Rupture des interactions mutualistes plantes à fruits charnus-vertébrés frugivores, et conséquences sur la régénération des forêts tropicales dans les Mascareignes

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THÈSE

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Rupture des interactions mutualistes plantes à fruits charnus-vertébrés frugivores, et conséquences sur la régénération des forêts tropicales dans les Mascareignes

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À MES PARENTS,

pour m'avoir transmis l'amour de la forêt,

À MES AMI-E-S,

pour leur participation indéfectible tout au long de cette aventure,

À SOLÈNE,

pour m'avoir tant soutenu dans la dernière ligne droite.

« Dans la morale de cette histoire, il n'y a pas de fruits défendus, la gourmandise n'est pas un péché, elle est au service de la vie. »

Jérôme Bouvier

« Les maires sont superbes et fiers. Ils se présentent avec un air sévère et inflexible et une bouche grande ouverte, très enjoués et audacieux. Ils ne bougent pas devant nous ; leur arme de guerre est la bouche, avec laquelle ils peuvent mordre férocement. Leur nourriture est constituée de fruits crus ; ils ne sont pas très bien parés, mais riches et gras, c'est pourquoi nous en avons amené beaucoup à bord, pour notre plus grand plaisir à tous. »

Missive anonyme néerlandaise, au sujet du Dodo nommé « maire », 1631

« Dans les jours que nous passâmes dans l'île s'y trouvaient aussi des pigeons sauvages que nous appelons de tour, en si grande quantité que les femmes, au moment même où elles préparaient le dîner, en tuaient par douzaines avec un bâton, jusque dans leur cuisine. »

Borghesi, probablement au sujet du Pigeon bleu ardoisé de Bourbon, 1703

« La relation des oiseaux et des mammifères avec les fruits est, à bien des égards, parallèle à celle des insectes et des fleurs, seuls les fruits dont la dispersion est effectuée par les oiseaux ou autres animaux ont des couleurs stimulantes. »

Wallace, 1879

« Ainsi, les agents de dispersion peuvent être responsables de la survie d'une espèce d'arbre dans un habitat qui favorise les prédateurs de graine. »

Janzen, 1970

« Il est clair que la défaunation est à la fois un élément omniprésent de la sixième extinction massive de la planète et un moteur majeur du changement écologique mondial. »

Dirzo, 2014

Avant-propos

Les introduction et discussion générales de cette thèse sont écrites en français, mais son coeur est en revanche composé de sept chapitres en anglais, ces chapitres ayant vocation à être publiés dans des revues internationales à comité de lecture. L'introduction générale en français s'attache à démontrer la pertinence des systèmes d'études insulaires et des Mascareignes en particulier, pour explorer les conséquences de la rupture des interactions de frugivorie sur la régénération des forêts. Les sept chapitres écrits en anglais sont précédés par un long résumé en français qui se veut davantage qu'une simple traduction de l'*abstract* habituellement concis. Le document s'achève par une discussion générale en français qui, outre le rappel des résultats principaux, a l'ambition d'ouvrir des perspectives pour la conservation et de délivrer un message volontariste face à la dégradation croissante des écosystèmes indigènes.

Foreword

The general introduction and discussion of this dissertation are written in French, but its core is composed of seven chapters in English intended for publication in international peer-reviewed journals. The general introduction in French aims to demonstrate the relevance of islands as study systems and Mascarenes in particular for exploring the consequences of the disruption of frugivory interactions on forest regeneration. The seven chapters in English are preceded by a long summary in French which is intended to be more than a simple translation of the usually concise abstract. The dissertation concludes with a general discussion in French which, in addition to recalling the main results, aims to open perspectives for conservation and to deliver a voluntarist message in the face of the increasing degradation of native ecosystems.

Table of contents

Table des matières

INTRODUCTION GÉNÉRALE

*Le Carpophage de Nouvelle-Zélande (*Hemiphaga novaeseelandiae*, Columbidae) avalant un fruit de* Beilschmiedia tarairi *(Lauraceae). Les pigeons frugivores jouent souvent un rôle clé dans la dispersion des arbres à grosses graines dans les forêts insulaires. Cliché issu de Wotton et Kelly (2011).*

INTRODUCTION GÉNÉRALE

L'importance de la frugivorie dans le fonctionnement des forêts

Les interactions plantes-animaux retiennent l'attention des biologistes depuis le $19^{\text{ème}}$ siècle. Dès 1802, Alexander von Humboldt ébauche le concept d'espèce clé de voûte en décrivant l'importance des fruits des palmiers *Mauritia flexuosa* pour l'avifaune des Llanos. Au moment où Darwin publie plusieurs articles et ouvrages sur la biologie de la pollinisation, Wallace (1877) définit une typologie de la coloration des plantes et des animaux, dont la dernière catégorie se nomme « *attractive colors of plants* ». Il y décrit diverses caractéristiques des fruits, *i.e.* couleurs et odeurs, qui les rendent plus ou moins attractifs pour les oiseaux et les mammifères. Wallace, visionnaire, plante ainsi le décor évolutif de ce qui sera nommé par la suite les « syndromes de dispersion », *i.e.* l'idée selon laquelle la co-évolution diffuse entre des groupes de disperseurs de graines et de plantes a façonné les caractéristiques des fruits pour faciliter leur localisation et la dispersion des graines (van der Pijl, 1969; Ridley, 1930). Pendant une longue période, ce mutualisme frugivores/plantes à fruits charnus reste pourtant en arrière-plan de la biologie des interactions plantes-animaux, dominée par l'herbivorie et la pollinisation. Il faut en effet attendre les travaux de Janzen (1970) et Connell (1971) pour que l'influence cruciale de la dispersion des graines sur la structure des populations et des communautés des plantes arrive sur le devant de la scène (**Fig.i.1**). Il a depuis été montré que de nombreux écosystèmes sont largement dominés par les plantes à fruits charnus, elles représentent par exemple entre 75 % et 90 % des plantes ligneuses dans les forêts tropicales humides d'Afrique centrale, de Papouasie ou du Costa Rica (Turner, 2001). Par conséquent, la frugivorie joue un rôle central dans le fonctionnement d'une grande partie des écosystèmes planétaires.

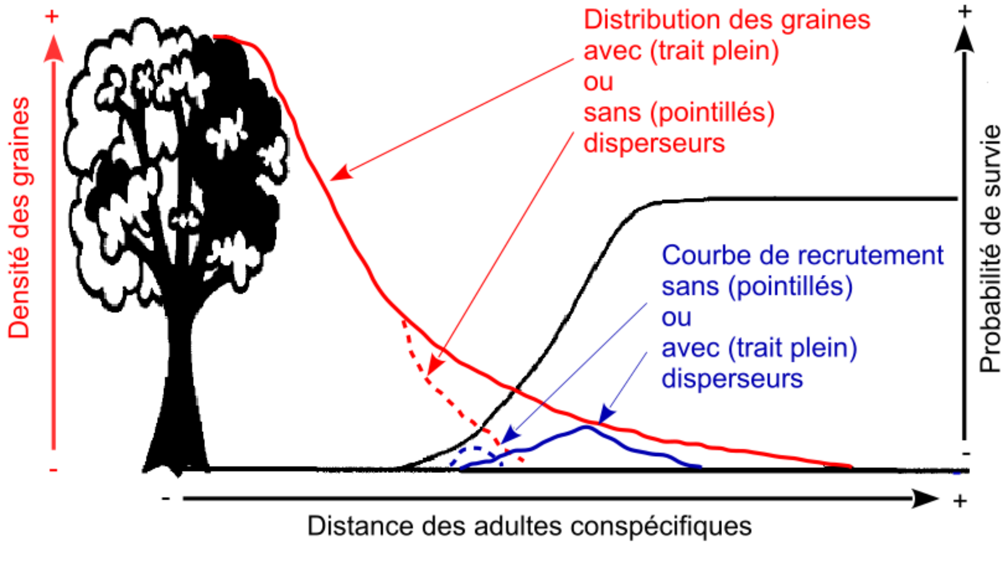


Fig.i.1 *Modèle de Janzen-Connell (Janzen, 1970, Connell, 1971) en trait plein montrant l'importance de la dispersion des graines pour échapper à diverses limitations du recrutement à proximité de l'arbre-mère. Les modifications de Terborgh et al. (2008) en pointillés prédisent une forte diminution du recrutement des plantules en cas de perte des agents de dispersion. L'axe x représente la distance à l'arbre focal, et les axes y rouge et noir représentent respectivement la densité des graines tombant au sol et la proportion de plantules échappant à une mortalité précoce. La courbe en bleu représente le recrutement de l'espèce focale.*

Jusqu'aux années 1990, de nombreux travaux concernant les interactions plantes-animaux frugivores étaient focalisés sur les questions de co-évolution ou sur des modèles simples d'interaction entre deux espèces avec une approche de biologie des populations (Heithaus et Fleming, 1978; Herrera, 1985; Howe et Estabrook, 1977; McKey, 1975; Snow, 1971). Avec l'accélération de la perte de diversité biologique et la défaunation au niveau global, les questions d'écologie des communautés et de biologie de la conservation des forêts tropicales sont petit à petit revenues au premier plan. Chercher à préserver une forêt dominée par des arbres à fruits charnus pourrait s'avérer totalement inefficace en l'absence des frugivores disperseurs (**Fig.i.1**) (Levey et al., 2002). Pire, l'effondrement de la faune de vertébrés pourrait compromettre la capacité même des écosystèmes à se reconstruire à une époque où la destruction des écosystèmes tropicaux se poursuit à large échelle (Chazdon, 2014) et où le réchauffement climatique rend d'autant plus cruciale la mobilité des végétaux (McConkey et al., 2012). L'effondrement global des populations de vertébrés que nous vivons actuellement pose donc de lourdes questions quant à la résilience des écosystèmes, d'autant plus que les vertébrés de grande taille qui sont les plus à même de disperser efficacement une multitude d'espèces ligneuses disparaissent en premier (Ceballos et al., 2017; Dirzo et al., 2014; Federman et al., 2016; Guimarães et al., 2008; Young et al., 2016).

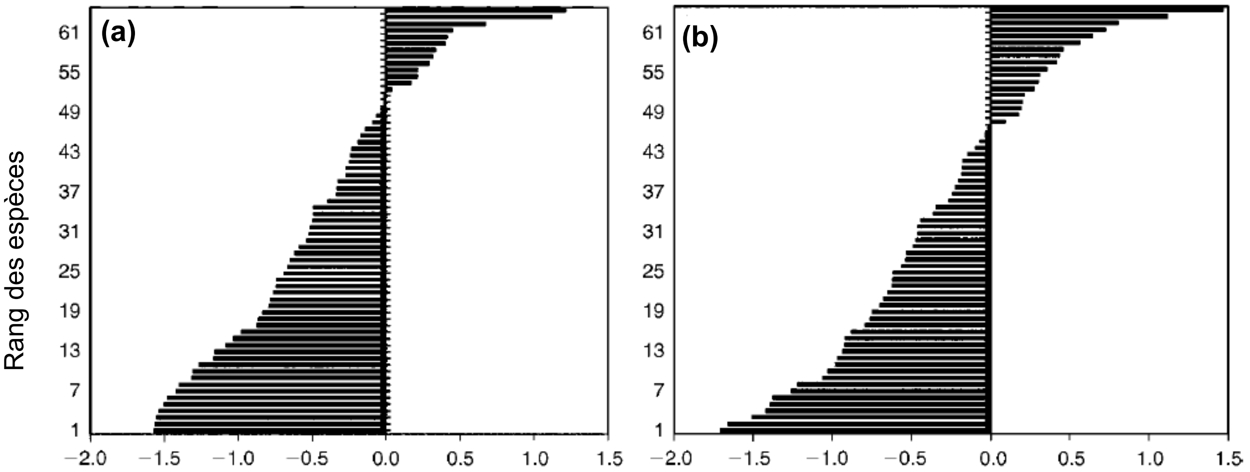


Fig.i.2 *Comparaison du recrutement de 65 espèces d'arbres entre un site défauné (Boca Manu) et un site non-défauné (Cocha Cashu) en Amazonie péruvienne. Les espèces gagnantes et perdantes à Boca Manu sont représentés par le ratio log([n baliveaux / n adultes]$_{Boca\ Manu}$ / [n baliveaux/ n adultes]$_{Cocha\ Cashu}$), montré pour* ***(a)*** *les grands baliveaux et* ***(b)*** *les petits baliveaux. L'hypothèse nulle du nombre égal de baliveaux par adulte pour les deux sites est représentée par la ligne verticale ; les ratios > 0 représentent les espèces dont les baliveaux sont relativement plus abondants à Boca Manu qu'à Cocha Cashu ; les ratios < 0 représentent les espèces dont les baliveaux sont relativement moins abondants à Boca Manu qu'à Cocha Cashu. Plus de 75 % des espèces présentent un recrutement beaucoup plus faible dans le site défauné et le phénomène est encore plus marqué pour les grands baliveaux. Cela montre que la dynamique forestière est gravement impactée seulement 30 ans après la défaunation des grands disperseurs. D'après Terborgh et al. (2008).*

Comprendre les conséquences de la rupture des interactions de frugivorie sur la régénération des forêts demeure un défi. Par exemple, la disparition massive de la mégafaune au Pléistocène a probablement eu de lourdes conséquences sur les écosystèmes (Federman et al., 2016; Guimarães et al., 2008; Young et al., 2016), mais il reste très difficile de les évaluer avec précision. Pour évaluer les conséquences actuelles des ruptures d'interaction de frugivorie, la durée de vie généralement importante des plantes à fruits charnus qui sont souvent des grands arbres (Diaz et al., 2004; Thompson et Rabinowitz, 1989) inscrit d'emblée ce type d'étude dans une temporalité longue. Les territoires qui ont été massivement défaunés et dont l'historique de la défaunation est connu, apparaissent dès lors comme des systèmes d'études privilégiés. Depuis les années 2000, des travaux comparant le recrutement entre des forêts où la grande faune est présente et d'autres où celle-ci a été extirpée, ont été menés en Amazonie péruvienne (Terborgh et al., 2008), en Afrique centrale (Effiom et al., 2013; Vanthomme et al., 2010) et dans les îles Mariannes (Wandrag et al., 2017). Bien que ces études s'inscrivent dans une temporalité n'excédant pas une trentaine d'années, les résultats sont éloquents: le recrutement dans le sous-bois montre un appauvrissement important de la diversité en plantes à fruits charnus et une augmentation en abondance des plantules d'espèces anémochores (**Fig.i.2**). Mais qu'en est-il sur des durées plus longues ? Turner et al. (1997) suggèrent que la forêt secondaire à Singapour serait appauvrie en arbres à fruits charnus après un siècle de défaunation des grands frugivores, mais aucune démonstration n'a été produite à ce jour. D'importants travaux sur une espèce modèle de palmier en Mata Atlantica ont récemment montré que la défaunation des frugivores agit comme la principale force micro-évolutive sur le changement de taille des diaspores en quelques générations (Carvalho et al., 2016; Galetti et al., 2013). Il reste que les études écologiques à l'échelle des communautés n'ont pas encore été menées sur une temporalité longue à notre connaissance.

Les îles ont été colonisées par l'Homme plus tardivement que les continents, mais elles ont subi une défaunation rapide et massive (Blackburn, 2004; Hansen et Galetti, 2009; Heinen et al., 2017; Steadman, 1995). Dans plusieurs archipels, la colonisation à partir des Grandes Découvertes s'est accompagnée d'une description relativement précise des faunes de vertébrés insulaires et de leur quasi-anéantissement parfois fulgurant (*cf* Cheke et Hume, 2008; Darwin et Rookmaaker, 1835). Les îles qui présentent de plus une flore généralement appauvrie et mieux connue que les flores continentales (Whittaker et Fernandez-Palacios, 2007), sont ainsi des systèmes d'étude particulièrement pertinents des conséquences de rupture d'interactions plante-animaux sur le long terme (Warren et al., 2015).

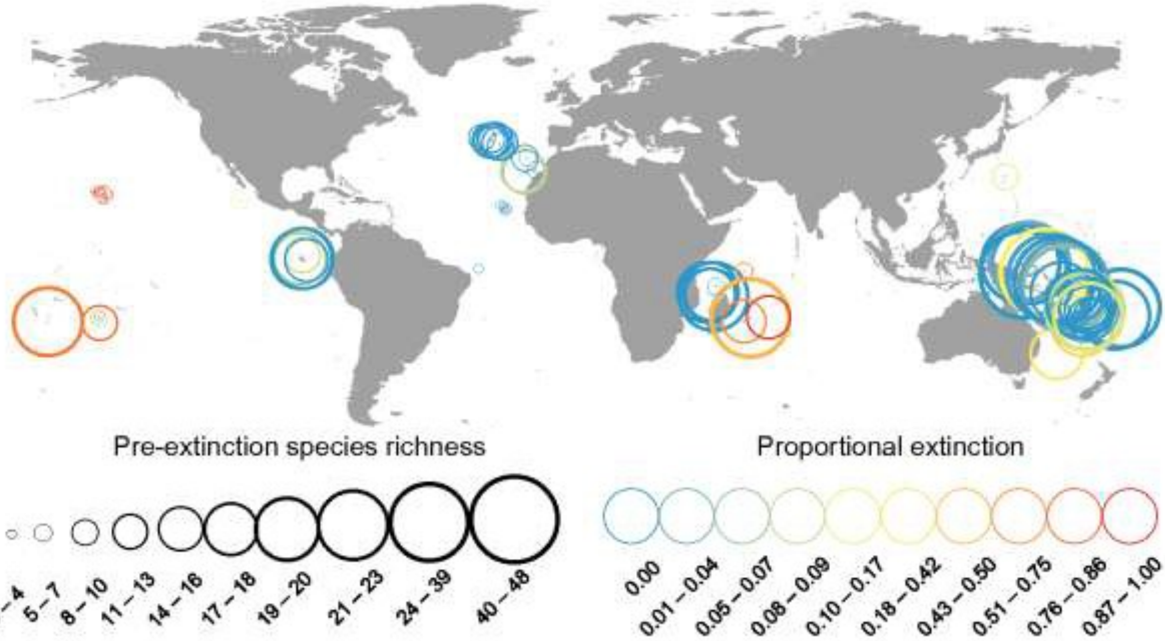


Fig.i.3 *Bilan des extinctions de frugivores dans 74 îles. La richesse spécifique pré-extinction et la proportion d'extinction sont respectivement illustrées par la taille du cercle et des couleurs allant du bleu (peu d'extinctions) au rouge (forte proportion d'extinctions). Seules les espèces de vertébrés frugivores indigènes (oiseaux, mammifères, reptiles) sont incluses. D'après Heinen et al. (2017).*

Les forêts insulaires en première ligne face à l'effondrement de la faune

L'effondrement des populations de vertébrés est aujourd'hui global, mais les îles ont connu un effondrement faunistique majeur avec la colonisation humaine. La plus grande vague d'extinctions connues chez les vertébrés à l'Holocène a ainsi eu lieu chez les oiseaux de Mélanésie, Micronésie et Polynésie où on estime qu'environ 2000 espèces ont disparu suite à la colonisation humaine (Blackburn, 2004; Duncan et al., 2013; Steadman, 1995). Il s'agissait surtout d'oiseaux terrestres (râles, pigeons, perroquets et passereaux), parmi lesquels figuraient de nombreuses espèces frugivores. Ces oiseaux insulaires ont principalement disparu en raison de la prédation par l'Homme et les mammifères introduits (rats, chats, chiens et cochons) qui ont rapidement décimé ces espèces dépourvues de comportement de fuite ou de protection face aux prédateurs, mais la destruction et la transformation des habitats indigènes a aussi joué un rôle important (Blackburn, 2004; Duncan et al., 2013; Steadman, 1995). Des travaux récents ont également montré comment la faune d'une île para-océanique comme Madagascar a été sévèrement modifiée dans les deux derniers millénaires (Albert-Daviaud et al., 2020; Goodman et Jungers, 2014). Parmi les frugivores, des lémuriens atteignant la taille des gorilles (*e.g.* *Archaeolemur*, *Palaeopropithecus*), des tortues géantes (*Aldabrachelys*) ou le plus gros oiseau du monde (*Aepyornis*) ont disparu dans le millénaire qui a suivi la colonisation humaine (Federman et al., 2016; Goodman et Jungers, 2014; Hansen et Galetti, 2009). L'étude au niveau global de Heinen et al. (2017) montre à quel point de nombreuses îles ont perdu une proportion considérable de leurs vertébrés frugivores indigènes (**Fig.i.3**). Les archipels d'Hawai'i, des Seychelles, des Tonga et des Mascareignes apparaissent particulièrement affectés. Certaines îles ont aujourd'hui perdu tous leurs frugivores indigènes, comme Oahu et Lanai dans l'archipel d'Hawai'i (Heinen et al., 2017) ou Guam dans l'archipel des Mariannes (Wandrag et al., 2017). Une question émerge dès lors : quel est le niveau de dépendance des communautés de plantes dans les forêts insulaires vis-à-vis de ces vertébrés frugivores indigènes ?

Tab.i.1 *Proportion d'espèces d'arbres indigènes produisant des fruits charnus ou zoochores dans divers habitats insulaires. [1] valeurs en considérant l'ensemble des espèces zoochores; [2] données pour les ligneux ornithochores uniquement; [3] données pour les arbres et les lianes confondus.*

Océan	Ile ou archipel	Territoire ou forêt	Proportion	Source
Atlantique	Macaronésie, Ténérife	Laurisylve d'Anaga	0,79	(Arévalo et al., 2007)
Atlantique	Puerto Rico	Forêts de l'île	0,75[2]	(Carlo et Morales, 2016)
Indien	Madagascar	Forêt littorale de Sainte Luce	0,80[1]	(Bollen et al., 2005)
Indien	Madagascar	Forêt sèche de Kirindy	0,69[1]	(Bollen et al., 2005)
Indien	Masc., La Réunion	Forêt de Mare Longue	0,83	(Strasberg, 1996)
Indien	Masc., Île Maurice	Forêt du Brise Fer	0,90	(Florens et al., 2017)
Pacifique	Chiloé	Forêts de l'île	0,67	(Armesto et al., 2001)
Pacifique	Hawai'i	Forêts sèches de l'archipel	0,54-0,76[1]	(Pau et al., 2009)
Pacifique	Juan Fernandez	Forêts tempérées de l'archipel	0,37	(Bernardello et al., 2006)
Pacifique	Mariannes	Forêts de Guam, Saipan et Rota	0,7[2]	(Wandrag et al., 2017)
Pacifique	Nlle-Calédonie	Forêt tropicale humide du Sud	0,59 ; 0,72[1]	(Carpenter et al., 2003)
Pacifique	Nlle-Zélande	Île du Sud – Péninsule de Banks	0,78	(Burrows, 1994)
Pacifique	Nlle-Zélande	Forêt tempérées de l'archipel	0,59	(Salmon, 1980)
Pacifique	Tonga	Forêts tropicales humides	0,79[1, 3]	(Meehan et al., 2002)

Jordano (2000) suggère déjà que les îles sont dominées par les plantes à fruits charnus tout comme les forêts tropicales continentales de basse altitude. Mais il ne s'appuie à l'époque que sur les travaux de Burrows (1994) en Nouvelle-Zélande et aucune étude n'a fait à notre connaissance un état des lieux entre-temps. Une revue de la littérature montre que les forêts insulaires de basse altitude des océans Atlantique, Indien et Pacifique atteignent souvent des niveaux comparables voire supérieurs aux forêts tropicales humides des continents (**Tab.i.1**). La palme revient à l'archipel des Mascareignes avec près de 90 % de plantes ligneuses qui sont endozoochores dans la forêt du Brise-Fer à Maurice. Il va sans dire que de telles proportions de plantes à fruits charnus parmi les plantes ligneuses montrent que ces écosystèmes dépendent étroitement des vertébrés frugivores pour leur dispersion.

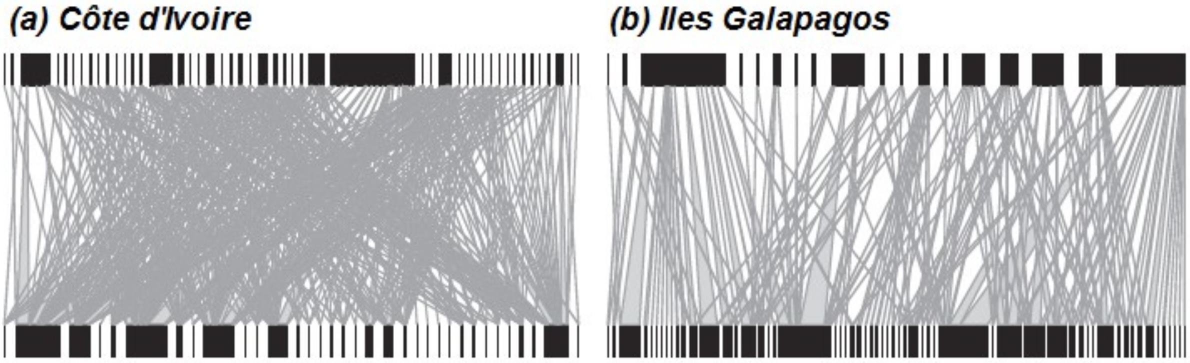


Fig.i.4 *Illustration du caractère asymétrique des réseaux de dispersion en milieu insulaire. Les interactions sont symbolisées par les lignes, les animaux et les plantes par les rectangles respectivement en haut et en bas. La largeur des rectangles et des lignes est proportionnelle à la fréquence des interactions (traduit et adapté depuis Schleuning et al. 2014).* ***(a)*** *Le réseau continental en Côte d'Ivoire présente une communauté de frugivores très diversifiée, la plupart des plantes étant visitée par plusieurs voire un grand nombre d'espèces animales.* ***(b)*** *Le réseau insulaire des Îles Galápagos est en revanche marqué par peu d'espèces animales. La plupart des plantes dépendent d'un unique ou de quelques animaux disperseurs partagés avec de nombreuses autres plantes, ce réseau est sujet à un effondrement fonctionnel.*

Les îles présentent des réseaux de dispersion hautement asymétriques, ce qui rend les espèces de plantes à graines insulaires très dépendantes de quelques espèces animales (**Fig.i.4**) (Schleuning et al., 2014). Cette asymétrie préexistait à la colonisation humaine qui l'a encore accentuée par les extinctions de vertébrés qu'elle a générées. La défaunation intense et rapide dans de nombreuses îles océaniques a probablement entraîné un effondrement fonctionnel des réseaux mutualistes de dispersion, affectant en cascade la régénération des forêts insulaires (Schleuning et al., 2014). Quelques d'études ont cherché à mesurer ces conséquences à l'échelle des populations, elles ont déjà montré un recrutement altéré dans les Baléares (Riera et al., 2002; Traveset et al., 2012), en Nouvelle-Zélande (Wotton et Kelly, 2011), à Madagascar (Bleher et Böhning-Gaese, 2001) ou dans les Mascareignes (Hansen et al., 2008). Ce dernier archipel a fait l'objet de travaux questionnant la perturbation des interactions de frugivorie à l'échelle des communautés de plantes ligneuses (Strasberg, 1994; Thébaud et Strasberg, 1997) et offre à l'instar d'Hawai'i ou des Galapagos, un remarquable système d'étude.

La terre du Dodo : un système d'étude unique au monde

Les Mascareignes sont avec les Galápagos le dernier grand archipel tropical à avoir été colonisé de manière permanente par l'Homme. Les faunes de vertébrés d'origine de ces archipels sont ainsi relativement bien connues car elles ont été décrites par les colons européens et les scientifiques explorateurs à partir du 17ème siècle. Avant cette époque, les Mascareignes étaient déjà connues par les navigateurs de la péninsule arabique (voir la Géographie d'Al Idrîsî de 1154) et les Portugais (mappemonde « de Cantino » de 1502) (Germanaz, 2016), mais aucun récit des biotes de l'archipel n'aurait été produit par ceux-ci (Cheke et Hume, 2008). Une première gravure néerlandaise en 1601 montre une faune et une flore originales à l'île Maurice avec la première description connue du dodo (*Raphus cucullatus*). Dubois et Leguat font respectivement en 1671 et 1707 les premières descriptions détaillées des vertébrés terrestres de La Réunion et de Rodrigues. Les nombreux récits qui suivent aux 17 et 18ème siècles convergent quant à la diversité et au caractère relativement dysharmonique et pléthorique de la faune d'origine dans l'archipel des Mascareignes (Cheke et Hume, 2008; Lougnon, 2005). A tel point que certains récits, comme celui de Leguat, ont été jugés fantaisistes tant la faune y semble exubérante en comparaison de ce qui est connu ailleurs à la même époque (**Fig.i.5**).

***Fig.i.5** Vertébrés frugivores dans les écosystèmes d'origine à La Réunion (à gauche), Maurice (au centre) et Rodrigues (à droite) : à gauche, trois espèces de pigeons, dont le founingo bleu ardoisé (*Alectroenas *sp., † 18ème siècle), et en arrière plan, la perruche verte (*Psittacula eques*, † 18ème siècle) ; au centre, la tortue géante de l'île Maurice (*Cylindraspis inepta*, † 1730) et trois espèces de perroquets, le perroquet gris de Thirioux (*Psittacula bensoni*, † 1750), le perroquet à bec large (*Lophopsittacus mauritianus*, † 1675), et la perruche verte (VU); à droite, le solitaire de Rodrigues (*Pezophaps solitaria*, † 1761), colombidé apparenté au dodo et incapable de voler. Illustrations reproduites avec l'aimable autorisation de J. Hume.*

Comme la plupart des archipels océaniques, les Mascareignes sont dépourvues de mammifères terrestres (et donc de primates), mais aussi de formes d'oiseaux continentales comme les calaos qui sont souvent d'importants frugivores dans les forêts tropicales de l'Ancien Monde (Snow, 1981). Ces absences offrent des niches vacantes qui sont occupées par des reptiles (tortues géantes terrestres et scinques), des chauve-souris (roussettes) et surtout des lignages d'oiseaux divers (bulbuls, huppes, pigeons, perroquets, râles, oiseaux-lunettes) (Whittaker et Fernandez-Palacios, 2007). Parmi les oiseaux, les Colombidés jouent dans les Mascareignes un rôle particulièrement important et comptent diverses espèces de founingo et deux espèces de dodo, ces deux dernières qui ont perdu la capacité de voler étant les plus emblématiques (**Fig.i.5**). Malgré la controverse (*cf* Mourer-Chauviré et al., 1999), de tels oiseaux n'ont probablement jamais existé à La Réunion du fait de la relative jeunesse géologique de l'île (Cheke et Hume, 2008).

Les tailles qu'atteignent les populations des vertébrés frugivores impressionnent particulièrement les premiers colons dans les Mascareignes. Les pionniers décrivent des

« nuages » de roussettes dans le ciel, pléthore de founingos s'égarant dans les cuisines des matrones, une multitude de bulbuls et de perroquets, d'immenses colonies de tortues terrestres géantes s'étendant en un rassemblement continu sur des centaines, voire des milliers de mètres, etc. (Cheke et Hume, 2008; Lougnon, 2005). A la lumière des travaux montrant la relation forte qui existe entre la taille des populations des frugivores et l'efficacité de la dispersion (**Fig.i.6**) (McConkey et Drake, 2006; McConkey et O'Farrill, 2016), nous avons toutes les raisons de penser que les espèces de plantes à graines qui étaient consommées par cette faune hyper-abondante bénéficiaient d'une dispersion particulièrement efficace. L'effondrement faunistique qui suit le début de la colonisation humaine au 17$^{\text{ème}}$ siècle soulève la question des conséquences délétères sur la régénération de nombreuses espèces de plantes qui se retrouvent sans aucun disperseur depuis plusieurs siècles.

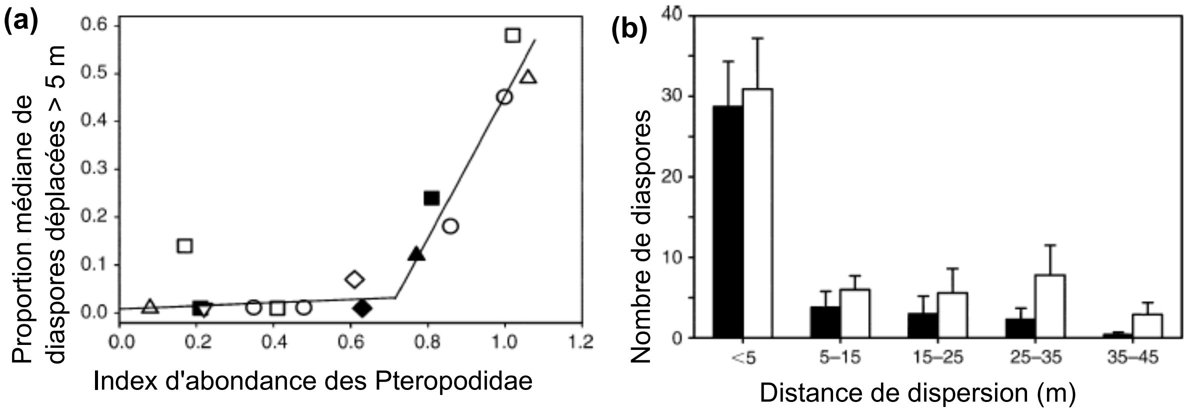


Fig.i.6 *Illustration du phénomène de « perte de la dispersion avant la perte des disperseurs » dans un archipel du Pacifique (issue de McConkey et Drake (2006)).* ***(a)*** *Relation entre l'abondance des roussettes et la proportion médiane de diaspores dispersées à plus de 5 m de l'arbre mère à Vava'u (Tonga, Polynésie). Deux tendances nettes apparaissent de part et d'autre d'un seuil d'abondance en deçà duquel les roussettes cessent de disperser les grosses diaspores.* ***(b)*** *Nombre moyen de diaspores dispersées par les roussettes à des intervalles de distance croissants depuis les couronnes des arbres. Les barres symbolisent l'intervalle de confiance. Les arbres sont distingués selon leur appartenance à des sites montrant l'abondance des roussettes au dessus (barres blanches) ou au dessous (barres noires) du seuil de fonctionnalité.*

Les témoignages des premiers explorateurs nous permettent de connaître de manière relativement précise l'historique de la défaunation des frugivores dans les Mascareignes. Le plus grand scinque du monde non décrit par les européens s'éteint probablement à Maurice avant le 16$^{\text{ème}}$ siècle (Hume, 2013), le Dodo dès le 17$^{\text{ème}}$ siècle et le Solitaire de Rodrigues au 18$^{\text{ème}}$ siècle. Les tortues géantes, la Rougette, les huppes, les founingos et l'ensemble des perroquets hormis la Perruche de Maurice, qui voient souvent leurs populations très réduites dès la fin du 18$^{\text{ème}}$ siècle, ont tous disparu de l'archipel dans la seconde moitié du 19$^{\text{ème}}$ siècle. Aujourd'hui, seuls subsistent de la faune de frugivores d'origine la Roussette noire, la Perruche verte et le Scinque de Telfair à Maurice, la Roussette de Rodrigues, ainsi que les bulbuls et oiseaux-lunettes. Ainsi, malgré la colonisation très tardive des Mascareignes par l'Homme, les vertébrés frugivores y ont été largement décimés. La fulgurance du phénomène apparaît troublante, en particulier à La Réunion où les populations de l'ensemble des grands vertébrés frugivores s'effondrent en 70 ans environ après l'installation de l'Homme et s'éteignent en moins de deux siècles de colonisation humaine permanente (Cheke et Hume, 2008; Lougnon, 2005). Bory de Saint Vincent (1804) qui arpente largement et longuement La Réunion note qu'il existe encore des forêts majestueuses dans le Sud-Est de l'île, mais que la grande faune en est totalement absente, lors de son passage en 1801. Ce terrible constat concernant l'état de la faune des Mascareignes dès la première moitié du 19ème siècle, explique peut-être aussi pourquoi Darwin s'attarde si peu sur son histoire naturelle lors de son bref passage en 1836.

Les Mascareignes sont donc un des rares endroits sur Terre où des écosystèmes tropicaux ont évolué jusqu'à l'époque moderne avec une influence humaine négligeable. Il est troublant de pouvoir y visiter des écosystèmes relativement jeunes, avec des arbres qui se sont établis dans une nature sans l'Homme. La Réunion abrite en effet le Piton de la Fournaise, volcan terrestre parmi les plus actifs au monde (Morandi et al., 2016), qui a largement contribué à nous faire parvenir des reliques de forêts préservées à basse altitude en raison du caractère inculte des sols (Meunier et al., 2010). L'ensemble des formations végétales installées sur des substrats d'âge différent constitue une chronoséquence, classiquement utilisée pour étudier la succession et qui permet théoriquement de substituer l'espace au temps (Walker et Moral, 2003). La chronoséquence des coulées de lave du Piton de la Fournaise a d'ailleurs fait l'objet de nombreux travaux concernant la dynamique de colonisation des plantes (Ah-Peng, 2007; Cadet, 1977; Chevennement, 1990; Strasberg, 1994), l'impact de la fragmentation (Thébaud et Strasberg, 1997) et les conséquences des invasions biologiques (Potgieter et al., 2014; Strasberg, 1994). Cette chronoséquence présente encore un remarquable potentiel d'étude qui ne manquera pas d'être exploré au cours de cette thèse.

Comme de nombreux archipels (Kueffer et al., 2010), les Mascareignes sont particulièrement sujettes aux invasions biologiques qui constituent une redoutable menace pour la conservation des écosystèmes relictuels (Florens et al., 2012; Macdonald et al., 1991; Strasberg et al., 2005). L'introduction de nombreuses plantes à fruits charnus et de vertébrés potentiellement frugivores soulève d'importantes questions quant aux nouvelles interactions de frugivorie et leurs conséquences pour la régénération des écosystèmes indigènes. Divers travaux menés dans l'archipel ont notamment contribué à décrire les synergies d'invasion (*invasional meltdown*) entre plantes exotiques à fruits charnus et frugivores introduits (Macdonald et al., 1991; Mandon-Dalger et al., 2004; Simberloff et Von Holle, 1999; Thébaud et Strasberg, 1997). Néanmoins, le rôle de certains vertébrés envahissants comme disperseurs potentiels de plantes indigènes demeure peu étudié à l'échelle globale malgré l'idée qu'ils pourraient partiellement remplacer les vertébrés indigènes éteints (Shiels et Drake, 2011; Williams et al., 2000). La question se pose d'autant plus dans les Mascareignes que cet archipel a été particulièrement touché par les extinctions de grands frugivores (Cheke et Hume, 2008). De même, s'il va de soi que les frugivores relictuels indigènes consomment les fruits des plantes indigènes, leur rôle comme disperseur potentiel de plantes exotiques à fruits charnus est probablement sous-estimé (Kueffer et al., 2009; Lavergne, 2000).

Les Mascareignes présentent enfin une remarquable diversité végétale malgré leur relatif éloignement (Strijk et al., 2012). La flore de l'archipel est aujourd'hui bien connue des points de vue taxonomique (Boullet et al., 2012) et fonctionnel (traits des plantes) en comparaison avec les grandes forêts continentales. Les patrons de diversification des principaux lignages et la biogéographie de l'archipel ont fait l'objet de récents travaux de recherche (Ahmad et al., 2016; Appelhans et al., 2014; Bone et al., 2012; Le Péchon et al., 2010; Linan et al., 2019; Malcomber, 2002; Olesen et al., 2012; Pelser et al., 2007; Plunkett et Lowry, 2010; Renner et al., 2010; Strijk et al., 2012). Ces éléments, combinés à la bonne connaissance de la faune d'origine de l'archipel et de sa cinétique d'extinction, contribuent à en faire un remarquable système d'étude des conséquences sur le long terme de la rupture des interactions mutualistes de frugivorie.

Objectifs et plan de la thèse

Cette thèse s'organise en trois grandes parties qui visent à (**i)** décrire les patrons de distribution spatiale des traits de dispersion des plantes ligneuses dans les Mascareignes et en étudier les implications pour l'extinction de la faune qui a été particulièrement fulgurante à La Réunion (chapitres 1 et 2) ; (**ii**) comprendre les conséquences de la rupture des interactions de frugivorie sur la reconstruction des écosystèmes forestiers sur les coulées de lave du Piton de la Fournaise (chapitres 3, 4 et 5) ; (**iii**) évaluer les conséquences de la rupture des interactions de frugivorie sur le maintien de la diversité dans les forêts des Mascareignes, établies avant la colonisation humaine permanente (chapitres 6 et 7). Cette thèse en écologie est donc constituée de sept chapitres qui font intervenir d'autres disciplines comme l'histoire (chapitres 2 et 4) ou la volcanologie (chapitre 3), et s'appuient sur des approches observationnelles et expérimentales à différentes échelles spatiales (de l'hectare à l'archipel) et temporelles (via l'utilisation d'une chronoséquence de plus de 600 ans). Les chapitres 2 et 6 utilisent à la manière de Wandrag et al. (2017) dans les Mariannes des comparaisons entre les principales îles des Mascareignes, Maurice et La Réunion, qui présentent aujourd'hui des différences notables quant à la conservation de leurs biotes: La Réunion présente encore plus d'un tiers de sa superficie couverte d'habitats indigènes peu transformés (Strasberg et al., 2005) mais a perdu tous les vertébrés frugivores indigènes dont la masse est supérieure à 55 g (Cheke et Hume, 2008), tandis que Maurice possède moins de 5 % d'habitats indigènes (Florens et al., 2012) mais conserve encore plusieurs grands vertébrés frugivores indigènes, notamment la Roussette noire ou la Perruche verte à écho (Florens et al., 2017a).

Dans le chapitre 1, l'objectif consiste à modéliser la distribution spatiale des types de fruit (charnu ou sec) à l'échelle de La Réunion pour comprendre quels sont les habitats les plus riches en espèces à fruits charnus et les plus vulnérables face à la disparition des vertébrés frugivores. Notre modélisation s'appuie sur des variables climato-topographiques qui nous offre l'opportunité d'explorer le rôle de l'environnement dans l'assemblage des communautés de plantes indigènes. Nous avons aussi choisi d'étudier la structure phylogénétique des communautés, ainsi que leur niveau d'endémisme. Les résultats montrent une chute spectaculaire des proportions de plantes à fruits charnus avec l'altitude et offrent de remarquables perspectives biogéographiques qui vont au delà du cadre de cette thèse. La principale implication découlant du puissant gradient mis en évidence est que les habitats de basse altitude sont probablement beaucoup plus vulnérables face à l'extinction de la faune à La Réunion. Nous nous concentrons donc sur ces habitats dans les parties II et III de cette thèse. Ce chapitre est publié dans *Journal of Vegetation Science*.

Dans le chapitre 2, il s'agit de mieux comprendre le paradoxe déjà évoqué précédemment quand on compare La Réunion et Maurice qui présentent respectivement « les forêts indigènes sans les grands vertébrés forestiers indigènes » et « les grands vertébrés forestiers sans les forêts indigènes ». Cette question a déjà été soulevée par Cheke et Dahl (1981), et nous pensons que les travaux menés dans le chapitre 1 apportent de nouveaux éléments qui méritent d'être discutés et mis en perspective avec les autres facteurs des extinctions classiquement évoqués. Elle mérite d'autant plus d'être explorée que le paradoxe observé dans les Mascareignes pourrait bien être le participe d'un patron global. Heinen et al. (2017) ont en effet montré que les îles océaniques hautes sont plus sensibles aux extinctions de vertébrés frugivores, mais les raisons sous-jacentes restent très peu discutées.

Dans le chapitre 3, nous développons une nouvelle méthode de datation des coulées de lave qui permet d'accroître notablement l'amplitude de la chronoséquence du Piton de la Fournaise sur laquelle repose les chapitres 4 et 5. Cette méthode de datation des coulées utilise la distribution diamétrique d'une espèce pionnière à vie longue, *Agarista salicifolia* (Ericaceae) ou Bois de rempart. Ce grand arbre est capable de s'installer très précocement sur des coulées de lave et de vivre plus de 600 ans, ce qui offre de remarquables perspectives pour dater des coulées de lave, en particulier celles antérieures au début de la colonisation humaine à La Réunion. La méthode consiste à calibrer un modèle basé sur les distributions diamétriques observées sur des coulées d'âge connu, pour ensuite estimer l'âge de coulées portant cet arbre indigène. Ce chapitre est publié dans *Journal of Volcanology and Geothermal Research*.

Dans le chapitre 4, nous utilisons la chronoséquence de plus de six siècles des coulées de lave du Piton de la Fournaise pour étudier s'il existe une corrélation entre l'âge des coulées (comme une approximation de la disponibilité en frugivores) et la diversité des traits de dispersion dans les communautés de plantes ligneuses. La combinaison entre le grand nombre de coulées datées du Piton de la Fournaise et la chronologie de la défaunation agit comme une « machine à remonter le temps ». Cette expérience naturelle unique permet de montrer que la disparition des populations de frugivores a profondément altéré la capacité des écosystèmes à se rebâtir dès le 18ème siècle à La Réunion. Ce chapitre est publié dans *Journal of Ecology*.

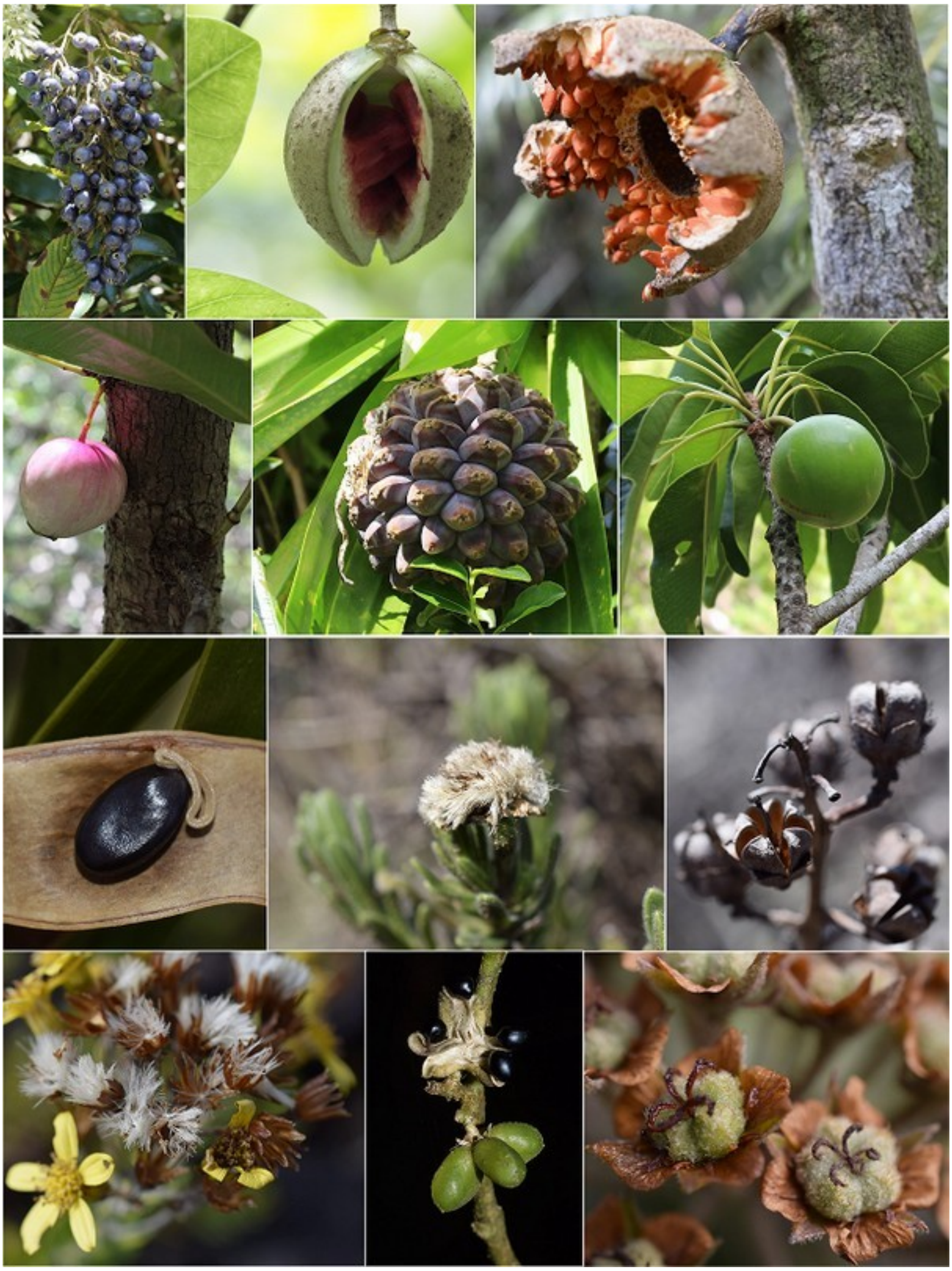
Dans le chapitre 5, nous réalisons une expérience de terrain pour démontrer que la rupture des interactions de frugivorie est bien le principal mécanisme à l'œuvre derrière l'effondrement de la diversité mis en évidence dans le chapitre 4. Sur la coulée historique de 1800, nous évaluons les limitations du recrutement agissant avant, pendant et après la dispersion, et montrons que les plantes exotiques envahissantes dominent la pluie de graines et le recrutement des plantules. Actant le caractère très appauvri de la pluie de graines en espèces indigènes, nous semons expérimentalement plusieurs espèces à grosses graines et montrons que l'absence de ces espèces sur cette coulée historique est bien la conséquence de la perte de la dispersion et ne peut être expliquée par les conditions environnementales, la compétition avec la végétation existante ou la prédation des graines. Cette expérimentation démontre enfin que des protocoles de restauration écologique relativement simples peuvent être mis en œuvre pour régénérer des arbres emblématiques de la forêt tropicale humide et lutter contre les invasions sur les coulées récentes du Piton de la Fournaise.

Dans le chapitre 6, nous comparons les structures diamétriques des plantes ligneuses dans les parcelles permanentes de Mare Longue (La Réunion) et Brise Fer (Maurice) et montrons que le maintien d'une partie de la grande faune de frugivores à Brise Fer permet un bien meilleur recrutement des plantes ligneuses qu'à Mare Longue, notamment pour les plantes à fruits charnus avec des graines de taille petite à moyenne. A Mare Longue, quelques espèces ligneuses ont probablement des difficultés à se maintenir du fait des conditions environnementales, mais l'appauvrissement en cours du système se poursuivra inexorablement si nous ne restaurons pas la fonction de dispersion pour nombre d'espèces à fruits charnus souvent absentes dans le sous-bois. Ce chapitre est soumis dans *Biological Conservation*.

Dans le chapitre 7, nous testons l'impact du nettoyage de la graine sur le recrutement de deux espèces d'arbres de Sapotaceae dans une expérimentation de terrain. Nous montrons que la persistance de la pulpe a un fort effet négatif sur le recrutement de ces deux espèces à grosses graines, et que la variabilité spatio-temporelle dans le comportement de la faune introduite peut moduler considérablement les résultats.

Enfin, dans la discussion générale, les résultats principaux des sept chapitres sont rappelés et mis en perspective pour dégager plusieurs pistes d'étude à ouvrir ou approfondir. Cette discussion se veut aussi tournée vers les acteurs locaux et régionaux de la conservation, elle intègre par conséquent nombre d'exemples d'actions de conservation.

PARTIE I. Distribution spatiale des traits de dispersion et implications pour les extinctions de frugivores dans les Mascareignes



Plantes ligneuses à fruits charnus (1ère et 2nde lignes) et à fruits secs (3ème et 4ème lignes) à La Réunion. De gauche à droite et de haut en bas: Bertiera rufa *(Rubiaceae),* Tabernaemontana mauritiana *(Apocynaceae),* Tambourissa elliptica *(Monimiaceae),* Syzygium cymosum *(Myrtaceae),* Pandanus purpurascens *(Pandanaceae) et* Mimusops balata *(Sapotaceae) ;* Acacia heterophylla *(Fabaceae),* Psiadia callocephala *(Asteraceae),* Agarista buxifolia *(Ericaceae),* Hubertia tomentosa *(Asteraceae),* Melicope borbonica *(Rutaceae) et* Dombeya punctata *(Malvaceae). Photo montage : S. Albert*

CHAPITRE 1. Pourquoi les plantes ligneuses sont-elles à fruits charnus à basse altitude ? Les enseignements d'une île océanique haute

RESUME

La composition en types de fruit, charnu *versus* sec, a une grande influence sur le fonctionnement des communautés de plantes. Par exemple, les forêts tropicales humides largement dominées par les plantes à fruits charnus dépendent étroitement des vertébrés frugivores pour la dispersion des graines. La littérature documentant les patrons de distribution spatiale des types de fruits est abondante à petite échelle spatiale. Cependant, les études à plus large échelle restent rares, en particulier sur les îles océaniques hautes qui présentent une grande hétérogénéité environnementale. A La Réunion, point culminant de l'océan Indien (3070 m) où des records de précipitation sont régulièrement enregistrés, nous étudions comment divers facteurs climato-topographiques influencent la proportion d'espèces à fruits charnus (**pFF**) dans les communautés de plantes ligneuses. Nous demandons (i) quels sont les facteurs abiotiques les plus corrélés à pFF, (ii) si, parmi les plantes à fruits charnus, les espèces d'arbres et arbustes réagissent différemment le long des gradients abiotiques et (iii) quelles sont les relations entre pFF, l'endémisme et l'apparentement phylogénétique des communautés ? En nous appuyant sur l'échantillonnage historique de T. Cadet, nous sélectionnons 429 relevés de végétation dans les habitats préservés et attribuons à 213 espèces ligneuses indigènes les types de fruits, formes de croissance et répartitions géographiques (*e.g.* endémisme Réunion ou archipel). Nous construisons un arbre phylogénétique pour chaque relevé et calculons un indice nomalisé de parenté. Nous utilisons des GLMs pour mesurer la relation entre pFF et les facteurs abiotiques, en contrôlant l'autocorrélation spatiale. Nous évaluons ensuite la relation entre pFF, l'indice normalisé de parenté et la proportion d'espèces endémiques. Le meilleur modèle explique 78 % de la variation de pFF. L'altitude est de loin le meilleur prédicteur de pFF, avec une diminution de 81% en moyenne à 50 m à 0% à 3000 m d'altitude. À basse altitude, pFF est plus élevée sur la côte-au-vent humide (81%) que sur la côte-sous-le-vent (70%) où l'agrégation phylogénétique est manifeste. Près de la moitié (48 %) des plantes ligneuses sont des arbres à fruits charnus à basse altitude. La proportion d'arbres à fruits charnus diminue fortement avec l'altitude et apparait significativement corrélée aux précipitations du mois le plus sec, contrairement à la proportion d'arbustes à fruits charnus qui présente un effet quadratique le long du gradient d'altitude et aucune corrélation avec les précipitations du mois le plus sec. À haute altitude, la plupart des assemblages de plantes sont phylogénétiquement agrégés et fortement dominés par des plantes endémiques à fruits secs. La relation très forte entre pFF et l'altitude, le *shift* des formes de croissance à fruits charnus le long des gradients climatiques et l'agrégation phylogénétique des assemblages soumis à des conditions climatiques difficiles suggèrent que les facteurs climatiques sont les principaux déterminants de la distribution des types de fruits à la Réunion. Pour expliquer l'absence d'espèces à fruits charnus aux hautes altitudes, nous faisons l'hypothèse que les lignages indigènes à fruits charnus n'ont pas le potentiel évolutif pour s'adapter et que les lignages à fruits charnus adaptés au froid ont de grandes difficultés à atteindre La Réunion, notamment en raison d'un forçage régional important. Enfin, si ces travaux ouvrent d'intéressantes perspectives macroécologiques, les principales implications dans le cadre de cette thèse concernent l'archi domination des plantes à fruits charnus à basse altitude : il est probable que les vertébrés frugivores éteints dépendaient étroitement des habitats indigènes de basse altitude (*cf* chapitre 2) et les vestiges de ces derniers sont probablement très vulnérables suite à la disparition de la plupart des vertébrés frugivores depuis plus de 250 ans (*cf* parties II et III).

Why are woody plants fleshy-fruited at low elevations? Evidence from a high-elevation oceanic island*

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ABSTRACT

The composition of fruit types, fleshy vs dry fruits, greatly influences the functioning of plant communities. Literature documenting spatial patterns of fruit types at fine scale is abundant. However, studies at larger geographical scale remain scarce, especially on high-elevation oceanic islands that provide a great environmental heterogeneity. Here, we investigated how abiotic factors explained the proportion of fleshy-fruited species (pFF) on Réunion (Mascarene archipelago). We asked (i) which abiotic factors were most related to pFF, (ii) if fleshy-fruited canopy species were more sensitive than fleshy-fruited shrubs to harsh climatic conditions and (iii) what are the relationships between pFF, endemism and phylogenetic relatedness ? We used a dataset of 429 vegetation plots and assigned fruit types, growth forms and geographical distribution to 213 native woody species. Phylogenetic trees were constructed for each plot. We used GLMs to measure the relationship between pFF and abiotic factors, controlling for spatial autocorrelation. We then assessed the relationship between pFF, the standardized net relatedness index and the proportion of endemic species. The top model explained 78% of the variation in pFF. Elevation was by far the best predictor, with pFF decreasing from 81% at 50 m asl to 0% at 3000 m asl. At low elevations, pFF was higher on the wet windward (81%) than on the leeward (70%) where phylogenetic clustering was evident. Almost half (48%) of woody plants was fleshy-fruited trees at low elevations. The proportion of fleshy-fruited trees declined sharply with elevation and was significantly related to precipitation of the driest month contrary to the proportion of fleshy-fruited shrubs that showed a hump shaped pattern along elevational gradient and no correlation with precipitation of the driest month. At high elevations, most plant assemblages were phylogenetically clustered and strongly dominated by single-island endemic dry-fruited plants. The striking relationship between pFF and elevation, the shift among fleshy-fruited growth forms along climatic gradients and the phylogenetic clustering of assemblages subjected to harsh climatic conditions, suggested that climatic factors were the main drivers of the distribution of fruit types on Réunion. To explain the absence of fleshy-fruited species at high elevations, we hypothesized that native fleshy-fruited lineages lacked the evolutionary potential to adapt and fleshy-fruited cold-adapted lineages had major difficulties reaching Réunion.

INTRODUCTION

Plant fruit type, *i.e.* fleshy versus dry, greatly influences seed dispersal strategy (Howe and Smallwood, 1982). Fleshy-fruited (FF) plants typically depend on vertebrates for their dispersal, *e.g.* endozoochory. On the contrary, dry-fruited (DF) plants are dispersed by diverse vectors, among which the wind. Because wind dispersal produces not directed and scattered distribution,

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Turner (2001) considers it as poorly effective in tropical rain forest. Investing in structures that attract and reward frugivorous animals implies a great cost for plants. This is evidenced by the fact that FF plants are overwhelmingly woody because they can allocate sufficient resources (Yu et al., 2017), Willson et al. (1989) reported for example that more than 90% of FF plants were woody at four Queensland sites. As a consequence, abiotic factors that strongly influence resource availability may play an important role in shaping the distribution of fruit types. Several studies have investigated climatic and geographical factors underlying broad-scale patterns in fruit type on tropical mainland (see Almeida-Neto et al., 2008; Chen et al., 2016; Correa et al., 2015), but none have on oceanic islands. High-elevation islands are relevant study systems because (i) they present strong ecological gradients and provide a suitable environmental heterogeneity to understand the composition of fruit type across assemblages (Irl et al., 2016); (ii) they possess impoverished and well-studied floras, *e.g.* taxonomy, phylogeny and geographical distribution of species. Hence, oceanic islands, with their small manageable areas for research in comparison to mainland provide a good opportunity to investigate the mechanisms underlying the distribution of fruit types (Santos et al., 2016).

Relationship between abiotic factors and the distribution of fruit types

On high-elevation oceanic islands, one may expect the proportion of FF species (pFF) in woody plant assemblages to decrease with elevation. In lowland island habitats, several fine-scale studies suggest that pFF is high, *i.e.* between 54% and 83% (Arévalo et al., 2007; Meehan et al., 2002; Pau et al., 2009; Strasberg, 1996), potentially reaching similar levels to that observed in continental tropical forests, *i.e.* between 46% and 89% (Jordano, 1992). Recent studies have shown that pFF decreases significantly with elevation on continents and have emphasized the role of climate and especially temperature as a primary driver of fruit type distribution (Buitrón-Jurado and Ramírez, 2014; Yu et al., 2017). On oceanic islands, the low mass elevation effect strongly influences climatic conditions (Irl et al., 2016). The rapid decline of soil fertility with decreasing temperature and increasing cloudiness (Carbutt et al., 2013; Tanner et al., 1998), and the presence of a trade wind inversion layer inducing lower water availability (Leuschner and Schulte, 1991), result in trade-offs in plant functional traits along elevational gradients. Anemochorous dry-fruited (DF) plants better adapted to high-elevation conditions (Buitrón-Jurado and Ramírez, 2014) may thus dominate high-elevation assemblages. However, in addition to environmental factors, biogeographic constraints may influence pFF with increasing elevation. Thus, the dominance of anemochorous species in tropical montane forests of Pacific islands may be a consequence of the great isolation of these oceanic islands (Chapman et al., 2016).

Because fleshy fruits are usually water-rich fruits, FF species may be more common where water availability is high (Yu et al., 2017). The latter is primarily related to the amount of precipitation. The positive influence of precipitation on richness and proportion of fleshy fruitedness has thus been shown at both regional (Almeida-Neto et al., 2008; Correa et al., 2015) and continental scales (Chen et al., 2016). On tropical high-elevation oceanic islands, trade winds generate a climatic divide, with a windward side wetter than leeward side. Consequently, FF species are expected to be more common on the former than on the latter. Furthermore, water availability may be related to topographic factors (Oddershede et al., 2015). Topographic factors might thus influence the distribution of fruit types, *e.g.* by saturating soils in water on flat lands or increasing drought on steep slopes.

On high-elevation islands, FF species are expected to be less common among tree canopy species when climatic conditions become harsher, *e.g.* in areas subjected to drought and/or to low temperatures. Trees may be more limited in the amount of water they can invest into fleshy fruits because they are more exposed to evapotranspiration than shrubs that grow in the understory and are buffered by the canopy (Yu et al., 2017). Thus, in the wet and fertile lowlands of oceanic islands, a large majority of species bearing fleshy-fruits is expected to be trees as observed on mainland (Chen et al., 2016). On the contrary, FF species that occur at higher elevations may mainly be shrubs benefiting from a DF plant canopy.

Relationship between phylogeny, endemism and the distribution of fruit types

Ecophylogenetics states that harsh environments should produce phylogenetically aggregated assemblages when key ecological traits are conserved (Webb et al., 2002), which is the case for fruit types on oceanic islands (García-Verdugo et al., 2014). Hence, investigating phylogenetic relatedness of woody species may help in better understanding the role of abiotic forces in constraining the distribution of fruit types (Santos et al., 2016).

On high-elevation oceanic islands, one may expect different spatial patterns of phylogenetic relatedness. Indeed, these islands show high levels of endemism at high elevations (Steinbauer et al., 2016), which may be a result of *in situ* radiations among DF lineages (García-Verdugo et al., 2014). Radiations of some lineages into a wide range of habitats may lead to phylogenetic overdispersion (Mouquet et al., 2012). At the same time, radiations may lead to phylogenetic clustering if species coexist at fine scale. In the latter case, a strong association between abiotic gradients and the degree of clustering within assemblages would help demonstrate the role of environment in shaping communities (Cadotte and Tucker, 2017).

In this paper, our primary goals were to investigate (i) which abiotic factors were most related to pFF, (ii) if fleshy-fruited canopy species were more sensitive than fleshy-fruited shrubs to harsh climatic conditions and (iii) the relationship between pFF, endemism and phylogenetic relatedness to unravel how abiotic factors shape the distribution of fruit types. We chose Réunion as a study system, which is host to the longest bioclimatic gradient in the South-West Indian Ocean and protection of its rich and unique biota is considered crucial (Mittermeier et al., 2004).

MATERIAL AND METHODS

Study area

Réunion, at 2512 km² is the largest and youngest (2-3 million years) volcanic island in the Mascarene archipelago, located in the Indian Ocean 750 kms east of Madagascar (**Fig.1.1a**). Its steep relief reaches 3070 m asl. in the oldest part of the island at the Piton des Neiges and 2630 m asl. in the southeast at the Piton de la Fournaise (**Fig.1.1b** & **1.1c**). Réunion experiences a tropical oceanic climate with the south-eastern trade winds generating orographic precipitation on the windward side of the island (**Fig.1.1d**). On the coast, annual precipitation ranges from 500-1500 mm on the leeward side, to 5000 mm on the windward, reaching up to 12 000 mm between 1300 and 1800 m asl. (Jumeaux et al., 2011). Annual mean temperature ranges from 26 °C at sea level to 11°C on the summits. A thermal inversion layer is usually encountered between 2000 and 2380 m asl, with the driest conditions and frequent frost in winter (up to 100 days of frost per year on the top of the island) (Ah-Peng, unpubl.). Consequently, high elevations are defined above 2000 m asl on Réunion.

The vegetation zonation along the elevational gradient is strongly associated with climatic conditions (Cadet, 1977). These zones range from tropical rain forest (windward) and semi-dry forest (leeward) at sea level, through to tropical mountain cloud forest then subalpine shrubland above 2000 m (Strasberg et al., 2005). According to Baider et al. (2010), Réunion hosts 550 native angiosperm species, of which 45% are woody. Native species are mainly found in well-preserved native habitats, which still cover one third of the island (**Fig.1.1e**). While native mountain habitats are well preserved, lowland habitats have been almost completely transformed. Two corridors of native forest remain relatively intact from sea level to the subalpine vegetation, one on the leeward side and one on the windward side on the active volcano, the Piton de la Fournaise (Strasberg et al., 2005). These corridors are crucial to understanding past vegetation assemblages at low elevations.

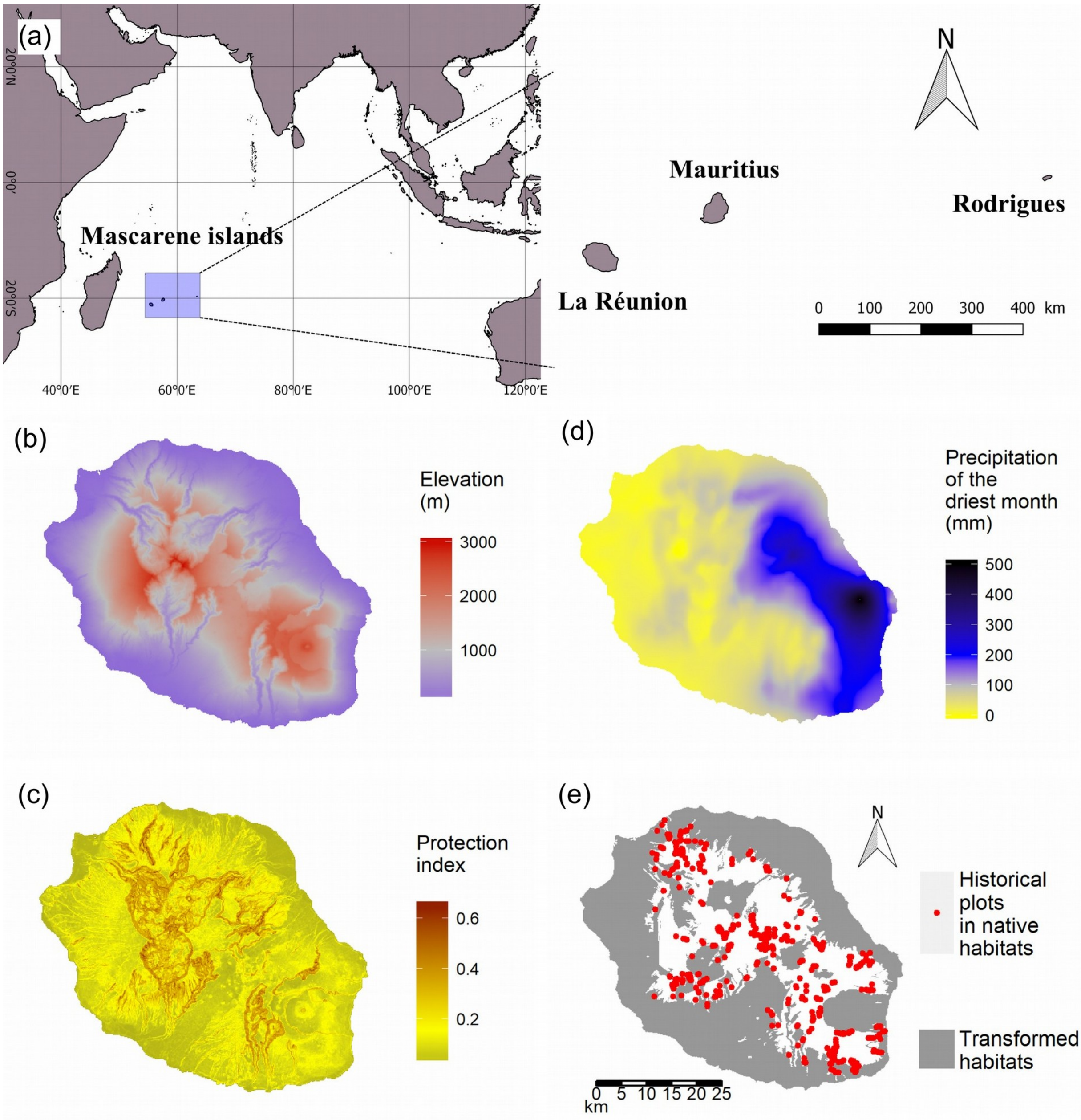

Fig.1.1 Maps of Réunion island. a) *Réunion is the westernmost and the largest island within Mascarenes.* ***(b)*** *The island peaks at 3070 m, almost half of its area is above 1000 m.* ***(c)*** *Protection index highlights the complex topography of Réunion with escarpments reaching 1000 m high.* ***(d)*** *Precipitation of the driest month (mm) shows the climatic divide between the dry leeward side in the West and the wet windward side in the East.* ***(e)*** *Since the 17th century, two-thirds of native habitats have been transformed (mask from Strasberg et al., 2005). The 429 historical plots selected for analyses are shown in red.*

Sampling

We used an historical dataset comprising more than 850 vegetation plots (quadrats) sampled in the 1970s, mostly in native habitats (Cadet, 1977). The sampling area ranged from 25 m² in high-elevation shrubland to 2500 m² in lowland tropical forests. In each plot, Cadet recorded the number and cover of vegetation strata. For each stratum, Cadet recorded the list of tracheophyta at species level and growth forms with the Braun-Blanquet semi-quantitative method.

We removed all plots occurring in secondary vegetation where native species were no-longer present, in highly disturbed forests where invasive species dominated or on lava flows of less than 300 years old to avoid successional biases. In the 429 selected plots, alien species were rare or assumed to have negligible effect on assemblage structure. A GIS points layer was created on the basis of geographical information provided by Cadet, *e.g.* elevation, topographic description, orientation, steepness, track proximity, and field knowledge of the authors (**Fig.1.1e**). The distribution of plots was not random, however, it encompassed most broad habitat units and environmental gradients, *e.g.* elevation (**App.1.1**), precipitation, topographic complexity.

We focused on woody plant species, *i.e.* woody angiosperms (208 species) and arborescent ferns (5 species), for the following reasons: (i) Most woody species were taxonomically named in the 1970s (Bosser et al., 1976 - ongoing; Rivals, 1952) compared to herbaceous species, which were often only determined to genus. (ii) FF species usually are woody plants that contribute significantly to the structure of tropical plant communities (Willson et al., 1989; Yu et al., 2017).

Relationship between the distribution of fruit types and abiotic factors

We categorized the fruit of each woody species as either fleshy or dry according to the description in the Flore des Mascareignes (Bosser et al., 1976 - ongoing). Fruits were classified as fleshy if they possessed noticeable fleshy pericarps, *e.g.* drupes, berries, or fleshy appendages when mature, *e.g.* aril, receptacle. Tree ferns, which produce spores, were assigned to dry fruits. For each plot, we calculated the FF and DF species richness (respectively nFF and nDF), and the proportion of FF species (pFF = nFF / woody species richness).

We categorized the growth form of each species as tree, shrub or climber according to the description in the Flore des Mascareignes. To assess the contribution of FF growth forms to pFF, we calculated the proportion of FF shrub species (pFFshr = FF shrub species richness / woody species richness) and the proportion of FF tree species (pFFtree = FF tree species richness / woody species richness). Climbers, *i.e.* creepers and lianas, were excluded from our analyses because only 20 species were found in Cadet‘s survey.

We extracted 19 bioclimatic variables (see http://www.worldclim.org/bioclim) from Météo France (Jumeaux et al., 2011). All climatic data spanned the years 1980-2010 and were computed using monthly means. Topographic data were derived from a digital elevation model provided by the IGN (http://professionnels.ign.fr/bdalti). The resolution of the digital elevation model was resampled to a raster resolution of 150 x 150 m and topographic variables extracted with the software SAGA version 5.0.0.

Fruit types, phylogenetic relatedness and geographical distribution of species

We constructed phylogenetic trees for vegetation plots based on the phylogeny from Zanne et al. (2013) (R package ‘brranching’). We assumed that the resolution of deep nodes was sufficient to assess the phylogenetic relatedness in our analyses.

Finally, we assigned a geographical distribution to woody species following Boullet et al. (2012). We calculated the proportion of single-island endemic species from Réunion (pSIE = endemic species richness / woody species richness) and the proportion of Mascarene-shared species (pMS = Mascarene-shared species richness / woody species richness), *i.e.* archipelago endemic species shared by Réunion and Mauritius and/or Rodrigues.

Tab.1.1 *List of environmental variables and their abbreviations used as explanatory variables in GLMs. The minimum and maximum values are extracted from the 429 historical plots.*

Variables	Description	Unit	Min	Max
Elevation	Elevation above sea level	m asl.	50	3000
Insolation	Annual direct insolation	kWh m^{-2}	488,90	2930,40
Mean diurnal range	Mean of the monthly temperature ranges (monthly maximum minus monthly minimum)	° C	5,77	11,13
Precipitation of the driest month	Total precipitation during the driest month	mm	6,62	495,49
Protection	Measure of the openness/protection calculated by analyzing the degree to which the surrounding relief protects the given cell	-	0,01	0,85
Topographic wetness	Index quantifying topographic control on hydrological processes	-	0,87	7

Statistical analyses

Relationship between the distribution of fruit types and abiotic factors

All statistical analyses were conducted in R ver. 3.4.3 (R Core Team). For data exploration, we used the framework proposed by Zuur et al. (2010). To minimize the effect of collinearity, we retained six environmental variables with variance inflation factors < 3 (**Tab.1.1**).

The relationship between binomial data responses (species proportion) and environmental variables were analyzed using generalized linear models (GLM) with binomial distribution (Guisan et al., 1999). We did not include interaction terms in regressions because of the limited increase in the models' explanatory power and the difficulties of assessing interactions between continuous variables (Aiken et al., 2003). To avoid inflation of type I & II errors in models, we accounted for the possible effects of spatial autocorrelation on parameter estimates. Firstly, we constructed models with environmental predictors only (E-GLM). The residuals of each model were tested for spatial autocorrelation using Moran's I (Dormann et al., 2007). A significant spatial autocorrelation was detected in the residuals of all E-GLMs. We then constructed environmental-spatial models (ES-GLM) using the Moran eigenvector filtering function (R package 'spdep') to remove spatial autocorrelation from the residuals (Griffith and Peres-Neto, 2006). For all E-GLMs and ES-GLMs, we assessed the best fitting GLM using Akaike information criteria (R package 'dredge'). Finally, we constructed spatial models without environmental predictors (S-GLM) to assess the contribution of Moran eigenvectors to the explained deviance of models. Pseudo-R^2 of models were calculated by the relationship "1 – residual deviance/ null deviance".

By interpolation, we predicted pFF on a spatial grid over Réunion constituted by 111 460 cells of 150 x 150 m using a partial regression, *i.e.* excluding Moran eigenvectors, on environmental variables (Le Rest et al., 2013). Due to the large transformation of native lowland habitats, spatial interpolation is a relevant method to understand what the former distribution of fruit types on Réunion may have been.

Fruit types, phylogenetic relatedness and geographical distribution of species

For each vegetation plot, we calculated the standardized net relatedness index (NRI) (R package 'Picante'), to estimate the influence of phylogenetic relatedness on the species pool (Webb et al., 2002). To infer phylogenetic structure, the observed NRI of assemblages was compared to a null expectation obtained by randomly sampling the species pool 1000 times while keeping species richness constant. Positive and negative NRI values respectively superior or inferior to the 5th or 95th quantiles of the simulated distribution were considered as significant and thus indicated phylogenetic clustering or over-dispersion.

To visualise the relationships between phylogenetic relatedness, geographical distribution and fruit type composition, a principal component analysis was conducted using NRI, pSIE, pMS and pFF.

RESULTS

Relationship between the distribution of fruit types and abiotic factors

A total of 213 woody species were identified, belonging to 65 families of tracheophyta (62 angiosperms and 3 ferns). 124 woody species were FF (58%, **App.1.2**). Across plots, pFF ranged from 0 to 89% (42 FF species in 47 woody species), pFFtree from 0 to 67% (20 FF tree species in 30 woody species) and pFFshr from 0 to 40% (6 FF shrub species in 15 woody species).

Tab.1.2 *Scaled coefficients and standard errors of the best fitting ES-GLMs (GLM with environment predictors and spatial filtering). "pFF", fleshy-fruited species proportion, "pFFtree", fleshy-fruited tree species proportion, "pFFshr", fleshy-fruited shrub species proportion, "^2" quadratic term; "Log" napierian logarithm term. Moran eigenvectors included in models are not shown here.*

	pFF (Pseudo-R²=0,78)		pFFtree (P-R²=0,74)		pFFshr (P-R²=0,50)	
	Coef	se	Coef	se	Coef	se
Intercept	0,47***	0,031	-0,62***	0,034	-1,22***	0,031
Elevation	-0,98***	0,034	-0,78***	0,041	-0,50***	0,042
Elevation^2	-0,26***	0,034	-0,29***	0,039	-0,32***	0,040
Insolation	-	-	-	-	0,05^{NS}	0,026
Precipitation of the driest month	0,15***	0,036	0,16***	0,031	-	-
Precipitation of the driest month^2	-0,07***	0,014	-0,12***	0,016	-	-
Log(protection index)	-0,06**	0,022	-	-	-	-
Topographic wetness index	-0,07**	0,026	-	-	-0,05*	0,026

The goodness of fit of ES-GLMs was substantial and not a consequence of including spatial filtering as a fixed effect (**App.1.3**). ES-GLMs no longer showed a significant spatial autocorrelation. In ES-GLMs, elevation was always the best predictor (**Tab.1.2**). pFF and pFFtree were highly influenced by precipitation of the driest month, whereas pFFshrub was not. Topographic wetness and protection had a negative influence on pFF, but this influence remained weak in comparison with climatic variables. Neither mean diurnal range, nor insolation had any significant effect (**Tab.1.2**).

pFF was very high at low elevations and decreased sharply with elevation (5% each 100 m loss in montane forest, maximum negative slope at 1500 m asl) (**Fig.1.2**). FF plants were rare above 2000 m asl (only 5 FF species in 39 woody species sampled in 43 vegetation plots) and absent above 2400 m asl. Almost half (48%) of all woody species were FF trees at low elevations. pFFtree declined sharply with elevation whereas pFFshrub showed a hump-shaped pattern with a peak around 750 m asl. At low elevations, pFF was higher in the wettest areas due to the strong presence of FF trees.

Spatial interpolation suggested that most native habitats may have been strongly dominated by FF plants prior to human transformation (**Fig.1.3**). In addition, lowland habitats were probably FF species-rich (**App.1.4**).

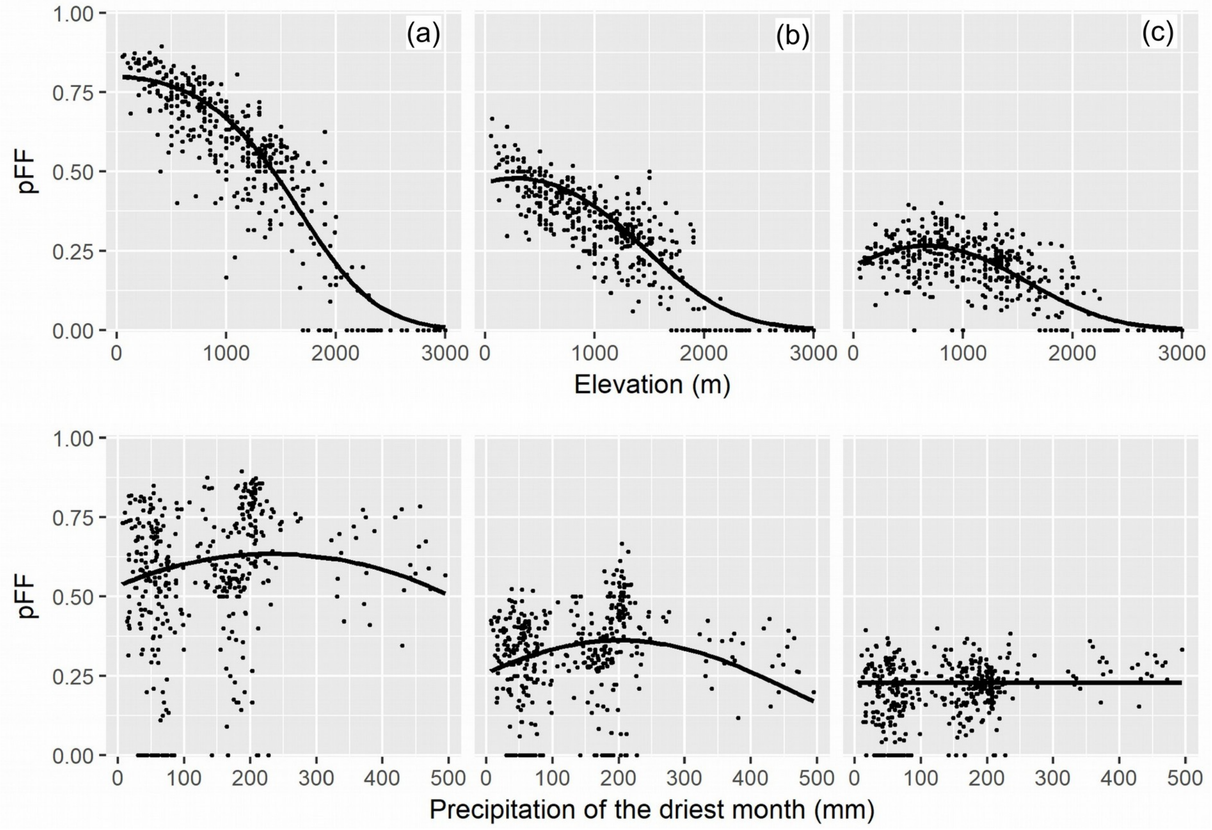

Fig.1.2 *Partial logistic regressions of the fleshy-fruited species proportion with elevation and precipitation of driest month. Columns (a) to (c) are respectively the fleshy-fruited species proportion (pFF), the fleshy-fruited tree species proportion (pFFtree) and the fleshy-fruited shrub species proportion (pFFshr). Predicted probabilities as fit by glm with analyses based on binary data are displayed by the black lines.*

Fruit types, phylogenetic relatedness and geographical distribution of species

No shift in fruit type occurred on Réunion among woody species radiations (**App.1.5**). The widest radiations belonged to DF lineages. Most of DF species (54%) were endemic, whereas FF species showed equal proportions (40%) between endemic and Mascarene-shared species. pSIE and pMS ranged respectively from 4% to 100% and from 0% to 59%. NRI ranged from -2.9 to 4.1, 51 and 44 woody species assemblages were respectively phylogenetically overdispersed and aggregated in a significant manner.

On the first PCA axis accounting for 72% of the total variance, pFF and pMS were strongly related, and both were negatively related to pSIE and NRI (**Fig.1.4**). Woody species-rich assemblages were sorted along the first axis depending on their elevation. On the second PCA axis accounting for 18% of the total variance, pSIE and NRI were negatively related. FF species-rich assemblages were sorted along the second axis depending on precipitation of driest month. In other words, at low elevations, FF species-rich assemblages were dominated by Mascarene-shared species. These assemblages were phylogenetically random or overdispersed in wet areas all across the year and more clustered in drier areas. At middle elevations where pFF decreased strongly, pSIE showed a strong increase and assemblages were phylogenetically random or overdispersed. At high elevations where FF species were absent, assemblages were dominated by endemic closely related species (**Fig.1.4**).

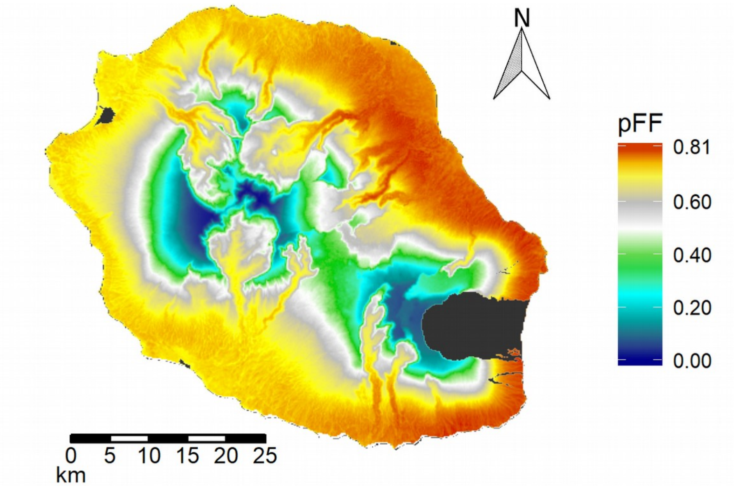

Fig.1.3 *Spatial modeling of the fleshy-fruited species proportion (pFF) by interpolation of ES-GLM coefficients. Fleshy-fruited and dry-fruited species-rich habitats are respectively shown in warm and cool colors. A dark grey mask is applied on recent lava flows and wetlands.*

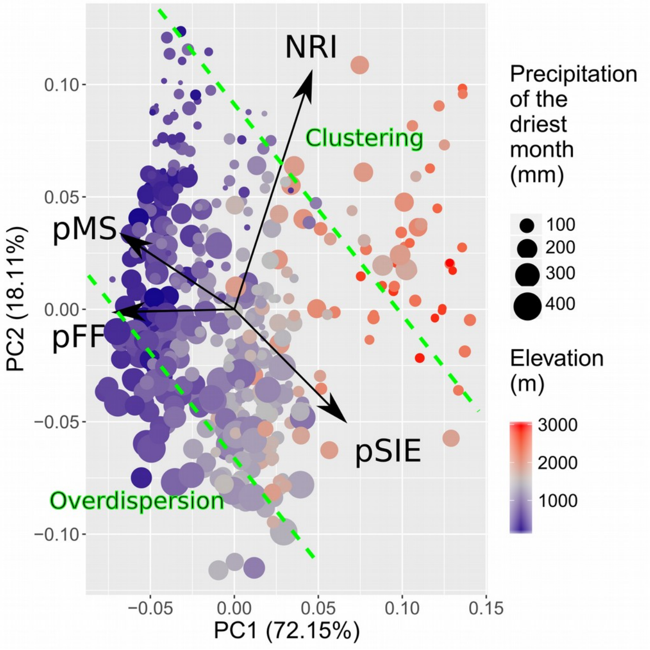

Fig.1.4 *PCA ordination plot showing the association between 429 historical plots and four descriptors of woody species assemblages: (1) standardized net relatedness index (NRI), green dashed lines indicate domains where assemblages are phylogenetically clustered or overdispersed in a significant manner; (2) proportion of single-island endemic species (pSIE); (3) proportion of Mascarenes-shared species (pMS); (4) proportion of fleshy-fruited species (pFF). For each plot, elevation is shown as a color gradient (cool and warm colors respectively for low and high elevations), precipitation of the driest month is shown as a size gradient (small and large disks respectively for low and high precipitation). The proportion of explained variance is given for each component.*

DISCUSSION

A striking elevational gradient in pFF

An overwhelming majority of woody species bear fleshy fruits at low elevations, while FF species are absent at high elevations (above 2400 m asl.) on Réunion. Although several works showed a significant decrease of pFF with elevation (Buitrón-Jurado and Ramírez, 2014; Chapman et al., 2016; Yu et al., 2017), to our knowledge this is the first time that such a striking change is highlighted (0% - 81%). The magnitude of this gradient at landscape scale on Réunion is greater than the one shown at continental scale by Chen et al. (2016). The sharp decrease of pFF with elevation on Réunion shows how important the last remaining vegetation corridors along environmental gradients are in understanding biodiversity patterns. In particular, our analyses show the singularity of lowland remnants where canopies are dominated by FF tree species. Moreover, we show that the distribution of fruit types is related to rather different patterns of endemism and phylogenetic structure depending on the climatic variables. These observations demonstrate the relevance of high-elevation oceanic islands as study systems of ecological trait distribution (Irl et al., 2015; Santos et al., 2016; Warren et al., 2015).

Abiotic factors as the main drivers of the fruit type distribution

The striking relationship between elevation and pFF suggests a strong bottom-up control of communities, *i.e.* the availability of resources controls the fruit type composition. FF plants strongly dominate assemblages at low elevations where the productivity is highest (Cleveland et al., 2011) and where the availability of nutrients is high, both crucial for fruit production (Kramer and Kozlowski, 1979). With increasing elevation, temperature declines, soil conditions deteriorate (particularly where the relief is steep) and cloudiness becomes more persistent, leading to lower nutrient availability (Bruijnzeel and Veneklaas, 1998; Carbutt et al., 2013; Dalling et al., 2016; Tanner et al., 1998) to make fleshy fruits.

The elevation at which frost appears may be a major threshold for tropical species adapted to warm conditions (Sarmiento, 1986) and for FF species where freezing of succulent cells is known to cause irreparable damage to the diaspore (Burke et al., 1976). Areas above 1500 m asl experience several days of frost a year on Réunion and frost is frequent in winter at high elevations in subalpine shrubland. In the latter, low temperatures combined with aridity are probably the main components of the strong environmental stresses that determine assemblages and promote the coexistence of anemochorous species belonging to radiations within Asteraceae and Ericaceae (Monasterio and Sarmiento, 1991; Pelser et al., 2007; Schwery et al., 2015; Strijk et al., 2012). FF species that occur in subalpine shrubland on Réunion are usually shared with Mauritius and have a wide elevational range (**App.1.6**). Extinction of endemic FF species with a narrow niche might have occurred, *e.g.* during the last explosive events of the Piton des Neiges some 230000-12000 years ago, but this explanation seems unlikely because the high levels of habitat diversity has allowed to maintain high richness of endemic DF plants with a narrow niche (Strijk et al., 2012). The absence of endemic FF plants at high elevations may rather reflect the inability of FF lineages to adapt to high elevation conditions. FF lineages that radiated on Réunion, *e.g.* six species within *Badula* (Primulaceae) despite the young age of Réunion (Bone et al., 2012), are well represented below 2000 m asl and may be limited by their tropicality along strong climatic gradients (Kerkhoff et al., 2014; Vetaas et al., 2018). In Hawai'i archipelago, 76 FF radiated species appeared in less than 1,5 million years within the genus *Cyanea* (Campanulaceae) and are all encountered below 2000 m asl. (Givnish et al., 2009), which is also the lower bound of subalpine shrubland. Thus, niche conservatism may be a major driver of diversification pattern on oceanic islands (Ibanez et al., 2018) and may explain why so many FF species cannot adapt to high elevation conditions.

In the lowlands, woody plants are more likely to bear fleshy fruits on the windward side where there is no dry season. The positive, linear influence of precipitation on pFF has already been shown for mainland worldwide (Almeida-Neto et al., 2008; Chen et al., 2016; Correa et al., 2015) and Madagascar (Bollen et al., 2005). Lower pFF on the leeward may be the consequence of higher water requirements for making fleshy diaspores. However, pFF remains high in the semi-dry forest, *i.e.* 70% at sea level (only about 10% lower than the windward side), which is probably because the dry season is moderate on Réunion in comparison with tropical dry deciduous forests (Cadet, 1977). The fact that phylogenetic clustering and randomness are respectively observed on the leeward and the windward shows that high levels of pFF in the semi-dry forest are reached among particular lineages on Réunion. This phylogenetic structure supports the idea that the ability to tolerate drought and fire shapes woody species distribution patterns at large scale (Slik et al., 2018).

The relationship between pFF and precipitation is more hump-shaped than linear on Réunion. At mid elevations particularly, massive precipitation and strong topographic wetness lead to lower pFF. Cadet (1977) raised the possibility that high precipitation, in areas where the edaphic drainage is weak, could have an inhibitory effect on forest dynamics. Pioneer DF plants that are less nitrogen demanding than FF plants may be less impacted by the difficulties with the uptake of nitrogen due to the reduced microbial metabolism in cool and very wet soils (Grubb, 1977). Topographic factors, however, have an overall weak influence on the distribution of fruit types in our analyses. The pattern of residuals of ES-GLM shows that pFF is systematically overestimated in a common mid-elevation habitat, *Erica* thicket, which often occurs on narrow ridges. This suggests that the resolution of topographic rasters, *i.e.* 150 x 150 m, is probably too low to correctly describe the effect of topographic factors on the distribution of fruit types (Oddershede et al., 2015).

Fleshy-fruited trees more sensitive to stressful conditions than fleshy-fruited shrubs

We find a shift within assemblages when we assess the contribution of FF growth forms to pFF, and show that spatial pattern of FF woody species is mostly driven by FF trees. As hypothesized, FF trees are probably more sensitive to the more stressful canopy conditions than FF shrubs (Yu et al., 2017). In our study, two main phenomena distinguish FF trees from FF shrubs: (i) pFFtree declines sharply with elevation whereas pFFshrub shows a hump shaped pattern. At low elevations, FF trees strongly dominate canopies (Strasberg, 1996) and the latter is increasingly enriched with DF trees in montane forest (**App.1.7**). At high elevations, FF trees disappear above 2000 m asl., whereas FF shrubs are encountered until 2400 m asl., possibly benefiting from the protection of the DF species canopy (Larcher, 2003). (ii) pFFtree is related to precipitation of the driest month whereas pFFshrub is not. In the lowlands, FF trees are thus more dominant within assemblages on the windward where precipitation is ample all year long. The fact that pFFshrub is not related to precipitation shows that shrubs growing in the understory probably experience far less evapotranspiration than canopy trees allowing them to invest more water in fleshy fruits (Yu et al., 2017).

Phylogenetic structure, fruit types and climatic conditions

We highlight phylogenetic clustering and a significant decrease of pFF in areas where climatic conditions are harsh, *i.e.* drought on the leeward at low elevations and drought combined to low temperature at high elevations. This relationship between compositional data, traits and climatic conditions demonstrates a strong influence of the environment in community structure (Cadotte and Tucker, 2017). Our analyses also show that there is a greater number of phylogenetically overdispersed assemblages (51 versus 44) that occur between low elevations and upper montane forest, in areas without any dry season. However, we lack elements to further discuss the potential mechanisms underlying this pattern. We note that many overdispersed assemblages display high levels of endemism in montane forest, while clustered assemblages are widely dominated by endemic dry-fruited species at high elevations. Thus, this observation demonstrates that high endemism at fine scale is not necessarily related to a certain phylogenetic pattern.

The role of dispersal limitation at landscape and regional scales

According to the traditional view of filters shaping communities, the dispersal filter is the first to act (Cadotte and Tucker, 2017). An oceanic island like Réunion allows one to explore the potential role of dispersal limitation at two geographical scales by asking the following questions: is the distribution of fruit types shaped by the ability of FF or DF species (i) to reach neighboring habitat patches at landscape scale or (ii) to reach Réunion at regional scale?

At landscape scale, we have several reasons to think that dispersal limitation may play a minor role in shaping the distribution of fruit types. Our results show that seed dispersal strategies are fundamentally different between assemblages at low and high elevations. In the lowlands, the rich frugivorous vertebrate fauna, *e.g.* giant turtle, skinks, fruit pigeons, flying foxes, described by the first settlers (Cheke and Hume, 2008) and attested by sub-fossil archives (Mourer-Chauviré et al., 1999), corroborates the large dominance of FF plants. Yet, even if this rich frugivorous fauna once occurred throughout the lowlands of Réunion, we show that FF species-rich assemblages are phylogenetically more clustered on the leeward where there is a dry season. In montane forest, frugivorous vertebrates were abundant until the late 19th century (Cheke and Hume, 2008), but pFF decreases sharply with elevation. Moreover, FF species are absent at high elevations, although opportunistic frugivorous birds probably disperse small-seeded FF plants above 2500 m asl. (Cheke, 1987a). Hence, most FF plants do (or did) not seem to have any dispersal limitation but are (or were) probably not able to grow because of harsh environmental conditions in these habitats.

Long distance-dispersal limitation may differentially influence the distribution of fruit types depending on elevation. At low elevations, FF assemblages are species-rich, phylogenetically diverse and mainly composed of Mascarene-shared or widespread species. This supports the idea that FF species have a high potential for inter-island colonization (Carvajal-Endara et al., 2017; García-Verdugo et al., 2014), despite the relative isolation of Réunion (Strijk et al., 2012). At higher elevations, biogeographic constraints may enforce the decrease of pFF. FF lineages preadapted to high elevation conditions, *e.g.* holarctic, austral antarctic taxa that maintain high levels in pFF in the Andes (Buitrón-Jurado and Ramírez, 2014), are almost absent on Réunion, except one single species of *Rubus* (Rosaceae). The closest source of subalpine FF preadapted lineages is at minimum 850 km away in Madagascar where subalpine shrubland covers small and disjunct areas (Crowley, 2004). Consequently, subalpine shrublands are very isolated habitats at regional scales and cold-adapted plant lineages may have major difficulties crossing unfavorable habitats (Slik et al., 2018). Moreover, subalpine shrublands show a striking resemblance on Réunion, Comoros, Madagascar and East Africa, and are all dominated by closely related species within the genus *Erica* (McGuire and Kron, 2005). This suggests that, at regional scale, (i) similar abiotic conditions probably drive vegetation patterns at high elevations (Irl et al., 2016) and (ii) species pool might be impoverished in FF preadapted lineages, resulting in a strong regional forcing of pFF on Réunion (Ibanez et al., 2018). A larger scale study is required to better understand the role of biogeographic constraints in shaping spatial patterns of fruit types within oceanic islands.

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CHAPITRE 2. Les vertébrés forestiers éteints de La Réunion et l'île Maurice - Une revue des causes d'un paradoxe

RESUME

L'archipel des Mascareignes est mondialement connu pour l'extinction massive de ses vertébrés indigènes depuis le début de la colonisation humaine au 16ème siècle. Pourtant, les extinctions y présentent d'étonnantes disparités entre les îles et entre les lignages de vertébrés forestiers partagés par les deux principales îles de l'archipel : le bilan des extinctions est plus sévère à La Réunion où subsiste plus d'un tiers des habitats indigènes en comparaison avec Maurice où plus de 95% de ceux-ci ont été transformés. Pour comprendre ce paradoxe, nous étudions la chronologie des extinctions et passons en revue les principaux facteurs impliqués depuis le début de la colonisation humaine. Nous évaluons (i) le nombre d'introductions de vertébrés exotiques en considérant en particulier les prédateurs connus pour leur impact dévastateur en milieu insulaire, (ii) la surchasse en discutant essentiellement les changements dans la démographie humaine et (iii) la transformation des habitats en considérant les caractéristiques altitudinales des habitats relictuels et les implications fonctionnelles sous-jacentes. Parmi les 23 genres étudiés, les râles aptères (*Dryolimnas*), geckos nocturnes (*Nactus*) et scinques frugivores (*Leiolopisma*) s'éteignent rapidement après le début de la colonisation dans les deux îles (hormis pour les deux derniers sur les îlots au Nord de Maurice). A l'exception du Busard de Maillard (*Circus*), l'ensemble de la grande faune étudiée s'effondre dès la première moitié du 18ème à La Réunion et concerne particulièrement les frugivores (*Alectroenas, Cylindraspis, Pteropus, Psittacula*), tandis qu'elle résiste mieux à Maurice même si des extinctions ont finalement lieu avec environ un siècle de déphasage. Considérant les facteurs impliqués, Maurice présente non seulement des introductions plus précoces de mammifères prédateurs (*Rattus*), mais aussi en plus grand nombre avec par exemple les macaques et les mangoustes qui n'ont jamais été introduits à La Réunion. Ces multiples introductions ont néanmoins épargné certains îlots au Nord de Maurice qui sont devenus d'importants sanctuaires pour diverses espèces de squamates. Les colons des deux îles étaient d'invétérés chasseurs, et même si La Réunion a subi une surchasse plus précoce que Maurice, l'explosion de la population humaine à Maurice dès la fin du 18ème siècle n'a pas mené pour autant à l'extinction totale de sa grande faune indigène. Ces deux facteurs ne peuvent donc expliquer à eux seuls le paradoxe observé. La destruction avant 1800 de la majorité des habitats les plus favorables à La Réunion et l'incapacité des habitats (sub-) montagnards et de haute altitude à agir comme des refuges efficaces pour des vertébrés issus de lignages de basse altitude, ont probablement joué un rôle crucial dans la fulgurance des extinctions. Ce phénomène est documenté en particulier pour les frugivores qui ont rapidement perdu la plupart des habitats de basse altitude dominés par les plantes à gros fruits. A l'inverse, Maurice présentait jusqu'à la fin du 19ème siècle des habitats relictuels hautement favorables et relativement compacts qui ont probablement permis à de nombreux vertébrés indigènes d'échapper, au moins pour un temps, aux multiples perturbations induites par l'Homme. D'importantes questions persistent en raison du caractère souvent lacunaire des récits historiques et du manque de travaux paléoécologiques, en particulier à La Réunion où ils mériteraient d'être développés. Plusieurs espèces de vertébrés relictuelles ont frôlé l'extinction à la fin du 20ème siècle, mais des mesures ambitieuses leur ont permis dans l'ensemble de revenir à des tailles de population moins inquiétantes. Enfin, en documentant la raison pour laquelle la destruction des habitats de basse altitude à La Réunion est probablement le facteur majeur derrière ce paradoxe d'une île défaunée malgré la persistance de vastes surfaces d'habitats indigènes, nous apportons une explication crédible au fait que les îles océaniques de haute altitude connaissent à l'échelle globale des taux d'extinctions de frugivores plus élevés.

Extinct forest vertebrates of Réunion Island and Mauritius - A review of the causes of a paradox in the light of recent spatial modelling*

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ABSTRACT

The Mascarenes are famous worldwide for the massive extinction of their native vertebrates since human colonization in the 16th century. However, the extinction pattern between islands and between lineages of forest vertebrates shared between the two main islands of the archipelago shows astonishing disparities: the rate of extinctions is more severe on La Reunion where more than a third of native habitats have remained compared to Mauritius where more than 95% of them have been transformed. To understand this paradox, we study the chronology of extinctions and review the main factors since first contacts with humans. We assess (i) the number of introductions of exotic vertebrates, considering in particular predators known for their devastating impact on island biotas, (ii) overhunting, mainly by discussing changes in human demography, and (iii) habitat transformation, considering the elevational characteristics of habitat remnants and the underlying functional implications. Among 23 studied genera, several went rapidly extinct on both islands after colonization began (except on northern islets of Mauritius). Most large-bodied vertebrates, especially frugivores, collapsed from the first half of the 18th century on Reunion (except the Réunion harrier), while several vertebrates that are now extinct on Mauritius survived until 1850. Considering the factors involved, Mauritius does not only show earlier but also more numerous introductions of mammal predators (except northern islets which have thus become important sanctuaries for several squamates). Settlers of both islands were inveterate hunters: Réunion was overhunted before Mauritius, but the explosion of human population in the latter in the late 18th century did not lead to the rapid extinction of large native vertebrates as on Réunion. These two factors alone therefore cannot explain the observed paradox. The early destruction of most favourable lowland habitats on Réunion and the inability of montane habitats to act as effective refuges for most vertebrates probably played a crucial role in rapid extinctions. Notably, frugivores rapidly lost most habitats dominated by large fleshy-fruited plants. Conversely, Mauritius presented highly favourable substantial habitats until the late 19th that probably allowed many native vertebrates to escape from multiple human-induced disturbances, at least for a time. Important questions persist due to the incompleteness of historical accounts and the lack of palaeoecological works particularly on Réunion where the potential for studies remains high. Finally, by documenting why the destruction of lowland habitats is probably the major factor underlying this paradox, we provide a credible explanation for the fact that high-elevation oceanic islands globally experience higher rates of frugivore extinctions.

> *"Reunion, though a larger island than Mauritius, is very mountainous and had a much smaller area of lowland tropical forest than Mauritius. As most suitable fruit-bearing trees are confined to this largely coastal zone, the available habitat was perhaps more easily scoured for bats than in Mauritius, where suitable habitat was originally spread all over the island."* (Cheke and Dahl, 1981)

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* *In preparation*

INTRODUCTION

The Dodo of Mauritius became one of the most emblematic species of human induced extinction but this species is only a symbol among numerous other insular species that constitute the bulk of documented extinctions at the Holocene (Alcover et al., 1998; Blackburn, 2004; Kier et al., 2009; Steadman, 1995; Whittaker and Fernandez-Palacios, 2007). Islands show indeed a more pronounced extinction rate than mainland ecosystems, which often leads to the global extinction of species due to high endemism. The primary drivers of vertebrate extinction are the destruction and fragmentation of habitats, the number of introduced vertebrate species and overhunting, all induced by human colonization (Blackburn, 2004; Cheke and Hume, 2008; Duncan et al., 2013; Heinen et al., 2017; Osuri et al., 2020; Triantis et al., 2010). However, biogeographic factors such as island isolation, small area size or high elevation, have also been shown to increase vertebrate extinction risk on islands (Blackburn, 2004; Duncan et al., 2013; Heinen et al., 2017).

Habitat destruction is a major cause of global diversity loss (Tilman et al., 1994; Triantis et al., 2010). It results in small and isolated populations that are susceptible to stochastic factors, such as erosion of genetic diversity or random fluctuation in demography, that can lead alone these populations to extinction in a few generations. These populations are however also susceptible to other human-induced factors. For example, the introduction of invasive predators has been a major cause of vertebrate extinctions on oceanic islands worldwide, because most islands have few native predators (Blackburn, 2004; Doherty et al., 2016). Invasive mammals are particularly damaging, having contributed to considerable species decline and extinction. Introduced rodents and cats have for instance been listed as causal factors in 44% of modern species extinctions of bird, mammal, and reptile (Doherty et al., 2016). In addition, introduced non-predator vertebrates can primarily compete for resources and nest sites, but they are also sometimes reservoirs of exotic diseases that can negatively impact native vertebrates (Jones, 1996; McClure et al., 2020).

Among biogeographic factors, island isolation increases the risk of vertebrate extinction (Heinen et al., 2017). Indeed, isolation may cause exaggerated ecological release, resulting in traits such as flightlessness that make species more prone to extinctions (MacArthur and Wilson, 1967). Smaller islands are also more prone to vertebrate extinctions because resources are limited as well as refuges in order to escape anthropogenic overhunting or deforestation (Blackburn, 2004; Duncan et al., 2013; Heinen et al., 2017). On the other hand, the positive effect of maximum elevation on extinction risk was unexpected by Blackburn (2004) and Heinen et al. (2017), notably because montane areas were expected to act as refuges. Heinen et al. (2017) suggest it might be explained by the great heterogeneity of habitat suitability along elevational gradients, making species more vulnerable to the destruction of lowland habitats. Actually, this “habitat suitability” hypothesis has been early proposed by Cheke and Dahl (1981) who discuss a striking paradox in the Mascarene islands: one of the two native species of fruit bats has survived on Mauritius despite the almost total destruction of native habitats, whereas they have long gone extinct on Réunion, where vast areas of native habitats have remained. Thiollay and Probst (1999) made a comparable assumption concerning the two extant Mascarene cuckoo-shrikes: the species confined to native remnants on Mauritius is doing better than on Réunion, where major conservation efforts are not succeeding in significantly raising population size (see Salmona et al., 2012). This hypothesis has in fact also been proposed in West Indies and Hawai‘i, where it has been postulated that the loss of dry lowland habitats long before the arrival of Europeans probably caused the extinction of numerous vertebrates (Olson and James, 1989).

Here, we use the Mascarene archipelago as a study system to explore the "habitat suitability" hypothesis. It is probably one of the only archipelagos worldwide where natural history has been so well documented since first human settlement both in terms of historical accounts (Cheke and Hume, 2008; Lougnon, 2005) and palaeontological works on extinct vertebrates (Arnold and Bour, 2008; Cheke and Dahl, 1981; Hume, 2007, 2011, 2013, 2014, 2019; Rijsdijk et al., 2009). With a filter effect (*sensu* Blackburn, 2004) which can be considered very low, we have a unique opportunity to study the chronology of extinctions in relation to the main drivers of vertebrate extinctions. Réunion is the highest island (3070 m asl) of the Mascarenes and still harbours 35% of native habitats (Strasberg et al., 2005), whereas Mauritius peaks at 828 m asl and retains less than 5% of native vegetation (Florens et al., 2012) (**Fig.2.1**). In that context, one would expect less extinctions on Réunion compared to Mauritius.

In the pristine Mascarenes, Réunion and Mauritius shared 23 forest vertebrate genera among which 12 genera went extinct on Réunion (55,2% of species involved) against five genera on Mauritius (31,4% of species involved) (**Tab.2.1**). Hence, the island with large native areas that might have acted as refugia, lost almost all its large forest vertebrates including every large-bodied frugivore species (**Tab.2.1**). This contrast between the two islands is all the more puzzling as the extinction of vertebrates on Réunion has been staggering (Cheke and Hume, 2008; Lougnon, 2005). We review the three main drivers of extinction, *i.e.* introduction of alien vertebrates, overhunting and deforestation, and compare the associated timeline on Réunion and Mauritius. In order to understand the extent to which suitable habitats for frugivores have been differentially destroyed on Réunion and Mauritius, the framework presented in chapter 1 (Albert et al., 2018) that shows a striking elevational gradient in the proportion of fleshy-fruited species on Réunion, will be extended to large fleshy-fruited plants on Réunion and Mauritius.

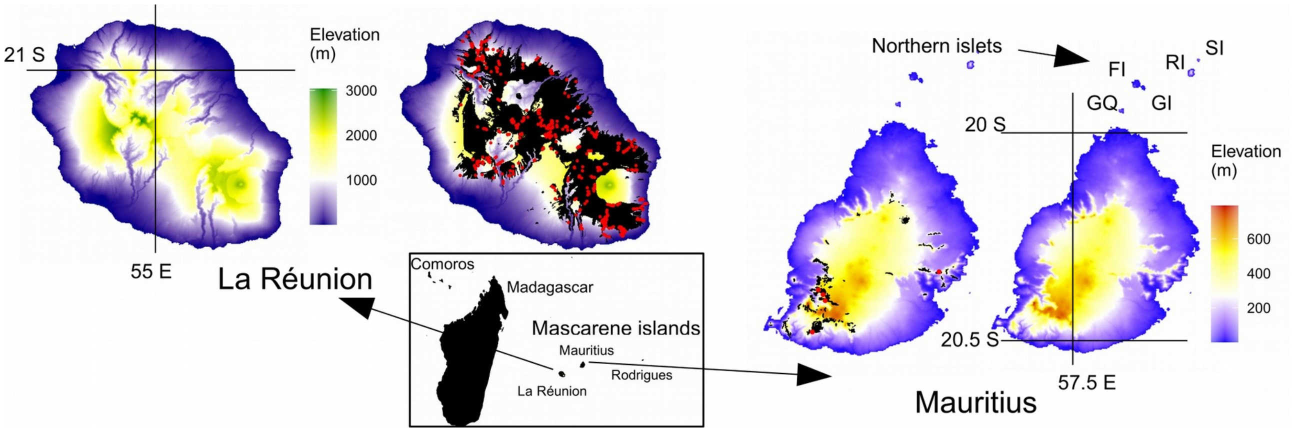

Fig.2.1 Topography and native forest remnants of the two main islands of the Mascarenes. *Réunion is a relatively recent high-elevation island with only one tiny islet, while geologically older Mauritius shows a much less rugged topography and a large number of islets. The northern islets that have played an important role for the conservation of several endemic reptiles are indicated by letters: from South to North, "GQ" Gunner's Quoin, "GI" Gabriel Island, "FI", Flat Island", "RI" Round Island and "SI" Serpent Island. The small Pigeon House Rock is not visible on the map. These six islets are located between 4 km (Gunner's Quoin) and 24 km (Serpent Island) from the mainland. Extant native forests and shrublands are shown in black. On both islands, they are mainly located at the highest elevations, but two native forest corridors between sea level and montane habitats still persist in the South-East and North on Réunion. Red points display the location of historical surveys used for analyses of plant diversity (430 and 5 plots on Réunion and Mauritius, respectively).*

Tab.2.1 Overview of forest vertebrate lineages shared by Réunion and Mauritius in the pristine Mascarenes. *For each species, diet, body size and status are given (“extinct” with the date of extinction or “extant” with the IUCN status). Red colours indicate when extant species on Mauritius are confined to northern islets. Diet: “**F**” frugivore, “f” occasionally frugivore, “G” granivore, “H” herbivore, “I” insectivore, “N” nectarivore, “R”: raptor. “?” putative date of extinction; “1” only flightless taxon shared by both islands; “2” species of which genus remains unclear (formerly* Necropsittacus*); “3” rough approximate value because substantial differences were found depending on the sources; “4” isolated individuals probably survived beyond this date on Réunion, and populations have survived between 1740 and 1850 on the northern islets on Mauritius; “5” a small population has been rebuilding in the East since the beginning of the 21st century; “6” several individuals recently observed, but this species has long been presumed extinct; “7” One of the two subspecies went extinct on Mauritius mainland. Source: Arnold and Bour, 2008; Cheke, 2013; Cheke and Hume, 2008; Dunning Jr, 2007; GCOI, 2019; Heinen et al., 2017; Hume, 2007, 2011, 2013, 2019; Slavenko et al., 2016; https://www.iucnredlist.org*

Taxonomy						Réunion		Mauritius	
	Genus	Species	Common name	Diet	Body size (g)	Extinct	Extant	Extinct	Extant
Aves	*Aerodramus*	*francicus*	Mascerene swiftlet	I	8,9		VU		DD
	Alectroenas	*nitidissima*	Pigeon Hollandais	**F**	170			1835	
		sp	Réunion blue pigeon	**F**	170	1715			
	Circus	*maillardi*	Réunion harrier	R	1000		EN	1630	
	Dryolimnas[1]	*chekei*	Sauzier's wood rail	I	300			1695	
		augusti	Réunion wood rail	I	300	1695			
	Falco	*punctatus*	Mauritius kestrel	R	350				EN
		duboisi	Réunion kestrel	R	350	1675			
	Foudia	*rubra*	Mauritius fody	f G	15				EN
		delloni	Réunion fody	f G	15	1675			
	Hypsipetes	*olivaceus*	Mauritius bulbul	**F**	55				VU
		borbonicus	Réunion bulbul	**F**	55		LC		
	Lalage	*typica*	Mauritius cuckoo-shrike	f I	32				VU
		newtoni	Réunion cuckoo-shrike	f I	32		CR		
	Mascarenotus	*sauzieri*	Commerson's lizard-owl	R	370			1860	
		grucheti	Gruchet's lizard-owl	R	370	1675?			
	Nesoenas	*mayeri*	Mauritius pink pigeon	f G H	300				VU
		duboisi	Réunion pink pigeon	f G H	300	1705			
		cicur	Mauritius turtle dove	f G H	300			1730	
		aff. *picturata*	Réunion turtle dove	f G H	300	1720?			
	Phedina	*borbonica*	Mascarene swallow	I	23,9		VU		DD
	Psittacula	*eques*	Echo parakeet	**F** G	220	1755			VU
		bensoni	Thirioux's grey parrot	**F** G	180	1735		1760	
		borbonicus[2]	Réunion red & green parrot	**F** G	300	1675			
	Terpsiphone	*bourbonnensis*	Mascarene flycatcher	I	11		LC		LC
	Zosterops	*mauritianus*	Mauritius grey white-eye	**F** I N	9				LC
		borbonicus	Réunion grey white-eye	**F** I N	9		LC		
		chloronothos	Mauritius olive white-eye	**F** I N	10				CR
		olivaceus	Réunion olive white-eye	**F** I N	10		LC		
Chelonii	*Cylindraspis*	*inepta*	Mauritius domed tortoise	**F** H	50000[3]			1850[4]	
		triserrata	Mauritius high-backed tortoise	**F** H	50000[3]			1850[4]	
		indica	Réunion giant tortoise	**F** H	50000[3]	1760[4]			
Mammalia	*Mormopterus*	*acetabulosus*	Mauritius free-tailed bat	I	7				EN
		francoismoutoui	Réunion free-tailed bat	I	7		LC		
	Pteropus	*rodricensis*	Golden bat	**F** N	254			1745	
		niger	Black-spined flying-fox	**F** N	450	1775[5]	(CR)		EN
		subniger	Rougette	**F** N	250[3]	1860		1865	
	Taphozous	*mauritianus*	Grey tomb bat	I	28		NT		NT
Squamata	*Cryptoblepharus*	*boutonii*	Bouton's skink	I	1,7		CR[6]		DD
	Gongylomorphus	*bojerii*	Bojer's skink	I	3,9	1865			CR[7]
	Leiolopisma	*mauritiana*	Didosaurus	**F** I	1120			15th?	
		telfairii	Telfair's skink	**F** I	68				VU
		ceciliae	Arnold's skink	**F** I	130[3]	1665?			
	Nactus	*serpensinsula*	Mauritius night-gecko	I	5,8				VU
		coindemirensis	Lesser night-gecko	I	0,8				VU
		soniae	Réunion night-gecko	I	2,1	1665?			
	Phelsuma	*cepediana*	Blue-tailed day-gecko	f I	4,6				LC
		rosagularis	Upland forest day-gecko	f I	3,4				DD
		ornata	Vinson's day-gecko	f I	3,7				DD
		guimbeaui	Guimbeau's day-gecko	f I	7,1				DD
		guentheri	Günther's day-gecko	f I	74,6				VU
		borbonica	Réunion forest day-gecko	f I	10		EN		
		inexpectata	Manapany day-gecko	f I	6		CR		
			Number of species			16	13	11	24

METHODS

Study site

Réunion (2512 km²) and Mauritius (1865 km²) are the two main islands of the Mascarenes (**Fig.2.1**). Rodrigues (109 km²), the smallest and easternmost island of the archipelago, was not included in this study. Indeed, the natural history of this island provides little information to disentangle the different drivers of extinctions due to the early and almost complete destruction of native habitats. Mauritius and Réunion have very different topographical characteristics. The first one is a shield volcano that peaks at 3070 m asl with 50% of areas located above 770 m. The island is marked by a very rugged relief that induces strong geographical barriers, the most obvious being the one that runs across the great diagonal, but many deep valleys also constitute radially oriented obstacles (**Fig.2.1**). Conversely, 50% of areas are located under 161 m on Mauritius and even if the island has some steep massifs that peak at 820 m asl, they are located in a rather lateral position. Indeed, Mauritius is marked by vast plains and a large plateau in a central position contrary to Réunion (**Fig.2.1**). Both islands experience a tropical oceanic climate, but the relief on Réunion induces far greater variations in terms of temperature and rainfall. Frost may appear above 1500 m and is frequent above 2000 m in winter, and the windward and leeward coasts respectively record the maximum (11000 mm) and minimum (450 mm) annual rainfall in the archipelago (Réchou et al., 2019). The result is a zoning of habitats that has been the subject of various typological works (Cadet, 1977; Dupouey and Cadet, 1986; Strasberg et al., 2005). On Mauritius, an altitudinal zoning of habitats has also been described although the whole island is included in the megathermic domain (Page and D’Argent, 1997; Vaughan and Wiehe, 1937). In this study, we actually used a common elevational typology that served as a surrogate for habitat suitability (please report to the next subsection for details).

Until the 17th century, Réunion and Mauritius were almost totally wooded (except at high elevations on Réunion) and were home to a particularly abundant and relatively diverse fauna for oceanic islands. Here, we focus on vertebrates that are closely dependent on forest habitats, which led us to exclude seabirds and vertebrates dependent on wetlands. Both islands shared 23 genera of forest vertebrates (14 Aves, one Chelonii, three Mammalia, five Squamata, **Tab.2.1**). However, Réunion and Mauritius were also home to 15 genera of forest vertebrates not found on the sister island. Réunion had other endemic bird species such as the solitaire (*Threskiornis*), the oiseau bleu ('*Cyanornis*'), the Mascarin parrot (*Mascarinus*), the hoopoe starling (*Fregilupus*) and the Réunion stonechat (*Saxicola*), but also insectivorous bats, *i.e.* the pale house bat (*Scotophilus)* and the Bory's white bat *(Boryptera*). Mauritius sheltered endemic flightless birds, the dodo (*Raphus*) and the red hen (*Aphanapterix*), but also the raven parrot (*Lophopsittacus*), the wood pigeon (*Columba*) that might have existed on Réunion (Hume, 2013) and the Mauritius starling (*Cryptopsar*) (Hume, 2014). More surprisingly, Mauritius also had several endemic snakes: the keel-scaled boa (*Casarea)*, the burrowing boa *(Bolyeria)* and the Carié's blind-snake *(Typhlops*). All these vertebrates went extinct since human colonization, except the stonechat on Réunion and the keel-scaled boa that survives on the northern islets (Cheke and Hume, 2008). In this study, we have only chosen the genera shared between Mauritius and Réunion by assuming that they shared enough characteristics to allow a direct comparison of the factors that led to involved species extinction.

Data collection & analyses

Introduction of alien vertebrates

We established a chronological overview of terrestrial vertebrate naturalizations on Réunion and Mauritius since the beginning of human colonization. We characterized the date of their introduction on Réunion, Mauritius mainland or Mauritius islets, as well as their diet. The aim was not to provide a complete picture of vertebrate introductions on both islands, but to present all those that potentially negatively impacted the native fauna or have impacted the extant fauna. This impact may be directly mediated via predation or indirectly via competition, sometimes between related lineages. We also presented vertebrates that potentially contribute to alter the structure of native habitats. Most of the data regarding vertebrate introductions were drawn from the appendices of Cheke and Hume (2008) and relative updated publications.

Overhunting

Overhunting is primarily related to human demography, and this was especially the case in the Mascarenes where the first settlers were known as inveterate hunters on both islands (Cheke and Hume, 2008; Lougnon, 2005). Using data available for Mauritius in Cheke and Hume (2008) and for Réunion in INSEE (2014), we compared the demography on Réunion and Mauritius since the beginning of human colonization. We also tried to document the extent to which marooning might have contributed to overhunting in both islands.

Deforestation: habitat suitability assessment since human colonization

We assessed the destruction of native forest habitats since the beginning of human settlement using digitized maps of native forest clearings in 1773, 1835, 1872, 1935 and 1997 available in Norder et al. (2017) for Mauritius. For Réunion, we created digitized maps of native forest clearings based on Selhausen's maps of 1793 and 1818. Earlier maps from before Selhausen were not used because they were far too inaccurate regarding forest clearings (Germanaz, 2016). We also produced a map of native forest clearings in 1925 (J.-C. Notter, unpubl. data), which marked the end of the *Pelargonium* cropping (Cheke and Hume, 2008), and used the recent work of Strasberg et al. (2005) as the most recent assessment of habitat transformation.

By cross-referencing the current habitat maps with those of the chronology of native forest destruction, we assessed the chronology of the destruction of different native habitats since the beginning of human colonization. Habitat maps were based on common altitudinal zoning: 0-400 m, lowland; 400-850 m, mid-elevation; 850-1200 m, submontane; 1200-2000 m, montane; 2000-3070, subalpine. This zoning generally follows the altitudinal boundaries already described. The “lowland” area here is close to the definition of Dupouey and Cadet (1986) on Réunion and the altitudinal boundary between the so-called humid and subhumid forests was probably a bit below on Mauritius (Vaughan and Wiehe, 1937). The elevation of 850 m corresponds more or less to the upper limit of the megathermic area (Cadet, 1977) and to the top of Mauritius. Numerous lowland tree species occur up to 1200 m in the “submontane” area on Réunion (Strasberg et al., 2005). The “montane” area then extends up to the average elevation of the trade-wind inversion (Cadet, 1977; Strasberg et al., 2005). The “subalpine” area also includes elevations above 2700 m which are actually in an "alpine" environment (Kitayama and Mueller-Dombois, 1992).

Forest habitats show wide disparities along elevational gradients in terms of plant functional diversity on Réunion (Albert et al., 2018; Strasberg, 1994). It is not easy to associate functional characteristics of habitats with their suitability to harbour the pristine fauna. Nevertheless, it can be achieved with regard to the diversity of dispersal traits which probably had (has) a strong influence on the distribution of frugivores (and *vice versa*). The distribution of fleshy-fruited plants on Réunion has already been discussed in chapter 1, but we wanted to go further here by studying the distribution of woody plants with fleshy fruits larger than 13 mm in diameter (called "large fleshy-fruited plants" hereafter). We therefore used a binomial GLM with spatial filtering to model the proportion of large fleshy-fruited species ($n_{\text{large fleshy-fruited species}}$ *versus* $n_{\text{other woody species}}$) as a function of a dozen climato-topographic variables. By interpolation of the best predictors, we modelled the proportion of large fleshy-fruited plants to understand what the former distribution of large-fruited plants on Réunion may have been. For more details, please report to the material and methods presented in chapter 1 for fleshy-fruited plant species (Albert et al., 2018). Such modelling could not be performed on Mauritius because extant forests are too scarce and do not currently display sufficient environmental heterogeneity (**Fig.2.1**). Nevertheless, Florens (2008) surveyed native forest remnants on the central plateau and in the Bambou Mountains, which enabled us to characterize roughly the dispersal trait diversity on Mauritius.

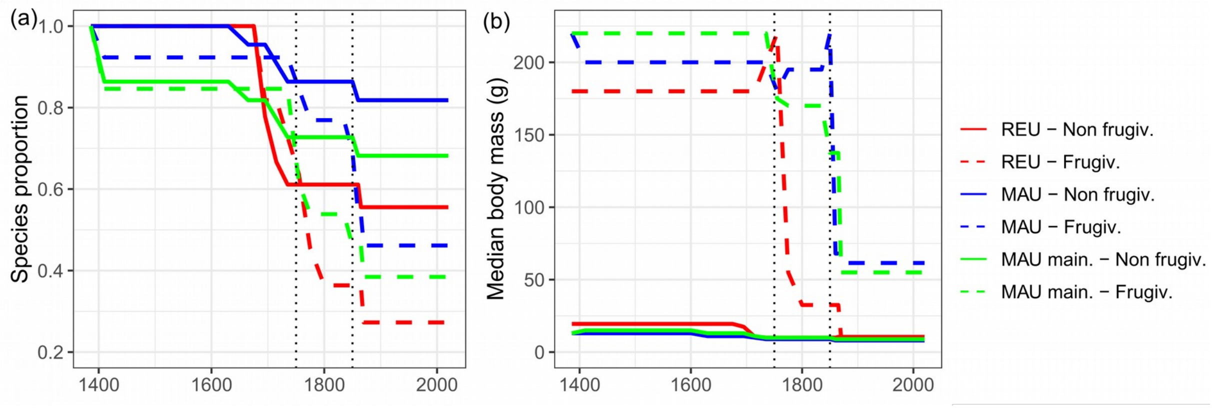

***Fig.2.2 Chronology of extinctions of native forest vertebrates in lineages shared between Réunion (REU) and Mauritius (MAU)**. **(a)** Decrease in the number of frugivore and non-frugivore species due to extinctions as proportions of initial species assemblages. **(b)** Median body mass of assemblages are shown for native forest vertebrates and native frugivores on each island. For Mauritius, there are two possible scenarios: considering mainland and the northern islets ("MAU") or excluding the latter ("MAU mainland").*

RESULTS

Extinctions within taxa of forest vertebrates shared by Réunion and Mauritius have probably begun in the 14th century on Mauritius mainland after the arrival of Arab traders (Hume, 2013) (**Fig.2.2** & **Tab.2.1**). Several reptile species may have survived only on the northern islets for several centuries. Most extinctions occurred from the second half of the 16th century on Mauritius which was colonized by the Dutch in AD 1638 (all dates hereafter in years AD), but also on La Reunion which followed the same trend after the beginning of permanent colonization in 1665. Common lineages of forest vertebrates were dominated by frugivores in terms of body mass (**Fig.2.2**). Frugivores went more extinct than other vertebrates and this phenomenon was much more marked on Réunion which lost a large part of its large frugivorous vertebrates as early as 1750 (**Fig.2.2**). Large-bodied frugivores have relatively well maintained for more than a century on Mauritius: giant tortoises went extinct on the northern islets in 1850 and the *Pigeon Hollandais* and the Rougette around 1870 on Mauritius mainland. The balance of extinctions, *i.e.* 15 and 10 species extinct on Réunion and Mauritius respectively, has remained unchanged since that time and Mauritius still has 68% of native forest vertebrates (**Fig.2.2** & **Tab.2.1**). The fact that several native species have survived until the recent era of conservation biology probably played a great role in their maintenance, especially on Mauritius where numerous species are today threatened but actively protected. The largest surviving native frugivore on Réunion for more than 150 years is the Réunion bulbul (the only larger extant forest vertebrate being the Réunion harrier). The median body size of frugivores remains much larger on Mauritius compared to Réunion due to the extant black-spined flying-fox, echo parakeet and Telfair skink (on northern islets only for the latter) (**Fig.2.2**).

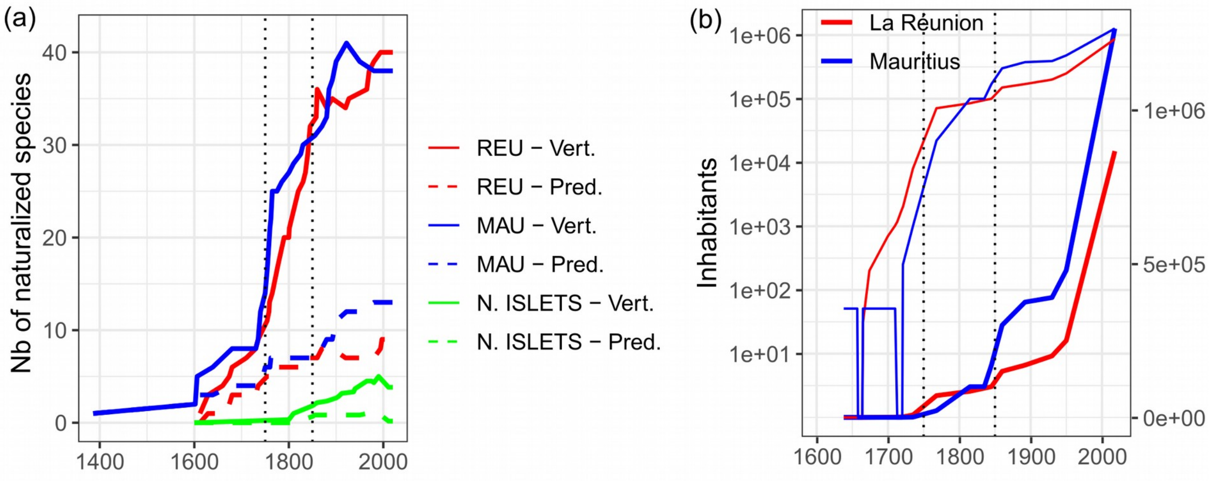

***Fig.2.3 Vertebrate naturalizations since first human arrival and human population growth on Réunion (REU) and Mauritius (MAU) since first arrival of humans**. **(a)** On each island, the total number of vertebrate naturalizations is given, as well as the number of naturalized predators. There are two possible scenarios for Mauritius: considering mainland and the northern islets ("MAU") or only the latter ("N. ISLETS"). For the northern islets, the mean by islet is given. The non-monotonicity of the curves shows that numerous species went extinct after lasting for decades or centuries (for more details, see **App.2.1**). **(b)** Population growth (note the log-scale for the left y-axis with associated thin line). There are no accurate estimates of the number of Dutch settlers who occupied Mauritius more or less permanently during the 17th century. Similarly, after the abandonment of Mauritius by the Dutch, the human population officially fell to zero even though there is evidence of maroons persistence before the French took possession.*

Introduction of vertebrates

Réunion and Mauritius have experienced the naturalization of about 50 vertebrate species that have potentially impacted native terrestrial biotas (**App.2.1**), excluding the two species of non-native tortoises voluntarily introduced on Round island as taxon substitutes of native giant tortoises (Cole, 2012; Griffiths et al., 2011). Mauritius mainland showed earlier introductions of vertebrates than Réunion, especially predators such as the ship rat introduced in the 14th century or the crab-eating macaque and the pig in the 16th century (Hume, 2013) (**Fig.2.3a**). Potentially harmful organisms among non-native birds and reptiles were introduced late except the Common Mynah in the mid-18th century (**App.2.1**). Hence, the main vertebrates involved in early extinctions were land mammals that were introduced before first permanent settlement on Réunion and Mauritius (**Fig.2.3a**).

The early introduction of predators of which the ship rat, the pig and especially the cat, caused a carnage among flightless birds, *e.g.* the wood rails (*Dryolimnas*), but also among other ground nesting birds (Cheke, 2013) and giant tortoises as reported many times by settlers and travelers (Cheke and Hume, 2008; Lougnon, 2005). Moreover, the absence of any mention in the historical literature of the world's greatest skink on Mauritius is likely the direct result of the early introduction of the ship rat by the Arab traders (Hume, 2013). As stated by Blackburn (2004), species most susceptible to introduced mammals probably went extinct rapidly on both islands, *i.e.* before 1750 (**Fig.2.3a**). However, several large vertebrates were able to survive on Mauritius until now despite the persistence of predators sometimes at high density while pigs went extinct in the meantime on La Reunion (**Tab.2.1**). Even taxa such as fruit pigeons (*Alectroenas*) that went extinct on both islands have lasted longer on Mauritius mainland than on La Reunion (**Tab.2.1**). This is all the more puzzling since several mammal species known for their severe impact such as the crab-eating macaque and the Indian mongoose, have been introduced on Mauritius, but never on Réunion (**App.2.1**). The northern islets experienced few introductions of vertebrates, and especially few and relatively late introductions of predators (**Fig.2.3a**), which is probably the main reason of the capacity of several endemic geckos and of the Telfair skink to have persisted until now (**Fig.2.2** & **Tab.2.1**). Northern islets also shelter endemic snakes that probably never existed on Réunion. Thus, introduced vertebrates have had a major impact on the native fauna of the archipelago, but apart from the northern islets which shelter several endemic reptiles, this factor cannot explain alone why all large forest vertebrates went extinct so quickly on Reunion compared to Mauritius.

Overhunting

The Dutch claimed Mauritius in 1598 and occupied the island between 1638 and 1710, with a pause between 1657 and 1664. During all this period, the European population of Mauritius never numbered more than 50 according to Hume (2013). When the French actually took control of Mauritius in 1721, Réunion already had about 2000 inhabitants (**Fig.2.3b**). On that date, flightless birds were extinct on both islands and many forest vertebrate populations were already strongly reduced or were collapsing, especially on Réunion where increasing demography led to a strong demand for meat. The local authorities actually early realized how quickly the populations of large vertebrates were collapsing, which particularly worried them because the French East India Company was using the native fauna to supply its ships free of charge (Lougnon, 2005). Large frugivores were particularly prized because they were, by necessity, large body-sized game (**Fig.2.2**). Settlers were literally obsessed with the areas that were still home to abundant wildlife at the beginning of the 18th century, areas known as “the land of food” (“*le pays des vivres” or “Mahavel”*) (Defos Du Rau, 1960). Attempts to legally regulate hunting on Réunion proved totally unsuccessful (Cheke and Hume, 2008). The arrival of the governor Mahé de La Bourdonnais in 1735 coincided with strong economic development based on sugar production and a sharp increase in the number of inhabitants on Mauritius. In 1768, the number of inhabitants was still three times larger on Réunion than on Mauritius, but the balance was reversed in the last decades of the century (**Fig.2.3b**). The number of inhabitants on Mauritius has remained higher since that date. What is puzzling is that the sharp increase in inhabitants on Mauritius has not led, as on Réunion, to the rapid extermination of all large native frugivores. However, settlers were known as active and efficient hunters on both islands (Cheke and Hume, 2008; Lougnon, 2005), deer hunting has for instance remained an institution on Mauritius since that time (Cheke and Hume, 2008).

Marooning, *i.e.* slaves fleeing their captive terrible condition, may have significantly contributed to overhunting of vertebrates in the archipelago. Indeed, maroons have early taken refuge in the remote forests of La Reunion and Mauritius, and lived largely on the fauna of both islands between the 17th and 19th centuries (Cheke and Hume, 2008; DACOI, 2017; Dijoux, 2013; Fontaine, 2017; Lougnon, 2005). We do not have accurate estimates of the number of maroons on both islands. The phenomenon has been quite intense in the first half of the 18th century on Réunion where small villages of maroons may have existed in the Cirques before the settlers launched man-hunts that gradually pushed the maroons back up to the highlands (Dijoux, 2013). Marooning was also prominent in the early phases of the colonization of Mauritius (Hume, 2013) and succeeded in posing severe difficulties to the first French settlers (Cheke and Hume, 2008). The phenomenon then seems to have been essentially confined to south-western Mauritius where large native forests have belatedly remained (**App.2.2**). On both islands, marooning probably contributed to increased pressure on wildlife in remote areas that could act as refuges. However, while overhunting has played an important role in the extinction of vertebrates on both islands, it fails to explain alone why the native fauna that had survived the arrival of introduced predators went extinct rapidly on Réunion compared to Mauritius.

Deforestation

Before permanent colonization, lowland forests (under 400 m asl) represented 31,8 % of total area on Réunion against 81% on Mauritius (**Fig.2.4a**). On Réunion, the belt of lowland habitats was rapidly destroyed by clearings which generated large-scale fires as reported by La Houssaye in 1698 on the leeward (Lougnon, 2005) and which eventually, during the 18th century, brought to an end a large part of the forests installed on land that could be cultivated on the windward. Despite the intense exploitation of ebony trees on Mauritius by the Dutch and the early use of fires (Gosling et al., 2017), the island was still largely wooded when the French took control in 1721. The permanent colonization of Mauritius led to an intense deforestation that has not stopped until the 20th century. Around 1800, 610 km² of native forests have been cut down on Réunion and Mauritius, which respectively represent *ca* 87 % and 40 % of lowland habitats (**Fig.2.4a**). Hence, Réunion lost its overall tropical lowland forest in less than 135 years of settlement, which probably had dramatic functional consequences for native forest vertebrates, notably in terms of dispersal trait diversity.

As already discussed in chapter 1, woody plant communities were dominated by fleshy-fruited plants up to 1500 m asl on Réunion. However, from 400-500 m asl, there was a sharp decrease in the proportion of large fleshy-fruited plants (**Fig.2.4b**). If large fleshy-fruited plants were still structuring at mid-elevations, these plants were scarcely present in submontane habitats and rare in montane habitats (**Fig.2.4b**). The early destruction of the lowland belt has thus led to the rapid loss of habitats highly favourable for frugivorous vertebrates.

Fleshy-fruited plants dominated woody plant communities on Mauritius even more than on Réunion (**Fig.2.4b**). The difference is all the more striking as it may be explained by a higher proportion of large-fruited plants: despite a large sampling on Réunion, the maximum proportion of large fleshy-fruited plants is reached with 27,1% compared to 40% on Mauritius (**Fig.2.4b**). Hence, even if the statistical modeling of fleshy-fruited plant distribution could not be performed on Mauritius due to the large destruction of habitats nowadays, native forest habitats are supposed to have been formerly highly favourable to native vertebrates throughout the island. And this shows that, with a comparable level of deforestation in 1800 (**Fig.2.4a**), native forests probably remained much more favourable to native frugivorous vertebrates on Mauritius than on La Reunion. In the 1830s, deforestation accelerated on Mauritius and the proportion of native forests fell to 25.2% in 1872. In fact, it was in this interval of time that the *Pigeon Hollandais* and the Rougette went extinct.

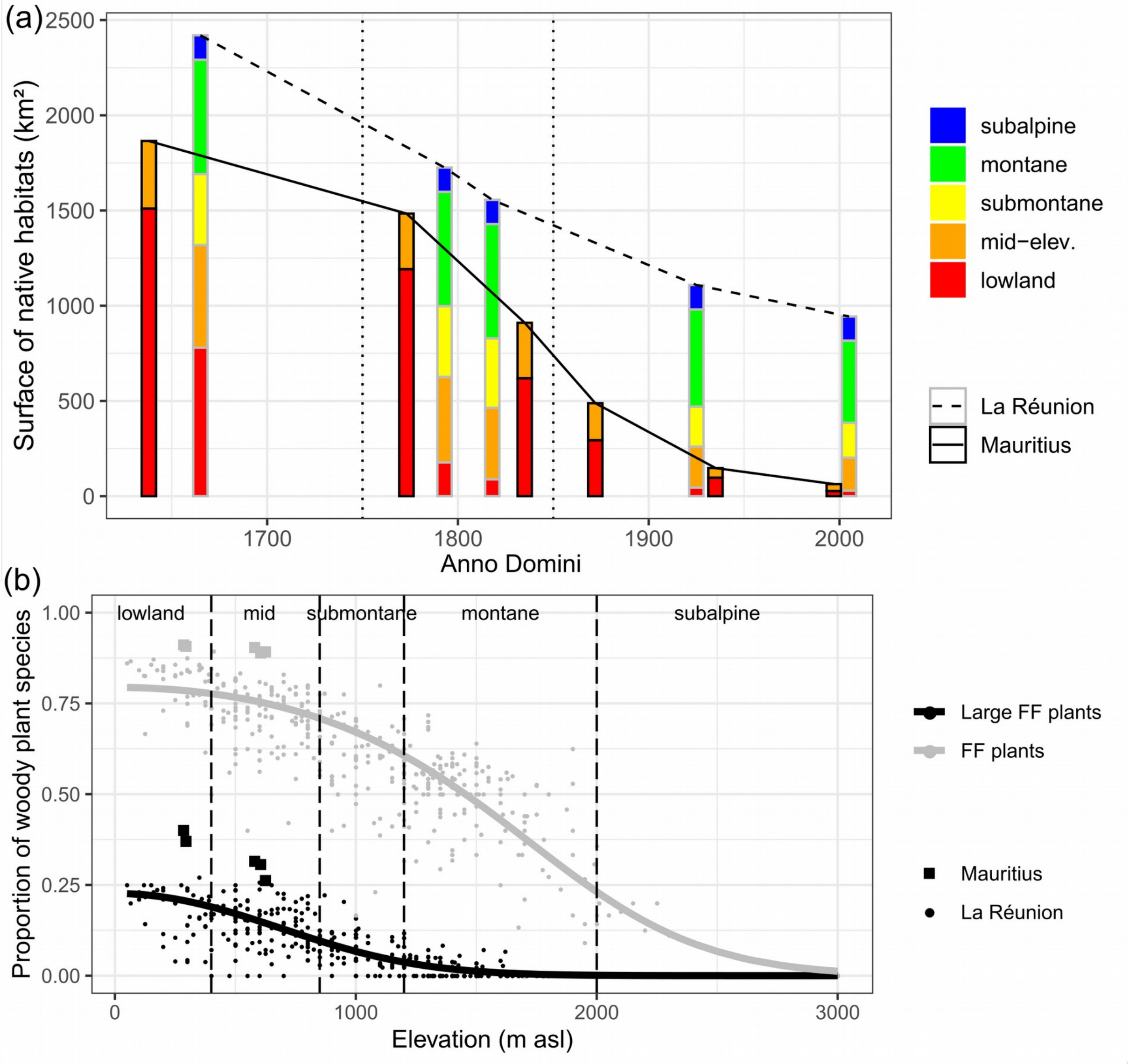

***Fig.2.4 Chronology of native habitat clearings and dispersal trait diversity depending on habitats on Réunion and Mauritius**. **(a)** The surface of native forests on Réunion and Mauritius are displayed by dashed and solid lines. The proportion of relictual habitats is given by bars with white and black contours for Réunion and Mauritius, respectively. For Réunion, approximately 100 km² of unfavourable areas (mostly in the caldera) have been excluded from analyses. **(b)** Grey and black colours respectively symbolize the proportions of fleshy-fruited (FF) and large fleshy-fruited plants among woody plant communities. Sampling plots on Réunion and Mauritius are respectively displayed by points and squares. For Réunion where vegetation sampling is substantial, predicted probabilities as fit by GLMs with analyses based on binary responses are displayed by lines.*

The configuration of habitat remnants has probably led to an even more fast degraded suitability on Réunion. Due to belt structuring, favourable remnants were systematically adjacent at lower elevations to cleared areas and subsequently subject to high hunting pressure, and at higher elevations to (sub)montane habitats where suitability rapidly decreased in terms of ressource (**Fig.2.5**). Thus, effective refuges were rare on La Reunion not only because the original area of favourable habitats was relatively small, but also because the relief accentuated the fragmentation of potentially suitable remnants (**App.2.2**). On the contrary, vast areas of highly suitable habitats have belatedly persisted on the central plateau of Mauritius. Until the 20th century, most native remnants on Mauritius took the form of compact areas with the possibility for native vertebrates to better escape, at least for a time, from the multiple human-induced disturbances (**App.2.2**).

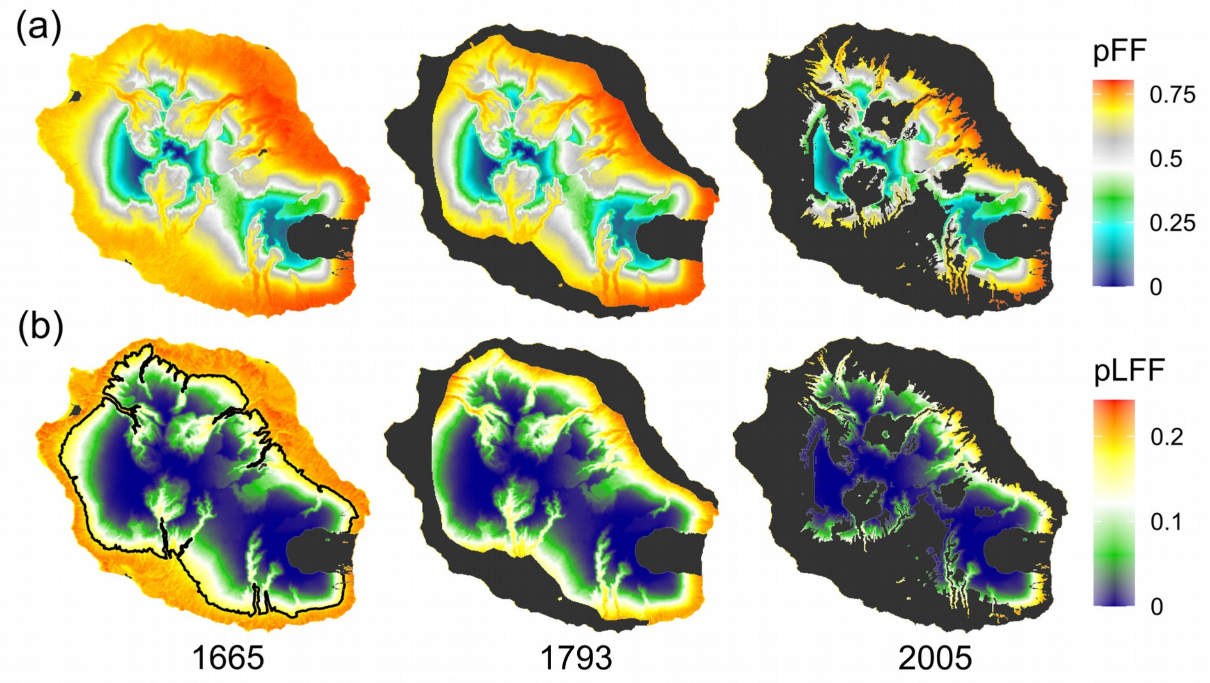

Fig.2.5 Spatial modeling of the distribution of dispersal trait diversity on Réunion with masks of habitat transformation in 1793 and 2005*. Areas rich and poor in native (large) fleshy-fruited plants are respectively shown in warm and cool colors* ***(a)*** *Proportion of fleshy-fruited plants among woody plant communities (pFF).* ***(b)*** *Proportion of large fleshy-fruited plants among woody plant communities (pLFF). The 400 m asl contour line is given by the black line. The spatial modeling of pLFF displayed a high pseudo-R² = 0,74.*

DISCUSSION

The deforestation of suitable habitats as the likely crucial cumulative factor

The majority of native forest vertebrates in the Mascarenes has disappeared since human colonization, but this phenomenon nevertheless shows important disparities in the archipelago (Cheke and Dahl, 1981; Cheke and Hume, 2008; Hume, 2013). By choosing vertebrates from lineages shared by Réunion and Mauritius, we seek to understand why the former, which still has 35% of native habitats, has lost all of its large forest vertebrates (except the Réunion harrier, *Circus*) while the latter, whose habitats have been almost completely destroyed, has retained a greater diversity of squamates (*Gongylomorphus*, *Leiolopisma*, *Nactus*), birds (*Falco*, *Foudi*, *Nesoenas*, *Psittacula*) and mammals (*Pteropus*). With the exception of the northern islets where the low number of predator introductions has allowed various squamates escaping extinction (Cheke and Hume, 2008; Cole, 2012), it seems difficult to invoke differential pressures of mammal invasion and overhunting between Mauritius and Réunion to explain this paradox. On the contrary, Mauritius shows a greater number of introductions of predators known for their negative impact, and overhunting that may initially have had a greater impact on La Reunion has not spared Mauritius, where the number of inhabitants has been higher than on Réunion since the late 18th century. The major difference between the two islands, however, is the rate of deforestation of lowland habitats since human colonization. On Réunion, lowland habitats were destroyed as soon as the early 18th century on the leeward and were massively destroyed during this century on the windward. The suitability of forest remnants has probably also been reduced due to the fragmentation caused by clearings in the lowlands and much less favourable habitats at higher elevations. Montane habitats were not only less favourable, and while they may have acted as refuges from overhunting especially in steep places, they were not a refuge from introduced mammal predators (Pinet et al., 2009; Thiollay and Probst, 1999). By contrast, habitats have long persisted on Mauritius as low-fragmented favourable forests despite major early fires (Gosling et al., 2017). Thus, extinctions have probably been early catalysed on Réunion due to a synergy between the rapid destruction of the most suitable habitats, the predation by introduced mammals and overhunting. Avian malaria has been mentioned as a possible cause of extinction of the hoopoe starling on Réunion in the 18th (Cheke, 2013), but vector-borne diseases seem unlikely to have decimated native vertebrates on Réunion but not on Mauritius where introductions of potentially host vertebrates have been earlier and more massive.

Large frugivorous vertebrates are more prone to extinction than other forest vertebrates, and their extinction has been especially rapid and massive on Réunion. As suggested by Cheke and Dahl (1981), we showed that lowland forest of pristine Réunion were widely dominated by fleshy-fruited plants (Albert et al., 2018) and we demonstrate here that this pattern is even more pronounced regarding large fleshy-fruited woody plants. These species probably provided crucial resources for frugivorous vertebrates on Réunion, as already demonstrated in the tropical Andes (Dehling et al., 2014), on Mount Kilimanjaro (Ferger et al., 2014) or in Papua New Guinea (Hazell, 2019) where the loss of large frugivores towards upland forest corresponds to a decrease in large fruits at high elevations. On the contrary, all forests on Mauritius were probably widely dominated by fleshy-fruited species with an even more pronounced proportion of large fleshy-fruited plants than on Réunion, which is the consequence of multiple radiations in large fleshy-fruited plant lineages including Ebenaceae, Myrtaceae, Rubiaceae or Sapotaceae (Ahmad et al., 2016; Dafreville, 2013; Florens, 2008; Linan et al., 2019). The consequence is that highly suitable habitats thus originally spread all over the island with the exception of a few steep peaks. The maintenance of more than 500 km² of low-fragmented forests until the second half of the 19th century probably played a key role in the survival of the *pigeon hollandais* until that time (see Morante-Filho et al., 2018) and in the maintenance of the black-spined flying-fox and echo parakeet until today. Even introduced *Coracopsis* parrots from Madagascar that naturalized in the 1790s on Réunion failed to survive in lowland forest remnants in the 19th century, while the ring-necked parakeet has naturalized in Mauritius in native forests since its introduction in the 19th century (Cheke and Hume, 2008).

It is more convenient to demonstrate how the suitability of habitats declines for frugivorous vertebrates compared to those with different diets. Indeed, habitat suitability goes beyond food availability and encompasses optimal environmental conditions and all resources needed to maintain a population through foraging, breeding, nesting, etc. The “habitat suitability” hypothesis proposed by Cheke and Dahl (1981) concerning frugivorous vertebrates is thus transposable to other forest vertebrates in the Mascarenes, as suggested by Hume (2011) for the extinct Mauritius turtle dove and by Thiollay and Probst (1999) for the Réunion cuckoo-shrike that might prefer the lowlands.

We do not know why the Réunion harrier has survived on Réunion but not on Mauritius (Hume, 2013). This shows that the destruction and fragmentation of lowland habitats in combination with the introduction of non-native vertebrates and overhunting cannot explain all extinctions of shared forest vertebrates in the Mascarenes. One may argue that our knowledge of extinct vertebrates is quite incomplete (see the subsection "palaeoecology") and the specific causes of extinctions remain difficult to attribute, since factors act in combination on islands that do not share exactly the same natural history (Triantis et al., 2010; Whittaker and Fernandez-Palacios, 2007). However, our results strongly suggest that the destruction of the most favourable habitats on Réunion is the crucial cumulative factor that explains why this island lost so quickly its large forest vertebrates despite the persistence of vast native areas. It would be relevant to test this hypothesis at global scale as the paradox observed in the Mascarenes belongs to a global pattern (Heinen et al., 2017).

Biogeographical implications

Elevational gradients generate strong environmental filtering at global scale (Malhi et al., 2017) and are generally stronger on oceanic islands (Irl et al., 2016). Therefore, the striking elevational gradient in the proportion of large fleshy-fruited species on Réunion may be consistent across high-elevation oceanic islands. Pending a larger scale study to demonstrate this, we can nevertheless rely on the works already mentioned in the continental tropics, which show a strong correlation between changes in dispersal trait diversity and the diversity of frugivores along elevational gradients (Dehling et al., 2014; Ferger et al., 2014; Hazell, 2019). Hence, the systematic destruction and fragmentation of insular lowland forests by human activities may have led globally to the early destruction of the most suitable habitats for frugivores vertebrates. That would ultimately explain why high-elevation islands experience higher rates of frugivore extinctions (Heinen et al., 2017) and show that the expected refuge effect in montane habitats does not stand up.

At intermediate spatial scale, the South-West Indian Ocean islands offer interesting biogeographical perspectives. Large forest vertebrates shared by Réunion and Mauritius belong to radiated lowland lineages (Hume, 2011; Kehlmaier et al., 2019). However, several of extinct forest vertebrates have been described as frequenting mid-elevation or even montane habitats on Réunion, with for example giant tortoises observed in steep and mountainous places (Cheke and Hume, 2008; Lougnon, 2005). These observations fuelled the idea that montane habitats may have acted as effective refugia. Likewise, vertical migrations were attributed to several bird species, of which passerines, pigeons and parrots (see accounts of Dubois and Boyer in Lougnon, 2005). As suggested for fruit pigeons *Alectroenas* in Madagascar, vertical migrations of pigeons on the leeward were probably associated with the rains, descending in the lowlands during the wet season, and returning in winter to the mid-elevations, probably because of food availability (Hume, 2011). Hence, this suggests that these forest vertebrates were capable of adapting to heterogeneous insular contexts, but that they probably remained highly dependent on lowland habitats. Four sympatric pigeons and doves related to the extinct Mascarene columbids have persisted in the Comoros where forests still remain along elevational gradients (Hume, 2011). In a context of increasing deforestation in this archipelago (FAO, 2014), this provides a good opportunity to better understand the capacity of these species to adapt to montane conditions that are presumed to be much less favourable.

Need for palaeoecological works, especially on Réunion

Paleontology plays a central role in the knowledge of the extinct fauna, but also of the factors that led to their extinctions. Reunion paleo-ecosystems remain the less well investigated island of the Mascarenes (Hume, 2013). The reasons are above all geomorphological as the island has few favourable sites (but see Mourer-Chauviré et al., 1999) compared to Mauritius and Rodrigues where many caves and limestone deposits have yielded numerous subfossil bones (Cheke and Hume, 2008; Hume, 2013). This leads to gaps in knowing the original fauna, understanding the composition of the paleo-vegetation, and documenting early human settlement (DACOI, 2017; Dijoux, 2013) (this probably applies to both islands for the last statement). This vacuum offers remarkable transdisciplinary perspectives; several research units are planning sediment sampling and coring in several sites such as ponds in mid-elevation or montane habitats which have not been the subject of any paleoecological investigation on Réunion.

Due to the lack of osteological material, several emblematic vertebrates have not yet been described, such as the Réunion blue pigeon, the Réunion turtle dove or the Réunion red & green parrot (Hume, 2011, 2013). Many vertebrates remain actually poorly known on Réunion. The existence of certain species remains putative, *e.g.* the Réunion wood pigeon (Hume, 2011), and Mourer-Chauviré et al. (1999) stated that the near absence of flightless birds on Réunion might be a sampling bias. Moreover, osteological details allow better understanding the ecology of extinct species of which we usually have very sketchy accounts. For example, the extinct Mauritius turtle dove differs from the Madagascar turtle dove in a number of osteological details, which shows that this subspecies was probably more terrestrial than the introduced Madagascar turtle dove (Hume, 2011). This example also shows that in potentially idiosyncratic contexts (Whittaker and Fernandez-Palacios, 2007), inferences from close taxa must be made with caution. Finally, osteological material can also be used to better trace the chronology of (i) the extinction of native vertebrates as well as of (ii) the introduction of predators. (i) Environmental changes are poorly documented on Réunion from 1735 to 1800 (Cheke and Hume, 2008) and palaeoecological works could help fill this gap. Within that time frame, Barré et al. (2005) believe that travellers no longer felt the need to mention the local fauna because most species went already extinct, but it is questionable whether some of them could have survived for another half-century in the most remote and suitable eastern areas on Réunion (**App.2.2**). For the low number of writings could also be linked to the fact that Mauritius, which was then the *Ile de France*, was receiving most of the attention since the governor Labourdonnais. (ii) It is by dating a mandible of ship rat collected from the Mare aux Songes that the first material evidence of contact between the Mascarenes and the Arab traders was obtained and at the same time, that a credible explanation for the early extinction of several endemic squamates on Mauritius mainland has emerged (Hume, 2013).

Spatial modeling suggests that Réunion lowland were dominated by tropical habitats rich in large fleshy-fruited plants, including the driest areas of the leeward that may have been the main habitat of several large vertebrates such as the giant tortoise or Arnold's skink. Because there is no longer any native vegetation in the driest lowlands of Réunion (**App.2.3**), spatial modeling in this sector was based on an extrapolation of data and should be taken with caution. However, the structure and composition of the whole coastal dry forest may have been early altered and the leeward lowlands early savannised as suggested by Houssaye who reported large areas of recently burned land in 1689 (Lougnon, 2005). At the same time, Houssaye specifically stated that the Pointe des Galets was forested (Lougnon, 2005), although this area receives only 580 mm annually (average 1981-2010) (Réchou et al., 2019). Moreover, Mourer-Chauviré et al. (1999) excavated a great amount of large seeds belonging to *Latania, Terminalia*, *Cassine*, *Foetidia*, *Pandanus* or *Sideroxylon* among giant tortoise bones in the swamp of l'Ermitage (Strasberg, unpublished data). These findings suggest that ecosystems more complex than a latan/benjoin savanna may have been encountered in this sector and whose composition might have been relatively close to what was revealed by Rijsdijk et al. (2009) at La Mare aux

Songes on Mauritius. Hence, we need a thorough palaeoecological work in order to better understand what may have been the main habitat of the largest forest vertebrates on Réunion.

A contrasting situation for extant species

While the majority of native forest vertebrate species are extinct, the situation is not rosy for extant ones. There is little doubt that many of them would have gone extinct if the conservationists had not taken action on both islands to face the extinction debt (Triantis et al., 2010). Conservation actions have focused on improving the quality of native remnants that are often severely degraded by exotic plants, and on combating poaching and introduced predators. While clearings no longer seem to be on the agenda and poaching seems to have declined significantly over the past several decades (Cheke and Hume, 2008), it is crucial to locally control introduced predators when necessary and to prevent new introductions in the archipelago of exotic vertebrates that would further increase the threats to native vertebrates in the Mascarenes (Blackburn, 2004).

The Réunion grey white-eye is probably the Mascarene vertebrate able to colonise all kinds of habitats as long as they are planted with trees or shrubs (Barré et al., 2005; Cheke and Hume, 2008). Likewise, the Mascarene swiftlet also holds up well as long as they are not disturbed in caves and lava tunnels. Réunion passerines (except the cuckoo-shrike) are widely distributed where native forest still remain, such as the Réunion bulbul even if the size of its populations has nothing to do with what it was until 1915, when they plummeted for reasons that are still unclear (Cheke, 1987b). The situation is much more contrasted on Mauritius where most forest birds that have escaped extinction are threatened and subject of much conservation effort. Birds of prey remain threatened in the Mascarenes, but the Réunion harrier and the Mauritius kestrel have recolonized a large part of their initial range in their respective island. The rescue of the latter is regarded as one of the most successful achievements in conservation biology (Cheke and Hume, 2008). The populations of the pink pigeon, the echo parakeet and the Mauritius olive white-eye which had resisted well on Mauritius until the second half of the 20th century, declined sharply after the disappearance of *Les Mares* in 1975 (Jones, 1987; Jones et al., 1998). This shows that there is probably a critical size of home-range for a given level of disturbance and that it is difficult to maintain these populations in a fragmented, disturbed landscape. Fortunately, the reintroduction of individuals reproduced in captivity has made it possible in recent years to significantly raise the size of populations of the pink pigeon and the echo parakeet. Nevertheless, the situation remains of great concern for the Mauritius olive white-eye. On Réunion, a lot of effort is devoted to the conservation of the Réunion cuckoo-shrike. This species, which previously had a much wider range down to the lowlands, is now confined to montane habitats to the north of the island (Barré et al., 2005). Efforts to control predators introduced into a specially created reserve (now part of the National park of Réunion) have been unsuccessful in increasing population size. Hence, this species might be a lowland species which survives in suboptimal habitat and the establishment of a second population in lowland remnants should be reconsidered (Thiollay and Probst, 1999).

All mammals have been extirpated since the 1990s from the northern islets where populations of native reptiles have reached satisfactory sizes since then (Cheke and Hume, 2008). Rewilding with substitute giant tortoises has even been undertaken to restore seed dispersal and herbivory on northern islets but also on *Ile aux Aigrettes* (Cole, 2012; Griffiths et al., 2011), which are now formidable labs for ecological restoration. The future of squamates on Réunion and Mauritius mainland is much more uncertain. Surveys continue on La Reunion where Bouton's skink may still survive in the coastal cliffs in the South. While Bourbon gecko's populations might be underestimated, those of the Manapany gecko are confined to a short portion of the southern coastline where new introduced competitors and/or predators have recently appeared (Sanchez and Probst, 2016).

The future of microbats mainly lies in the preservation of breeding and roosting habitats on both islands, especially caves for the free tailed bat (Cheke and Hume, 2008). The black-spined flying-fox that inspired the idea of Cheke and Dahl (1981) is facing a massive slaughter for demagogic reasons on Mauritius while their role in the functioning of indigenous forests is no longer to be demonstrated (Florens, 2015). Anyway, we want to finish on a note of optimism with the pleasing prospects opened up by the recent return of this species to Réunion after more than two centuries of absence (GCOI, 2019). We hope that this species will not have to face hunters and/or persecutors and will succeed in recolonizing native forests where it has a crucial role to play as a seed disperser (Albert et al., 2020a; Florens et al., 2017a). Needless to say, this will depend on the ability of conservationists to learn from the socio-ecological context and create the conditions for consent.

ACKNOWLEDGEMENTS

We would like to thank Jean-Cyrille Notter at Reunion National Park who provided support for the production of digitized maps.

PARTIE II. Conséquences de la rupture des interactions de frugivorie sur la reconstruction des écosystèmes : les coulées de lave du Piton de la Fournaise comme système d'étude

*Vue aérienne prise au pied des Grandes Pentes dans l'Enclos Fouqué (caldeira du Piton de la Fournaise dont on devine le rempart septentrional de Bois Blanc à l'arrière plan). On peut voir au premier plan une coulée du 18ème siècle portant des arbres pionniers qui atteignent 20 m de haut (*Sideroxylon borbonicum*). A droite de la photo, on perçoit bien les coulées de lave de 2002 et 2004 dont la couleur beige provient essentiellement du lichen* Stereocaulon vulcanii*. L'intense activité volcanique du Piton de la Fournaise crée ainsi une mosaïque de formations végétales d'un âge très variable qui témoignent de la capacité des écosystèmes à se reconstruire à une date donnée. L'étude de cette chronoséquence peut ainsi être perçue comme une machine à remonter le temps. Photo de drone : Hugo Santacreu.*

CHAPITRE 3. Accroître la chronoséquence du Piton de la Fournaise en datant les coulées récentes grâce à la distribution diamétrique du Bois de rempart (*Agarista salicifolia*)

RESUME

La datation des coulées de lave récentes est une question essentielle pour évaluer les risques volcaniques pour les populations humaines avoisinantes, mais aussi pour les études en écologie car les coulées de lave constituent souvent des expériences naturelles privilégiées pour analyser la reconstruction des écosystèmes forestiers. Cependant, en l'absence de données historiques, les méthodes traditionnelles telles que la datation au radiocarbone 14 ne sont souvent pas applicables. Nous proposons ici une méthode statistique simple qui associe l'âge des coulées de lave du volcan Piton de la Fournaise (PdF) à la taille d'*Agarista salicifolia* (Ericaceae), un arbre pionnier qui s'établit rapidement après une éruption et peut vivre plus de 600 ans. Nous mesurons le diamètre à la base de 711 arbres sur 20 coulées de lave datées (entre 1401 CE et 2007 CE). Nous utilisons un modèle linéaire log-log pour évaluer la relation entre le diamètre maximum à la base d'*Agarista salicifolia* et l'âge des coulées de lave, et montrons une très forte corrélation ($R^2=0,987$, $p< 10^{-15}$). Nous utilisons ensuite ce modèle calibré pour estimer l'âge de 11 coulées de lave de Saint-Joseph à Sainte-Rose entre 1447 CE (Intervalle de Confiance : 1349-1531) et 1823 CE (IC : 1806-1839). Ces nouveaux âges, combinés aux âges radiocarbone connus et aux enregistrements historiques, indiquent trois groupes d'éruptions (1460-1630, 1690-1840, depuis 1970 CE) affectant à la fois la caldeira et les flancs du PdF. Nous interprétons ces dynamiques discontinues composées de périodes d'activité intense et de faible activité comme la preuve d'impulsions d'apport de magma élevé depuis au moins le 11ème siècle. Nous proposons aussi que l'énigmatique coulée de 1820 relatée dans la presse locale pourrait bien s'être produite dans les hauts de Basse-Vallée et être descendue depuis les Puys Ramond. Notre travail montre que la datation des coulées de lave avec un calibrage basé sur la distribution de la taille des arbres pionniers à vie longue représente une méthode alternative pertinente pour redéfinir la carte des risques du PdF. L'existence d'arbres pionniers à vie longue dans d'autres aires volcaniques du Chili aux Comores en passant par Hawai‘i et la Nouvelle-Zélande pourrait permettre d'utiliser cette méthode afin de mieux y comprendre les patrons de récurrence d'éruption. Enfin, nos travaux permettent de compléter la datation des substrats sur lesquels sont installés les derniers vestiges de forêt tropicale humide de basse altitude: il persiste de tels vestiges dans la caldeira du PdF, et des reliques floristiquement proches de la forêt de Mare Longue sont installées sur des substrats d'âge comparable sur les pentes externes (Brûlé de Takamaka, Le Tremblet) et dans la vallée de Langevin. Ainsi, cette étude étoffe notablement la chronoséquence des coulées de lave du Piton de la Fournaise, ce qui permet de mieux étudier la capacité des écosystèmes forestiers de basse altitude à se reconstruire dans les chapitres 4 & 5.

Dating young (<1000 yr) lava flow eruptions of Piton de la Fournaise volcano from size distribution of long-lived pioneer trees[*]

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ABSTRACT

Dating recent lava flows is a critical issue to assess the volcanic hazards for nearby human populations, but traditional methods such as radiocarbon dating are often not applicable. We propose here a simple statistical method that relates the age of lava flows of the Piton de la Fournaise volcano (PdF) to the size of *Agarista salicifolia* (Ericaceae), a long-lived pioneer tree that quickly establishes after eruption and able to live more than 600 years. We measured the diameter at base of 711 trees on 20 dated lava flows (between 1401 CE and 2007 CE). We used a log-log linear model to assess the relationship between maximum diameter at base of *Agarista salicifolia* and the age of lava flows, and. showed a very strong correlation ($R^2 = 0.987$, $p < 10^{-15}$). We then used this calibrated model to estimate the age of 11 lava flows between 1447 CE (Confidence Interval: 1349-1531) and 1823 CE (CI: 1806-1839). These new ages, combined with existing radiocarbon ages and historical records, indicate three clusters of eruptions (1460-1630, 1690-1840, since 1970 CE) affecting both the caldera and the flanks of PdF. We interpret such discontinuous dynamics made of periods of intense and low activity as evidencing pulses of high magma supply since at least the 11th century. Overall, our work shows that dating lava flow with calibration based on the size distribution of long-lived pioneer trees represents an accurate alternative method to redefine the hazard map of lava flow inundation. The existence of long-lived pioneer trees in several volcanic areas provides the opportunity to use the same framework in order to better understand eruption recurrence patterns.

INTRODUCTION

Dating recent lava flows is a critical issue to characterize the eruption recurrence pattern and subsequently to assess the volcanic hazards for nearby human populations (Le Pennec et al., 2008; Negro et al., 2013; Trusdell, 1995). Historical archives can provide reliable sources used for reconstructing the recent geological history of volcanoes. However, such written sources may be scarce or inaccurate especially in volcanic areas where human settlement was late or infrequent (Michon et al., 2013; Neri et al., 2011). Therefore, several methods are commonly used in order to date recent (<1000 years) lava flows. First, radiocarbon dating on sampled charcoals coming from trees burned by lava flows is frequently applied (Madeira et al., 1995; Rubin et al., 1987). Yet, charcoal often remains inaccessible, particularly in areas where lava flows are numerous and/or thick, and where erosive processes are too young or insufficient to totally incise the lava flows and excavate the underlying paleo-soils. Second, secular variations of the Earth's magnetic field can also be used to date recent lava flows (Holcomb et al., 1986; Roperch et al., 2015; Tanguy et al., 2011). However, this method requires independently dated lavas in order to trace the path of the directional secular variation for the study periods and may not be suitable in

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densely vegetated areas where root development may disturb the initial orientation of lava blocks. Third, cosmogenic nuclides such as ^{36}Cl, ^{3}He, ^{10}Be or ^{26}Al have been used to date Late Holocene surfaces like lava flows (Alcalá-Reygosa et al., 2018; Dunbar, 1999; Staudacher and Allègre, 1993) or moraines (Shakesby et al., 2008). However, dating accurately surfaces younger than 1000 yr is challenging and requires good estimates of the cosmogenic isotope production rate, time-invariant scaling methods and to be able to evaluate possible erosion of the initial surface (Jomelli et al., 2016; Young et al., 2015). It has therefore, to our knowledge never been applied to date lava flow eruptions younger than 1000 yr.

Finally, vegetation characteristics can be considered as alternative to date lava flow eruptions. Surface dating methods such as lichenometry or dendrochronology may be used in primary succession context, with the idea that the development stage of the vegetation growing on lava flows mostly depends on the age of the substrate (Atkinson, 1970), that is on the date of the eruption that produces the lava. Lichenometry is a method based on the known growth rate of lichen thalli, but it allows potentially to date eruptions on a short time range only in lowland tropical regions where lichens are totally replaced by vascular plants in less than 150 years after eruption (Kurina and Vitousek, 1999). Dendrochronology has been carried out on volcanofluvial terraces (Pierson, 2007), tephra deposits (Druce, 1966; Yamaguchi, 1983), post-eruptive ravines (Franco-Ramos et al., 2017) and exceptionally applied to lava flow (Alcalá-Reygosa et al., 2018; Yamaguchi et al., 1990). However, most plant species do not form distinct annual growth rings in tropical regions (Jacoby, 1989; Stahle, 1999) and dendrochronology has never been used to date lava flows in these areas, despite unsuccessful attempts on La Réunion (Catry and Daux, unpublished data) and the recent development of new methods coupled with classical dendrochronology (Jacquin et al., 2017; Poussart et al., 2004; van der Sleen et al., 2017). Moreover, destructive methods may affect population survival of the model species and not be adapted to the legal framework regarding sampling in protected natural areas. Other vegetation features, such as biomass for instance, can also serve as an indirect proxy for the age of lava flow. Li et al. (2018) recently used the Normalized Difference Vegetation Index (NDVI) derived from satellite images as a proxy for vegetation development and biomass on lava flows produced by three volcanoes located in a tropical setting (Nyamuragira, Democratic Republic of Congo; Mt Cameroon, Cameroon; Karthala, Comoros Archipelago). They could determine a relationship between NDVI values and lava flow ages, which however becomes invalid for ages older than 388, 333 or 93 years depending on the volcano.

Considering chronosequences of lava flows traditionally used in ecological studies (Walker and Moral, 2003), we propose here an original method that relates the age of lava flows to size of pioneer trees. The calibrated relationship is then used to estimate unknown ages based on the size distribution of pioneer trees. This approach focuses on pioneer tree species because these plants (i) can be easily reached and sampled in a simple manner, (ii) are able to establish on recent lava flows within less than five years after eruption (Cadet, 1977; Strasberg, 1994) and (iii) grow in diameter all along their life due to cambium functioning. Because in general, the bigger the trees within a population, the older they are (Worbes et al., 2003), one may expect maximum size observed on lava flows to be strongly related to flow age. One important condition is nevertheless to be able to sample trees that benefited from the most favourable conditions on each flow, *e.g.* where the growth of vegetation may be facilitated by external soil sources (Deligne et al., 2013) or smaller distance to seed source (Li et al., 2018). Moreover, if we want to use the model to date lava flows on a large time range, trees must not only belong to pioneer species, but they also need to be long-lived. Long-lived pioneer trees can reach 700 years old (Lusk, 1999), they notably play an important ecological role on (sub) tropical islands across all the world's oceans (Atkinson, 1970; Cadet, 1977; Clarkson, 1990; Elias et al., 2004; Kamijo et al., 2002; Tagawa et al., 1985). Hence, this method might be a relevant alternative to date lava flow eruptions in several (sub)tropical volcanic areas.

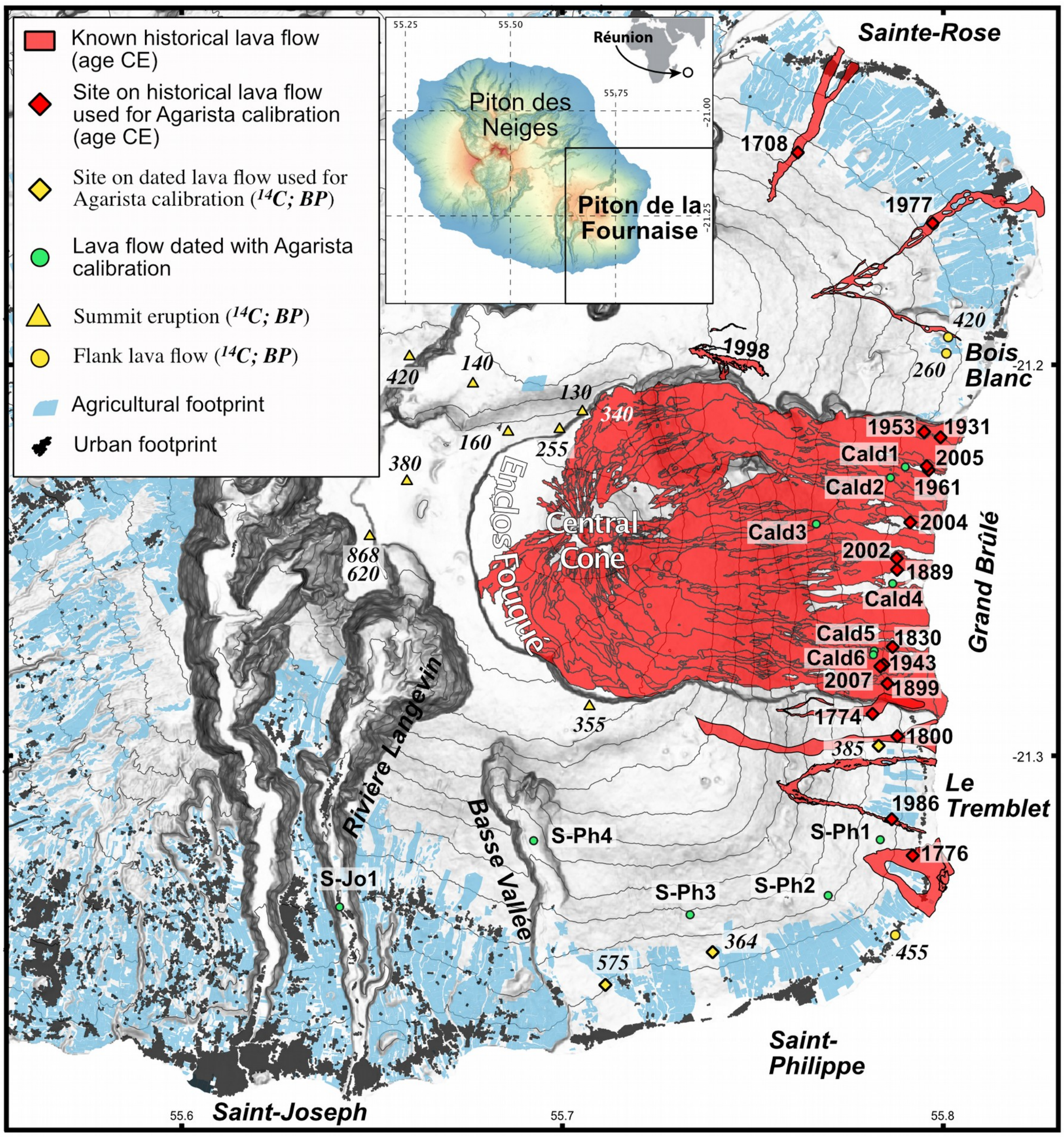

Fig.3.1 *Historical and recent (<1000 yr) volcanic activity of Piton de la Fournaise volcano, Réunion Island. Pre-historical or unreported eruptions have been dated with radiocarbon method (Morandi et al. 2016). Radiocarbon ages of the summit eruptions have been obtained from charcoal sampled below tephra deposits. Here, we further constrain the recent volcanic activity from a size/age relationship based on* Agarista *tree development to date the recent lava flows of Piton de la Fournaise. Agricultural and urban footprints from www.peigeo.re. Contour lines every 200 m.*

La Réunion is an oceanic island that hosts the Piton de la Fournaise volcano (PdF) (**Fig.3.1**), one of the most active in the world (Morandi et al., 2016; Roult et al., 2012), and a common long-lived pioneer tree, *Agarista salicifolia* (Ericaceae), which plays a crucial role in early ecological succession (**Fig.3.2**) (Cadet, 1977; Meunier et al., 2014; Strasberg, 1994). Due to the late settlement of the island (1646 CE; Common Era), historical observations of eruptions do not exist before that (see Lénat, 2016; Michon et al., 2013; Stieltjes, 1986). Only six radiocarbon dated eruptions affected the lower flanks of PdF in the last thousand year (**App.3.1**), but field observations suggest that more recent eruptions may have occurred on lower flanks which are now inhabited (Cadet, 1977; Strasberg, 1994). Thus, there is a crucial need to improve our knowledge on the temporal distribution of this volcanic activity to better assess the volcanic hazards in this inhabited area. In this respect, we first use the size distribution of *Agarista salicifolia* on dated lava flows of PdF to calibrate a statistical model relating flow age to tree size. Second, the size distribution of *Agarista salicifolia* on undated lava flows is used as a proxy to estimate the age of these flows based on the previously calibrated model. Finally, we integrate these new dates in a larger analysis of eruption events to describe and better understand the eruption recurrence pattern and evolution of the PdF dynamics that is likely understated.

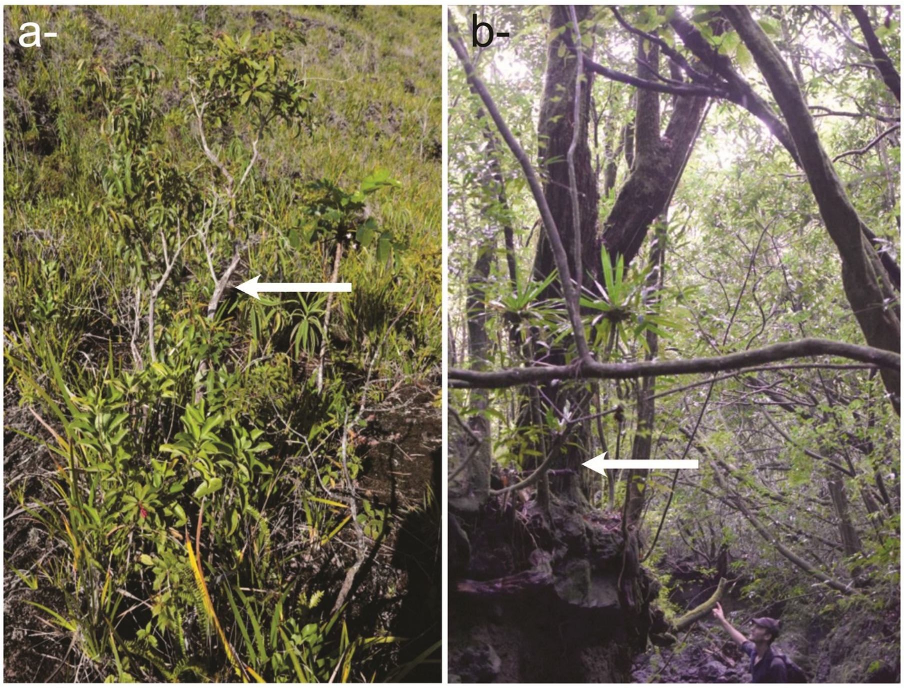

Fig.3.2 Agarista salicifolia *at different stages of growth (white arrows).* ***a-*** Agarista *sapling settled on the 1986 lava flow at Saint-Philippe.* Agarista *is usually the first native woody plant to settle rapidly after the initial lava cooling at low elevations, as reflected on this recent lava flow.* Agarista *further provides shade to newly settled plants and produces litter locally, thus bringing organic matter to the system.* ***b-*** Agarista *tree settled on the 1708 lava flow at Sainte-Rose. Note the Pāhoehoe lava that overhangs the ravine due to the higher weathering of underlying soil.*

MATERIAL AND METHODS

Study site

La Réunion is a 5 Ma old basaltic volcanic edifice that is composed of two main shield volcanoes: Piton des Neiges (inactive) and Piton de la Fournaise (PdF) that expands across the south-eastern third of the island (**Fig.3.1**). PdF is a highly active volcano with more than 238 eruptions that have been recorded since human settlement in the second half of the 17th century (Morandi et al., 2016; Roult et al., 2012). The historical activity of PdF is mostly restricted to the uninhabited Enclos Fouqué caldera and its downslope continuity named Grand Brûlé (97% of the post 1708 CE eruptions), and rarely propagated along the NE and SE inhabited volcano flanks (**Fig.3.1**) (Michon et al., 2013; Villeneuve and Bachèlery, 2006). Only seven eruptions have been observed on these flanks since the settlement of this part of the island during the 18th century.

They occurred during two eruptive clusters: four and three eruptions during the 18th and 20th centuries, respectively, with a pause of 177 years between 1800 and 1977 (**Fig.3.1**) (Michon et al., 2013). Beside this observed “historical” activity, the activity of the last thousand years was constrained by 16 radiocarbon ages spanning between 868 ± 30 BP and 130 ± 30 BP (**App.3.1**) (Morandi et al., 2016). Only six of these dated eruptions affected the lower flanks, despite numerous observations reporting potential recent eruptions (Cadet, 1977; Strasberg, 1994).

PdF area experiences a humid tropical climate throughout the year below 800 m asl, i.e. annual mean temperature ranges from 18 to 25°C and precipitation of driest month ranges from 75 to 400 mm, with large inter- and intra- annual variations (Réchou et al., 2019). Where the lower flanks of PdF have not been cleared for croplands or urbanisation, they harbour tropical rainforest of which *Agarista salicifolia* is an important pioneer tree species (Cadet, 1977; Strasberg, 1994).

Radiocarbon ages of eruptions

Radiocarbon method has long been used to date the lava flows and tephra layers related to past eruptions of PdF volcano that occurred during the last thousands of years (see the synthesis in Morandi et al., 2016). To ensure their intercomparison, each radiocarbon age has been recently calibrated by Morandi et al. (2016) using the online Calib program (Stuiver et al., 2019) and the IntCal13 calibration curve (Reimer et al., 2013). However, radiocarbon ages obtained on tree rings that grew at the same time in opposite hemispheres present a shift, with samples of the southern hemisphere being older than in the northern one (McCormac et al., 1998). We therefore calibrated for this work the radiocarbon ages with Calib and the SHCal13 calibration curve determined for the southern hemisphere (Hogg et al., 2013), and obtained an average interhemispheric difference for median probabilities of 41 yr between both calibrations (**App.3.1**).

Focal species

Agarista salicifolia (Ericaceae), hereafter referred to as *Agarista*, is a long-lived tree that is native on La Réunion but occurs also in Mauritius, Madagascar and East Africa. It is well known as a pioneer species and is usually the first native woody species to establish on newly formed lava flows on La Réunion (Cadet, 1977; Strasberg, 1994; **Fig.3.2**). *Agarista* produces numerous tiny seeds that are dispersed by wind away from mature mother trees and a recent study shows that this species does not suffer any dispersal limitation in the whole study area (Albert et al., 2020a). Seedlings of the species are commonly observed on recent lava flows as soon as a few years after the eruption (Cadet, 1977). Once settled, *Agarista* trees are able to survive during the complete course of ecological succession to mature forests in which it occurs as large trees up to 15-20 m high settled in the canopy. Importantly, the species does not regenerate under vegetation cover: individual settlement stops as the vegetation cover develops and becomes continuous. As a consequence, on a given lava flow on which primary ecological succession happens without further disturbance events, its populations consist in cohorts made of individuals of the same age rather homogeneous in size. The species occurs from sea level up to ca. 1200 m asl, but we sampled below 800 m asl in the tropical rainforest biome where climatic conditions for *Agarista* growth are assumed to be comparable. *Agarista* identification on the field is easy, notably because of the longitudinally cracked reddish bark.

Sampling

To calibrate a statistical model of flow age vs tree size, we selected 20 lava flows with *Agarista* populations on them. Most of these flows, 17, occurred after 1708 and were historically recorded (see Michon et al., 2013; **Fig.3.1**). To extend temporal sampling, we considered two additional lava flows emplaced before human colonization (575 ± 75 BP and 364 ± 25 BP; Morandi et al., 2016) and dated a third one with radiocarbon method 385 ± 25 BP (**App.3.1**). We included the median probability of these dates in the *Agarista* calibration procedure.

We then selected 11 lava flows for which no date was known, but which were described as "young lava flows" by Cadet (1977). Six lava flows were located in the Grand Brûlé, downslope in the PdF caldera (Cald1 to Cald6) and five along south volcano flanks: four in Saint Philippe municipality (S-Ph1 to S-Ph4) and one in the inhabited valley of Langevin (S-Jo1; **Fig.3.1**).

On each studied lava flow, we characterized the size distribution of *Agarista* in order to estimate the maximum size reached by the species. In this prospect, the first crucial step was to identify the spatial limits of each lava flow. Lava flows can be of very variable width, occur at different elevations and sometimes reach the sea. Their lateral margins are generally perpendicular to elevation contours. Recent lava flows (< 1000 years old) show a very thin topsoil (in the order of mm) on continuous rock (Meunier et al., 2010), with tree roots running on the lava. One can easily distinguish a single lava flow outside the Grand Brûlé when looking along elevation contours for a deep soil that materialise the flow limits. At elevations <500 m asl, these deep soils are usually cultivated. Thus, some lava flows are easily distinguishable, especially outside the Grand Brûlé where recent lava flows rarely overlap. In areas where lava flows overlap, features as changes in the type of lava flow or in the size of the largest *Agarista* trees were carefully identified to prevent any sampling issue. In any event, *Agarista* trees in doubtful areas were not sampled.

Once the flow boundary is clearly delineated, at least 30 *Agarista* trees should ideally be sampled per flow and special attention must be paid to large trees so that they are not forgotten. The sampling area can be highly variable and depends on the density of the trees and the difficulty in accessing some locations because of remoteness, plant invasion or relief complexity. This may limit the possibility of reasonably extending the sampling.

In order to take into account all *Agarista* cohorts including seedlings and saplings of small height, we measured diameter at base (at ground level) and height using a caliper, a tape measure and a telescopic rule depending on the size of the plants. *Agarista* does not display buttresses, but older individuals often show a very irregular base that was sometimes difficult to measure. Diameter at base was consequently defined as the cross-sectional wood area expressed as a circle. Heights above 8 m were eye-estimated and total length was estimated instead of height for large trees whose trunks could have a section growing sub-horizontally.

Statistical analysis of size-age relationship

Our analysis is based on the simple observation that tree size increases with time (Worbes et al., 2003). After visual inspection of the observed relationship between the two study variables (age flow and maximal tree size), we first consider a simple power-law model as it is simple and allows for non-linearity. Considering that the largest trees on a lava flow are the oldest and have settled shortly after the flow, we therefore assume: $\text{Age} = a \times D_m^b$, where D_m is an estimator of the maximal size reached by the trees on the flow and *Age* the age of the flow. After log-transformation, we obtain model: $\log(\text{Age}) = a' + b \times \log(D_m)$. In order to account for potential non-linearity on the log-log scale, we finally consider a quadratic model as full model and test its components: $\log(\text{Age}) = a' + b \times \log(D_m) + c \times \log(D_m)^2$.

For maximal tree size, we consider three different estimators of D_m on each lava flow. D_m is successively estimated by the absolute maximum of the diameter distribution of censused trees

(D_{max}), the 95th percentile of the diameter distribution (D_{95}), and eventually the mean of the five larger diameters observed (D_5). We obtain the best model for each estimator of Dm using analyses of variance. We finally retain the estimator of D_m of which the best linear model displays the highest adjusted R-squared. All models were fitted using ordinary least squares regression using R ver. 3.4.4 (R Core Team).

RESULTS

The mean number of measured plants across all lava flows is 30.1 and varies from a minimum of five individuals to 46 on the 2007 and 1559 lava flows, respectively (**Fig.3.3**). For the former, the limited sample size relates to *Agarista* seedlings established in 2012 being very rare on the 2007 flow. These seedlings however demonstrate that *Agarista* is able to settle on a lava flow < 5 years old. The 95th percentile of the diameter distribution ranges from 0.19 cm on the 2007 lava flow to 177.47 cm on the 1401 lava flow. 711 and 255 *Agarista* trees were respectively sampled for the calibration model (elevation mean: 198 m, precipitation of driest month mean: 226 mm) and dating purpose (elevation mean: 354 m, precipitation of driest month mean: 210 mm).

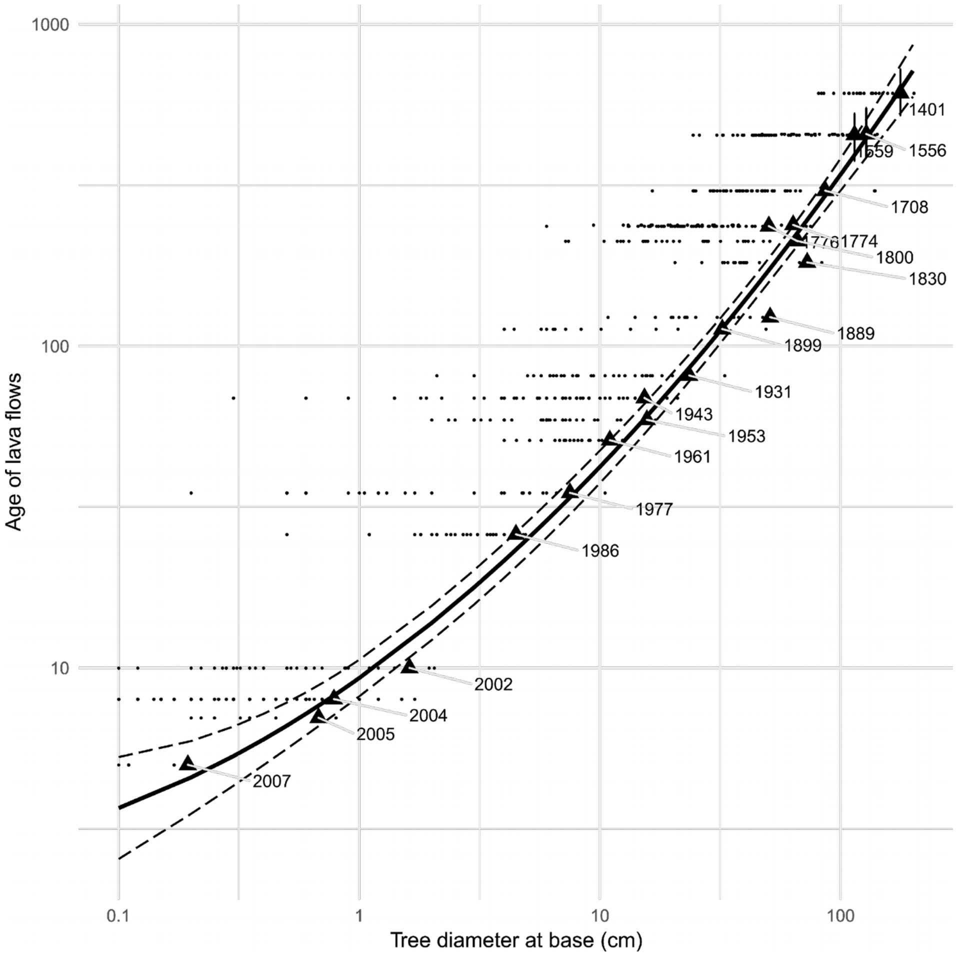

***Fig.3.3** Calibration of volcanic activity dating based on the relationship between age of lava flows and maximum diameter at base of* Agarista*. Dots and triangles respectively display* Agarista *measurements and the 95th percentile of the diameter distribution of* Agarista *populations; solid and longdash lines respectively display mean and upper/lower bounds of confidence interval predicted by the best linear model. The date of the lava flows on which* Agarista *trees were measured is given. The year of eruption is based on ^{14}C dating for the three oldest lava flows (errors bars are consequently shown) and is exactly known for the 17 historical lava flows.*

Among the three linear models that estimate the maximal size reached by *Agarista* (D_m), the 95th percentile of the diameter distribution (D_{95}) displays the highest adjusted R-squared, with small differences however compared to the other estimators: ($R^2_{D95} = 0.988 > R^2_{D5} = 0.986 > R^2_{Dmax} = 0.983$). The best model using a logarithmic linear regression with a quadratic form (**App.3.2**) is as follows:

$\log(Age) = 0.969 + 0.530 \times \log(D_{95}) + 0.126 \times (\log(D_{95}))^2$ ($n = 20$, $R^2 = 0.988$, $p < 10^{-15}$),

where D_{95} is the 95th percentile of the diameter distribution in cm and *Age* the age of lava flows on which *Agarista* trees were measured (**Fig.3.3** & **App.3.3**). The explicative power of the quadratic term remains weak compared to the linear trend (**App.3.2**). The study of model residuals shows no significant relationship between residuals and elevation or precipitation of driest month (**App.3.4**). Hence, climatic heterogeneity has no particular effect on the discovered relationships.

Using the calibrated model, 11 lava flows are dated between 1447 (CI: 1349-1531) at S-Ph1 and 1823 (CI: 1806-1839) at S-Ph4 (**Tab.3.1**). These new dates show that (i) at least one eruption occurred 422 years ago in a currently urbanised valley (S-Jo1: 1598 CE), (ii) several eruptions occurred along the South flanks at historical times (S-Ph2, S-Ph3, S-Ph4: 1726, 1765 and 1823 CE, respectively) and (iii) the caldera still hosts old-growth native forests settled at low elevations on lava flows that occurred before permanent human settlement (Cald-5: 1581 CE) (**Tab.3.1**).

Tab.3.1 *Dating of lava flows based on calibrated* Agarista *model. Id: Lava flow with* Agarista *population; D95: 95th percentile of the diameter distribution of* Agarista*; n: number of* Agarista *tree measurements; Age: age predicted by the calibrated mode; Date: 2012 – Age; CI min: minimum confidence interval value; CI max: maximum confidence interval value.*

Id	D95	n	Age	Age CI max	Age CI min	Date	Date CI min	Date CI max
Cald1	82.97	24	281.65	312.03	254.23	1730	1700	1758
Cald2	76.42	25	259.24	285.93	235.03	1753	1726	1777
Cald3	73.62	20	249.70	274.92	226.79	1762	1737	1785
Cald4	79.14	28	268.52	296.71	243.02	1743	1715	1769
Cald5	125.10	20	431.04	492.79	377.02	1581	1519	1635
Cald6	57.17	20	194.57	212.45	178.19	1817	1800	1834
S-Jo1	120.43	16	414.04	471.69	363.43	1598	1540	1649
S-Ph1	160.93	26	564.67	662.55	481.25	1447	1349	1531
S-Ph2	84.24	25	286.04	317.18	257.96	1726	1695	1754
S-Ph3	72.78	26	246.85	271.64	224.32	1765	1740	1788
S-Ph4	55.54	25	189.18	206.45	173.35	1823	1806	1839

Field work revealed a strong observer bias to estimate the height of trees > 8 m by eye. Consequently, we did not retain this method for lava flow dating. We note nevertheless that the 95th percentile of the height distribution allows a good prediction of lava flow age despite sample bias, which offers promising perspectives for future work (**App.3.5**).

DISCUSSION

A relevant alternative method to date past volcanic activity

We show evidence of a very strong relationship between the maximum diameter at base of *Agarista* trees and the age of lava flows. Hence, we demonstrate for the first time that dating volcanic activity from size distribution of pioneer trees is a relevant method, especially when no ^{14}C, paleomagnetic secular variations assessments nor historical records are available. Classical dendrochronology has recently developed in the humid tropics (Giraldo et al., 2020), but could not be successfully tested on *Agarista* because of indistinct ringing in wood (Catry and Daux, unpublished data). Coupling dendrochronology to X-ray densitometry or to the analysis of stable isotopes offers promising prospects to obtain independent dating of *Agarista* trees (Jacquin et al., 2017; Poussart et al., 2004). However, the former is cumbersome to implement, while the latter can cause substantial uncertainties in the interpretation because of major methodological issues, *e.g.* model parameterization used to calculate carbon and oxygen isotope fractionation or potential confounding effects of ontogenetic changes on isotope ratios (van der Sleen et al., 2017). Li et al. (2018) have also recently proposed dating volcanic activity from remote sensing techniques. However, this technic was limited to the last few centuries (between 93 and 388 years depending on the volcano) and does not allow having access to longer time spans. On the contrary, the longevity of *Agarista* enables to date lava flows as old as 1447 CE. This method is also interesting because it implements undestructive, simple and cheap methods, i.e. diameter measurement using tape measure. By contrast with remote sensing methods, good knowledge of the field and good physical condition are required to access remote locations and to measure numerous trees, which may be time consuming and demanding. Dating volcanic activity from size distribution may be tested in areas where long-lived trees also play a major role as an early shade-intolerant pioneer species on volcano slopes: *Metrosideros* spp. in Hawai‘i (Atkinson, 1970; Drake and Mueller-Dombois, 1993) and New Zealand (Clarkson, 1990); *Weinmannia* spp. in Chile (Lusk, 1999), New Zealand (Clarkson, 1990) and in Comoros (Charahabil et al., 2013); *Casuarina* spp. in Indonesia (Tagawa et al., 1985).

Dating volcanic activity from size distribution relies on (i) undisturbed pioneer cohorts of *Agarista* since their initial establishment on a newly-formed lava flow, (ii) accurate measurement of the maximum diameter at base among well-identified cohorts and (iii) use of the model in an area where climatic conditions for *Agarista* growth are relatively homogeneous. One would otherwise undoubtedly underestimate the age of this lava flow.

Alcalá-Reygosa et al. (2018) emphasize that dating a lava flow using pioneer tree may provide minimum ages and that the discrepancy between pioneer tree age and lava flow age may be substantial. They state that “this may be due to the impact of fires, the volcanic activity or the natural mortality in a pioneering community”. In our study, the calibration model based on 20 lava flows shows a strong correlation that makes very unlikely a strong disturbance of pioneer cohorts since their establishment. The question arises above all with regard to lava flows that were dated with *Agarista* model and that do not have other independent dating. Natural mortality within *Agarista* population on lava flows does not lead to new recruitment of younger cohorts. On older lava flows, senescent *Agarista* individuals are replaced by late successional canopy tree species (Albert et al., 2020a; Cadet, 1977; Strasberg, 1994) and isolated individuals can occasionally survive because of favourable light conditions, such as forest gaps. Before the beginning of forest clearings for agriculture in this wet area in the late 18th century, fires were probably related to volcanic activity. Two situations must be distinguished: the lower flanks of PdF outside the caldera and the Grand Brûlé. On the former, the low occurrence of eruptions makes unlikely the destruction of previous *Agarista* populations. In the caldera where lava flows frequently occur, it cannot be ruled out that the growth of *Agarista* population in the kipukas was not disturbed by adjacent lava flows (fire, gas) and thus might lead to an underestimation of the flow age. Hence, future work aimed at obtaining independent dating could first focus on the caldera where disturbances have been numerous.

One other limitation is the difficulty to identify the boundaries of each single lava flow to precisely sample tree cohorts and their whole size distribution. A great attention should especially be given to lateral margins of lava flows. Indeed, field observations show that *Agarista* trees can be bigger and higher at the edge of lava flows than in the middle part. This pattern suggests a front of plant colonization from the nearest source of seeds (Li et al., 2018), not only from *Agarista*, but also from numerous species. This might strongly facilitate the growth of *Agarista* that might benefit from a higher nutrient availability and from buffering environmental stress (Walker and Moral, 2003). In addition, the type of basaltic lava might have a significant influence on the growth of *Agarista*, Cadet (1977) reported for instance that vegetation growth was faster on Pāhoehoe lava than on ‘A‘ā lava and field observations show that tree roots are able to penetrate through Pāhoehoe lava probably to access nutrients below (see **Fig.3.2b**). Because several eruptions produced mixt Pāhoehoe-‘A‘ā lava (*e.g.* 1401, 1559, 1977, 2004), future work at finer scale to include these factors in a multiple linear regression may substantially improve our capacity to date volcanic activity from size distribution of pioneer tree.

Finally, *Agarista* model was calibrated in an area where climatic heterogeneity probably has a minor influence on the estimation of the age of lava flows (**App.3.4**). We used *Agarista* model to date lava flows up to 800 m asl, which characterizes the upper limit of the tropical rainforest biome on La Réunion (Albert et al., 2020a; Cadet, 1977; Strasberg, 1994). At higher elevations where *Agarista* is at edge-range or absent, one could attempt to use other ecological “analog” species that could help in dating some lava flows and associated eruptions.

An underestimated lava flow recurrence along the volcano flanks of PdF

The analysis of the historical reports of PdF recently revealed that the volcanic activity in the Enclos Fouqué caldera evolved from an intense, continuous lava lake dynamics at the top of the Central Cone between at least the first summit observations (1751 CE) to 1860 CE, to the current dynamics made of short, frequent eruptions on the flanks of the Central Cone and on the floor of the Enclos Fouqué caldera (Michon et al., 2013). This study also proposed that the edification of the Central Cone was almost complete before 1750 and ended in 1860 with a main phreatomagmatic eruption following the emptying of the last lava lake (Maillard, 1862; Michon et al., 2013). The cone growth resulted from a twofold evolution characterized by a lava fountain dynamics building a first cone until the collapse of a large pit crater that was subsequently filled by a lava lake activity centred on the Bory crater, which led to the formation of the Bory shield until around 1750 (Michon et al., 2013; Peltier et al., 2012). Despite a lack of any direct dating of the beginning of the Central Cone activity nor observations before 1751, Michon et al. (2013) interpreted the absence of unconformity between the lava sheets forming both the basal cone and the Bory shield as indicative of a long-lasting continuous activity. This interpretation is supported by radiocarbon ages between 340 and 130 BP (median ages of 1560 and 1856 CE) of eruption fall deposits preserved on the northern rim of the Enclos Fouqué caldera (**App.3.1** & **Fig.3.1**; Morandi et al., 2016). However, despite an increasing amount of evidence for an intense volcanic activity affecting the summit area before the 19th century, our knowledge of its impact on the volcano flanks was based on only 4 radiocarbon ages of lava flows and a few historical reports after 1708 CE.

Our alternative method of dating lava flows with *Agarista* allows to track the volcanic activity on the flanks of PdF (11 newly dated lava flows). Figure 3.1 indicates that at the exception of the Grand Brûlé where sampling is relatively dense, our dating sites are homogeneously distributed in the volcano lower flanks (i.e. about <400 m asl). Furthermore, as mentioned above, lava flows emplaced since the 15th century, on which *Agarista* trees are still present, are not covered by any deep soils. By contrast, the spatial distribution of the agricultural activity gives insight in the location of lava flows on which deep soils had time to develop. Thus, Figure 3.1 reveals that our analysis of the lower flanks takes most of the areas not covered by crops into account and therefore correctly integrates the areas affected by recent lava flows. The main sampling bias in the lower slopes of PdF would therefore result from the 0.8 km wide area located between the lava flow of Piton Nelson dated at 260 BP and the northern limit of the Grand Brûlé, where no soil developed.

Altogether the eruptions observed outside the Enclos Fouqué and Grand Brûlé structures since 1708 and those dated either from radiocarbon or *Agarista*-calibrated methods form a comprehensive database of 34 ages that allows determining the temporal evolution of the volcanic activity during the last millennium (**Fig.3.4**). We split the database considering the location of the eruption sites, i.e. inside or outside the Enclos Fouqué and Grand Brûlé structures, in order to evaluate potential differences in the central versus flank dynamics. Outside the Enclos Fouqué caldera, the evolution is characterized by 24 ages. The relative probability distribution of these ages shows three main peaks, the last one been defined by the three eruptions that recently occurred between 1977 and 1998 (**Fig.3.4b**). Interestingly, the temporal distribution of the 10 ages related to eruptions located in the Enclos Fouqué caldera reveals an overall evolution similar to the one deduced outside the caldera. Lava flows emitted from the Central Cone or adjacent eruptive fissures have partly resurfaced the Grand Brûlé area since the 19th century. However, the occurrence of a few small scattered kīpuka allowed to date older lava flows between 1581 and 1817 CE (**Tab.3.1** & **Fig.3.4**). Moreover, the probability distribution of the observed lava flows entering the ocean in Grand Brûlé since 1753 confirms an intense activity of PdF until around 1820 that progressively declined until a renewal since around 2000 (**Fig.3.4b**). Thus, these data suggest (1) a similar dynamics outside and inside the Enclos Fouqué caldera and (2) the existence of three successive periods of intense activity drawn by three clusters of eruption and lava flow ages (1460-1630, 1690-1840, 1970-present).

We show above that the Central Cone of PdF results from a long-lasting period of intense lava fountaining and lava lake activity between at least the 16th and 19th centuries (Michon et al., 2013; Peltier et al., 2012). The present work reveals that the volcano flanks and the summit area experienced two successive periods of intense activity before the 19th century (clusters 1 and 2 in **Fig.3.4b**). Considering these results, we tentatively propose that both the building of the Central Cone and the eruption occurrence outside the Enclos Fouqué caldera, in the summit zone and the volcano flanks, result from large magma supply. Moreover, the distribution in clusters could indicate a pulsating rather continuous magma supply. Such pulses could yield large overpressures in the magmatic system promoting lateral migrations and eruptions and lava flows outside the Enclos Fouqué caldera (**Fig.3.5**). Such magmatic pulses would be comparable to those experienced by the Hawaiian volcanoes during the last centuries (Klein, 1982). Thus, our data give potential insights to refine the periods of edification of the Central Cone (15th-19th centuries) for which chronological constraints were lacking. Indirectly, they raise the question of the volcanic structures existing in the Enclos Fouqué caldera between this period of intense activity and the large explosive eruptions dated at around 2140 BP possibly related to the last Enclos Fouqué caldera collapse events (Morandi et al., 2016). Only the remnant relief of Puy Mi-Côte at the northwestern base of the Central Cone (Michon et al., 2013) could attest of a volcanic activity within the Enclos Fouqué caldera during this time span. Finally, if the two first magmatic pulses led to the building of the Central Cone with a long-lasting lava lake activity, the eruptive dynamics of the third, current cluster clearly differs and is characterized by frequent, few hours-to-few months long eruptions located of the floor of the Enclos Fouqué (Roult et al., 2012).

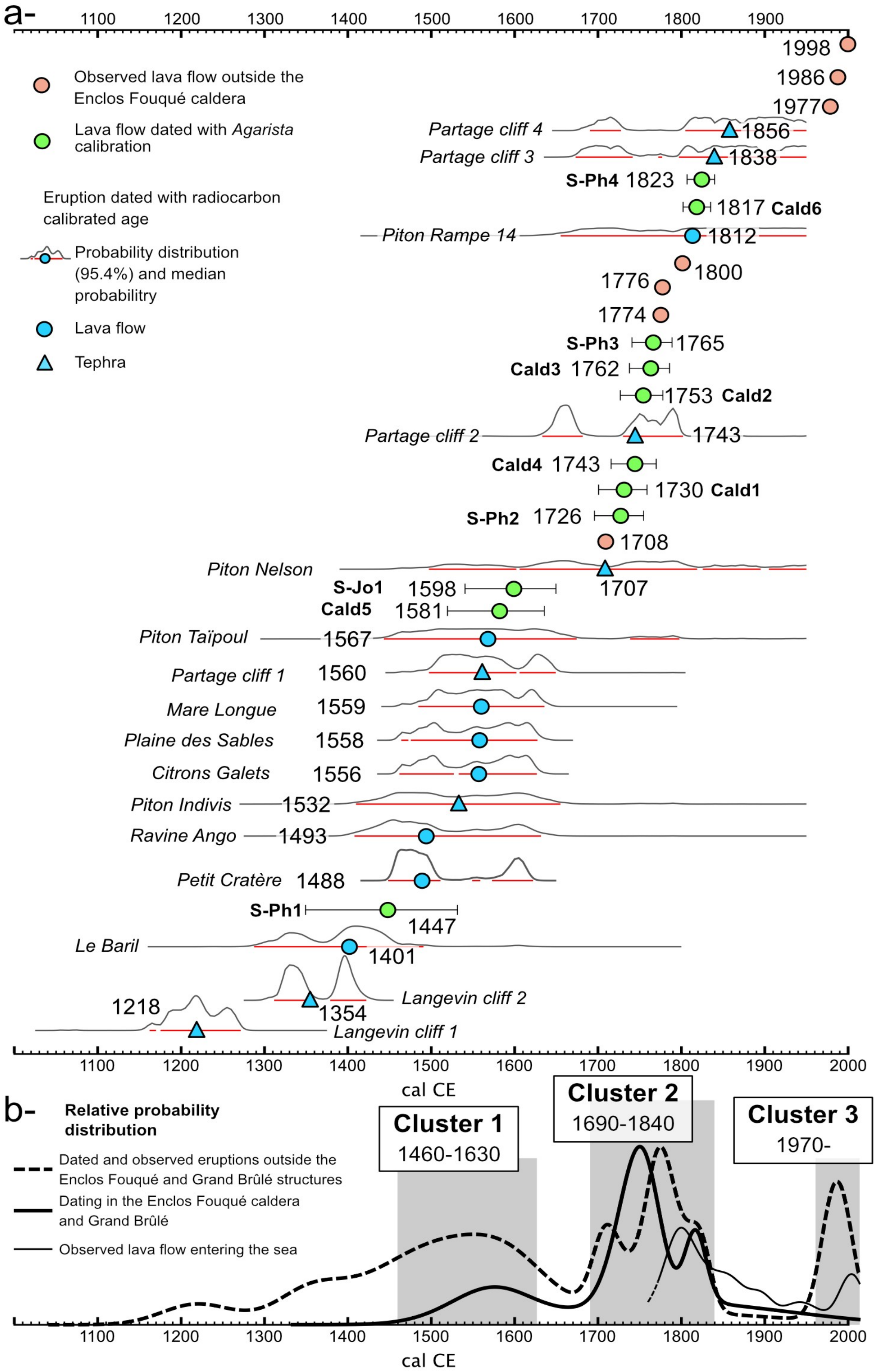

Fig.3.4 a- *Temporal distribution of the dated and observed eruptions of Piton de la Fournaise since the 12th century.* ***b-*** *Relative probability plot determined for eruptions or lava flow that occurred outside the Enclos Fouqué and Grand Brûlé structure (thick line), inside the Enclos Fouqué caldera and in Grand Brûlé (thick dashed line), and observed lava flows reaching the sea in Grand Brûlé. It is worth noting that the observation in Grand Brûlé are totally lacking before 1759 and sparse until 1774. Two clusters (1460-1630; 1690-1850) of eruption and lava flow occurrence are defined by calibrated radiocarbon,* Agarista-*calibrated ages and observations both inside and outside the Enclos Fouqué caldera. Interestingly, the probability low highlighted by dates outside and inside the Enclos Fouqué and Grand Brûlé structures between around 1850 and 1977 (thick lines) also corresponds to a lower rate of observed lava flow entering the ocean within Grand Brûlé (thin line).*

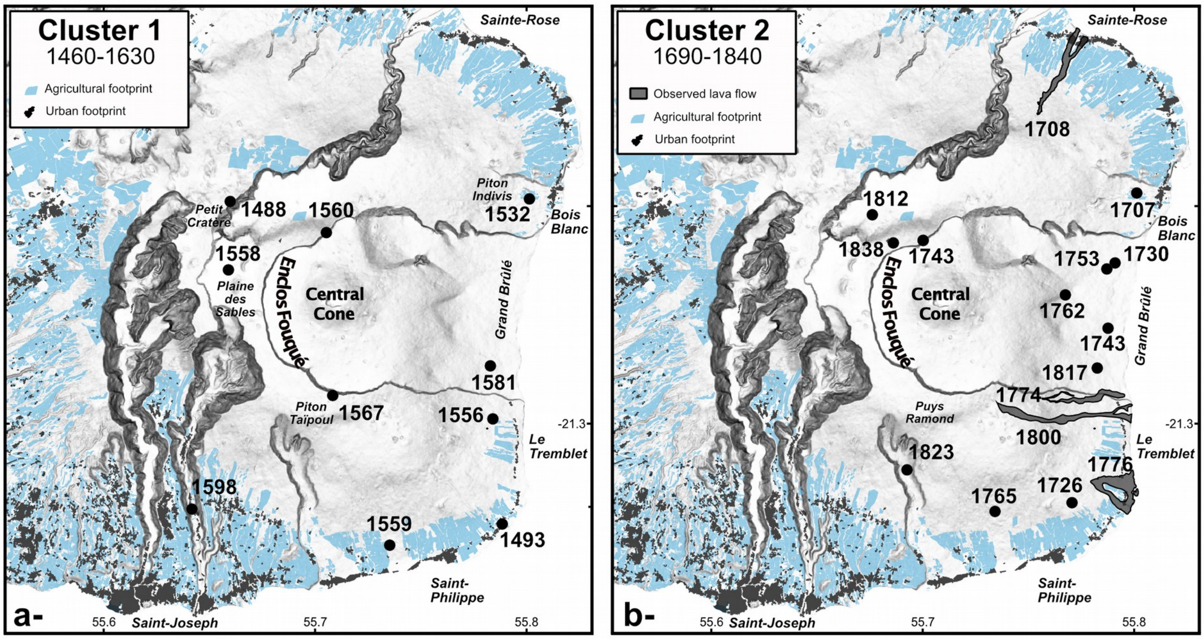

Fig.3.5 *Spatial distribution of the dated sites (^{14}C and* Agarista *calibration) that give insights into the eruption occurrence related to the two first clusters of volcanic ages determined from* ***Fig.3.4b*** *between 1460-1630 and 1690-1840.*

In terms of hazard assessment, our work also shows that dating lava flow with *Agarista* calibration represents an accurate alternative method to refine the hazard map of lava flow inundation. At least 24 lava flows covered the volcano slopes since 1401 CE (**Fig.3.4**). It appears that 18 out of 24 lava flows were located on the south and north flanks nowadays inhabited. Most of them affected the southern and southeastern slopes (13 out of 18) where they were either channelized in the deeply incised valleys (Rivière Langevin and Basse Vallée, **Fig.3.5**) or resurfaced the volcano flanks. The spatial distribution of the lava flows might indicate a higher lava flow hazard in Saint-Joseph, Saint-Philippe and Le Tremblet areas, than in Sainte-Rose despite the recent 1977 lava flows (**Fig.3.1**). This is supported by the almost continuous footprint of the agricultural surface in the lower part of the northern flank compared to the south flank (**Fig.3.1** & **Fig.3.5**) It is also important to note that the valley incised in the southern flank can efficiently channelize the lava flows related to eruptions located in the summit zone. Such an effect is supported by the Plaine des Sables eruption that occurred between 1424-1628 cal CE (median probability at 1558 CE), which fed a lava flow that flew down in the upper part of the Rivière Langevin valley (Principe et al., 2016). This lava flow whose downstream continuity is not established could correspond to the remnant of the lava flow that we dated dated with *Agarista* at 1598 CE (CI between 1540-1649) at 285 m above sea level in the now inhabited Rivière Langevin canyon (**Fig.3.5a**). However, if the lava flows of the Plaine des Sables and in the lower part of the valley are not related, it suggests a lava flow inundation hazard even higher in the now inhabited Rivière Langevin canyon (**Fig.3.5a**). The Basse Valley canyon would have played a similar role with lava flows emitted from the Puys Ramond area (**Fig.3.5b**). To this respect, the recent lava flow dated at 1823 CE (CI between 1806-1839) with *Agarista* could correspond to the mysterious eruptions of 1820 described by (Hoarau and Vinet, 1820) but never identified in the field so far. Finally, the higher volcanic hazard of the southern flank of PdF must be confirmed by future sampling north of the Grand Brûlé (*e.g.* Bois Blanc; **Fig.3.5**) where several eruptions have already been reported in Morandi et al. (2016) and where several undated eruptions might have occurred before 1700 CE.

CONCLUSION

We built from a statistical approach a robust relationship between the age of secular lava flows of Piton de la Fournaise and the size of the long lived pioneer tree *Agarista salicifolia*. This relationship allows to date 11 lava flows that covered the volcano lower southern and eastern slopes between the 15th and 19th centuries. Combining ages obtained with ^{14}C and *Agarista* calibration methods, and observed historical lava flows between 1700 and 1800, the timing of the eruptions of PdF is now constrained by 31 ages between 1000 and 1900 CE. The temporal distribution of these dates is organised in three clusters (1460-1630, 1690-1840, 1970-present) interpreted as the result of pulses of high magma supply. This intense dynamics during the two first identified pulses may have led to the building of the Central Cone with a lava lake activity in the Enclos Fouqué caldera and the occurrence of eruptions outside the caldera and on the volcano flanks which are now inhabited. The third pulse may explain the activity renewal outside the Enclos Fouqué caldera and a higher rate of lava flow entrance in the ocean. Finally, our original approach of dating lava flows from size distribution of pioneer trees might be tested in numerous areas where long-lived trees also play a major role as an early pioneer on volcano slopes: *Metrosideros* spp. in Hawai‘i and New Zealand; *Weinmannia* spp. in Chile, New Zealand and in Comoros archipelago; *Casuarina* spp. in Indonesia.

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CHAPITRE 4. L'effondrement de la diversité des traits de dispersion sur les coulées historiques révèle un fort impact négatif de la disparition des frugivores sur la résilience forestière

RESUME

Comprendre comment la rupture des interactions entre les plantes à fruits charnus et les animaux frugivores peut altérer la diversité et la dynamique des communautés végétales sur le long terme demeure un défi. En raison de la durée de vie généralement importante de ces végétaux, de telles études doivent en effet s'inscrire dans une temporalité longue, mais les études à l'échelle des communautés ont jusqu'à présent étudié les conséquences de moins d'un demi-siècle de défaunation. Ici, nous utilisons une chronoséquence de plus de six siècles pour comparer les changements dans la richesse et la composition de différents assemblages basés sur les traits de dispersion au sein de communautés établies avant et après la colonisation humaine de l'archipel des Mascareignes. Notre étude est située à La Réunion sur les pentes du Piton de la Fournaise, l'un des volcans les plus actifs au monde. En utilisant l'échantillonnage historique de T. Cadet, nous analysons 151 relevés de végétation sur des coulées de lave datées entre 1401-AD et 1956-AD, et en forêt tropicale humide sur des substrats plus anciens. Nous définissons cinq classes d'âge de substrat, selon la chronologie bien connue de la défaunation des frugivores indigènes : “vieux subtrats” et [1401, 1665[quand les frugivores sont abondants et diversifiés avant la colonisation humaine permanente ; [1665, 1800[quand les populations des grands frugivores sont fortement réduites; [1800, 1900[quand les grands frugivores sont éteints et les petits frugivores encore abondants; [1900, 1956] quand les populations de petits frugivores déclinent. Nous caractérisons 146 espèces ligneuses indigènes selon leurs traits de dispersion : anémochores, à petits fruits charnus ou à gros fruits charnus, ces derniers ne pouvant être théoriquement avalés par les frugivores relictuels. Les changements dans la diversité des traits de dispersion sont fortement corrélés à la chronologie de la défaunation. Les communautés avec une grande richesse spécifique établies avant la colonisation humaine sont largement dominées par les espèces à fruits charnus. Les plantes à gros fruits charnus dans les communautés établies peu après le début de la colonisation humaine déclinent très fortement et disparaissent quasiment après 1800. La richesse des plantes à petits fruits charnus diminue moins vite le long de la chronoséquence, avec des niveaux moyens sur les coulées de lave de [1665, 1800[et [1800, 1900[, puis faibles sur les coulées de lave du 20ème siècle. En revanche, la richesse des plantes anémochores ne change pas de manière significative. L'isolement des relevés qui résulte notamment de la fragmentation des forêts par les coulées de lave, a aussi un impact négatif sur la richesse des communautés, mais cet effet est surtout visible sur les coulées historiques, montrant que la perte des grands frugivores a probablement gravement altéré la capacité de dispersion à longue distance. Considérant la diversité béta, les communautés établies avant la colonisation humaine ont une composition comparable. Les assemblages de plantes à fruits charnus montrent une forte perte d'espèces le long de la chronoséquence, tandis que les assemblages anémochores montrent un fort remplacement d'espèces, probablement en raison d'une faible barrière à la dispersion. Nos résultats montrent pour la première fois l'impact considérable de l'extinction des frugivores sur la dynamique de colonisation des plantes sur plus de 300 ans. L'effondrement de la diversité des plantes à fruits charnus sur les coulées de lave historiques souligne le rôle irremplaçable joué par les frugivores, en particulier les espèces de grande taille. La conservation des interactions mutualistes plantes-animaux est primordiale, et des efforts de refaunation doivent être entrepris dans les zones où les frugivores ont disparu.

Collapse of dispersal trait diversity across a long-term chronosequence reveals a strong negative impact of frugivore extinctions on forest resilience*

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ABSTRACT

Understanding how seed dispersal disruption may alter plant community diversity and dynamics over a large temporal scale remains a challenge. Here, we use a long-term chronosequence to compare changes in the richness and composition of different dispersal trait assemblages in communities established before and after human colonisation in the Mascarene archipelago. Our study was located on Réunion on the slopes of the Piton de la Fournaise, one of the most active volcanoes worldwide. We analysed 151 vegetation surveys on lava flows dated between 1401-AD and 1956-AD and in tropical rainforests established on older substrata. We defined five classes of substratum age, according to the well-known chronology of native frugivore defaunation: “old substrata” and [1401, 1665[when frugivores were abundant and diverse before permanent human settlement; [1665, 1800[when large-bodied frugivore populations were strongly reduced; [1800, 1900[when large-bodied frugivores went extinct and small-bodied frugivores were still abundant; [1900, 1956] decline in the population of small-bodied frugivores. Based on dispersal traits, we categorised 146 native woody species as anemochorous, small fleshy-fruited or large fleshy-fruited, *i.e.* plant of which fruit could not theoretically be dispersed by extant frugivores. Changes in dispersal trait diversity strongly correlated with the chronology of defaunation. Species-rich communities settled before human colonisation were strongly dominated by fleshy-fruited species. Large fleshy-fruited plants in the oldest communities settled after human colonisation declined markedly and almost disappeared after 1800. The richness of small fleshy-fruited plants decreased less rapidly across the chronosequence, with medium levels on [1665, 1800[and [1800, 1900[lava flows and low levels on [1900, 1956] lava flows. Conversely, the richness of anemochorous plants remained unchanged. Communities settled before human colonisation had a similar composition. Fleshy-fruited assemblages showed strong species loss across the chronosequence, while anemochorous assemblages showed strong species turnover, which was probably due to lower dispersal limitation. Our results provide the first insights into the tremendous impact that frugivore extinction has on plant colonisation dynamics over 300 years. The dramatic loss of fleshy-fruited plant diversity on historical lava flows highlights the irreplaceable dispersal role played by frugivores, especially large-bodied species. The conservation of plant-animal mutualistic interactions is invaluable and refaunation efforts need to be undertaken in areas where frugivores have been extirpated.

INTRODUCTION

The decline in large vertebrates is a global phenomenon (Blackburn, 2004; Dirzo et al., 2014; Hansen and Galetti, 2009; Steadman, 1995; Young et al., 2016). For decades it has been raising serious concern with regard to the consequences for plant-animal mutualistic interactions (Bond,

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1994; Emmons, 1989; Janzen, 1974). Notably, frugivore vertebrates (hereafter referred to as "frugivores") play a prominent role and their extirpation alters seed dispersal process (Babweteera and Brown, 2009; Jordano et al., 2007; McConkey and Drake, 2006; Meehan et al., 2002; Riera et al., 2002; Wotton and Kelly, 2012; Young et al., 2016). Ecological and evolutionary consequences at plant population level include altered regeneration (Levi and Peres, 2013; Wotton and Kelly, 2011; Zeng et al., 2019), reduced connectivity (Pérez-Méndez et al., 2018), downsized dispersal traits (Galetti et al., 2013) and altered genetic diversity (Carvalho et al., 2016). Recent studies reported the transforming effects of frugivore loss on plant communities, by comparing seedling recruitment between intact and defaunated sites (Effiom et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010; Wandrag et al., 2017; Wright et al., 2007). However, to our knowledge, no study has yet examined how seed dispersal disruption may jeopardise whole tree communities over a period exceeding thirty years. Our research uses a long-term chronosequence of lava flows that spans a frugivore defaunation time range of 300 years on Réunion, an oceanic island that belongs to the Mascarenes. It has been one of the latest tropical archipelagos to be colonised by humans in the 17th century, which makes it a unique study system, particularly since: (1) the kinetics of frugivore extinction is well documented by subfossil records (Hume, 2013; Mourer-Chauviré et al., 1999) and historical archives (Cheke and Hume, 2008; Lougnon, 2005); and (2) high volcanic activity has produced numerous lava flows, which provide an ideal natural experiment to date and explain patterns of plant community changes (**Fig.4.1**).

Seed dispersal is a key process for ecosystem recovery after disturbance, such as lava flows. Dispersal is the only possible pathway by which plant colonise disturbed areas where the living biomass, including soil seed banks, has been totally destroyed (Walker and Moral, 2003). In relation to seed dispersal strategies, fruit traits are important for understanding plant colonisation mechanisms: plants with large or small fleshy fruits mainly depend on frugivores for their dispersal, whereas most plants with dry fruits depend on abiotic dispersal vectors, *e.g.* wind (Howe and Smallwood, 1982; van der Pijl, 1982). In most tropical rainforests, frugivorous vertebrates are key components of forest succession, since they play a far greater role than wind in dispersing woody plants (González-Castro et al., 2019; Ingle, 2003; Whittaker et al., 1989). Hence, past and present frugivore defaunation probably has severe consequences on ecosystem recovery and forest dynamics after disturbance. This is especially the case on tropical oceanic islands, where a mass extinction of frugivore vertebrates has frequently followed human colonisation (Blackburn, 2004; Heinen et al., 2017; Steadman, 1995). Therefore, we would expect drastic changes in the diversity and composition of fleshy-fruited plant assemblages on lava flows, before and after human colonisation, compared to anemochorous dry-fruited (ADF) plant assemblages, which remain unaffected.

The fruit of fleshy-fruited plants varies considerably in size, typically ranging from a few millimetres to over 50 cm (Guimarães et al., 2008). This suggests that different sized frugivores are required for effective dispersal (Hansen and Galetti, 2009; Naniwadekar et al., 2019). Critical fruit size thresholds exist among plant communities: for example, the early extinction of megafauna limited the dispersal of many large-seeded plants (Federman et al., 2016; Guimarães et al., 2008). Fruit size of ca 13 mm is documented as a critical threshold, both on the mainland (Dowsett-Lemaire, 1988; Galetti et al., 2013) and on oceanic islands (McConkey and Drake, 2015). As defaunation primarily extirpates large vertebrates (Dirzo et al., 2014), most oceanic islands are strongly depauperate in large-bodied frugivores (McConkey and Drake, 2015; Schleuning et al., 2014). In some places, including Réunion, they have been totally extirpated and therefore absent for several centuries (Heinen et al., 2017). In addition to the contrast between ADF vs fleshy-fruited species, we would also expect to see dramatic changes in diversity and composition within fleshy-fruited species given that large fleshy-fruited (LFF) plant assemblages are likely to have been impacted for a longer period (since human colonisation) than small fleshy-fruited (SFF) plant assemblages.

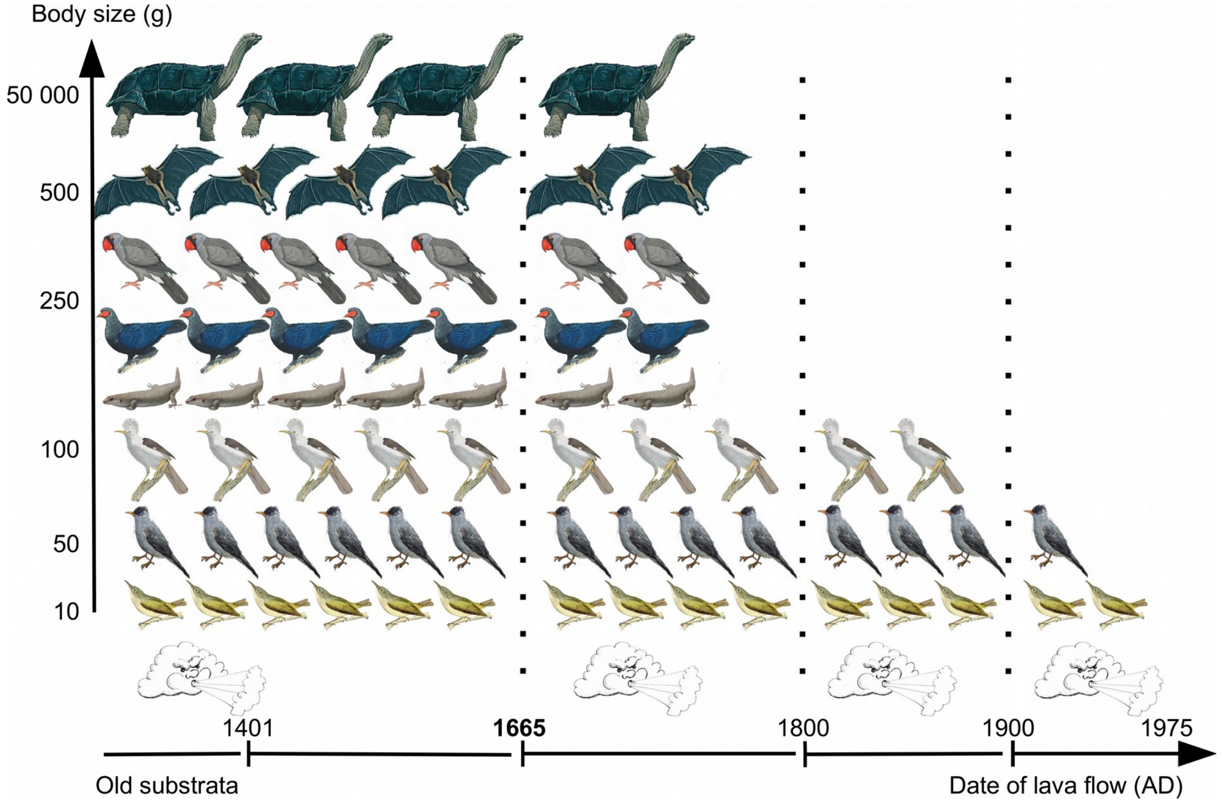

Fig.4.1 *Historical milestones in relation to availability of dispersal agents on Réunion across a long-term chronosequence of lava flows. Availability through time in native frugivores (from top to bottom: giant tortoises, flying foxes, parrots, fruit pigeons, starlings, skinks, bulbuls and white-eyes) is inferred from Cheke and Hume (2008) and Lougnon (2005). Native frugivore assemblages were diversified and oversized until the first human settlements were established in 1665 AD. After 135 years of human settlement throughout the lowlands, habitat destruction and overharvesting led to the extinction of large-bodied frugivores by 1800. The Réunion bulbul was abundant until the beginning of the 20th century, when populations declined sharply. They have remained at low levels throughout the 20th century until Cadet's sampling in 1975. Wind is assumed to be constantly present across the chronosequence. The giant tortoises, flying foxes, parrots, fruit pigeons and starlings were illustrated by Julian Hume, the white-eyes by John Gerrard Keulemans, the skinks by Josh Noseworthy and the bulbuls by Dominique Strasberg. For more details about frugivores, see* ***App.4.1****.*

In this paper, we use a comparative approach to investigate whether dispersal failure caused by defaunation leads to severe diversity loss in plant communities studied across a long-term chronosequence of lava flows. We focus on changes in the richness and composition of ADF, SFF and LFF plant assemblages settled on substrata belonging to five age classes, which we consider as a proxy of dispersal agent availability (**Fig.4.1**). We compare plant communities settled before permanent human settlement in 1665-AD, when frugivores were abundant and diverse, to more recent communities established after the extinction of large-bodied frugivores and the decline in the population of small-bodied frugivores began. First, we test whether changes in richness relate to the availability of frugivores. We expect the richness of LFF and SFF plant to be high on ancient lava flows that were colonised when frugivores were still abundant. In theory, LFF plant richness should decrease faster across the chronosequence (from oldest to youngest lava flows) than SFF plant richness because large-bodied frugivores became extinct sooner than small frugivores. On the contrary, dispersal limitation for ADF plants is low, therefore, variation in ADF plant richness should be independent of the defaunation history. It may even increase across the chronosequence because early primary successional stages are often dominated by ADF species (Walker and Moral, 2003). Second, we analyse β-diversity and its two components, *i.e.* nestedness and turnover, which respectively result from the loss (or gain) of taxa and from the replacement of taxa (Baselga, 2010), to detect variation in plant community composition across the chronosequence. We expect strong dispersal limitation in fleshy-fruited species to lead to a significant increase of nestedness across the chronosequence, especially for LFF plants. On the contrary, if ADF species suffer no major dispersal limitation and can all reach lava flows, we should detect higher species replacement or species gain on recent lava flows (Wandrag et al., 2017).

MATERIAL AND METHODS

Study area

Réunion (2512 km²) is the largest island in the Mascarene archipelago. It is located in the biodiversity hotspot that characterises the South-West Indian Ocean islands (Mittermeier et al., 2004) (**Fig.4.2**). The study site is located in the South-East of Réunion on the slopes of the Piton de la Fournaise. This shield volcano is one of the most active in the world. More than 238 eruptions have been recorded since the second half of the 17th century (Morandi et al., 2016). For 5000 years, most lava flows have occurred in the most recent caldera of the Piton de la Fournaise. Eruptions have also occurred outside the caldera along three rift zones (Morandi et al., 2016). The Piton de la Fournaise area has a humid tropical climate throughout the year below 750 m asl, *i.e.* annual mean temperature ranges from 19 to 25°C and precipitation in the driest month ranges from 75 to 350 mm, with large inter- and intra- annual variations (Jumeaux et al., 2011). This area shelters almost all that remains of the tropical rainforest on Réunion and represents the last sanctuary of its kind in the Mascarene archipelago (Strasberg et al., 2005).

Data collecting

Vegetation sampling and frugivore guild characterisation

We used a historical dataset sampled in the 1970s by the French botanist Cadet (1977). It is invaluable because it includes forests that have since been destroyed (**App.4.2**). We retained 151 vegetation plots sampled in pristine or relatively undisturbed habitats, where alien plants were rare or had little overall cover (**Fig.4.2**). Twenty-eight plots were settled on well-developed soils as reported by Cadet (1977) in his technical notes. We did not have proper dating for these substrata, but based on the very likely slow pedogenesis, we assumed that they were at least 1000 years old (Meunier et al., 2010). One-hundred and twenty-three plots were located on 27 lava flows dated between 1401 AD and 1956 AD: (i) three lava flows were dated by ^{14}C (Morandi et al., 2016), (ii) sixteen lava flows were known from historical sources (Cadet, 1977; Stieltjes, 1986) and (iii) eight lava flows were dated using an indirect approach based on the size distribution of long-lived ADF pioneer trees found on lava flows (Albert et al., 2020b). Because ^{14}C dating could not be used in several areas such as the caldera that, however, hosted isolated old remnant forests, the tree size method allowed to expand the chronosequence and to add some heterogeneity in the sampled ecological situations.

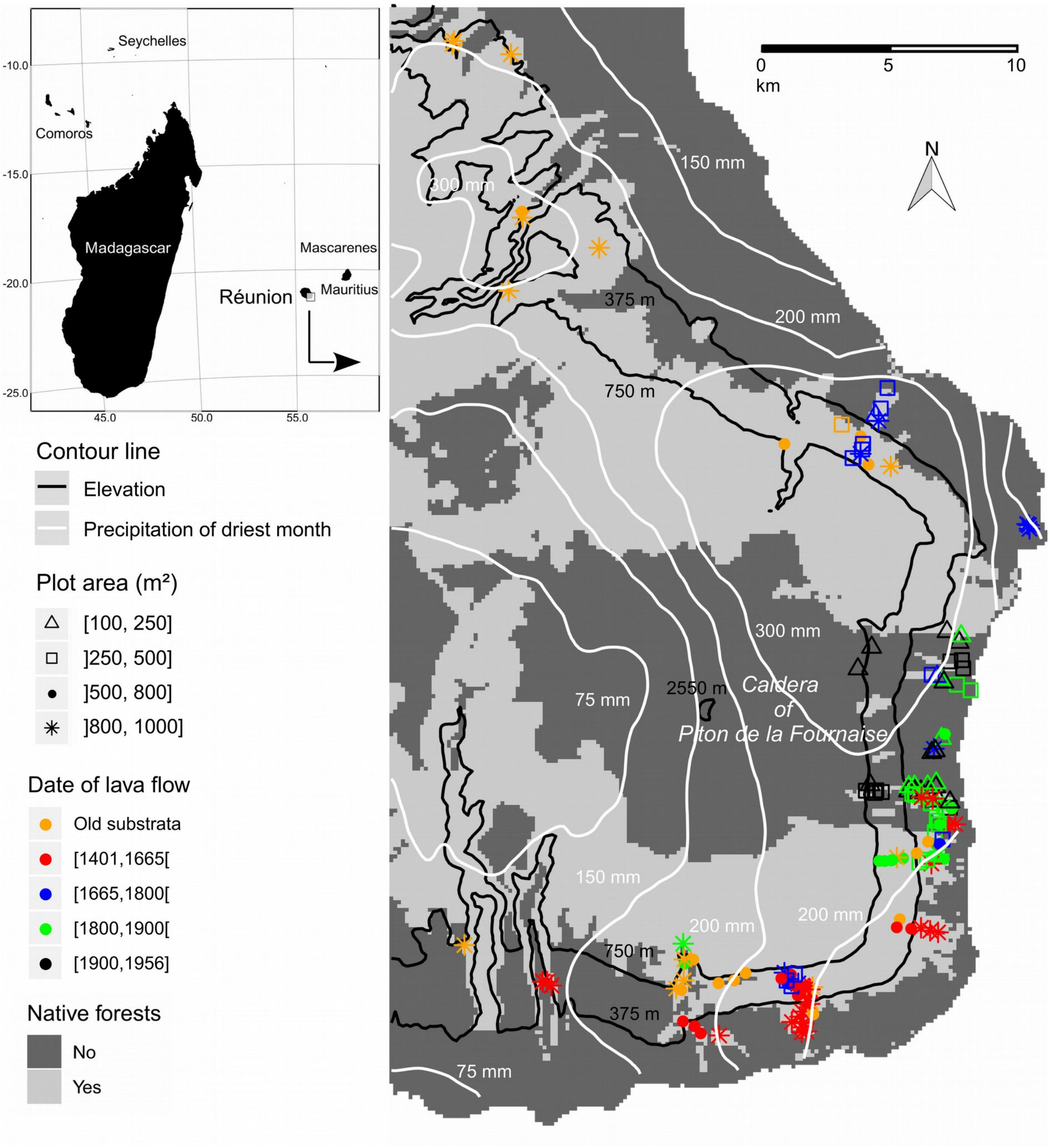

Fig.4.2 *The study site on Réunion in the Piton de la Fournaise area. Réunion is an oceanic island in the South-West Indian Ocean, situated between Madagascar and Mauritius in the Mascarenes. The massif of the Piton de la Fournaise extends across the South-Eastern third of the island (white rectangle). The 151 vegetation plots are located on the windward side below 750 m asl and shown according to lava flow dating: 123 plots in four classes are located on lava flows that occurred between 1401 and 1956; and 28 plots are found on old substrata,* i.e. *over 1000 years old.*

We assigned the 151 vegetation plots to five substrata age classes, defined according to the availability of dispersal agents, as documented by subfossils records (Hume, 2013; Mourer-Chauviré et al., 1999) and historical archives (Cheke and Hume, 2008) (**Fig.4.1**). Namely, the first class was “old substrata” on which plant communities assembled when frugivores were numerous and where pedological conditions were supposed to be more favorable. This class therefore included our reference control plots (n = 28 plots); the second class was [1401, 1665[, when frugivores were still numerous and diverse (n = 36 plots); the third class was [1665, 1800[, when large-bodied frugivore populations were severely reduced, while small-bodied frugivore populations were less impacted (n = 23 plots); the fourth class was [1800, 1900[, when large-bodied frugivores were extinct and small-bodied frugivores, especially the native bulbul (*Hypsipetes borbonicus*) and the hoopoe starling (*Fregilupus varius*), were still abundant (n = 37 plots); the fifth and most recent class was [1900,1956], when populations of extant small-bodied frugivores further declined to extremely low densities (n = 27 plots) (**Fig.4.1**).

Spatial distribution of study plots was not random given the volcanic eruption pattern, as well as difficulties in accessing some remote locations (**Fig.4.2** & **App.4.3**). All plots on "old substrata" were outside the caldera; plots on [1401, 1665[lava flows were all located in the southern half of the Fournaise area, whereas those on [1665, 1800[lava flows showed a wider distribution; plots located on [1800, 1900[and [1900, 1956] lava flows were respectively located in south-central Fournaise area and in the caldera. In the latter area, old growth native forests were already rare and very fragmented in 1975. Cadet (1977) also used different sampling areas ranging from 500 to 1000 m² on pre-defaunation lava flows and from 100 to 1000 m² on historical lava flows (**Fig.4.2**).

For each plot, Cadet (1977) recorded the cover of tree, shrub and herbaceous strata and maximum canopy height. For each stratum, he recorded the list of tracheophyta at species level, including seedlings with the Braun-Blanquet semi-quantitative method. These data allowed us to quantify species richness, composition and vegetation structure. We focused on woody species, *i.e.* woody angiosperms and arborescent ferns because they were taxonomically well known in the 1970s, unlike herbaceous species. In addition, they contribute significantly to the structure of plant communities from the early stages of vegetation development (Cadet, 1977).

Dispersal traits of woody species

Woody species were assigned to three functional groups based on dispersal traits. Fleshy-fruited plants that were originally dispersed by a rich native frugivore fauna (**Fig.4.1** & **App.4.1**) were assigned to two dispersal trait groups based on fruit size (Izhaki, 2002; McConkey and Drake, 2015): small fleshy-fruited (SFF) and large fleshy-fruited (LFF) species. These two groups were defined according to the mean value for fruit (or arillate seed) diameter, *i.e.* above or below 13 mm, which is the maximum gape width of *Hypsipetes borbonicus*, the largest extant frugivore on Réunion (body mass = 55 g) (Cheke, 1987a). Plants that use wind dispersal mechanisms and do not depend on animal dispersal were categorised as anemochorous dry-fruited (ADF). Dry-fruited plant species whose dispersal strategy remained unclear were included in the overall analysis of diversity, but not assigned to a specific dispersal trait group. These species are not common in lowland forests on Réunion.

Statistical analyses

We constructed a presence-absence matrix for each plot and each dispersal trait group based on species presence at any growth stage, *i.e.* in any vegetation stratum. Species could thus be present at seedling or sapling stage only.

Plant species richness across the chronosequence

We modeled plant species richness across the chronosequence using a multiple regression approach to take into account the relative influence of plot area, elevation, precipitation of driest month and isolation that substantially varied across study plots (**App.4.3**). To assess plot isolation, we used a habitat map to construct a binary raster of native closed-canopy forests at 100 m resolution and calculated the proportion of native forests in the 100 hectares surrounding each plot. The five variables used for analyses showed moderate collinearity with maximum variance inflation factors < 4.

The relationship between count data responses (species richness of all woody plants, ADF, SFF, LFF and not-assigned plants) and explanatory variables including the five variables and four interaction terms, *i.e.* age of lava flow x (isolation + elevation + precipitation + area), were analysed using generalized linear models (GLMs) with a Poisson distribution (O'Hara and Kotze, 2010). Using a type-II analysis of deviance, we dropped the non-significant terms for each GLM. We used the Moran eigenvector filtering function (R package "spdep") to account for possible effects of spatial autocorrelation on parameter estimates (Bivand et al., 2005). Pseudo-R^2 of GLMs were calculated by the relationship "1 – residual deviance/null deviance". We finally estimated the standardised values of species richness (S_{st}) across the chronosequence by fixing the four other variables to their mean value (sampling area = 591 m², elevation = 354 m asl, precipitation of driest month = 226 mm, isolation = 46 % of native forests).

Community composition across the chronosequence

We performed pairwise dissimilarity analyses between vegetation plots and used the beta.pair function (R package betapart) to decompose total β-diversity (measured by Sorensen dissimilarity) into its two components, nestedness and turnover (measured by Simpson dissimilarity) (Baselga and Orme, 2012). We then constructed six distance matrices by calculating the absolute values of the difference between each pair of plots for age of lava flow, sampling area, elevation, precipitation of driest month and isolation. Because age of lava flow was an ordinal variable, we converted the five age classes to numerical values from 1 (old substrata) to 5 ([1900; 1956]). We also calculated the Euclidean geographical distance for each plot pair. To take into account the influence of sampling area, elevation, precipitation of driest month, isolation and Euclidean distance on dissimilarities across the chronosequence, we could not use a multiple regression as we did for species richness because of obvious violation of the assumption on independence (Anderson et al., 2011). Consequently, we performed partial Mantel tests with 1000 permutations (R package ecodist) to examine the influence of age of lava flow on each dissimilarity while controlling for other variables, and vice versa (Goslee and Urban, 2007).

RESULTS

Species richness across the chronosequence

The age of lava flow was by far the best predictor of species richness for woody plants overall (n = 151, p = 1.7e-27; pseudo-R^2 = 0,87), small fleshy-fruited (SFF) plants (p = 4.7e-27; pseudo-R^2 = 0,84) and large fleshy-fruited LFF plants (p = 6.2e-41; pseudo-R^2 = 0,87) (**App.4.4** & **App.4.5**). Conversely, elevation was the best predictor for anemochorous dry-fruited (ADF) plant richness (p = 3.7e-16; pseudo-R^2 = 0,70). Isolation also had a strong influence on the richness of the four groups, but only on post-defaunation lava flows for all woody plants, SFF and LFF plants.

The estimated standardised species richness (S_{st}) for woody plants overall decreased considerably across the chronosequence, *i.e.* with decreasing substrata age (**Fig.4.3a**): S_{st} was similar on pre-defaunation substrata, *i.e.* 32.9 and 35.4 in "old substrata" and [1401; 1665] respectively, then declined markedly to 17.6 in [1665; 1800[and [1800; 1900[, and dropped down to 11.5 species in [1900; 1956]. This general downward trend across the chronosequence concealed very different changes that were evidenced when dispersal trait groups were considered separately (**Fig.4.3a**). S_{st} for ADF plants ranged from 4.8 to 6.2 species and showed no significant trend across the chronosequence. Changes in species richness of fleshy-fruited plants drove the general trend of woody plant species. S_{st} for SFF plants was similar on pre-defaunation substrata, *i.e.* 20.9 and 22.5 in "old substrata" and [1401; 1665], respectively, then strongly decreased in [1665; 1800[to 10.8 species. It was similar in [1800; 1900[with 11.3 species and dropped down to 5.4 species in [1900; 1956]. S_{st} for LFF plants followed a similar pattern to SFF plants, although their decline was more abrupt: LFF plant richness was similar on pre-defaunation substrata, *i.e.* 6.1 and 7.3 in "old substrata" and [1401; 1665], respectively. It showed a strong decrease to 1.1 species in [1665; 1800[, fell to 0.4 species in [1800; 1900[and 0 in [1900; 1956] (**Fig.4.3a**).

Lastly, the independently standardized estimated richness across dispersal trait groups overall summed to the overall richness of woody species with a low average relative difference of 0.5%, which suggested a good accuracy of the separate estimates (**App.4.6**).

Community composition across the chronosequence

The total β-diversity measured by Sorensen dissimilarity with control plots as reference ("old substrata") showed a highly significant increase across the chronosequence for woody plants overall (from 0.35 to 0.90), as well as within each dispersal trait group (ADF, from 0.35 to 0.78; SFF, from 0.35 to 0.89; LFF, from 0.33 to 0.62) when other variables were controlled (partial Mantel test, $p< 0.001$) (**Fig.4.3b** & **App.4.7**). For woody plants overall, turnover and nestedness increased significantly across the chronosequence (partial Mantel tests, $p<0.001$ & $p<0.001$). However, turnover was the main driver of composition changes, in relation with fleshy-fruited (both LFF and SFF) and ADF species dominating assemblages on old and recent lava flows, respectively (**Fig.4.3a**). Within dispersal trait groups, the general increase in Sorensen dissimilarity concealed very different situations evidenced when the two components of β-diversity were considered separately.

For ADF assemblages, the turnover strongly increased across the chronosequence from 0.26 to 0.64 (partial Mantel test, $p<0.001$), whereas nestedness was low and stable (partial Mantel test, NS) and mostly influenced by elevation and isolation (**Fig.4.3b** & **App.4.7**). For SFF assemblages, the turnover was mostly influenced by elevation and showed a weak increase from 0.26 to 0.32 across the chronosequence (partial Mantel test, $p = 0.04$), whereas nestedness strongly increased from 0.09 to 0.57 (partial Mantel test, $p<0.001$). For LFF assemblages, dissimilarity analyses involve a shorter chronosequence, given that LFF plants are totally absent on [1900; 1956] lava flows, and showed similar trends as SFF assemblages. The turnover was mostly influenced by elevation and remained stable between 0.19 and 0.29 (partial Mantel test, NS), whereas nestedness strongly increased from 0.12 to 0.37 (partial Mantel test, $p<0.001$) (**Fig.4.3b** & **App.4.7**). Overall, species replacement was the main phenomenon driving species composition of ADF assemblages across the chronosequence, while SFF and LFF plant assemblages that remained on recent lava flows constituted a subset of the communities found on "old substrata".

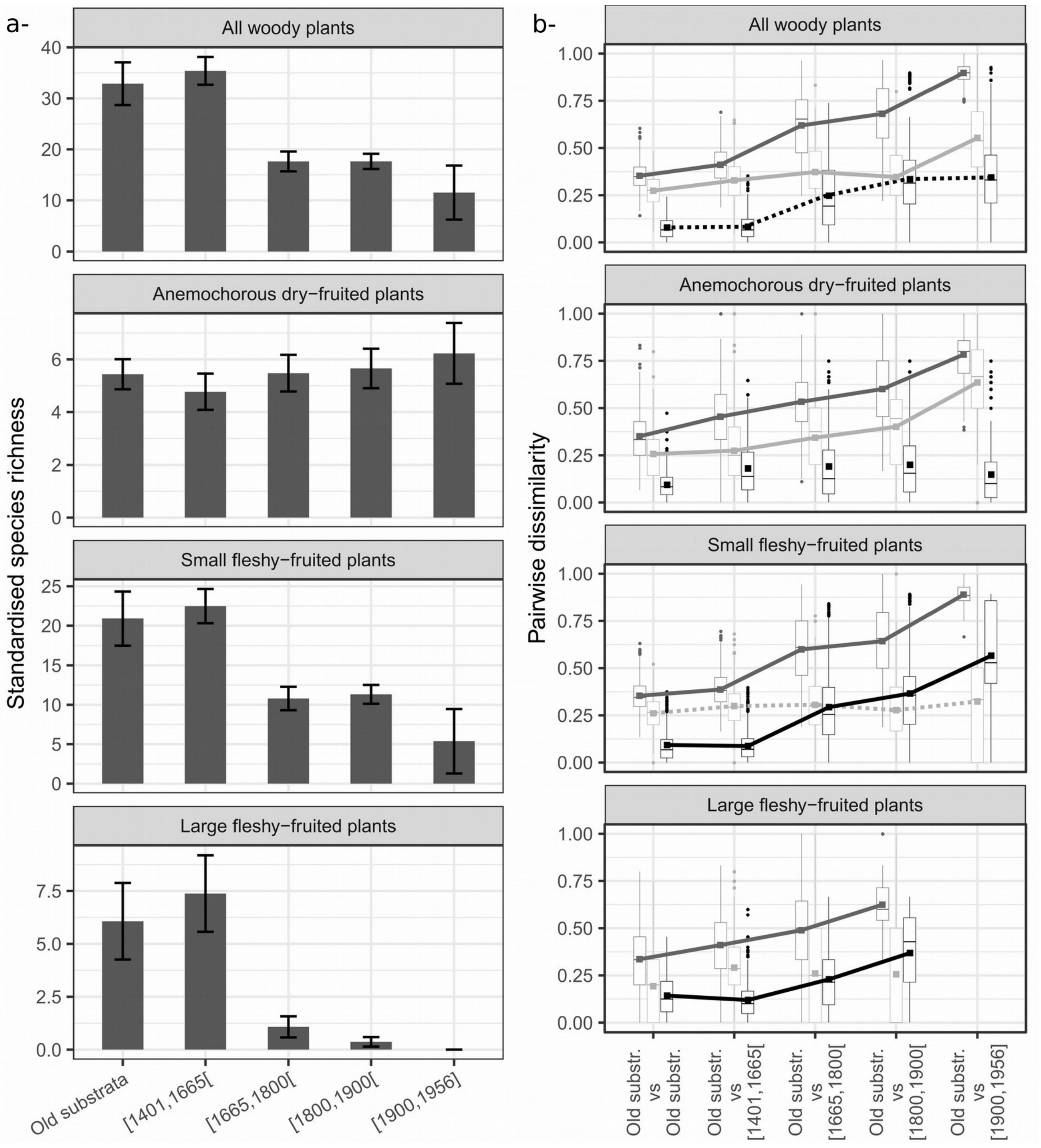

Fig.4.3. *Plant diversity assessment for woody plants overall and for three dispersal trait groups: anemochorous dry-fruited, small fleshy-fruited and large fleshy-fruited plants that respectively depend on wind, frugivores of various size and large-bodied frugivores.* ***(a)*** *Estimated standardised richness of native woody plants at any growth stage across the chronosequence (sampling area fixed at 591 m², elevation at 354 m asl, precipitation of driest month at 226 mm, isolation at 46% of native forests). Confidence intervals at 95% on estimated standardised richness are given by error bars. Note that large fleshy-fruited plants are completely absent on the most recent lava flows.* ***(b)*** *Pairwise Sorensen (dark grey), turnover (light grey) and nestedness (black) dissimilarities between native plant assemblages on old substrata (used as reference) and native plant assemblages in each lava flow age class. Boxplots and squares respectively display raw and mean values for each age class. Solid lines are displayed when the age of lava flow is the most explanatory variable apart the effect of area, elevation, precipitation of driest month, isolation and geographical distance (****App.4.3****). Dotted lines are displayed when the age of lava flow has a significant effect, but is not the most explanatory variable. Note that large fleshy-fruited plants are completely absent on the most recent lava flows.*

DISCUSSION

Frugivory disruption as a major cause of fleshy-fruited plant diversity loss

Plant dispersal trait diversity is strongly related to the availability of dispersal agents across a long-term chronosequence on the Piton de la Fournaise volcano. This suggests that the extinction of large-bodied frugivores has severely limited dispersal for many plant species since the early 18th century, *i.e.* less than a century after the first human settlements. It appears to be a major cause of the fleshy-fruited plant diversity loss on historical lava flows. The negative impact of frugivore defaunation on tree recruitment has already been shown at community level (Effiom et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010; Wright et al., 2007). Nevertheless, to our knowledge, our study is the first to reveal such a dramatic collapse of dispersal trait diversity of the temporal scale of several centuries. Our research was made possible because frugivore defaunation in the Mascarene archipelago has been well documented (Cheke and Hume, 2008; Lougnon, 2005) and because the high volcanic activity on Réunion provides numerous lava flows that constitute a natural experiment acting as a “time machine”.

Forests on old substrata and lava flows that occurred before permanent human settlements are widely dominated by fleshy-fruited species (Albert et al., 2018). They include LFF plants, that are usually big trees (Diaz et al., 2004; Thompson and Rabinowitz, 1989) with an important structural role in native forests (**App.4.8** & **App.4.9**). LFF plants are far less present on lava flows that occurred while the large-bodied frugivores were strongly decreasing in number. Hence, it is likely that effective dispersal at ecosystem level was disrupted before the dispersers of most LFF species actually went extinct, as shown elsewhere (McConkey and O’Farrill, 2016). LFF plants, including seedlings, are very scarce on lava flows that occurred after the extinction of all large-bodied frugivores in 1800. This shows that the latter play an extremely important role because they can swallow large fruits and are more likely to deposit seeds away from the parent tree (Naniwadekar et al., 2019; Wotton and Kelly, 2012). This also suggests that potential dispersal alternatives are very unreliable, *e.g*. secondary dispersal by introduced vertebrates or cyclone-mediated seed dispersal (Babweteera and Brown, 2009; Federman et al., 2016). The richness of SFF plants also decreases on lava flows that occurred after 1665, despite the abundance of several important frugivores for this species group, the native bulbul and the hoopoe starling. Large-bodied frugivores do not just eat LFF plants and also play an important role in SFF plant dispersal (Bollen and Elsacker, 2002; Florens et al., 2017a; Oleksy et al., 2017). In fact, their extinction has probably led to a decrease in the dispersal efficiency of most fleshy-fruited plants (Babweteera and Brown, 2009; Carvalho et al., 2016) and to the inability of many SFF plants to reach isolated post-defaunation lava flows (Jordano et al., 2007; Wotton and Kelly, 2012). We show that SFF richness eventually collapses on lava flows from the 20th century, as already suggested (Chevennement, 1990; Strasberg, 1994; Thébaud and Strasberg, 1997). We also reveal that the few fleshy-fruited species that colonise these areas are usually present on older substrata. Conversely, ADF plant richness remains unchanged across the chronosequence, despite strong species replacement. This finding suggests that successional changes occur within ADF assemblages across the chronosequence, but only rarely in fleshy-fruited assemblages (Wandrag et al., 2017).

Potential post-dispersal limitations

The pattern that we detected could partly be explained by post-dispersal factors, such as environmental filtering, *e.g.* light requirements, depth soil, or biotic interactions, *e.g.* seed predation (Wang and Smith, 2002).

We have consistent evidence that the total absence of many fleshy-fruited plant species, even at early life stages, on lava flows dating from [1665; 1800[and [1800; 1900[is not a consequence of environmental filtering. Although shade tolerance or light requirements were not considered in our analyses, it is likely that some SFF understorey shrubs have difficulty germinating in open canopy vegetation, especially on the most recent lava flows (Thornton, 1997). However, the proportions of LFF and SFF plants do not depend on canopy cover (**App.4.10**). Many vegetation plots on historical lava flows show a well-developed canopy, but totally lack a LFF tree that is very common on pre-defaunation lava flows (*Labourdonnaisia calophylloides*, Sapotaceae, **App.4.11**). Moreover, the presence of long-lived pioneer trees across the chronosequence provides relevant insights: a SFF pioneer tree (*Sideroxylon borbonicum*, Sapotaceae) is common on lava flows that occurred when small frugivores were abundant, but is much less prevalent on [1900; 1956] lava flows, despite favorable light conditions. On the contrary, an ADF pioneer tree (*Agarista salicifolia*, Ericaceae) is present across the entire chronosequence (**App.4.11**) (Albert et al., 2020b). Finally, soil type is another factor that might limit recruitment, but our analyses show a standardised richness as high on old substrata as on [1401, 1665[lava flows and a low β-diversity between these categories. Hence, most big trees found on well-developed soils are able to establish and develop on [1401, 1665[lava flows that usually display a very thin soil on continuous rock (Meunier et al., 2010) (**App.4.12**).

Seed predation may also be an important mechanism that limits plant recruitment (Forget et al., 2005; Hubbell, 1980; Janzen, 1970). Rats are usually the main seed predators on oceanic islands (Shiels and Drake, 2015) and probably reached high densities in the late 17th century, after their introduction on Réunion (Cheke and Hume, 2008). Since then, rat populations may have remained at high levels. It is however unlikely that seed predation by rats could explain the temporal shift observed between LFF and SFF plants across the chronosequence. A few LFF plants are common at all growth stages in extant mature rainforest on pre-defaunation lava flows, despite the abundance of rats (Strasberg, 1996), whereas they are totally absent from post-1800 lava flows. Hence, seed predation may play a secondary role in limiting recruitment, as shown by Wotton and Kelly (2011) in New Zealand.

Primary succession disruption and implications for conservation

Our analyses show that, in less than five centuries, primary succession on lava flows has led to plant assemblages of woody plants similar in richness and composition to those found on old substrata. The fact that LFF plants probably lost their dispersal capacity after 1800 shows that they were already present on historical lava flows in 1800. Hence, well under 200 years might have been enough for the establishment of most shade-tolerant tree species. This temporal scale is consistent with Thornton (1997), who documents the assembly of the Krakatau Islands ecosystem after its destruction in 1886, *i.e.* three years after the islands' sterilisation: despite the sea barrier (12 km from the closest source and 40 km from mainland Java and Sumatra), six zoochorous plants were recorded as soon as 1896, 23 in 1905, 35 in 1920, 68 in 1934 and 124 species in 1992. In the case of the Krakatau Islands, Whittaker and Jones (1994) emphasise the crucial role played by fruit pigeons able to transport large-seeded plants that became established in the decades following the initial disturbance.

The absence of many native species on historical lava flows has probably had severe consequences on succession processes. For instance, the absence of LFF tree species may have caused competition release (Hurtt and Pacala, 1995), possibly benefiting alien plants with low dispersal limitation. Recent surveys on post-1800 lava flows reveal the presence of the same native plant communities as those surveyed by Cadet (1977), as well as the generally low or absent regeneration of native species (Albert et al., 2019), suggesting arrested succession (Cohen et al., 1995). Together, these findings demonstrate that plant communities of different ages do not follow the same trajectory and that the vegetation stages originally described by Cadet (1977) do not represent successional seres (Walker et al., 2010). Therefore, it is unlikely that the structure and diversity of native plant communities on historical lava flows will ever be as rich as the tropical rainforests on pre-defaunation substrata.

The persistently high LFF plant richness on pre-defaunation lava flows supports the fact that, despite the loss of all large-bodied frugivores since 1800, plant communities can display a high level of resilience in situ, but a very low level of resilience by migration (Grubb, 1987). The plant communities on pre-defaunation lava flows are among the most important and well-preserved testimony of Mascarenes' lowland ecosystems (Strasberg, 1996), and their protection is considered crucial (Mittermeier et al., 2004). Our results confirm that their loss would be particularly dramatic because these ecosystems have lost their resilience. Although most of the remaining lowland ecosystems are protected as part of the Réunion National Park, the high frequency of lava flows in this area of Réunion may lead to their gradual destruction. In 2007, for example, the last fragment of tropical rainforest at sea level was destroyed (**App.4.2**). Moreover, the apparent maintenance of diversity on pre-defaunation lava flows is probably due to the fact that our study uses presence/absence data and does not take into account a potential failure of local recruitment for many species of the canopy. Several shade-tolerant long-lived trees hardly regenerate (Strasberg, 1996) and long-lived pioneer trees are often unable to reach gaps nearby, which makes them particularly sensitive to local extinction in the near future (Wandrag et al., 2017).

Today, frugivory disruption combined with alien plant invasion (see Potgieter et al., 2014) leads to the development of novel ecosystems with extremely low taxonomic and functional diversity. Given the dramatic loss of native fleshy-fruited plant diversity on recent lava flows, conservation strategies should include the lack of native vegetation recovery as a matter of urgency. Restoring the seed dispersal function will be necessary in defaunated ecosystems (Correia et al., 2017), as has already been done on several islands in the Indo-Pacific region (Griffiths et al., 2011; Hansen et al., 2010; Pedrono et al., 2013). The fact that there will be no altitudinal escape for most fleshy-fruited plants in the context of climate change makes the situation even more urgent (McConkey et al., 2012).

CONCLUSION

Defaunation can cause negative impacts on ecosystem functioning comparable with those from major drivers of global change (Young et al., 2016). However, its long term impact on dynamics of very long-lived trees is not sufficiently documented. Our study brings a first evidence of frugivore defaunation effect at community level over a temporal scale of 300 years. The studied chronosequence of lava flows acting as a "time machine" and harboring plant communities settled before and after human colonisation provides a natural experiment on one of the last tropical islands colonised by humans. To our knowledge, this is the first time that such a collapse of dispersal trait diversity has been shown. It strongly argues in favour of restoration programs targeting the re-establishment of seed dispersal interactions by promoting native frugivore populations and rewilding projects focusing on large vertebrates.

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CHAPITRE 5. L'évaluation des limitations du recrutement agissant avant, pendant et après la dispersion révèle un fort impact négatif de la perte des frugivores et des invasions biologiques sur la dynamique forestière

RESUME

Les forêts tropicales sont aujourd'hui essentiellement secondaires ou très dégradées, et leur résilience dépend fortement des frugivores qui assurent la dispersion de la plupart des ligneux. L'effondrement global des grands vertébrés laisse donc craindre un fort impact négatif sur la résilience des forêts, d'autant qu'elles font face dans le même temps à d'autres menaces. L'introduction et l'invasion de vertébrés et de plantes à fruits charnus exotiques peuvent par exemple mener à diverses limitations post-dispersion (prédation des graines, compétition avec les plantes envahissantes) qui compliquent notre compréhension de la dynamique de colonisation des plantes. A La Réunion, la chronoséquence du Piton de la Fournaise offre un remarquable système d'étude de la résilience forestière après perturbation majeure. Elle a récemment permis de montrer une dramatique perte de diversité sur les coulées intervenues depuis la disparition des frugivores indigènes. Cependant, les conclusions de cette étude observationnelle nécessitent une validation expérimentale mesurant rigoureusement les processus. Pour cela, nous avons choisi une coulée de lave post-défaunation (1800) portant une végétation indigène très appauvrie, notamment en plantes à grosses graines. Elle est bordée par une forêt ancienne avec une haute diversité des traits de dispersion. Sur toute sa largeur (100 m environ), nous avons installé 20 placettes expérimentales, mesuré la pluie de graines avec 40 trappes pendant 18 mois et estimé la disponibilité en fruits dans les 2,5 ha environnants. Le recrutement des plantules a également été caractérisé. Quatre arbres indigènes (*Calophyllum tacamahaca, Syzygium cymosum, Diospyros borbonica, Sideroxylon borbonicum*) qui ne sont plus (ou rarement) dispersés ont été semés sur la coulée post-défaunation dans un plan factoriel qui teste à la fois l'impact de la prédation des graines et la compétition avec la végétation existante. Quarante-quatre et 31 espèces à fruits charnus ont été respectivement observées en fruits et piégées au moins une fois. La taille de graine est le principal facteur qui influence la pluie de graines, devant la disponibilité en fruits. La plante invasive *Clidemia hirta* (0,3 mm de diamètre) domine très largement la pluie de graines. Si quelques espèces indigènes à petites graines sont encore assez bien dispersées, celles à graines moyennes le sont très peu et aucune graine > 8 mm n'a pu être piégée. Le fort effet de la distance à la lisière sur la pluie de graines suggère que le principal oiseau frugivore indigène, *Hypsipetes borbonicus*, est un disperseur mineur là où la canopée est ouverte. A l'inverse, le principal frugivore exotique, *Pycnonotus jocosus*, se nourrit surtout de plantes exotiques et semble beaucoup plus actif en milieu ouvert. Le recrutement des plantules est dominé par *Clidemia hirta* et surtout *Psidium cattleianum* dont l'invasion s'est amplifiée depuis les relevés de Cadet en 1972. Le faible recrutement spontané en plantules indigènes montre que la régénération de la forêt indigène est fortement compromise. Les trois espèces d'arbres à grosses graines semées sont néanmoins capables de s'établir dans l'ensemble des placettes et les deux facteurs post-dispersion testés ont un impact faible. La capacité des plantes à grosses graines à s'installer dans les larges zones perturbées suggère que la perte de la dispersion entraîne “une victoire par forfait” des plantes envahissantes, ce qui accroît l’impact négatif des invasions. Ainsi, le semis direct peut servir de fer de lance à des opérations de restauration écologique, notamment en coeur de Parc national où les forêts indigènes ont perdu la capacité de se reconstruire sur de vastes superficies sur les coulées historiques. Parallèlement, favoriser le retour de vertébrés indigènes telle la roussette noire dont le rôle d’espèce clé de voûte est largement démontré, devrait être une priorité.

Assessment of recruitment limitation by ecological filters acting before, during and after dispersal evidences strong negative impacts of frugivory disruption and non-native plant invasion on forest dynamics*

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ABSTRACT

Most tropical forests are now severely degraded and their resilience is highly dependent on frugivores which ensure seed dispersal for most woody plants. The global collapse of large vertebrates therefore raises major concerns about tropical forest succession, but few studies have addressed this issue, in particular field experiments that can unravel underlying mechanisms. On Réunion (Mascarenes) where all large frugivores went extinct in 1800, the Piton de la Fournaise volcano provides a relevant experimental setting: a post-defaunation lava flow marked by low dispersal trait diversity, bordered on both sides by diverse old-growth forests. Over the entire flow width, we set up 20 experimental plots where we measured seed rain for 18 months, monitored the recruitment of seedlings and sowed four fleshy-fruited native trees that are no longer dispersed to test their ability to settle and the impact of two post-dispersal factors (seed predation and competition with invasive vegetation). Fruit availability was estimated in the surrounding 2.5-ha all along the experiment. Forty-four and 31 fleshy-fruited species were respectively observed in fruits and trapped at least once. Seed size was the main factor influencing active seed rain, ahead of fruit availability. The alien tiny-seeded plant *Clidemia hirta* overwhelmingly dominated seed rain. Although some native small-seeded plants were fairly well dispersed, those with medium seeds were poorly dispersed and no seeds wider than 8 mm were trapped. Moreover, the strong effect of distance to old-growth forest margin suggests that the main native frugivore bird played a minor role in open-canopy landscape. Conversely, the main alien frugivore bird fed mainly on alien plants and was probably a more effective disperser in that landscape. The spontaneous recruitment of seedlings was largely dominated by alien plants and showed low rates for native plants, which is particularly worrisome. Sown large-seeded species were able to establish in all plots whatever the treatment, which suggests that loss or poor dispersal of numerous native plants leads to winning-by-forfeit of invasive plants. Our study emphasizes the fundamental role of dispersal loss in ecosystem stable-state shifts and the urgency to restore this function through large-scale sowing and frugivore rewilding actions.

INTRODUCTION

The majority of tropical forests is today secondary or severely degraded (Chazdon, 2014) and this proportion increases year by year (Rozendaal et al., 2019). Because most tropical forest regeneration occurs via natural forest succession, it is critical to analyse the capacity of recovery and expansion of fragmented ecosystems in the matrix of surrounding disturbed habitats (Rozendaal et al., 2019). After severe disturbances as conversion to agriculture, landslides or lava flows, forest regeneration cannot rely on the soil seed banks, seedling and sapling cohorts that have been destroyed (Quintana-Ascencio et al., 1996; Walker and Moral, 2003). Under such

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* *In preparation for Ecology*

conditions, seed dispersal is all the more essential (Carlo and Morales, 2016; Tabarelli and Peres, 2002; Whittaker et al., 1997).

Frugivorous vertebrates play a prominent role in transporting seeds from old-growth tropical forests to degraded areas (Caves et al., 2013; Ingle, 2003), sometimes by crossing long distances (Whittaker et al., 1989; Wotton and Kelly, 2012). Because tropical forests are worldwide dominated by fleshy-fruited species (Chazdon, 2014; Turner, 2001), the global decline of frugivores raises severe concern for seed dispersal mutualism (Dirzo et al., 2014; Heinen et al., 2017; Young et al., 2016). Several studies have shown frugivore loss alters seed dispersal and limits recruitment at community level (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008) and recent work using a long-term chronosequence shows that frugivore defaunation has a dramatic negative impact on plant colonization dynamics (Albert et al., 2020a). However, studies that measure processes to disentangle limitations in the context of ecological succession remain scarce, especially those that rigorously quantify the result of seed dispersal by measuring the seed rain (but see Caves et al., 2013; Costa et al., 2012; Wijdeven and Kuzee, 2000).

Extinctions among native frugivores have been massive on islands since human colonization, with one third of native frugivore communities being lost worldwide (Heinen et al., 2017). In fact, this average hides strong disparities and some archipelagos such as Tonga islands, the Marianas or the Mascarenes have been very severely defaunated (Heinen et al., 2017), with dramatic consequences for the regeneration of tropical insular forests (Albert et al., 2020a; Meehan et al., 2002; Wandrag et al., 2017). Islands have at the same time experienced multiple introductions of potentially frugivorous vertebrates such as passerines and land mammals (Blackburn, 2004). Because they often act as frugivores or secondary dispersers on continents, one may expect them to functionally replace extinct frugivores, at least partially (Pejchar, 2015). Some works have shown that they sometimes remain the only dispersers of several native plants (Duron et al., 2017; Foster and Robinson, 2007; Shiels and Drake, 2011; Vizentin-Bugoni et al., 2019), but they are nonetheless more widely reported as facilitator of plant invasion (Mandon-Dalger et al., 2004; Pejchar, 2015; Shiels, 2011; Simberloff and Von Holle, 1999; Spotswood et al., 2012; Vizentin-Bugoni et al., 2019; Williams and Karl, 1996) and/or as native seed predator (Campbell and Atkinson, 2002; Shiels and Drake, 2015; Towns et al., 2006; Williams et al., 2000). The disperser/predator continuum may be related to the size of seeds and frugivores, with large-seeded plants rarely benefiting from potential new frugivory interactions (Williams et al., 2000).

The strong downsizing of native frugivore communities on oceanic islands (Heinen et al., 2017) particularly threatens large-seeded plants that are typical species of old-growth tropical forests (Albert et al., 2020a; Federman et al., 2016; Guimarães et al., 2008). Large-seeded plants are usually absent in degraded/open areas in defaunated landscapes, but may nevertheless be able to establish (Martínez-Garza and Howe, 2003). Bypassing acute dispersal limitation with experimental sowing of these species is relevant to assess the extent to which seed dispersal drives seedling recruitment (Poulsen et al., 2012). Other potential confounding factors, *e.g.* seed predation (Campbell and Atkinson, 2002; Poulsen et al., 2012; Shiels and Drake, 2015; Towns et al., 2006) or plant competition (Cohen et al., 1995; Yurkonis et al., 2005), may also alter plant recruitment and must be disentangled. Such experiments will also help in accelerating succession to mature forests (Martínez-Garza and Howe, 2003) and increasing the habitat suitability prior to future rewilding.

Here, we conduct a field experiment to assess how frugivory disruption shapes community assembly in a species-rich fragmented landscape on Réunion. We choose as a study system a lava flow that spread in 1800 (Bory de Saint Vincent, 1804) and bears a depauperate plant community established after the extinction of all large-bodied native frugivores. This post-defaunation lava flow is bordered on both sides by an old-growth tropical rainforest (Albert et al., 2020a) (**Fig.5.1** & **App.5.1**). First, we measured the active seed rain in the post-defaunation community. We expect active seed rain to be depleted in native plants and devoid of large-seeded ones regardless of the availability of fruits in the pre-defaunation community in the vicinity. We also expect active seed rain to be enriched with invasive plants that have been reported to be very attractive for native and introduced frugivores. Second, we studied the natural regeneration of seedlings in the post-defaunation community to understand the extent to which the active seed rain explains the recruitment of seedlings. Finally, we sowed undispersed large-seeded trees to test whether these species could establish in the post-defaunation community and examined additional post-dispersal limiting factors (plant competition, seed predation).

METHODS

Study site

The study was conducted on Réunion, the westernmost oceanic island of the Mascarenes. The study site was located on the lower flanks of the Piton de la Fournaise volcano at 350 m asl, at Le Tremblet, municipality of Saint-Philippe (374,330 N; 7,644,500 W) (**Fig.5.1**). The study system consisted of the historical ‘A‘ā lava flow of 1800 (Bory de Saint Vincent, 1804) bordered on both sides by a Pāhoehoe lava flow that occurred in 1565 (Albert et al., 2020b). The 1800 and the 1565 lava flows respectively bear a depauperate vegetation with an open low canopy and a species-rich old-growth forest with a closed high canopy (**App.5.1**). Annual rainfall at Le Tremblet averages 400 cm per year (Réchou et al., 2019). There is no dry season at study site where the habitat is classified by Strasberg et al. (2005) as lowland tropical rainforest.

Setup of experimental plots

Prior to the field experiment, we used a 300 m trail within dense vegetation on the 1800 lava flow opened with the authorization of the Parc National de La Réunion and of the Office National des Forêts. This trail forms a transect perpendicular to the edge of the old-growth forests (**Fig.5.1**). In the low vegetation on the lava flow, we identified areas where the microtopography was not too rugged and enabled to set up experimental plots. In December 2018, we established 20 experimental plots to measure the active seed rain, spontaneous seedling recruitment and large-seeded plant establishment after sowing (**Fig.5.1**).

Assessment of diaspore availability

A 800 m track was established to monitor fruiting. Overall, 49 fleshy-fruited plants (44 native and 5 alien) representing all fleshy-fruited species in the 2.5 hectares surrounding the traps were monitored every month between December 2018 and July 2020 (**Fig.5.1**). The fruit trail was divided into three zones: old-growth forest North, 1800 flow and old-growth forest South. The presence of fruits in each area was noted for each species, and their abundance ranked on a semi-quantitative scale from zero to three: zero, no fruits; one, 1 to 100 fruits ; two, 100 to 1000 fruits; three, > 1000 fruits. This method allowed us to quickly monitor the large number of species in the three spatial areas. We finally calculated a fruit availability metric F for each species:

$$F=\sum_{i=1}^{3}\sum_{j=1}^{18} f_{i,j}$$

where *i* is the area of monitoring, *j* the month of monitoring and *f* corresponds to numeric scores assigned to each level of the semi-quantitative fruiting scale (0: 0; 1: 10; 2: 100; 3: 1000). Finally, we obtained the seed availability metric by multiplying F by the mean number of seeds per fruit.

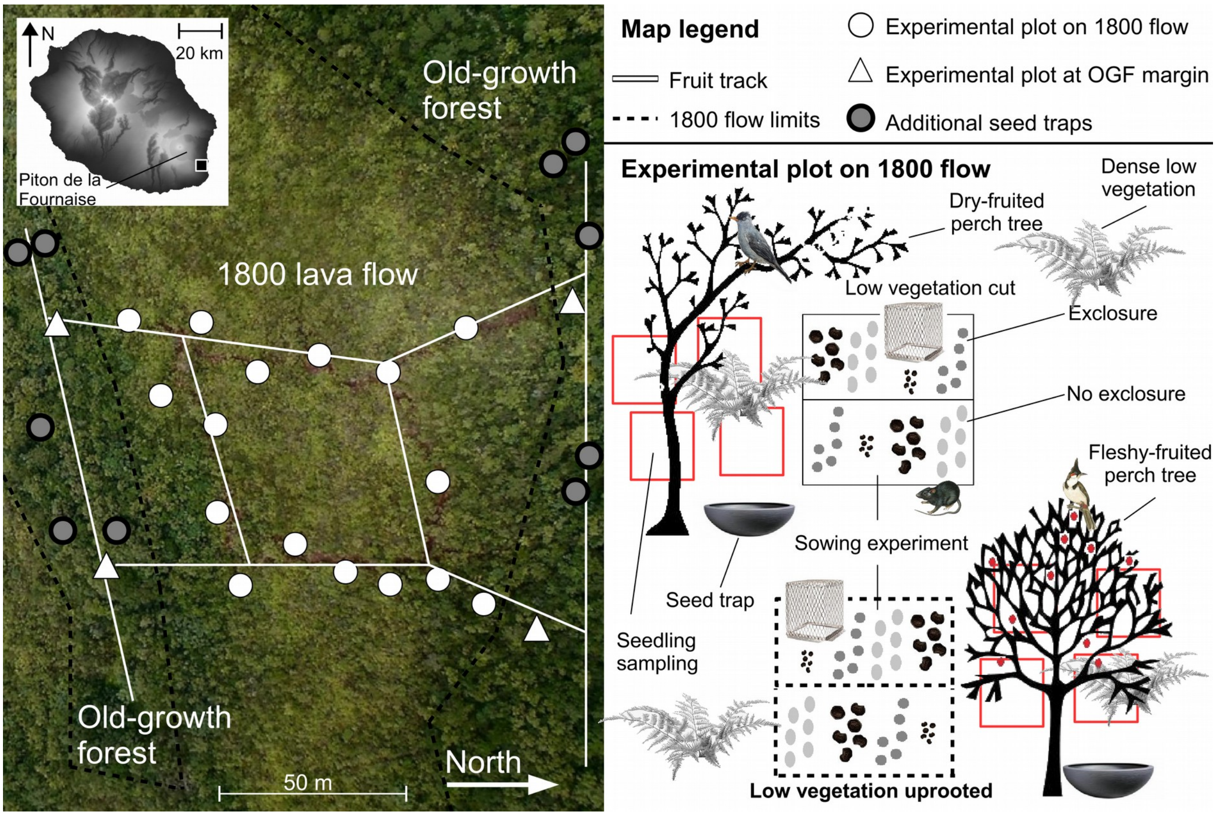

***Fig.5.1 Study site.** Le Tremblet is located on the windward south-east of Réunion (black rectangle). Our field experiment took place on lower flanks of Piton de la Fournaise at 350 m asl 1 km south of the caldera. It occupied the entire width of the 1800 lava flow between two areas of old-growth forest (OGF). 16 and four experimental plots were respectively settled on the 1800 flow (white disks) and in the understory of old-growth forest near the 1800 flow margin (white triangles). Each plot on the 1800 flow consisted of (i) two seed traps settled under dry-fruited and fleshy-fruited perch trees to measure active seed rain, (ii) an area of 2 m² to sample spontaneous seedling recruitment, (iii) a 2 m² sowing area for the experiment testing three factors: sown species, plant competition and seed predation. Experimental plots at old-growth forest margin were located in understory without dense low vegetation, so the 2×1m² sowing areas replicated the factors “exclosure” and “sown species”. Additional seed traps were settled in the understory of old-growth forests (grey disks). The main frugivores (*Hypsipetes borbonicus *and* Pycnonotus jocosus*) and seed predator (*Rattus rattus*) at Le Tremblet are shown. Fruit availability was monthly estimated along an 800 m track (white lines). Drone image: Hugo Santacreu.*

Assessment of active seed rain

To identify trapped seeds, we built a seminotheque of the plant community (**App.seed catalog**). This method was relevant at the study site because phylogenetic overdispersion observed in the community (Albert et al., 2018) minimized the difficulties for seed identification at species level.

The open-canopy landscape allowed to consider isolated trees as perches for volant or arborical frugivores (**App.5.1**). Seeds that were trapped under heterospecific perch trees were hence considered as actively dispersed (biotically or abiotically). Associated to each plot, we settled two circular seed traps (diameter=52 cm, area=0.21 m²) under either dry-fruited or fleshy-fruited isolated perch trees to sample the seed rain (**Fig.5.1**). The surroundings of each trap were cleaned every month to avoid possible pollution. Seed traps were covered with metal mesh (2×2 cm) to keep introduced mammals out (McAlpine et al., 2016). This mesh size was large enough to allow almost all seeds in the community to go through (except *Pandanus purpurascens*, most seeds of *Mimusops balata,* and the largest of *Calophyllum tacamahaca* & *Artocarpus heterophyllus*). Seed traps were open to other seed dispersal syndromes, *e.g.* wind. We did not need to control ants since they were rare at Le Tremblet and did not act as secondary dispersers.

Using nylon fabric, contents of seed traps were collected once a month and dried which was essential for separating seeds from debris. Seeds with diameter >0,3 mm were identified using the seed catalog and counted. Count of small seeds (diameter <0,8 mm) was estimated by area based extrapolation using a binocular loupe. Finally, to check whether dispersal of large-seeded plants might occur over very short distances, we added 10 open seed traps of 0,5×1 m (mesh of 8 mm) suspended in the understory of the old-growth forest North and South of the study site. We placed them in the close vicinity of large-seeded plants although far enough so that their diaspores could not enter traps by gravity only (**Fig.5.1**).

Assessment of spontaneous seedling recruitment

In late June 2020, we monitored spontaneous recruitment of seedlings in each plot where the vegetation had not been treated (**Fig.5.1**). We identified and measured all plants of which height was higher than 2 cm within an area of 4×0,25 m² at the foot of each perch tree, resulting in 40 m² of sampling. The sometimes difficult identification of seedlings could be based on a catalog recently compiled (Strasberg et al., unpublished data).

Sowing of large-seeded tree species

In each plot, we sowed in 2x1m² subplots to test the influence of three factors in a cross-factorial design (sown species, competition with invasive plants and seed predation; **Fig.5.1**). In December 2018, we collected fruits at the foot of four fleshy-fruited tree species at Saint-Philippe: three large-seeded shade-tolerant trees were absent on the 1800 lava flow: *Calophyllum tacamahaca* (Calophyllaceae), *Diospyros borbonica* (Ebenaceae), *Syzygium cymosum* (Myrtaceae); one medium-seeded pioneer tree was rare on the 1800 lava flow: *Sideroxylon borbonicum capuronii* (Sapotaceae) (**App.5.2**). For each species, 1440 seeds were hand-cleaned and sown on 30/12/2018 using 18 seeds per modality. The second factor concerned the treatment of the surrounding vegetation with three levels (**Fig.5.1**). On the 1800 flow, dense low vegetation dominated by *Dicranopteris linearis* and to a lesser extent by *Psidium cattleianum* was mechanically treated, by preserving as much as possible the surrounding vegetation. Low vegetation that shows high capacity of resprouting was (i) cut down to ground level in half of plots or (ii) uprooted in the other half. The third level consisted in four plots settled in the understory at old-growth forest margin that served as control. The last factor concerned mammal exclosure. Exclosures of 100×50×25 cm were constructed with metal mesh (0.8×0.8 cm) and firmly staked to the ground around half of subplots. Tests prior to the experiment showed that introduced rodents were not able to breach exclosures (**App.5.3**). The steel mesh remained in place for the first six months of the experiment before removing it to allow seedlings to grow unconstrained.

Assessment of frugivory interactions

In order to monitor plant-animal interactions, we first noted frugivory events observed with binoculars in particular during monthly assessment of fruit availability. We also used four camera traps Bushnell TrophyCam which have been placed in trees and shrubs mainly in the understory, but also on the ground to detect secondary dispersal (or seed predation). We also tried to identify "who defecated what" directly into seed traps. While bird droppings were easily disaggregated by frequent heavy rains and hard to discriminate in the contents of seed traps, entire rat feces were often trapped. We hence tried to collect as much data as possible while keeping in mind that the purpose was not to build an exhaustive seed dispersal network at study site.

Statistical analyses

Active seed rain

To understand what are the main drivers of seed dispersal at Le Tremblet, we took into account all fleshy-fruited species that produced diaspores as well as those that were dispersed although absent from the site. The response, *i.e.* cumulative number of seeds per trap and per species over the study period, was obtained by constructing a community table with fleshy-fruited species in rows and traps in columns. We used 13 predictors belonging to three groups (**Tab.5.1**): (1) characteristics of perch trees (*e.g.* attractiveness, position on lava flow), (2) traits of potentially dispersible fleshy-fruited plants and availability in diaspores at study site; (3) distance between perch trees and the closest mother plant of potentially dispersible species. Species present in the seed rain but of which mother trees were absent from the study site were assigned to "low" availability in fruits & seeds and "high" distance to the closest mother tree (**Tab.5.1**). For categorical predictors, classes have been defined to be as balanced as possible.

***Tab.5.1 Overview of predictors used to model the active seed rain**. Abbreviations: "OGF" old-growth forest, Predictors preceded by "L" were log-transformed prior to statistical analyses, but raw data are described here.*

Group	Predictor	Type	Description
Perch trees	Production of fleshy fruits	Categorical	2 levels: Yes; No
	Emergence above canopy	Continuous	Range: 0 – 6,95; Median: 2,3 (m)
	Distance to OGF margin	Categorical	3 levels: Low: < 5 < Mid < 25 < High < 55 (m)
	Height	Continuous	Range: 2,5 – 18,2; Median: 5,1 (m)
FF plants	Fruit availability	Categorical	3 levels: Low < 300 < Mid < 2000 < High
	Lfruit diameter	Continuous	Range: 0,3 – 26,7; Median: 1,02 (cm)
	Lfruit mass	Continuous	Range: 8.10^{-3} – 7.10^{3}; Median: 0,59 (g)
	Lseed diameter	Continuous	Range: 0,03 – 3,23; Median: 0,31 (cm)
	Lseed mass	Continuous	Range: 5.10^{-5} – 12; Median: $3,6.10^{-2}$ (g)
	Lseed number	Continuous	Range: 1 – 1071; Median: 3,9
	Seed availability	Categorical	3 levels: Low < 450 < Mid < 6000 < High
	Status	Categorical	2 levels: Native; Non-native
Both combined	Distance to the closest mother plant from perch trees	Categorical	3 levels: Low < 20 < Mid < 50 < High (m)

The relationship between the response (cumulative number of seeds per trap per species) and predictors was analysed using zero-inflated General Linear Mixed Models (GLMM) with a negative binomial distribution (Brooks et al., 2017). In order to account for potential autocorrelation in the data, we used two random effects, "species" and "plot". We first performed univariate regressions to assess the relationship between the response and the 13 predictors. Some relationships were not linear, we therefore tested usual transformations, *e.g.* quadratic.

Before performing multiple regression, we studied collinearity between predictors. Most of them were highly correlated, as visible in the three components of the multivariate mixed analysis (**Fig.5.2**). We selected in each group of correlated variables the one showing the highest correlation in univariate GLMMs (**App.5.5**). Surprisingly, "fruit availability" showed the strongest correlation with the response when one might have expected "seed availability". This was all the more interesting since this variable was poorly correlated with "log(seed diameter)" in comparison with “seed availability”. We finally retained a set of five predictors with low collinearity (“log(seed diameter)”, “fruit availability”, “status”, “distance to old-growth forest margin”, “emergence”, **Tab.5.1**). We tested all possible combinations including interactions, and selected the best GLMM with the lowest AIC.

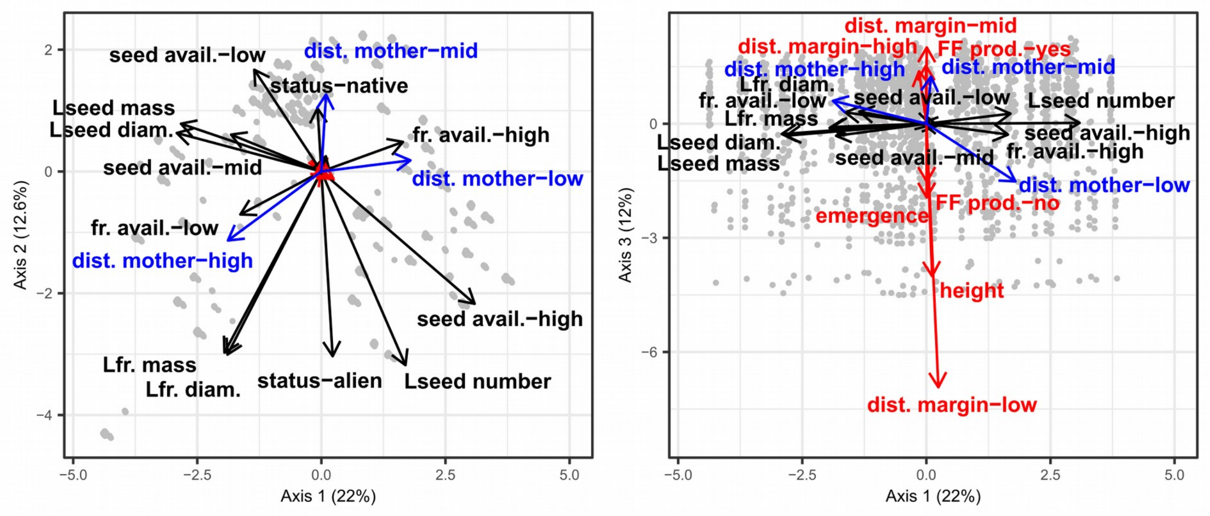

Fig.5.2 Assessment of relationships between predictors of active seed rain using a multivariate mixed analysis. *Predictors related to perch trees, dispersible fleshy-fruited species and both combined are displayed by red, black and blue colours, respectively. For factors, levels are displayed following “-”. Abbreviations: “avail”, availability; “diam”, diameter; “dist. margin”, distance to old-growth forest margin; “dist. mother”, distance to the closest mother plant; “FF prod”, production of fleshy fruits; “fr.”, fruit. Variables or factor levels with a very low contribution in each two-dimensional representation are not shown. For more details about predictors, please report to* ***Tab.5.1****.*

Diversity analysis of active seed rain and spontaneous seedling recruitment

To compare the diversity across plant life stages in experimental plots, rarefaction curves (Oksanen et al., 2013) were estimated on trapped seeds and recruited seedlings according to “plant status” and “distance to old-growth forest margin” (**Tab.5.1**).

To better understand variations in dispersal trait diversity, we calculated the plot-weighted seed diameter mean for native and non-native seedlings. The relationship between the latter and the two predictors (“plant status” and “distance to old-growth forest margin”, **Tab.5.1**), was analysed using a GLMM with a Gaussian distribution.

Sowing of large-seeded plants

The relationship between count data response (number of seedlings) and experimental factors, *i.e.* sown species, plant competition and seed predation, was analysed using a GLMM with a poisson distribution. We accounted for a potential spatial structure using the “plot” variable as a random effect. The whole procedure for selecting the best model was the same as the one presented above. For temporal monitoring, a GLMM was performed for each date.

To understand the extent to which experimental factors influence the growth of seedlings, we used the maximum height per modality as a proxy. The relationship between the maximum height of seedlings and experimental factors was analysed using a GLMM with a Gaussian distribution. All statistical analyses were conducted in R ver. 3.4.3 (R Core Team).

RESULTS

Forty-five (35 native and 10 alien) fleshy-fruited species were reported fruiting between January 2019 and July 2020 at study site (**Fig.5.3**). *Antirhea borbonica* produced the largest number of fruits (18,4% of the total) and native plants produced the bulk (70,7%) that, however, only represented 19,5% of seed availability. This was mainly due to *Clidemia hirta*, an invasive tiny-seeded species which represented 12,1% of fruits, but 75,7% of seed availability. Several species were difficult to monitor, especially climbers running on the high canopy, *e.g. Toddalia asiatica*, and their fruit availability was probably underestimated.

Of the 45 fleshy-fruited species that produced fruits, 29 (23 native and 6 alien) were trapped at least once (**Fig.5.3**). Ten small-seeded species remain unidentified at the end of this study, the majority being represented by a very small number of small seeds (**Fig.5.3**). *C. hirta* accounted alone for over 93% of seed dispersal. However, the next six species in decreasing order were native trees and one climber: *Ficus reflexa*, *Psiloxylon mauritianum*, *Polyscias repanda, Ficus densifolia, Mussaenda arcuata* and *Aphloia theiformis*. Two non-native species were trapped despite the absence of mother plants at study site: *Litsea glutinosa* and *Solanum* sp. Only 45 seeds > 5 mm in diameter were trapped and the largest seed belonged to *Syzygium borbonicum* (diameter 8 mm). Despite the production of thousands of fruits, plants with larger seeds could not be trapped even once (**Fig.5.3**). In addition, no large seeds or fragments that could not have entered the traps because of the 2×2 cm wire mesh were seen despite careful monthly examination. Additional seed traps set up in the understory of the old-growth forest only showed two seeds with large diameter: a single seed (12 mm) of the native *Labourdonnaisia calophylloides* with the closest parent tree at 10 m and a single seed of *Livistona sinensis* with no conspecific at study site.

Active seed rain of dry-fruited plants was overwhelmingly dominated by two anemochorous plants: the invasive shrub *Boehmeria penduliflora* was the most dispersed plant (57,2% of the total) just before the native long-lived pioneer *Agarista salicifolia* (40,4%) (**App.5.4**). The diversity of dry-fruited plants was higher in seed traps on the 1800 lava flow where canopy was very low. In that context, *Casuarina equisetifolia* was capable of reaching seed traps despite the absence of conspecific at study site (**App.5.4**).

The spontaneous recruitment was dominated by alien fleshy-fruited plants that accounted for 70% of small seedlings (2<<25 cm high) and for 87,9% of large seedlings (25<<200 cm high) (**Fig.5.3**). Two species mainly explained this phenomenon: *Clidemia hirta* and *Psidium cattleianum* accounted respectively for 27,3% and 33,9% of small seedlings, and 20,4% and 63,4% of large seedlings. Some native species were frequently encountered as small seedlings, but were rare as large seedlings (*e.g. Molinaea alternifolia, Doratoxlyon apetalum, Piper borbonense*). Moreover, some native or alien species were not sampled at least once at the seedling stage despite their noticeable presence in the seed rain and while this is not surprising for hemi-epiphytic species (*e.g. Ficus densifolia*), other species do not seem to be able to settle on the 1800 flow (*e.g. Psiloxylon mauritianum, Mussaenda arcuata*; **Fig.5.3**). On the contrary, various large-seeded plants were encountered as small or large seedlings, but the few sampled recruits were actually found at the old-growth forest margin (*e.g. Labourdonnaisia calophylloides, Syzygium cymosum*). Finally, the recruitment of dry-fruited plants was very low compared to fleshy-fruited plants and accounted for only 1,6% and 2,6% of small and large seedlings, respectively (**App.5.4**). Contrary to trapped seeds, all the seedlings could be identified at Le Tremblet.

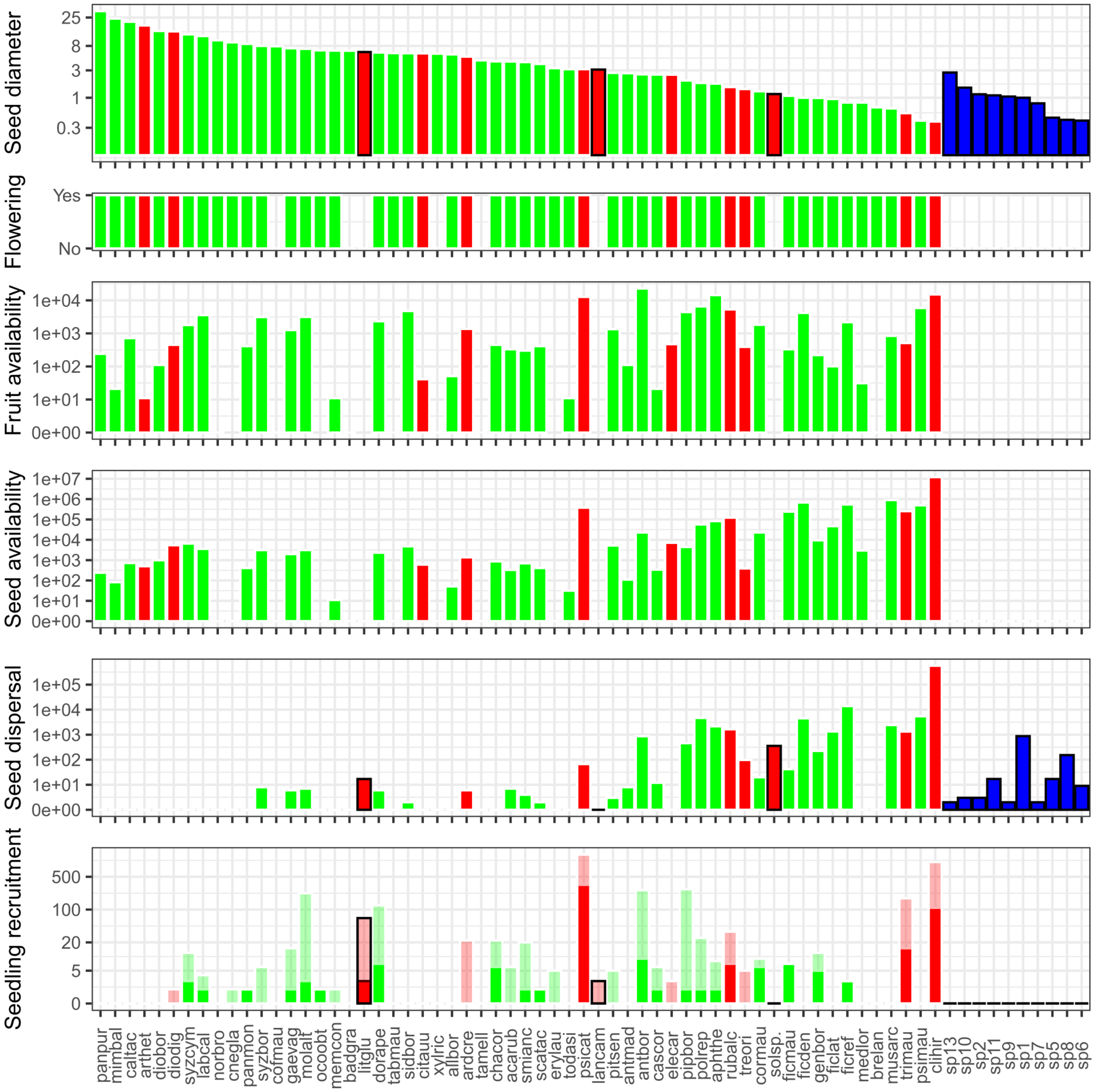

Fig.5.3 Assessment over 18 months of diaspore availability, active seed rain and spontaneous seedling recruitment in relation to mean seed diameter of fleshy-fruited plant species at study site. *Fleshy-fruited species are ranked-ordered by seed diameter (in mm). It is mentioned if the species have bloomed at least once. Index of fruit and seed availability are based on semi-quantitative data. Seed dispersal and seedling recruitment are derived from count data. For seedling recruitment, transparent and solid colours indicate small seedlings (2< <25 cm high) and large seedlings (25< <200 cm), respectively. Green, red and blue bars are native, alien and unidentified plant species, respectively. Bars framed in black represent species encountered in seed rain or seedling recruitment but without conspecific adult at study site. Species abbreviations in alphabetic order: ACARUB,* Acanthophoenix crinita; *ALLBOR*, Allophylus borbonicus*; ANTBOR,* Antirhea borbonica*; ANTMAD*, Antidesma madagascariense; *APHTHE,* Aphloia theiformis; *ARDCRE*, Ardisia crenata; *ARTHET*, Artocarpus heterophyllus; *BADGRA,* Badula grammisticta; *BRELAN*, Bremeria landia; *CALTAC*, Calophyllum tacamahaca; *CASCOR*, Casearia coriacea; *CHACOR*, Chassalia corallioides; *CITAUU*, Citrus aurantium; *CLIHIR,* Clidemia hirta;

CNEGLA, Cnestis glabra; *COFMAU,* Coffea mauritiana; *CORMAU*, Cordyline mauritiana; *DIOBOR*, Diospyros borbonica; *DIODIG*, Diospyros digyna; *DORAPE*, Doratoxylon apetalum*; ELECAR,* Elettaria cardamomum; *ERYLAU*, Erythroxylum laurifolium*; FICDEN,* Ficus densifolia; *FICLAT*, Ficus lateriflora*; FICMAU,* Ficus mauritiana; *FICREF*, Ficus reflexa; *GAEVAG*, Gaertnera vaginata; *GENBOR*, Geniostoma borbonicum; *LABCAL*, Labourdonnaisia calophylloides; *LANCAM*, Lantana camara; *LITGLU*, Litsea glutinosa; *LIVCHI*, Livistona chinensis; *MEDLOR*, Medinilla loranthoides; *MEMCON*, Memecylon confusum; *MIMBAL*, Mimusops balata; *MOLALT*, Molinaea alternifolia; *MUSARC,* Mussaenda arcuata; *NORBRO*, Noronhia broomeana; *OCOOBT*, Ocotea obtusata; *PANMON*, Pandanus montanus?; *PANPUR*, Pandanus purpurascens; *PIPBOR*, Piper borbonense; *PITSEN*, Pittosporum senecia; *POLREP*, Polyscias repanda; *PSIMAU,* Psiloxylon mauritianum; *RUBALC*, Rubus alceifolius; *SCATAC*, Scaevola taccada; *SIDBOR*, Sideroxylon borbonicum; *SMIANC*, Smilax anceps; *SOLSP.*, Solanum *sp.; SYZBOR*, Syzygium borbonicum*; SYZCYM,* Syzygium cymosum; *TABMAU*, Tabernaemontana mauritiana; *TAMELL,* Tambourissa elliptica; *TODASI*, Toddalia asiatica; *TREORI*, Trema orientalis; *TRIMAU*, Tristemma mauritianum; *XYLRIC,* Xylopia richardii.

Active seed rain

The best predictors of the cumulative number of seeds per trap per species were “log(seed diameter)” with quadratic transformation (Wald Chisquare test, p<2,2e-16), followed by “fruit availability” (p=9,9e-6), the interaction between “log(seed diameter)” with quadratic transformation & “distance to old-growth forest margin” (p=2,7e-4), “emergence” (p=4e-3) and the interaction between “fruit availability” & “plant status” (p=0,09; **App.5.6**). On the contrary, the best predictors of probability of absence were “fruit availability” (p=1,9e-14), followed by the interaction between “fruit availability” and “status” (p=1,8e-5), the interaction between “distance to old-growth forest margin” and “log(seed diameter)” with quadratic transformation (p=1,5e-3), “emergence” (p=2,4e-3) and “log(seed diameter)” with quadratic transformation (p=0,05; **App.5.6**).

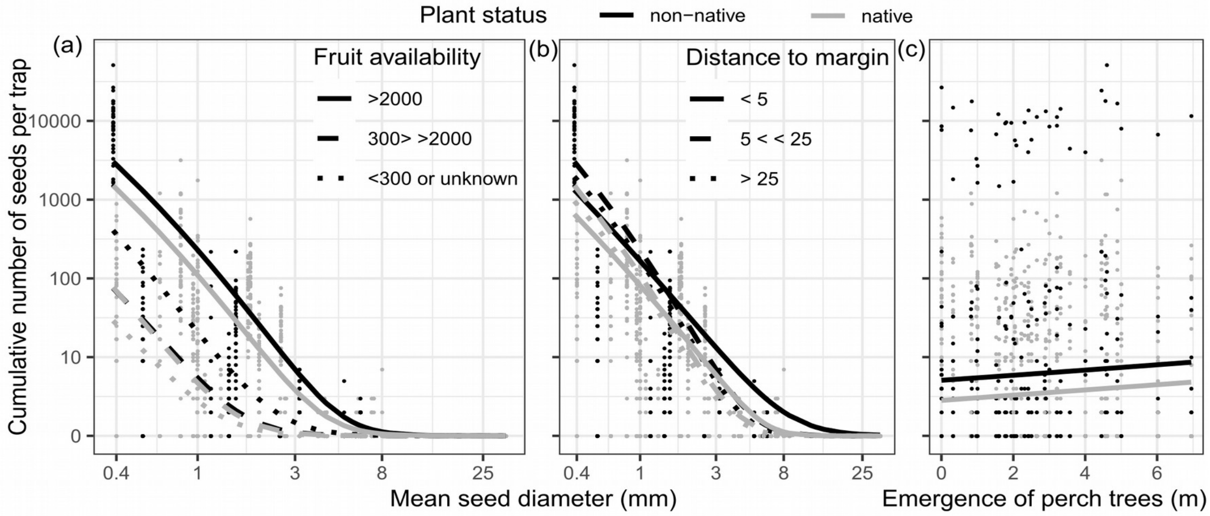

Fig.5.4 Assessment of cumulative seen rain over 18 months depending on five predictors. *The cumulative number of seeds per trap per species is estimated depending on* ***(a)*** *mean seed diameter, fruit availability and status of fleshy-fruited plants with emergence of perch trees fixed at 6,9 m and distance to old-growth forest margin at medium level,* ***(b)*** *mean seed diameter, distance to old-growth forest margin and plant status with emergence fixed at 6,9 m and fruit availability at high level,* ***(c)*** *emergence above canopy and plant status with seed diameter fixed at 1,7 mm, fruit availability at high level and distance to old-growth forest margin at medium level.*

The estimated cumulative number of seeds per trap decreased strongly between 0,3 and 5 mm in seed diameter and remained very low above 5 mm whatever fruit availability. This decrease was all the more important with seed diameter as perch trees were far away from the edge (**Fig.5.4**). For plants of which seed diameter > 5 mm, detailed results actually showed that native species were mostly found at the 1800 flow margin where the vegetation was more structured while alien plants were dispersed throughout the entire 1800 flow (**App.5.7**). Small- and medium-seeded plants were much more dispersed when fruit availability was high, especially for native plants (**Fig.5.4**). However, alien species of which mother trees were absent from the study site showed an estimated number of seeds per trap rather high, which shows their fruits were particularly attractive to frugivores. *Litsea glutinosa* for instance was responsible for most of the seed rain all over the 1800 flow for alien species of which seeds > 5 mm in diameter (**App.5.7**). Emergence of perch trees had a weak but significant positive influence on the response (**Fig.5.4**). The influence of emergence of perch trees was actually much more noticeable when considering the accumulated richness in fleshy-fruited plants per trap (**App.5.8**). The fact that trees of medium height but emerging from the canopy presented the highest richness shows these trees were particularly attractive to frugivores. On the contrary, seed dispersal of anemochorous plants was independent of the size of perch trees (**App.5.9**).

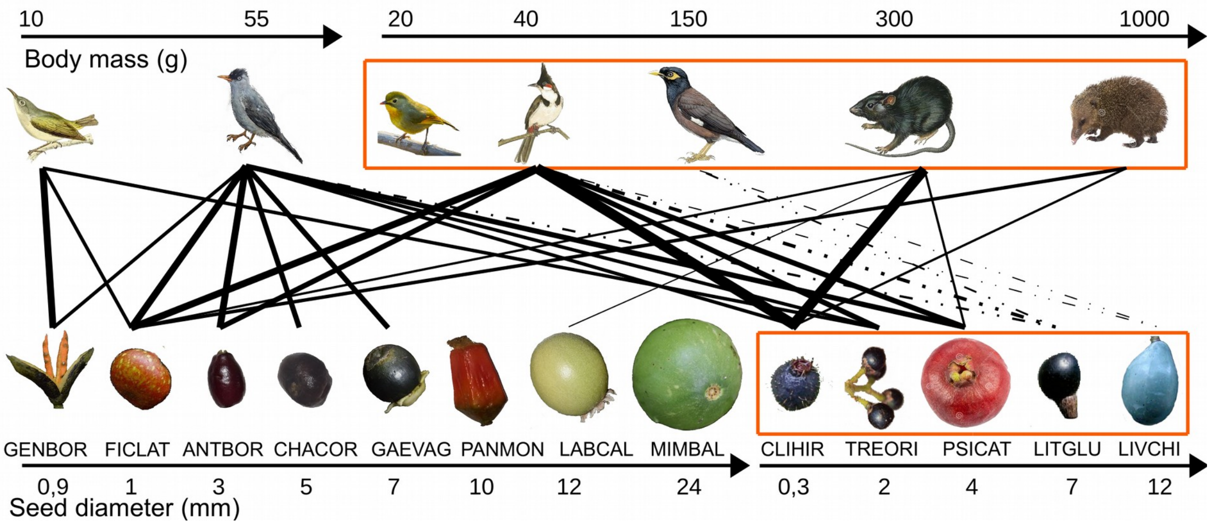

Fig.5.5 Simplified seed dispersal network at Le Tremblet. *Top, from left to right, extant native frugivores (two species of* Zosterops, Hypsipetes borbonicus*) and alien frugivores in orange box (*Leiothrix lutea, Pycnonotus jocosus, Acridotheres tristis, Rattus rattus, Tenrec ecaudatus*). Bottom, from left to right, examples of native and alien (in orange box) fleshy-fruited plants (for abbreviations, see* ***Fig.5.3****). Frugivores and fleshy-fruited plants are ranked by increasing body size and seed diameter, respectively. The thickness of lines is proportional to putative seed dispersal effectiveness. Dotted lines display frugivory interactions observed in the vicinity of study site. Only two events of large-seeded plant dispersal were recorded in additional seed traps in old-growth forests. For more details, see* ***App.5.10****.*

Frugivory interactions at Le Tremblet were recorded between 25 fleshy-fruited species and six species of frugivores (*Leiothrix lutea* was only seen moving twice; **Fig.5.5** & **App.5.10**). The overwhelming majority of frugivory interactions in birds involved *Hypsipetes borbonicus* (native) and *Pycnonotus jocosus* (alien). While both fed on native and alien fleshy-fruited plants, the former preferentially fed on native plants especially on understory shrubs, and the latter mostly fed on exotic plants including fruits on the ground. *Rattus rattus* was also recorded as a major consumer of *Clidemia hirta* and potential disperser of several native plants of which large-seeded trees by food wasting. A unique seed of an invasive palm found in additional seed traps suggested that *Acridotheres tristis* might have dispersed this plant from a remote mother tree (**Fig.5.5** & **App.5.10**). *Tenrec ecaudatus* also consumed fleshy fruits on the ground (*e.g. Ficus mauritiana*), but potential seed dispersal provided by this species could not be measured with our experimental design due to the terrestrial behaviour of this mammal.

Diversity analysis of active seed rain and spontaneous seedling recruitment

Rarefaction curves showed that seed traps and seedling sampling were able to capture the bulk of plant diversity in seed rain and recruitment of seedlings, respectively (**Fig.5.6a**). Regarding native plants, seed rain diversity was particularly depleted in the centre of the 1800 flow (see also **App.5.8**), but depletion of seedling diversity was observed over the vast majority of 1800 flow. This shows that various native species were not able to establish on the 1800 flow despite their notable presence in seed rain. On the contrary, diversity of small and large seedlings was higher at old-growth forest margin, where a highly significant increase in plot-weighted seed diameter of small seedlings was observed (**Fig.5.6b**). This was mainly due to the large number of small seedlings belonging to medium-seeded species and to the presence of seedlings of large-seeded species (**Fig.5.3**). However, many native species encountered at the “small seedling” stage (**App.5.11**) had difficulty in reaching the “large seedling” stage, resulting in the decline of plot-weighted seed diameter of large seedlings (**Fig.5.6b**). At this stage, plot-weighted seed diameter no longer showed a significant difference between native and alien fleshy-fruited plants, except at old-growth forest margin.

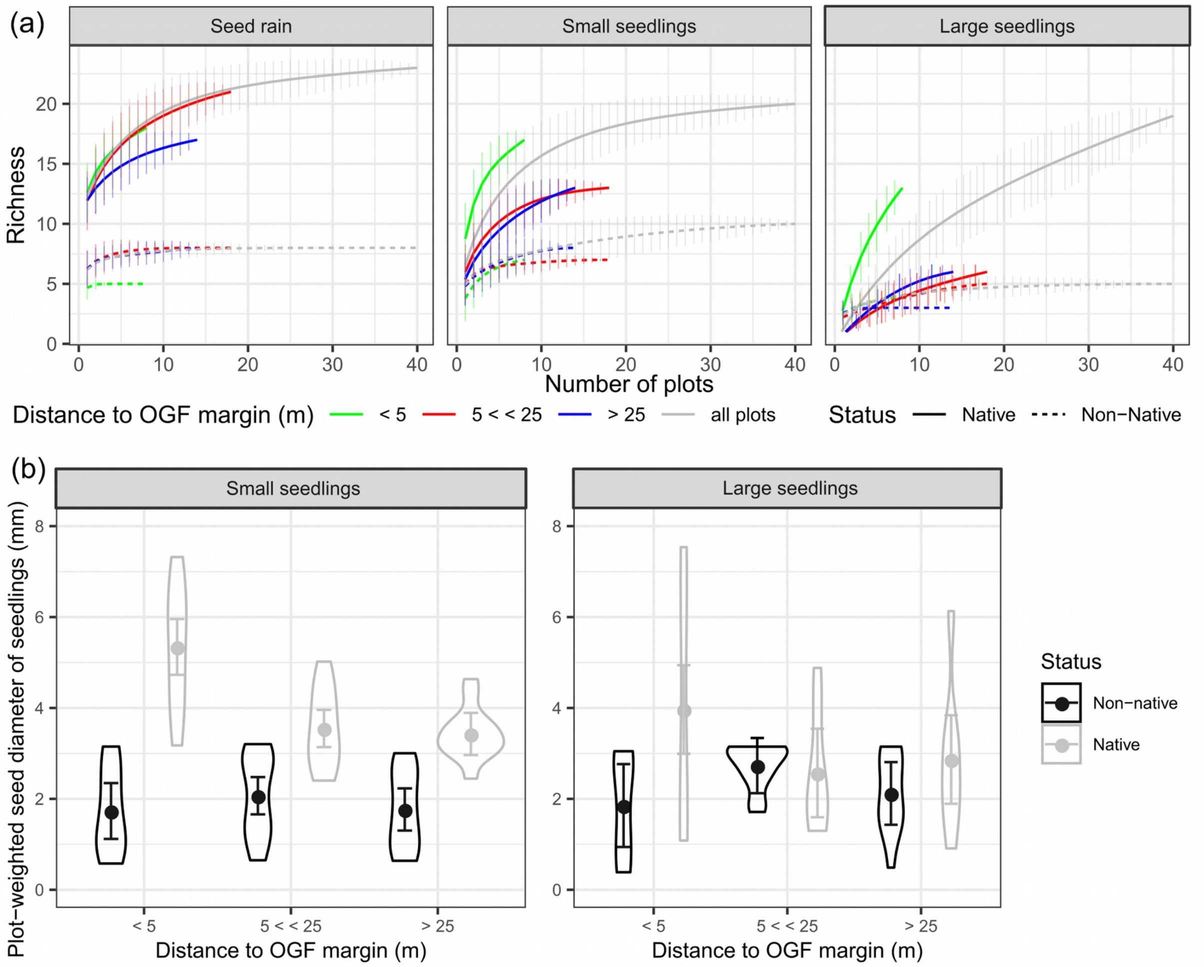

Fig.5.6 Assessment of diversity of spontaneous recruitment. (a) *Rarefaction curves for active seed rain and spontaneous seedling recruitment. Curves are evaluated depending on distance to old-growth forest margin (colours) and plant status (linetype). Confidence intervals are given by error bars.* ***(b)*** *Evaluation of plot-weighted seed diameter of seedlings depending on distance to old-growth forest margin and plant status. Violin plots, points and error bars display observed distributions, standardized values and confidence intervals predicted by GLMM, respectively.*

Diversity levelling from the bottom was observed across life stages for native and alien plants (**Fig.5.6a**). Although the diversity of seedlings of non-native species remained stable between dispersal and establishment of seedlings, it also underwent a significant decline when large seedlings were considered. The strong limitation at this stage was probably associated with the dominance of several invasive plants: two fleshy-fruited alien plants (*Psidium cattleianum* and *Clidemia hirta*; **Fig.5.3**) and the fern *Dicranopteris linearis*.

Sowing of large-seeded plants

The four selected species were sown on the assumption that they were no longer (or very poorly) dispersed on post-defaunation lava flows. Our results were consistent for the three large-seeded species, as well as for *Sideroxylon borbonicum* of which a single seed was caught over 18 months of monitoring (**Fig.5.3**). Once dispersal was reinstated, large-seeded species were quite capable of germinating, growing and surviving sometimes at very high levels all over the 1800 flow, without exclosure nor root mat uprooting, sometimes among invasive alien plants that we did not control after sowing (**App.5.12** & **App.5.13**). Species reached their maximum number of seedlings between five and six months after sowing. The results for the different treatments remained relatively stable during the rest of the experiment (**App.5.13**).

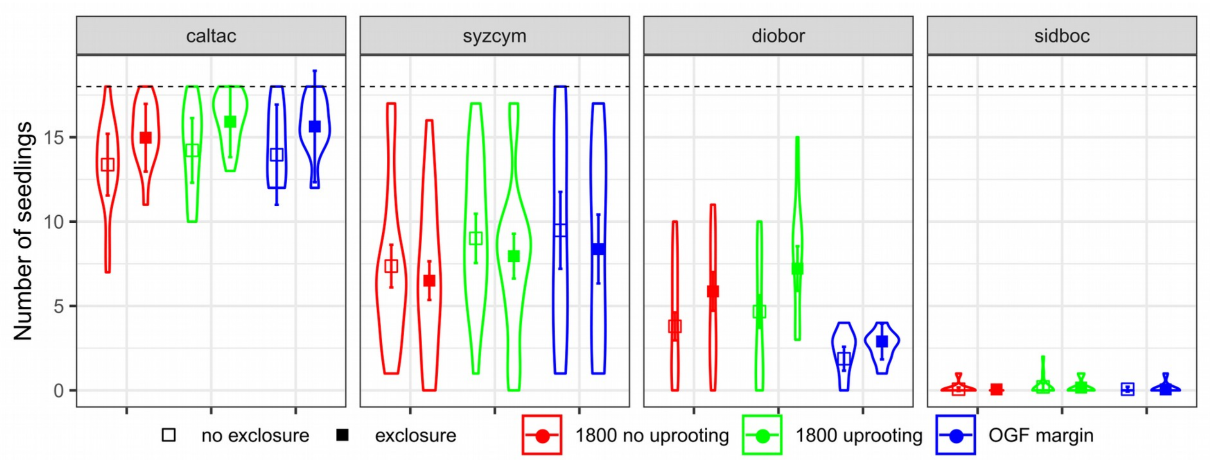

Fig.5.7 Seedling recruitment six months after experimental sowing and just before exclosure removal. *Three factors were tested (1) sown species: (“caltac”:* Calophyllum tacamahaca*; “diobor”:* Diospyros borbonica*; “syzcym”:* Syzygium cymosum*; ”sidboc”:* Sideroxylon borbonicum*); (2) competition with invasive plants (levels displayed by colors, “OGF”: old-growth forest); (3) seed predation (levels displayed by empty or full squares). 18 seeds per modality were sown (dashed lines). Violin, squares and error bars respectively displayed raw data, and estimates and confidence intervals predicted by GLMM.*

Six months after sowing just before exclosure removal, the most influential factors in the number of seedlings were “sown species” (Wald Chisquare test, $p<10^{-16}$; **App.5.14**), followed by the interactions between “sown species” & “plant competition” (p=4,5e-5) and “sown species” & “seed predation” (p=3e-4), “plant competition” (p=0,018) and “seed predation” (p=0,023). *C. tacamahaca* was by far the species with the highest number of seedlings (82,4% in average), followed by *S. cymosum* (44,7%), *D. borbonica* (26,9%) and *S. borbonicum* (0,6%; **Fig.5.7**). Competition with invasive plants and seed predation mainly had an effect on the number of seedlings of *D. borbonica*: its recruitment was lower at old-growth forest margin and higher where introduced mammals were excluded. In fact, the study of the spatial structure of GLMM residuals showed that seed predation was particularly strong in five plots, despite the presence of rats on the entire site (**App.5.15**). Surprisingly, exclosure had a weak but significant negative impact on *S. cymosum* (**Fig.5.7**). Overall, rootmat uprooting had no impact on the number of seedlings six months after sowing. However, using seedling height 21 months after sowing, seedlings were significantly higher where the low vegetation had been uprooted, especially those belonging to *Calophyllum tacamahaca* (**App.5.16**).

DISCUSSION

The evaluation of the limitations acting before, during and after seed dispersal shows that the low diversity of dispersal traits of native communities settled on a 220-yr lava flow is primarily the consequence of frugivory disruption. All large frugivores were already extinct when the focal lava flow occurred, while the old-growth forest nearby was established in 1565 (Albert et al., 2020b) when giant tortoises, flying-foxes, fruit pigeons, parrots and starlings were particularly abundant. Since the 19th century and despite likely high fruit availability, relictual frugivores have been unable to disperse the bulk of native plant diversity for physical (*e.g.* gape size) or behavioural (*e.g.* limited movement in open-canopy landscape) reasons. In particular, large-seeded fleshy-fruited plants, which are typical species of old-growth forests, have been unable to participate in the reconstruction of the tropical rainforest on the 1800 flow, although they are quite capable if dispersal is reinstated. This study thus corroborates experimentally the main conclusion of our recent analysis at larger scale that shows a collapse of dispersal trait diversity on all historical lava flows of the Piton de la Fournaise volcano (Albert et al., 2020a). These results are also consistent with several works showing depauperate seed rain in defaunated landscapes (Caves et al., 2013; Costa et al., 2012; Wijdeven and Kuzee, 2000), but our study is one of the first to characterize at which stage of the seed dispersal loop the various limitations are (Wang and Smith, 2002). Moreover, by coupling lava flow dating and defaunation chronology, the Piton de la Fournaise study system is probably unique in demonstrating the inability of native ecosystems to rebuild over the long term. Today, the situation is all the more dramatic as successful plant species are non-native and dominate both seed rain and spontaneous recruitment on the 1800 flow. In a world dominated by secondary or severely degraded forests (Chazdon, 2014; Rozendaal et al., 2019) and where the destruction of all populations of large native vertebrates is in progress (Ceballos et al., 2017; Dirzo et al., 2014; Heinen et al., 2017), our study emphasizes once again the urgent need to protect native frugivores which play a central role in the resilience of ecosystems.

The seed rain very depleted in native plants on the 1800 flow

The seed rain is particularly depauperate in native plants despite the high availability and diversity of fruiting plants in nearby old-growth forests. As expected, seed diameter has a strong negative effect on probability of dispersal. Plants of which seed diameter is > 5 mm are very little dispersed on the 1800 low and the largest seeds that we trapped during 18 months have a diameter of 0.8 cm. These seeds are probably dispersed by frugivorous birds that can swallow fruit up to 1.2 cm in diameter and subsequently seeds of a lower diameter (Cheke, 1987b; Mandon-Dalger et al., 2004). The absence of large seeds in the seed rain also shows that extant small-bodied birds cannot disperse effectively large seeded-plants by partially consuming their fruits away from parent trees. Moreover, introduced vertebrates larger than *Hypsipetes borbonicus* do not play a functional replacement of extinct large-bodied frugivores despite rare events of synzoochory in the vicinity of several mother trees. Hence, most native large-seeded plants can be considered as “anachronisms”, such as the alien *Artocarpus heterophyllus* introduced by humans in old-growth forests at study site (Guimarães et al., 2008).

While our results are consistent with several studies measuring depauperate seed rain in defaunated landscapes (Costa et al., 2012; Wijdeven and Kuzee, 2000), the persistence of *Hypsipetes borbonicus*, the most important native frugivore at Le Tremblet, may have led one to expect more encouraging results than in Guam where all native birds were extirpated (Caves et al., 2013). Yet, the concentration of the few native medium-sized seeds near the old-growth forest margin shows that this forest songbird is a low efficient disperser in open-canopy landscapes and that it may be even more sensitive to disturbances than the closely related Malagasy *Hypsipetes* (Scott et al., 2006). The limited effectiveness of legitimate frugivores in open-canopy landscapes is in fact consistent with Carlo and Morales (2016), who furthermore show that secondarily frugivorous kingbirds and mockingbirds play a central role in the early stages of plant recolonization in Puerto Rico. On Réunion, omnivorous vertebrates foraging in open areas such as the insectivore-frugivore extinct Hoopoe starling might have played an important role in forest recovery. Similarly, flying-foxes were not only capable of moving the largest fruits of native plants such as *Mimusops balata* (Florens et al., 2017a), but could defecate small seeds of native plants in flight very far away from mother trees (Muscarella and Fleming, 2007). As for giant tortoises often described in open areas on the leeward on Réunion, they might have played a key role in dispersal of large-seeded plants on recent lava flows (Cheke and Hume, 2008; Lougnon, 2005). While these hypotheses about the behaviour of extinct frugivores remain speculative, the recent return of the native flying-fox on La Reunion (GCOI, 2019) may soon provide an opportunity to study the role of this large frugivore in plant colonization dynamics.

Due to the lack of data on the behaviour of extinct frugivores, including at archipelago scale, we did not build a null model that would have helped to understand the extent to which results deviated from the pre-defaunation seed rain (see Carlo and Morales, 2016). There has probably always been a strong effect of seed size on the number of seeds dispersed, as shown by low seed rain around 1 seed.m^{-2}.yr^{-1} for most large-seeded plant species in neotropical preserved forests (Levi and Peres, 2013; Terborgh et al., 2011). However, the huge abundance of the extinct fauna described by first settlers (Cheke and Hume, 2008) might have generated an impressive seed rain on recent flows which is all the more difficult to imagine since no contemporary tropical ecosystem is home to a comparable abundance of frugivorous vertebrates. This hypothesis of an early and abundant seed rain is suggested by the fact that the Marelongue forest settled on a 16th century flow does not show any notable spatial variation in the diversity of dispersal traits, even when at a distance from the flow margin (Albert et al., 2020a).

Seed rain is very depleted on the 1800 flow, but is probably higher than it was in the second half of the 20th century, when populations of *Hypsipetes borbonicus* were at their lowest historical size and before the outbreak of *Pycnonotus jocosus* (Cheke, 1987b), that is probably the most abundant bird at study site today. In fact, our results show that alien vertebrates and plants now play a major role in seed dispersal networks in open-canopy landscapes.

The open-canopy landscape dominated by new frugivory interactions

Alien plant species are much more dispersed than native species, but this is especially due to *Clidemia hirta* of which seed dispersal highly exceeds all other plants at study site. This result is strikingly consistent with the recent work in Hawai'i of Vizentin-Bugoni et al. (2019). In this study, *Clidemia hirta* is yet dispersed by other alien songbirds, which shows the great flexibility of highly invasive plants to switch partners at global scale. Even if almost all frugivores including *Hypsipetes borbonicus* consume this plant at Le Tremblet, it is indeed alien vertebrates that disperse it massively, starting with *Pycnonotus jocosus* (Mandon-Dalger et al., 2004). The rapid expansion of *Clidemia hirta* and *Pycnonotus jocosus* on Réunion since the 1970s is in fact a typical example of “invasional meltdown” (Simberloff and Von Holle, 1999). In addition, the record number of seeds at study site is reached in hotspots of activity of rats, which disperse massively *Clidemia hirta*, as already reported in Hawai‘i (Shiels, 2011; Shiels and Drake, 2011). Hence, this plant is able to attract the whole range of frugivores throughout the year thanks to its particularly attractive fruits (Kueffer et al., 2009) and may outcompete most native plants whatever their fruit production (Aslan and Rejmánek, 2012).

Fruits of *Clidemia hirta* are mostly consumed by alien frugivores, but this is also true for alien fleshy-fruited plants in general at study site, as elsewhere (Jones, 2008; Vizentin-Bugoni et al., 2019). Most frugivory interactions with other alien plants such as *Rubus alceifolius*, *Psidium cattleianum* or *Citrus aurantium*, actually involve *Pycnonotus jocosus* and *Rattus rattus* whether in old-growth forests or on the 1800 flow. In addition, our results show that the former is only interested in a small group of native species, which is consistent with this songbird to be primarily an important disperser of invasive plants worldwide (Mandon-Dalger et al., 2004; Simberloff and Von Holle, 1999). *Rattus rattus* is interested in a wider range of native plants, but plays an ambivalent role of disperser/seed predator that is often difficult to disentangle (Carpenter et al., 2020). *Rattus rattus* is able to disperse endozoochorously several small-seeded plants, but may rather be a seed predator beyond 1 mm in diameter. Although it sometimes disperses large-seeded plants synzoochorously, its limited range and the great variability of its behaviour (see Loayza et al., 2020) probably make it a low-effective disperser.

Even if extant native frugivores consume numerous native small-fruited plants endozoochorously as demonstrated by other ongoing works (Fabien Jan, pers. comm.), it does not prevent them from dispersing alien fleshy-fruited plants. For example, *Zosterops borbonicus* and *Hypsipetes borbonicus* are known to frequently feed on invasive *Trema orientalis* and *Psidium cattleianum* (Cheke, 1987b), respectively. However, while we have shown that *Hypsipetes borbonicus* also feeds on *Clidemia hirta* (see Kueffer et al., 2009), this endemic passerine has not been able to spread this plant throughout Réunion as *Pycnonotus jocosus* did from the 1970s onwards (Mandon-Dalger et al., 2004). This is probably because *Pycnonotus jocosus* is highly mobile and moves easily between native and transformed habitats, while *Hypsipetes borbonicus* usually do not (**App.5.17**; Jones, 2008). Moreover, the high mobility of *Pycnonotus jocosus* might be the cause of the presence of several alien plant species in active seed rain (or spontaneous recruitment) despite the absence of mother plants at study site.

Our results also show that the structure of vegetation has a strong influence on active seed rain at study site where the width of the 1800 flow does not exceed 100 m. Indeed, *Hypsipetes borbonicus* may not be an important disperser in open-canopy landscape where *Pycnonotus jocosus* is probably the main disperser of various species, such as the native *Ficus* spp and above all the invasive *Clidemia hirta* or *Litsea glutinosa* (Jones, 2008). The latter plant is for example mostly dispersed in the centre of the 1800 flow despite its relatively large seed size (diameter=7 mm), while native plants of equivalent diameter are confined to marginal areas, probably because they are mostly dispersed by *Hypsipetes borbonicus*. Thus, invasive plants dominate the seed rain all the more the further away from the old-growth forest margin because *Pycnonotus jocosus* plays a primordial role as a disperser of alien plants in open-canopy landscapes. Ultimately, the refaunation with alien vertebrates has mainly benefited the alien fleshy-fruited plants (Vizentin-Bugoni et al., 2019), and the consequences for plant colonization dynamics are particularly dramatic where native closed canopies give way to more open or transformed habitats.

The spontaneous recruitment overwhelmed by alien fleshy-fruited plants

Non-native plant species are not only more dispersed, but also show a much higher recruitment than native species on the 1800 lava flow. This is consistent with the high invasion rates of several recent lava flows of the Piton de la Fournaise, as already reported by Strasberg (1994). At Le Tremblet, two species known to be highly invasive worldwide share more than 80% of recruitment, *Psidium cattleianum* and *Clidemia hirta*. The former is capable of invading native vegetation by massively producing seedlings and suckers (Huenneke and Vitousek, 1990). If this medium-seeded but large-fruited plant does not display a remarkable level of dispersal despite an abundant fruit consumption, it nevertheless remains fairly well dispersed compared to native plants with similar seed size and is thus capable of creating new invasion sites. The latter was absent from vegetation surveys in the 1970s (**App.5.19**; Cadet, 1977) and its rapid spread in the meantime has been possible thanks to huge seed dispersal (Kueffer et al., 2009; Vizentin-Bugoni et al., 2019).

The few native fleshy-fruited species that show some recruitment at study site are those that are still well dispersed, particularly *Antirhea borbonica*. Similarly, native species that usually recruit on recent lava flows (Albert et al., 2020a; Strasberg, 1994) are those that are well dispersed at study site. Yet, several of these species are not able to establish or have great difficulty in reaching the sapling stage on the 1800 flow, which shows that post-dispersal limitations are likely at work (Balcomb and Chapman, 2003).

Seed predation is all the stronger the larger the seeds (Carpenter et al., 2020) and its weak impact on sown species suggests that rats play a minor role in germination failure of native still-dispersed plants. Rather, invasive plants probably lead to strong competition that may not only prevent the germination of various species through allelopathy or attacking plant mutualists (Kato-Noguchi et al., 2012; Pinzone et al., 2018), but may also cause high mortality of young seedlings through the diversion of resources (Tng et al., 2016). At Le Tremblet, competition for water and nutrients may play a crucial role since a large part of the flow is covered by a root mat primarily made up of the fern *Dicranopteris linearis* whose uprooting has a positive effect on the growth of seedlings (**App.5.18**). Difficulty for native woody plants to settle in fernlands is documented elsewhere (Cohen et al., 1995) and the experimental uprooting revealed that native trees generally do not prospect this upper soil horizon (**App.5.18**). On the contrary, *Psidium cattleianum* can prospect this root mat and gradually invades the post-defaunation flow as revealed by comparison with Cadet (1977) (**App.5.19**). Thus, *Dicranopteris linearis* which still dominates most areas of the open-canopy landscape on the 1800 flow does not allow this ecosystem to resist alien plant invasions as Russell et al. (1998) had expected.

Large-seeded plants able to establish in all experimental plots

Large-seeded plants are sometimes still common in neighbouring old-growth forests, but they are particularly threatened by the loss of large frugivores in this naturally fragmented landscape (Albert et al., 2020a). Our results demonstrate experimentally that these plants are nevertheless capable of settling on the post-defaunation lava flow where they have always been absent or very rare: dispersal loss is indeed the major limiting factor in comparison with environmental and abiotic post-dispersal factors, as already shown elsewhere (Wotton and Kelly, 2011). Native large-seeded plants are actually much more capable of establishing than still dispersed medium-seeded plants, which do not benefit from a possible competition release where the vegetation has been treated (**App.5.12**). The capacity to settle in disturbed vegetation may be modulated by seed traits, which suggests that invasions also result from winning-by-forfeit in defaunated areas

(Hurtt and Pacala, 1995). In other words, the loss of dispersal of native large-seeded species has not only seriously disrupted plant succession for centuries (Albert et al., 2020a), but may have also increased the severity of invasions on Réunion.

After 21 months of monitoring, an important question concerns the survival of seedlings of sown species in the coming years. Indeed, conditions for seedling survival are often more stringent than conditions for germination (Balcomb and Chapman, 2003; Turnbull et al., 2000) and the question arises particularly for *Syzygium cymosum* and *Diospyros borbonica* which showed very low growth during the last six months of monitoring (**App.5.16**). However, the very high rates of germination and the vigour of *Calophyllum tacamahaca* make it an essential species for future ecological restoration projects on historical lava flows.

The old-growth forest used as a diversity reference at study site is probably already depleted in native large-seeded plants, as evidenced by the low number of saplings in the understory and the presence of isolated endangered large-seeded species just beyond the monitoring perimeter. Indeed, the loss of frugivores has probably largely contributed to their strong depletion in most tropical rainforest remnants as demonstrated by ongoing work in the Mascarenes (chapter 6) and various studies worldwide in continental forests (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010). Isolated mother trees still produce a large amount of fruits, which offers the opportunity to multiply direct sowing to better understand the limitations at work. By the way, other ongoing experiments on Réunion offer promising prospects in terms of restoration ecology on recent lava flows.

All of this demonstrates that arrested native succession (Albert et al., 2020a) and invasion on historical lava flows are not a fatality, and that massive direct sowing of large-seeded plant species could enable the enrichment of vast areas on Réunion, as elsewhere (Shaw et al., 2020). However, these human-led sowing actions should not hinder our efforts to rewild native ecosystems (Falcón and Hansen, 2018; Griffiths et al., 2011), as nothing will ever replace large native frugivores in perpetual search for food and space.

ACKNOWLEDGEMENTS

This experiment carried out in the *Parc National de La Réunion* and in the *domaine ONF* has benefited from the kind permission of the competent authorities. Facilities and financial support were provided by Reunion University (OSUR, Marelongue Research Station) and FEDER 1.02 (Divines project). We would like to thank all those who participated in the setting up of the experiment, as well as in the experiment monitoring. Special thanks to Alexis Gorissen who patiently and meticulously photographed the seeds for the catalog.

PARTIE III. Conséquences de la rupture des interactions de frugivorie sur le maintien de la diversité dans les forêts anciennes des Mascareignes

***À gauche**, vue prise dans le sous-bois de la forêt du Brise-Fer qui constitue la plus grande relique de forêt indigène à l'île Maurice. Cette forêt abrite une diversité et un endémisme importants chez les plantes ligneuses, et de grands vertébrés frugivores indigènes tels que la roussette noire (*Pteropus niger*) ou la perruche verte à echo (*Psittacula eques echo*). ***À droite**, vue prise dans la forêt de Mare Longue. Cette forêt constitue un des rares témoignages de forêt de très basse altitude dans les Mascareignes où les arbres peuvent atteindre 25 m de haut. Si elle abrite encore une diversité des traits de dispersion importante, le plus grand frugivore qu'on y rencontre depuis plus de 150 ans est le bulbul de La Réunion (*Hypsipetes borbonicus*), passereau forestier pesant environ 55 g. Photos : Claudia Baider & Alexis Gorissen.*

CHAPITRE 6. Avec ou sans frugivores ? Les roussettes soutiennent le recrutement des plantes ligneuses sur la terre du Dodo (archipel des Mascareignes)

RESUME

A l'échelle globale, la perte accélérée des vertébrés frugivores modifie profondément la régénération des forêts tropicales continentales quelque soit leur statut de protection. Aucune étude n'a pourtant été menée sur le maintien de la diversité des arbres dans les forêts anciennes et protégées des îles océaniques où les enjeux de conservation sont considérables. Dans les Mascareignes, les plus grands frugivores, dont le Dodo, ont disparu après la colonisation humaine. L'île Maurice, dépourvue de presque tous ses habitats indigènes, conserve tout de même une importante population de roussettes (masse corporelle moyenne = 450 g), tandis que La Réunion, encore largement couverte par des habitats indigènes, a perdu tous ses grands frugivores depuis plus de 150 ans et conserve un bulbul indigène (55 g) comme principal frugivore relictuel. En utilisant les parcelles permanentes non-envahies de 3 hectares de Mare Longue à La Réunion (REU-ML) comme traitement et Brise Fer à Maurice (MAU-BF) comme pseudo-contrôle, nous étudions l'impact de la perte des frugivores sur la régénération de 130 espèces ligneuses à croissance secondaire comptant 33 500 tiges avec un diamètre à hauteur de poitrine >1 cm. Nous montrons que la plupart des plantes à fruits charnus ont des cohortes juvéniles très appauvries à REU-ML en comparaison avec MAU-BF, les plantes à fruits charnus à grosses graines se régénérant mal dans les deux sites. Le recrutement bien meilleur à MAU-BF est d'autant plus marquant que la richesse spécifique est beaucoup plus élevée à MAU-BF (100 espèces) qu'à REU-ML (50 espèces). Nos résultats suggèrent que le bulbul de la Réunion, plus gros frugivore encore présent dans cette île, ne disperse pas efficacement la plupart des espèces ligneuses à REU-ML, en particulier les grands arbres de la canopée. Inversement, la roussette noire permet un recrutement massif de nombreuses plantes à petites et moyennes graines à MAU-BF, mais elle ne semble pas disperser efficacement les plantes à grosses graines dont elle se nourrit pourtant. Si d'autres processus, tels que la prédation des graines ou l'herbivorie par des mammifères introduits sont aussi à l'œuvre, ils agissent probablement comme des limitations secondaires. Alors que les plantes à fruits charnus à grosses graines théoriquement adaptées au sous-bois se régénèrent très mal en moyenne, les espèces à fruits secs ne semblent pas bénéficier d'un relâchement de compétition en raison de l'absence de plantes anémochores à grosses graines dans les Mascareignes. Bien que ces conclusions soient basées sur l'analyse des distributions diamétriques, la perte de diversité observée dans les cohortes de diamètre conduira probablement à long terme à un appauvrissement important de la canopée à REU-ML et à une modification de la composition de la canopée à MAU-BF. Ainsi, nos résultats montrent qu'à MAU-BF où l'invasion par *Psidium cattleianum* a été contrôlée dans les années 1990, la forêt conserve une certaine résilience grâce au maintien de la grande faune, tandis que la forêt non-envahie de REU-ML, souvent considérée comme un des plus beaux témoignages de forêt tropical humide dans l'écozone, continuera à perdre inexorablement en diversité si rien n'est fait. Il ne suffit donc pas de créer des aires de protection administrative et lutter contre les invasions pour protéger efficacement des forêts tropicales qui dépendent étroitement de la faune : la dispersion des graines doit être rétablie dans les forêts tropicales défaunées par tous les moyens. Si des semis directs peuvent être facilement entrepris, les frugivores clés de voûte qui existent encore devraient être une priorité de conservation et le ré-ensauvagement envisagé partout où les conditions le permettent.

With or without frugivores? Flying foxes sustain woody plant regeneration on the land of the Dodo (Mascarene archipelago)*

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ABSTRACT

Frugivore loss has the potential to alter the regeneration of tropical hyperdiverse forests. However, no study has investigated tree diversity maintenance within old-growth protected forests on tropical oceanic islands where conservation stakes are considerable. In the Mascarenes, the largest frugivores including the Dodo went extinct after human colonization. Mauritius, devoid of almost all of its native habitats, retains an important population of flying foxes, while Réunion, still largely covered by native habitats, has lost all native frugivores out of one bulbul for more than 150 years. Using census data of 130 woody species from 3-ha permanent plots of Brise Fer (MAU-BF) and Mare Longue (REU-ML), we show that most fleshy-fruited species regenerate poorly at REU-ML, in contrast to MAU-BF, large-seeded fleshy-fruited species being negatively impacted at both sites. The difference in recruitment is all the more striking because local woody plant diversity is twice as high at MAU-BF as at REU-ML. Changes observed in the understory will probably lead to strongly impoverished canopy at REU-ML, and to canopy shift composition at MAU-BF. Hence, the protected but highly fragmented forests on Mauritius are more resilient than those on Réunion usually considered as pristine among the ecoregion. Although processes other than seed dispersal may be at work, flying foxes probably ensure effective dispersal of numerous native fleshy-fruited plants on Mauritius, contrary to bulbuls on Réunion. To efficiently protect tropical rainforests on islands and continents alike, there is an urgent need to protect extant frugivores populations and reinstate seed dispersal function wherever necessary.

INTRODUCTION

Vertebrates play an important role as mutualistic pollinators or seed dispersers in most tropical forests worldwide (Dirzo et al., 2014; Turner, 2001). Recently, it has become clear that their loss has the potential to deeply alter tropical forest composition (Albert et al., 2020a; Dirzo et al., 2014; Effiom et al., 2013; Terborgh et al., 2008; Trolliet et al., 2019; Wandrag et al., 2017). Most conservation strategies have for decades involved integrating forest habitats into protected areas. However, preserving forests in which mutualistic vertebrates are absent or at low density might be ineffective when their functioning highly depends on plant-animals interactions (Laurance et al., 2012).

Various life history strategies of trees complicate the assessment of the impact of frugivore extirpation, but studies at community level indicate an alteration of the recruitment for numerous fleshy-fruited plants in defaunated protected forests of the Neotropics (Terborgh et al., 2008), Central Africa (Effiom et al., 2013; Trolliet et al., 2019) and Borneo (Harrison et al., 2013).

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* *Submitted to Biological Conservation*

This alteration of recruitment was detected just a few decades after frugivore decline or loss, being mainly the consequence of the negative distance- and/or density-dependent effects on germination or seedling survival close to maternal trees (Comita et al., 2014; Connell, 1971; Janzen, 1970). Other works have also shown how fruit consumption by frugivores may enhance the recruitment of fleshy-fruited plants by removing potential physical/chemical dormancy (Soltani et al., 2018; Traveset et al., 2008) or more simply, by cleaning the seed of flesh that could attract pathogens and seed predators causing propagule mortality (Levi and Peres, 2013). Hence, frugivores play a central role in closing the loop of dispersal in habitats largely dominated by fleshy-fruited plants (Wang and Smith, 2002).

In theory, tropical forests worldwide should be threatened by frugivore decline and extirpation, not only on continents, where hyperdiverse forests occur (Harrison et al., 2013; Terborgh et al., 2008), but also on oceanic islands (Hansen et al., 2008). Despite their isolation and small areas, oceanic islands can indeed host substantial richness in fleshy-fruited species, *e.g.* one forest patch on Mauritius harbours >60 tree species per hectare of which 89% are fleshy-fruited (Florens et al., 2017a, 2012). This relative diversity is comparable to some African continental tropical rainforests (Turner, 2001). Hence, one may expect a higher negative impact of frugivore loss on diversity maintenance on tropical oceanic islands since most frugivores went extinct after human colonization (Hansen and Galetti, 2009; Heinen et al., 2017), and having no options of alternative seed dispersal systems (Guimarães et al., 2008).

Fleshy-fruited plant species vary in their vulnerability following the extinction of frugivores. Plants with large fruits and/or large seeds are particularly at risk because large vertebrates often constitute the first guild to be extirpated (Dirzo et al., 2014; Hansen and Galetti, 2009; Heinen et al., 2017). Several studies have shown that insular large-seeded tree species experience recruitment failure at plant population level due to disperser loss (Carpenter et al., 2018; Hansen et al., 2008; Wotton and Kelly, 2011). Although large-seeded species are reputedly well adapted to the strong competition encountered in tropical understory (Leishman et al., 2000), their seedlings/saplings can be strongly depleted at community level in defaunated sites (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008; Trolliet et al., 2019). The relationship between recruitment patterns inferred from static size-distributions and defaunation has never been carried out before on islands, where one may expect a strong negative impact of large-bodied frugivore extinction on large-seeded plant recruitment.

This study aims to assess the impact of frugivore extinction on forest regeneration by comparing diameter size class distribution of woody plant species within two islands sharing a close biogeographic history with different trajectories since human colonization (Cheke and Hume, 2008). Mauritius and Réunion had lowland species-rich forests dominated by fleshy-fruited species (Albert et al., 2018; Florens et al., 2017a; Strasberg, 1996). On Réunion, primary succession dynamics have been severely altered after frugivore extinctions and great uncertainty remains about the capacity of established forests to maintain diversity in the near future (Albert et al., 2020a). Permanent plots at Brise Fer (MAU-BF) on Mauritius and Mare Longue (REU-ML) on Réunion are used to monitor the remnants of evergreen wet tropical rainforest in the Mascarenes for conservation purposes (**Fig.6.1**) (Cadet, 1977; Florens et al., 2012; Safford, 1997; Strasberg et al., 2005). These plots allow investigation of forest regeneration in two contrasting contexts of native frugivore defaunation, while accounting for biotic composition and environmental differences (**Tab.6.1**). The extirpation of large frugivores from Réunion dates 200 years ago, and the persistence of parrots and especially flying foxes on Mauritius (Cheke and Hume, 2008), provides a relevant opportunity to use these two main islands of the Mascarenes as pseudo-replicates, and to isolate the effects of seed dispersal from other factors (**Fig.6.1**). *Pteropus niger* is a keystone species on Mauritius which feeds on a large proportion of woody plants (Florens et al., 2017a). With a mean body mass of 450 g, this flying-fox is about nine times larger than *Hypsipetes borbonicus*, the largest extant frugivorous bird on Réunion (Cheke and Hume, 2008). However, Mauritius also lost its largest frugivore species that were able to swallow large fruits (**Fig.6.1**) and their extirpation has probably not been fully compensated for by those remaining taxa (Meehan et al., 2002; Trolliet et al., 2019). Hence, Mauritius cannot be considered as a strict control in terms of frugivory interaction.

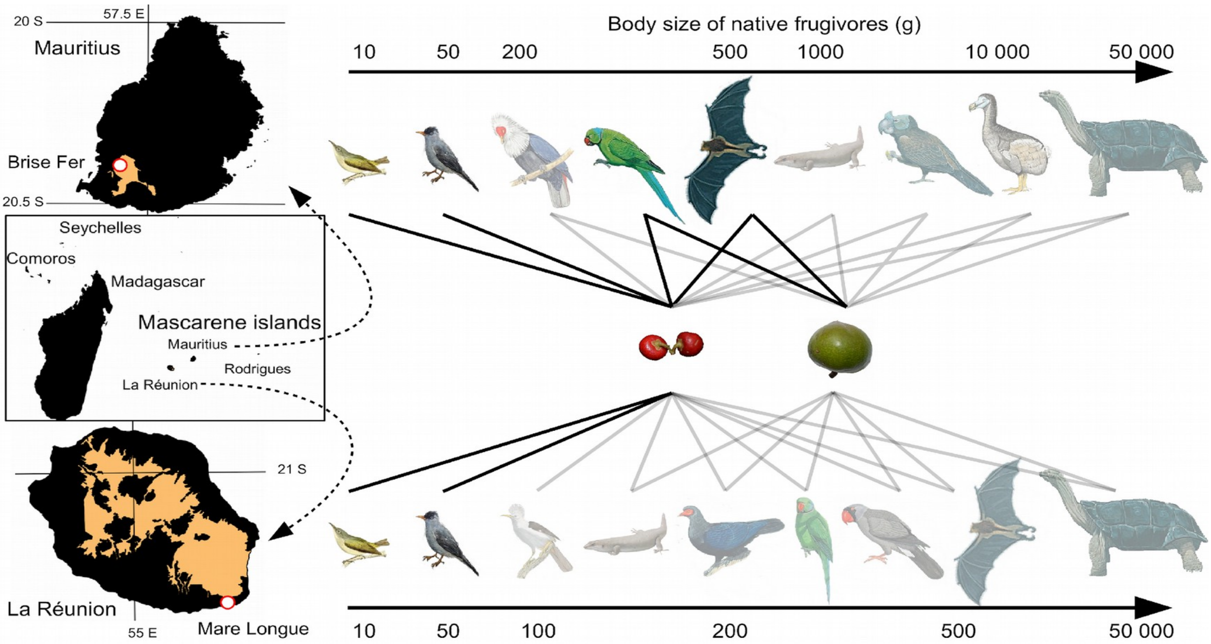

***Fig.6.1 Study sites**. Réunion and Mauritius are the two main islands of the Mascarenes. Permanent plots of Mare Longue and Brise Fer (circles) are located in the National Parks of Réunion and Mauritius, respectively (in orange). Réunion and Mauritius hosted a diverse and plethoric fauna of frugivores until the 17th century (from right to left, in descending order of body size): giant tortoises, dodo (Mauritius only), broad-billed parrot (Mauritius only), giant skink (Mauritius only), flying foxes, Mascarin parrot (Réunion only), parakeets, fruit pigeons, skinks, starlings (Réunion only), bulbuls and white-eyes. Extant frugivores and frugivory interactions are shown in bright colors. The red and green berries respectively symbolize fruit lower and higher than 13 mm in diameter. The diversity of fleshy-fruited plants is oversimplified, the Mascarenes actually showed highly asymmetric dispersal networks with relatively few species of frugivores compared to the diversity of plants (Schleuning et al., 2014). Illustrations: giant tortoises, dodo, flying foxes, parrots, fruit pigeons, starling by J. Hume; white-eyes by J.G. Keulemans; skinks by J. Noseworthy; bulbuls by D. Strasberg. For more details, see **App.6.1**.*

Our main objective is to test three complementary hypotheses. First, we assume that plant diversity is better maintained at MAU-BF (Mauritius) because of more effective dispersal than at REU-ML (Réunion). In particular, at community level, we expect that the diversity among juveniles should be similar or greater than that of adults at MAU-BF, whereas it should be lower at REU-ML. Second, within species, we assume a higher number of juveniles relative to adults at MAU-BF than at REU-ML. Indeed, few juveniles at a given time may indicate a declining population (Condit et al., 1998). Third, we hypothesize seed traits to have a strong influence on plant diversity and juveniles ratio. The extinction of all Mascarene frugivores able to swallow fruit >13 mm in diameter probably led to recruitment failure of large-seeded fleshy-fruited plants on both islands, although the extant flying foxes might have to some extent replaced the function of these extinct large frugivores on Mauritius. However, some plants, especially small-seeded species, might have difficulties in regenerating in the understory because of successional processes (Leishman et al., 2000), independently of their ability to be dispersed. This could be particularly true at REU-ML where the canopy is higher and the understory darker than at MAU-BF.

METHODS

Study area

Réunion (2512 km², 2-3 million years) and Mauritius (1865 km², 7.8 million years), the two largest islands of the Mascarene archipelago in the tropical Indian Ocean, are respectively 750 and 900 km east of Madagascar (**Fig.6.1**). They are part of the biodiversity hotspot of South-West Indian Ocean islands (Mittermeier et al., 2004). The Mascarene islands share most of their animal and plant lineages, with a great number of endemic species given their relatively small terrestrial area (Kier et al., 2009). Mauritius and Réunion host 691 flowering plant species (273 single island endemic and 150 Mascarene endemic) and 550 species (165 single-island endemic and 140 Mascarene endemic), respectively (Baider et al., 2010). Extinct and threatened species make 10.9% and 81.7% on Mauritius, while 1.2% and 50.9% on Réunion (Baider et al., 2010). Lower rates of extinction and threat on Réunion is attributed to its higher native cover (30%), although lowland habitats have mostly disappeared on Réunion (Strasberg et al., 2005).

Tab.6.1 Descriptors of permanent plots at MAU-BF and REU-ML*. Main environmental factors are shown: elevation ("m asl": meter above sea level) and annual precipitation ("Precip."). Basal area and number of stems are also displayed depending on diameter cohorts. Basal area and number of stems account for all woody species.*

Site	Plot	Elevation (m asl)	Precip. (mm)	Sampling year	Basal area dbh>1 cm (m².ha^{-1})	Basal area dbh>10 cm (m².ha^{-1})	Number of stems with dbh>1 cm	Number of stems with dbh>10 cm
Mauritius	BF1	560-600	2400	2011	41.6	34.8	6369	1026
	BF2	560-600	2400	2011	58.9	48.7	8003	1631
	BF3	560-600	2400	2010	65.2	58.4	5799	1463
Réunion	ML1	310-320	4540	2012	74.6	69.6	5807	984
	ML2	300-310	4520	2012	80.1	76.7	4580	935
	ML3	140-150	4375	2014	60.8	57.9	3098	814

Mare Longue

The three 1-ha plots at REU-ML (21°21'13'' S, 55°44'40'' E) belong to a reserve (68 hectares), now included in the National park of Réunion (**Fig.6.1**). This reserve is at the base of the last corridor of vegetation in the Mascarenes that is uninterrupted from 100 m asl to the volcano summit. This forest corridor is flanked by secondary vegetation and sugar cane fields. The studied plots are situated between 130 and 340 m asl and receive *ca* 4000 mm of mean annual rainfall (Réchou et al., 2019) (**Tab.6.1**). The forest at REU-ML is classified as a lowland tropical rainforest with no deciduous species (Cadet, 1977). It is set on pahoehoe basaltic lava flow not yet significantly altered, whose age has been estimated to be *ca* 430 years old (Albert et al., 2020b). Trees can reach 25 m high and canopy is about 15 m on average, with *ca* 900 stems >10 cm dbh and over 70 m².ha^{-1} basal area in average (**Tab.6.1**). The area is considered little invaded.

Brise Fer

The three 1-ha plots at MAU-BF (20°22'20'' S, 57°26'10'' E) are near the western edge of Mauritius central plateau, in the Black River Gorges National Park (**Fig.6.1**). This National Park has the largest remnants of native forests on Mauritius (Florens, 2013). The studied plots are located at 560-600 m asl and receive *ca* 2400 mm of mean annual rainfall (**Tab.6.1**). The forest at MAU-BF is classified as a tropical rainforest. Trees can reach 18 m high and canopy is about 12-15 m on average. MAU-BF has over 1000 stems >10 cm dbh but lower basal area than REU-ML (**Tab.6.1**). The area has been weeded of alien plant species since 1996.

Sampling

Monitoring of permanent plots began in the 1990s (at REU-ML), but we used the data sampled between 2010 and 2014 to avoid temporal bias. We used saplings reaching 1 cm diameter at breast high (dbh), as this was the threshold for measurements at REU-ML. We calculated an equivalent dbh for plants that had two or more stems.

We categorized the growth form of each woody species as either tree, shrub or climber according to the description in the *Flore des Mascareignes* (Bosser et al., 1976–ongoing) or newer publication, if available. Shrubs could reach up to 15 cm dbh, while trees reached a maximum of 94 cm at MAU-BF and 148.8 cm dbh at REU-ML (**App.6.2**).

Definition of diameter cohorts

We categorized the growth form of each woody species as either tree or shrub according to the description in the *Flore des Mascareignes* (Bosser et al., 1976-ongoing) and expert knowledge of the local floras. We excluded from analyses climbers and species without secondary growth (*e.g.* Monocots, fern trees). We defined “young”, “intermediate” and “adult” cohorts as stems with dbh of [1; 3[cm, [3; 10] cm and >10 cm, respectively for trees, and [1; 1.5[cm, [1.5; 3] cm and >3 cm, respectively for shrubs (**Fig.6.2**). For each permanent plot, we extracted the number of young, intermediate and adult cohorts for each species.

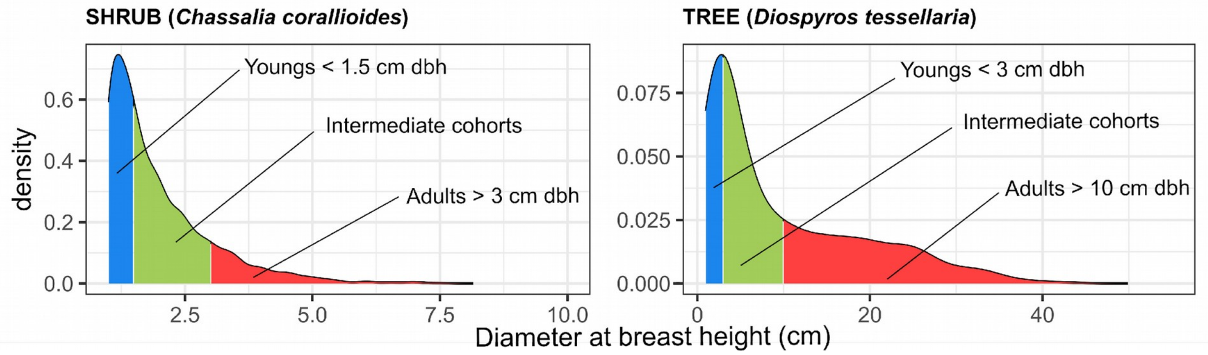

Fig.6.2 Definition of diameter cohorts according to growth forms*. Young cohorts of shrubs and trees show a diameter at breast height (dbh) of [1; 1.5[cm and [1; 3[cm (blue), respectively. Intermediate cohorts of shrubs and trees have a dbh of [1.5; 3[cm and [3; 10[cm (green), respectively. Adult cohorts of shrubs and trees have a dbh>3 cm and >10 cm (red), respectively. Two species with a left-skewed diametric distribution illustrate the assignment.*

Dispersal traits

We categorized the fruit type of each woody species as either fleshy (FF) or dry (DF), using the *Flore des Mascareignes* (Bosser et al., 1976-ongoing). Fruits were classified as fleshy if they had noticeable fleshy pericarps or fleshy appendages when mature. In the Mascarenes, most DF plants rely on abiotic agents for their dispersal.

We used seed length as a proxy for seed size as this trait was known for nearly all species, based on the *Flore des Mascareignes* (Bosser et al., 1976-onwards) and field measurements. At MAU-BF and REU-ML, seed length of woody species ranged from 0.06 cm (*Weinmannia tinctoria*, Cunoniaceae) to 5.3 cm (*Elaeocarpus integrifolius*, Elaeocarpaceae), which represented an order of magnitude of 10^6 in seed mass.

Depending on analyses, we used mean seed length as a continuous or categorical variable (**App.6.3**). For the latter case, we assigned seed length to three size classes: small-seeded plants [0.06; 0.6] cm, medium-seeded plants [0.6; 1.5] cm and large-seeded plants [1.5; 5.3] cm (as in Corlett and Primack, 2006; Costa et al., 2012). Large seeds cannot be swallowed by the extant frugivores. Fruit type and categorized seed length showed a strong dependence (χ^2 test, $p<10^{-4}$). We consequently combined both factors to create a “dispersal trait” factor with four levels: (1) all DF (as there were no large-seeded and few medium-seeded species) and FF species that were (2) small-seeded, (3) medium-seeded and (4) large-seeded.

Analyses

Dominance-diversity across diameter cohorts

To analyze changes in woody species dominance-diversity across diameter cohorts, we used rank-log abundance plots showing log-transformed species abundance for each species ranked in declining abundance order (Matthews and Whittaker, 2015). This allows to describe the full distribution of commonness and rarity in relation to diameter cohorts and dispersal traits within each permanent plot and for the whole woody community at each site.

Demographic status assessment

The demographic status of a tree population can be assessed via the ratio of juveniles to adults (Condit et al., 1998). We therefore calculated the proportion of young and intermediate cohorts to the adult plants for each woody species. This method included rare species, *e.g.* a single canopy tree without any conspecific individual in the understory. We used three explanatory variables to model proportions of young and intermediate cohorts within populations: (1) two factors (*site*: MAU-BF versus REU-ML) and (2) *fruit type* (fleshy versus dry), and a continuous variable, (3) *seed length*. The two factors *site* and *fruit type* showed no significant dependence (χ^2 test, p=0.23). *Seed length* was log-transformed prior to analyses. *Log(seed length)* and *site* showed no dependence whereas *log(seed length)* and *fruit type* were correlated (**App.6.3**), resulting in weak collinearity.

We analysed the relationship between binomial data responses (young and intermediate cohorts proportions) and explanatory variables using GLMMs, accounting for overdispersion (R package glmmTMB with a beta-binomial distribution). We also used two random effects: (1) a nested hierarchical taxonomic effect (Order/Family/Genus) to account for phylogenetic autocorrelation (Bolker et al., 2009), (2) a plot effect nested within site to account for intra-site spatial heterogeneity. Because the relationship between *log(seed length)* and responses was not linear, we tested a quadratic transformation. All models with these factors alone, in combination, possibly including interactions, or just the intercept, were considered. To select the best fixed effects structure, we performed analyses of deviance of the conditional model and dropped non-significant terms. From the best models, we estimated marginal means and 95% confidence intervals.

We used sensitivity analyses to evaluate the influence of cohort definition on demographic status assessment. We defined six different dbh classes for trees (**Fig.6.2**, upper limits of youngs: 2, 3 cm and upper limits of intermediate: 8, 10, 12 cm) and shrubs (**Fig.6.2**, upper limits of youngs: 1.5, 1.75 cm and upper limits of intermediate: 3, 4, 5 cm), resulting in 36 combinations. We tested these combinations of diameter cohorts using the same methods as above. Statistical analyses were done in R ver. 3.4.3 (R Core Team).

RESULTS

Total woody species richness was higher at Brise Fer (MAU-BF, 100 species: 65 trees, 35 shrubs) than at Mare Longue (REU-ML, 50 species: 42 trees, 8 shrubs) (**App.6.4**). Woody plants were mostly fleshy-fruited (FF) (92% at MAU-BF; 88% at REU-ML). Proportions of dispersal traits were similar across diameter cohorts at both sites. MAU-BF and REU-ML shared only 20 of the 130 species studied, but shared 35 genera, or 51% of those at MAU-BF and 81% at REU-ML (**App.6.5**). Eight other genera present at REU-ML, but absent at MAU-BF do exist on Mauritius. However, among the 33 genera present at MAU-BF but absent at REU-ML, 19 were present on Réunion (often in subhumid habitats, *e.g. Pleurostylia, Pyrostria, Securinega, Scutia*) and 14 only occurred on Mauritius (**App.6.5**). MAU-BF showed 1.47 species per genus on average against 1.16 species per genus at REU-ML.

Dominance-diversity across diameter cohorts

The S-shaped dominance-diversity curve of adult cohorts was comparable between permanent plots of each site, despite environmental differences (REU-ML) and/or different management practices (MAU-BF) (**Fig.6.3**). At REU-ML, we detected a strong increase in the steepness of the dominance-diversity curves across diameter cohorts (from adult to young), showing that some woody species excessively dominated young cohorts, and that rare species were more numerous despite depauperate richness among intermediate and young cohorts. However, we detected no steepness increase nor shape changes in the dominance-diversity curves at MAU-BF, except a tailing-off of rare species in all hectares (**Fig.6.3**). The extent of diversity loss at REU-ML can be measured using only presence-absence data. Woody species richness decreased across diameter cohorts from 34 to 23.3 species.ha^{-1} on average at REU-ML, whereas it was rather stable across diameter cohorts at MAU-BF from 65 to 67 species (with a slight peak about 70 species) (**App.6.6**). In the latter site, the stability of species richness concealed opposite trends when considering dispersal trait groups.

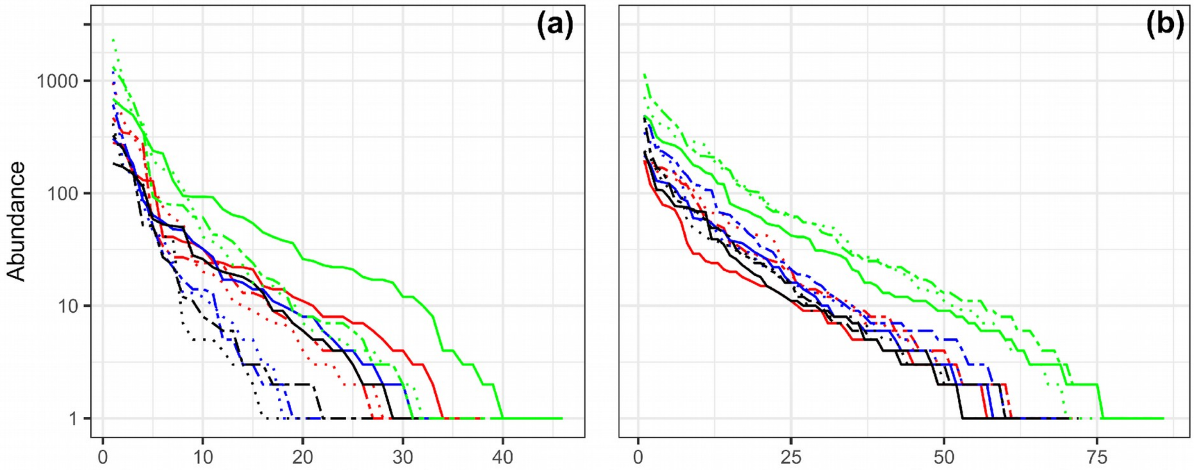

Fig.6.3 Rank-abundance diagrams for woody species overall at (a) REU-ML and (b) MAU-BF. *Solid, dashed-dotted and dotted lines respectively displayed adult, intermediate and young cohorts. Green, red, blue and black lines displayed all hectares, ha1, ha2 and ha3 at each site, respectively. Note the different scale for the x-axis.*

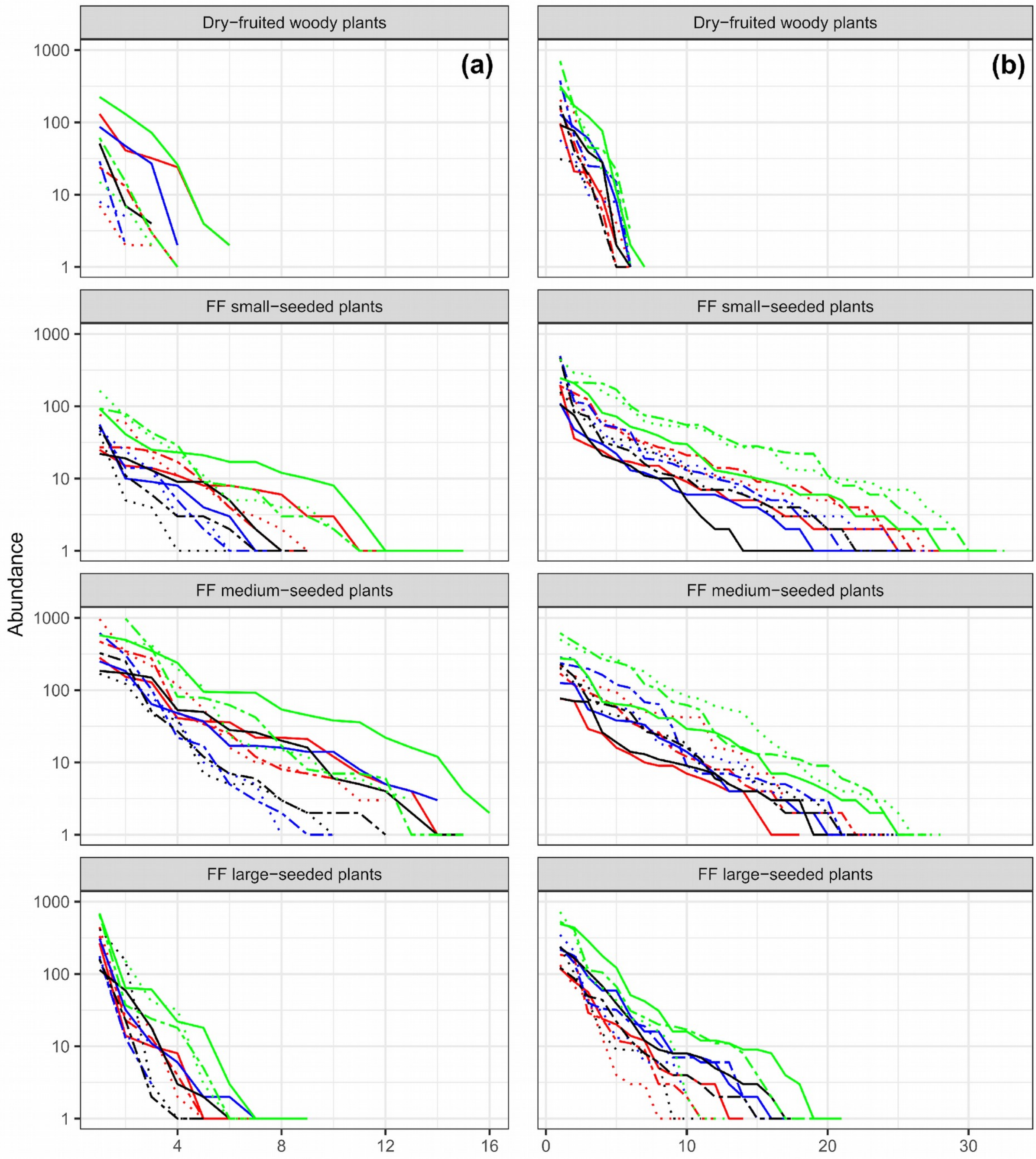

Fig.6.4 Rank-abundance diagrams according to dispersal traits at (a) REU-ML and (b) MAU-BF*. Solid, dashed-dotted and dotted lines displayed adult, intermediate and young cohorts, respectively. Green, red, blue and black lines displayed all hectares, ha1, ha2 and ha3 at each site, respectively. Dry-fruited plants were mainly anemochorous at both sites. Seed length of fleshy-fruited (FF) small-seeded, medium-seeded and large-seeded plants of [0.06; 0.6[, [0.6; 1.5[and [1.5; 5.3] cm, respectively. Note the different scales for the x-axis.*

At REU-ML, we detected a strong increase in the steepness of all dominance-diversity curves across diameter cohorts (**Fig.6.4**), with a noticeable decline in richness for all groups of dispersal traits (**App.6.6**). One or several dominant species were encountered within each group except dry-fruited plants. For instance, the proportion of large-seeded plant stems remained stable across diameter cohorts, about 0.23, but this was mainly due to *Labourdonnaisia* *calophylloides* (Sapotaceae). However, the dominance-diversity curve of adult large-seeded plants was interestingly steep in comparison with other FF groups, with numerous singletons despite depauperate diversity (**Fig.6.4**). Finally, the proportion of DF plant stems decreased across diameter cohorts from 0.12 to 0.01 on average per plot.

At MAU-BF, permanent plots showed a very high number of juvenile stems of FF small-seeded and medium-seeded plants (**Fig.6.4**) and a higher species richness across diameter cohorts of these dispersal trait groups (**App.6.6**). On the contrary, the strong increase in the steepness of dominance-diversity curve for FF large-seeded plants (**Fig.6.4**) was accompanied by an important decline in species richness (-5,7 species on average per plot) (**App.6.6**). Large-seeded species were more diverse and abundant in MAU-BF canopy compared to REU-ML canopy: four tree species on average exceeded 50 stems per plot at MAU-BF compared to only 1.33 tree species at REU-ML (**Fig.6.4**). The proportion of large-seeded plant stems decreased across diameter cohorts from 0.37 to 0.21 on average, for the benefit of FF small-seeded and medium-seeded plants. Hence, the tailing-off of the global dominance-diversity curve at MAU-BF was mainly due to diversity loss of large-seeded plants among young cohorts.

Demographic status assessment

Raw data showed wide disparities depending on site and fruit type. Median proportions of young and intermediate cohorts were notably higher at MAU-BF ($\text{prop}_{\text{young MAU-BF}}= 0.61$, $\text{prop}_{\text{int., MAU-BF}}= 0.63$) than at REU-ML ($\text{prop}_{\text{young, REU-ML}}= 0.23$, $\text{prop}_{\text{int., REU-ML}}= 0.30$). Median proportions of young and intermediate cohorts were much higher among FF plants ($\text{prop}_{\text{young, FF}}= 0.52$, $\text{prop}_{\text{int., FF}}= 0.53$) than among DF plants ($\text{prop}_{\text{young, DF}}= 0.12$, $\text{prop}_{\text{int., DF}}= 0.34$).

In statistical models, taking into account taxonomy and intra-site variability, *site* had the strongest influence on the proportions of young ($p_{\text{young}}<0.001$, Wald chi-squared test) and intermediate cohorts ($p_{\text{int.}}<0.001$, WC test), followed by *fruit type* ($p_{\text{young}}<0.001$ & $p_{\text{int.}}<0.01$, WC tests) and the interaction between the quadratic term of *log(seed length)* and *site* ($p_{\text{young}}<0.001$ & $p_{\text{int.}}<0.01$, WC tests) (**App.6.7**).

The estimated proportion of young cohorts, *i.e.* $n_{\text{young}}/(n_{\text{young}}+n_{\text{adult}})$, was about three times higher at MAU-BF than at REU-ML for small-seeded FF plants and this difference was particularly strong up to 3 mm in diameter (**Fig.6.5**). This proportion remained significantly higher at MAU-BF up to 10 mm in seed length, a value at which the proportion was 1.75 times higher than at MAU-BF. The estimated proportion of intermediate cohorts, *i.e.* $n_{\text{int.}}/(n_{\text{int.}}+n_{\text{adult}})$, weakly decreased with seed length from 0.65 to 0.55 at MAU-BF and remained significantly higher than at REU-ML up to 10 mm in seed length (**Fig.6.5**). At REU-ML, the hump-shaped curve hardly reached a maximal estimated proportion of 0.4, but sensitivity analysis revealed that estimated proportion for the large-seeded plants was rather inaccurate at REU-ML (**App.6.8**). However, sensitivity analysis showed overall consistent results when using 36 different diameter cohorts as response variables.

The estimated proportion of DF young and intermediate cohorts was higher at MAU-BF than at REU-ML, but this difference was only significant for small-seeded DF plants (Fig.6.5). Finally, taxonomy had a strong influence on the proportion of young and intermediate cohorts (**App.6.7**). At MAU-BF, most large-seeded plants belonging to radiations within *Eugenia*/*Syzygium* (Myrtaceae) and *Diospyros* (Ebenaceae) had a very low proportion of young cohorts, resulting in phylogenetic autocorrelation (**Fig.6.5**).

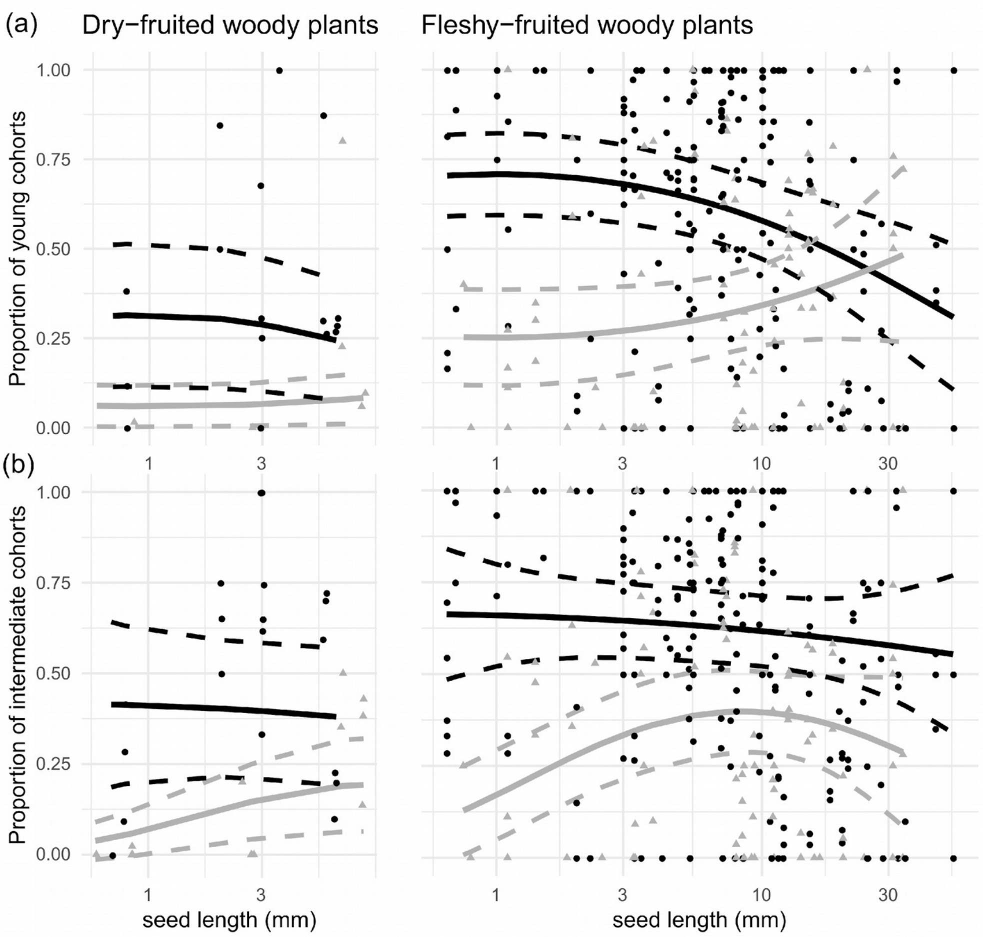

Fig.6.5 *Proportion of young and intermediate cohorts of woody plants in relation to site (MAU-BF: black; REU-ML: light grey), fruit type (fleshy versus dry) and mean seed length (mm). Points, solid lines and dashed lines display proportions of juveniles for each woody species in each permanent plot, estimates and confidence intervals from GLMMs, respectively. (a) Proportion of young cohorts,* i.e. $n_{young}/(n_{young}+n_{adult})$; *(b) Proportion of intermediate cohorts,* i.e. $n_{int}/(n_{int}+n_{adult})$. *A value of 0.5 means that a species has as many juveniles as adults. A value of 0.25 means that a species has three times as many adults as juveniles.*

DISCUSSION

Comparing three one-hectare plots of Mare Longue on Réunion (REU-ML) and Brise Fer on Mauritius (MAU-BF), famous for being the land of the Dodo, is a unique opportunity to explore the consequences of frugivores extinctions on the maintenance of diversity within tropical forests, as initiated by Terborgh et al. (2008) in Peru. On Réunion, all large-bodied frugivores went extinct for 200 years and the largest extant frugivore, a native bulbul *Hypsipetes borbonicus*, weighs 50 g on average (Cheke and Hume, 2008). On Mauritius, the largest frugivores (including the dodo), are also extinct, but MAU-BF still hosts native parakeets and an important population of flying foxes (*Pteropus niger*) weighing 450 g on average (Florens et al., 2017a). Given this discrepancy, we could test a set of assumptions using REU-ML as treatment (defaunated forest) and MAU-BF as pseudo-control: (1) diversity is better preserved at MAU-BF than at REU-ML; (2) number of juveniles relative to adults is larger at MAU-BF than at REU-ML, indicating stronger forest regeneration at MAU-BF; (3) large-seeded plants have difficulties in regenerating in the understory at both sites. Our results support these hypotheses, indicating that the loss of frugivores probably has a severe impact on the regeneration of lowland tropical forests in the

Mascarenes. Hence, even protected forests on oceanic islands would be just as much at risk as tropical forests in Neotropics (Terborgh et al., 2008), in Central Africa (Effiom et al., 2013; Trolliet et al., 2019) and in Borneo (Harrison et al., 2013).

Concern about strong diversity loss at REU-ML, encouraging situation at MAU-BF

Woody species richness strongly decreases across diameter cohorts (from adult to young) at REU-ML, whereas it is stable at MAU-BF and only decreases among large-seeded plants. This shows that diversity loss can be detected using only presence/absence data within diameter cohorts. Over a third (35.1%) of woody species do not have even a single sapling in the understory at REU-ML, compared to less than a fifth (17.9%) at MAU-BF. Moreover, proportions of intermediate and young cohorts are notably higher at MAU-BF than at REU-ML, except for large-seeded FF species, for which the recruitment of youngs is weak at both sites. Although REU-ML forest has been considered as the best well-preserved tropical rainforest in Mascarene islands (Strasberg, 1996), the extent of diversity loss in the understory and the poor recruitment of saplings for most species, questions the long term sustainability of Réunion native forests. The observed important regeneration of numerous species at MAU-BF shows that weeding since mid-1990s (Florens et al., 2012; Lorence and Sussman, 1986; Monty et al., 2013), has allowed the today promising recruitment (**App.6.9**), despite the presence of invasive alien mammals as pigs, deer or macaques (that are absent from Réunion (Florens, 2013)). This indicates that when immediate threats are removed, there are still ongoing problems, as our results also show that most large-seeded plants cannot recover despite conservation actions (Krivek et al., 2020). Therefore, it is likely that MAU-BF forest will probably experience a shift in composition in the future with considerably less large-seeded plants present in the canopy, as predicted elsewhere (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008).

One may argue that we did not study community dynamics, and that caution must be taken about the demographic status of plants, as few juveniles at a given time would not necessarily translate in a population decline (Condit et al., 1998). Indeed, the non left-skewed diametric distribution might reflect the normal depletion in the understory of a fast-growing species sampled at an unfavourable time window. However, fast-growing species are rare in the Mascarene flora (Cadet, 1977; Florens et al., 2017b) and the lack of recruitment of numerous large-seeded plants that are theoretically adapted to understory with strong competition (Leishman et al., 2000) suggests that anomalies in static diameter distribution truly derive from failure in forest regeneration because of strong dispersal limitation. The difficulty now lies in disentangling the mechanisms underlying this pattern of diversity, particularly since factors other than the availability in frugivores, such as vegetation structure or other post-dispersal factors, fluctuate between the two sites.

The likely crucial role of flying foxes in woody plant dispersal on Mauritius

Diversity loss at both sites primarily involves FF plants that make the bulk of woody plants at both sites. The disparities observed in the results between REU-ML and MAU-BF may be strongly influenced by a more or less significant alteration of mutualism networks at archipelago scale (Schleuning et al., 2014). Such a discrepancy in diversity maintenance and sapling recruitment of FF plants, except for large-seeded ones, may be mainly due to the persistence of an important population of flying foxes on Mauritius. This species is today a keystone species at MAU-BF due to the extinction of other large-bodied frugivores and the low level of the extant population of the Mauritius bulbul (Cheke and Hume, 2008). Flying foxes are known to feed upon numerous native species on Mauritius (Florens et al., 2017a; Nyhagen et al., 2005) and the role of Pteropodidae as effective seed dispersers of small-seeded and medium-seeded plants is well-known throughout the Paleotropics (Bollen and Elsacker, 2002; McConkey and Drake, 2006; Oleksy et al., 2017; van Toor et al., 2019). Flying foxes probably ensure island-scale mobility for numerous small-seeded native species (Muscarella and Fleming, 2007; Oleksy et al., 2019), even those not present adults, ultimately allowing maintenance of local diversity at MAU-BF. On REU-ML, the largest frugivore is the Réunion bulbul, which occurs at small density since the beginning of the 20th century (Cheke and Hume, 2008), which might not ensure effective dispersal of many plant species even though it can swallow their fruits (McConkey and O'Farrill, 2016).

Unlike other FF woody plants, large-seeded plants do not regenerate any better at MAU-BF than they do at REU-ML on average. The weak increase of large-seeded plant recruitment at REU-ML relative to smaller-seeded plants might be counterintuitive because of the extinction of every large native frugivore since 1800, but it may be artefactual. Indeed, many endangered large-fruited plants may have already gone extinct within permanent plots and hardly regenerate in their very vicinity, *e.g. Sideroxylon majus* (Sapotaceae)*, Hernandia mascarense* (Hernandiaceae)*, Scolopia heterophylla* (Salicaceae), which probably leads to the overestimation of the rate of large-seeded plant saplings. These isolated large-seeded species might soon go locally extinct, thus further impoverishing local diversity and at the same time increasing beta diversity at larger spatial scale (Wandrag et al., 2017). Exceptions exist, large-seeded *Labourdonnaisia calophylloides* dominates plots at REU-ML and regenerates well. Invasive alien rats may act as secondary seed dispersers (Shiels and Drake, 2011). However, while rats can occasionally move large fruits, they may be poor effective dispersers because dispersal distance is limited with most seeds usually destroyed and hoarded inside trees. Poachers that have made glue from fruit flesh extracted in the forest for several centuries might rather have acted as effective dispersers. This hypothesis, which is supported by ongoing field experiments showing a strong negative impact of flesh persistence, what would decrease the regeneration of this species without seed cleaning, has been demonstrated elsewhere (Levi and Peres, 2013).

At MAU-BF, flying foxes feed upon large-seeded plants (Florens et al., 2017a), some of which fail to recruit in the understory. Despite their large body mass that allows them to move large fruits, flying foxes cannot swallow large seeds. This incapacity has two major implications as already demonstrated at MAU-BF for the endangered endemic shrub *Syzygium mamillatum* (Myrtaceae): seeds are dispersed close from parents trees resulting in increased Janzen-Connell effects and seeds are not cleaned properly, leading to the persistence of potential dormancy-inducing or pathogen-attracting compounds, or increased attraction of introduced mammals (Hansen et al., 2008). Anyhow, the effectiveness of large-seeded plant dispersal by extinct large-bodied frugivores was probably much higher in the past. Entire lineages that had likely complementary functional roles in frugivory went extinct at both sites: fruit pigeons including the dodo (Meehan et al., 2002; Whittaker and Jones, 1994; Wotton and Kelly, 2011, 2012), parrots (except the extant endangered parakeet), skinks (Zuël et al., 2012) or giant tortoises (Hansen et al., 2008). Their absence probably plays a major role in recruitment failure of numerous large-seeded plants at both sites.

Potential post-dispersal factors: seed predation, herbivory and light availability

Recruitment failure in some large-seeded species may also be due to seed predation. Field observations at MAU-BF show that seeds of large-seeded species such as *Canarium paniculatum* (Burseraceae) are often predated by introduced rats. However, seed predation by invasive mammals may be a secondary cause of recruitment failure as already shown at MAU-BF

(Hansen et al., 2008), on Réunion (Albert, unpubl. data) or in New Zealand (Wotton and Kelly, 2011).

Seedlings and saplings may also be impacted by invasive herbivores, such as macaques or deer, as already reported by Thompson in the late 19th century (Cheke and Hume, 2008). Large-seeded plants such as Sapotaceae or *Diospyros* spp. may have specific vegetative traits which would make them more palatable than other plants (Cheke and Hume, 2008). Again, herbivory might be a secondary limitation on large-seeded plants that would primarily have difficulty establishing because of dispersal limitation.

One may argue that several species are shade-intolerant and have major difficulties in regenerating under closed canopy where competition for light is strong. This is especially true for numerous DF trees that include the smaller-seeded woody plants in the Mascarenes, as elsewhere (Leishman et al., 2000). The fact that saplings of anemochorous long-lived pioneer species such as *Agarista salicifolia* (Ericaceae), *Homalium paniculatum* (Salicaceae) or *Nuxia verticillata* (Stilbaceae) are absent or very rare at REU-ML is therefore logical (Cadet, 1977; Strasberg, 1996), which contributes to the observed decline in diversity. This influence of light availability is shown at MAU-BF where DF plants such as *Homalium integrifolium* or *N. verticillata*, only regenerate well where canopy cover is the lowest (**App.6.10**). Canopy tree species with large, wind-dispersed seeds are absent in the Mascarenes, a common feature of oceanic islands (Whittaker et al., 1997). Therefore, a gradual replacement of large-seeded FF plants in the understory, as shown in continental tropical forests (Harrison et al., 2013; Terborgh et al., 2008), is not possible.

Finally, native large-fruited light-demanding trees are usually absent in gaps at REU-ML because they are not dispersed to such areas (Wandrag et al., 2017) and most native tree species do not have a seedling/sapling bank prior to disturbance. These gaps are often occupied by alien FF small-seeded plants that benefit from high levels of dispersal by small frugivores (Baret et al., 2008; Mandon-Dalger et al., 2004), indicating the importance of seed dispersal in forest dynamics.

RECOMMENDATIONS FOR CONSERVATION

The protected tropical rainforest of REU-ML has severe regeneration of most its species because of large-bodied frugivore loss, while those of MAU-BF shows an important recruitment of FF plants, indicating their capacity of being effectively dispersed. There is consequently an urgent need to protect flying foxes that face mass cull on Mauritius (Florens et al., 2017a) and to promote the recolonization of larger forested areas by this species, which has now a small population on Réunion after more than 200 years of absence. While the ideal would be to rewild ecosystems with large-gape frugivores as already undertaken in several South-West Indian Ocean islands (Griffiths et al., 2011; Pedrono et al., 2013), direct sowing actions of large-seeded species should nevertheless be considered to support their recruitment. Ultimately, we provide additional evidence that there will be no future for diverse tropical rainforest without reinstating seed dispersal wherever necessary.

ACKNOWLEDGEMENTS

We would like to thank all those who participated in the data collection within Mascarene permanent plots.

CHAPITRE 7. La persistance de la pulpe diminue le recrutement de deux arbres indigènes dans la forêt tropicale humide de Mare Longue

RESUME

La perte des grands vertébrés frugivores mène à la rupture de la dispersion pour les arbres à grosses graines et à l'accumulation au pied des semenciers de fruits non consommés. Dans ce contexte, la principale cause des difficultés de régénération est généralement associée aux effets de Janzen-Connell. Pourtant, la persistance de la pulpe pourrait seule générer une forte limitation du recrutement, mais cette hypothèse demeure peu explorée. Ici, nous utilisons une expérience de terrain pour tester l'impact de la persistance de la pulpe sur le recrutement de *Labourdonnaisia calophylloides* et *Mimusops balata*, deux grands arbres à grosses graines (Sapotaceae) de la forêt tropicale humide à La Réunion. Le site d'étude se trouve à l'ilet Tessan dans le corridor forestier de Mare Longue qui matérialise à basse altitude une coulée de lave du 16ème siècle. Notre expérimentation se déroule dans une forêt indigène appauvrie où des semis peuvent être réalisés sans semencier conspécifique à proximité et dans des contextes variables d'ouverture du milieu. Après récolte des fruits mûrs au pied des semenciers à Mare Longue, nous nettoyons avant chaque semis manuellement 480 graines et conservons un nombre équivalent de graines au sein des fruits mûrs pour chaque espèce (nb graines.fruit^{-1} > 2 pour *M. balata*). Après avoir contrôlé les plantes envahissantes qui occupent la strate arbustive, nous semons 960 graines par espèce en janvier 2018 et novembre 2019 à raison de 20 graines par modalité (graine nettoyée manuellement *vs* fruit X sous-bois *vs* trouée). Pour évaluer l'impact potentiel des prédateurs de graines et disperseurs secondaires, nous contrôlons le nombre de diaspores dans le plan d'expérimentation et utilisons des pièges caméras pour identifier la faune impliquée. Nous comparons le recrutement des plantules au moment où les taux de recrutement sont maximaux, environ 6,5 mois après semis. Nous testons l'influence des quatre facteurs binaires (nettoyage manuel de la graine, espèce, année de semis, ouverture du milieu) et de leurs interactions sur le recrutement via des GLMs avec une transformation binomiale et conservons le modèle avec le plus faible AIC. Le nettoyage manuel de la pulpe montre un très fort impact positif sur le recrutement (x 3,2 en moyenne) et constitue de loin la variable la plus influente. Il existe pourtant de fortes variations du recrutement entre les années de semis, les milieux et les espèces. *M. balata* est l'espèce qui profite le plus du nettoyage manuel de la pulpe, mais les fluctuations les plus surprenantes sont associées à l'action différentielle d'*Achatina immaculata* qui parvient quasiment à restaurer le recrutement de *L. calophylloides* en se nourrissant massivement de pulpe dans le sous-bois en novembre 2019. De même, nos résultats montrent une forte variabilité comportementale de *Rattus rattus* qui se désintéresse des diaspores semées en janvier 2018, mais prédate plusieurs graines de *M. balata* et surtout emporte de nombreux fruits de *L. calophylloides* du plan d'expérimentation en novembre 2019. Notre expérience montre que la persistance de la pulpe contribue seule à réduire considérablement le recrutement des plantules chez deux espèces de Sapotaceae via deux mécanismes principaux: en créant une dormance exogène non innée et en handicapant les plantules ayant levé dans le péricarpe. Le relatif bon maintien des espèces focales dans les forêts anciennes apparaît dès lors paradoxal, mais pourrait provenir du rôle ambivalent joué par la faune introduite. De même, nos résultats suggèrent que les chasseurs à la glu pourraient avoir maintenu de hauts niveaux de dispersion de *L. calophylloides* dans les sous-bois des forêts anciennes. Enfin, nous démontrons avec cette expérimentation que coupler des semis directs à la lutte contre les plantes envahissantes constitue une méthode pertinente de restauration écologique.

Flesh persistence decreases tree recruitment in a defaunated tropical rainforest*

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ABSTRACT

The loss of large frugivores leads to regeneration failure of numerous large-seeded trees. Altough the main underlying cause is generally associated with Janzen-Connell effects, flesh persistence alone may generate a strong limitation of recruitment. In this study, we used a field experiment to test the impact of flesh persistence on the recruitment of *Labourdonnaisia calophylloides* and *Mimusops balata*, two big large-seeded trees (Sapotaceae) from tropical rainforest on La Réunion. Our experiment was located in the Mare Longue forest corridor on a recent pāhoehoe flow bearing an impoverished native forest without conspecific mother trees nearby. After sampling ripe fruits, we hand-cleaned 480 seeds and kept an equivalent number of seeds within pericarp for each species. We controlled invasive plants that occupied the shrub stratum and sowed 960 seeds per species in January 2018 and November 2019 at a rate of 20 seeds per modality (seed cleaning *vs* fruit X understory *vs* gap). To evaluate the potential impact of secondary dispersers or seed predators, we controlled the number of diaspores in the experiment and used camera traps to identify the fauna involved. We compared the recruitment of seedlings at maximum rates about 6,5 months after sowing. We tested the impact of four binary factors (seed cleaning, species, year of sowing, canopy closure) and their interactions on recruitment via GLMs with binomial transformation and kept the model with the lowest AIC. Seed cleaning showed a strong positive impact on seedling recruitment (x 3,2 in average) and was by far the most influential variable. However, there were significant variations in recruitment between species, years and light environments. *M. balata* was the species that benefited the most from seed cleaning. Surprisingly, *Achatina immaculata* almost restored *L. calophylloides* recruitment in the understory in November 2019. Similarly, *Rattus rattus* showed a strong behavioural variability: focal species were not impacted in January 2018, but in November 2019, several seeds of *M. balata* were predated and many fruits of *L. calophylloides* were removed from the experiment. Hence, flesh persistence due to frugivore loss contributes to significantly reduce seedling recruitment in two Sapotaceae species by creating an exogenous no innate dormancy and handicapping seedlings that grow up within pericarp. However, introduced animals and humans play a complex role in native ecosystems, which might explain why *L. calophylloides* is sometimes common in old-growth forests while our experiment suggests that it should regenerate poorly in the absence of flesh consumption.

INTRODUCTION

The loss of frugivorous vertebrates leads to seed dispersal disruption for numerous tropical fleshy-fruited species, among which large-seeded trees are particularly vulnerable (Albert et al., 2020a; Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010; Wotton and Kelly, 2011). This disruption primarily leads to the inability to move away from parent trees and the persistence of flesh around seeds, both resulting in the accumulation of

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* *In preparation for Biotropica*

unconsumed fruits at the foot of parent trees. To explain the recruitment failure of many tree species that lost dispersal, Janzen-Connell effects have long been thought to be the central process (Comita et al., 2014; Connell, 1971; Hansen et al., 2008; Janzen, 1970; Terborgh, 2012). However, Levi and Peres (2013) have shown that the absence of seed cleaning by frugivorous vertebrates is a primary cause of recruitment failure of *Manilkara bidentata* (Sapotaceae) and have suggested that flesh persistence in defaunated forests might strongly decrease the recruitment of numerous fleshy-fruited tropical trees. Since this work, studies investigating the processes involved in the lack of *in situ* recruitment as a result of defaunation remain scarce.

The non-consumption of fruits by frugivorous vertebrates may lead to seed dormancy, *i.e.* seeds do not have the capacity to germinate under favourable environmental factors for a while. In particular, flesh persistence can lead to exogenous dormancy which is or is not combined with endogenous dormancy (Baskin and Baskin, 2004). Consequently, the loss of frugivores can theoretically make all seeds of a fleshy-fruited species dormant when those that were previously cleaned by frugivore action were not. This “no innate dormancy” may be induced by germination inhibitors (“chemical dormancy”), low water potential and/or mechanical resistance within the pericarp (or other fleshy appendage such as aril) (Baskin and Baskin, 2004). Exogenous dormancy may be especially problematic for numerous tropical rainforest trees that generally show fast germination and possess recalcitrant seeds, *i.e.* they have a high moisture content and easily lose their viability because of low tolerance to dehydration (Vazquez-Yanes and Orozco-Segovia, 1993). Thus, delaying germination beyond a critical threshold of dryness would lead to a lower recruitment for these species that usually stock seedlings on the forest floor rather than storing seeds in soil banks (Hopkins and Graham, 2006). Regarding physical dormancy which is a type of endogenous dormancy, it has been shown that the alteration of water-impermeable seed coat in the gut of frugivores may enhance germination rate for numerous species (Barnea et al., 1991; Traveset, 1998). However, even if Rick and Bowman (1961) reported that the only way of breaking seed dormancy in the native Galápagos tomatoes was through ingestion by giant tortoises, ingestion of seeds by frugivorous vertebrates is rarely essential (Soltani et al., 2018; Traveset, 1998) contrary to what has long been believed (see Temple, 1977).

Flesh is the reward produced by plants to attract frugivores, but its persistence due to frugivore loss can paradoxically entice natural enemies, possibly resulting in decreasing recruitment (Hansen et al., 2008; Levi and Peres, 2013; Wyse Jackson et al., 1988). In particular, it has been claimed that fungal pathogens may be an important cause of regeneration failure of Sapotaceae trees (Levi and Peres, 2013; Wyse Jackson et al., 1988). In fact, the latter studies do not allow to disentangle whether fungi become pathogenic to seeds that have become dormant due to flesh persistence or whether they merely degrade seeds that are no longer viable. The persistence of flesh may similarly attract seed predators such as rodents in continental tropical forests (Levi and Peres, 2013), but also in island forests where they have been introduced since human colonization (Hansen et al., 2008; Shiels and Drake, 2011). For example, Hansen et al. (2008) have shown on Mauritius that ship rats are only interested in diaspores of *Syzygium mamillatum* (Myrtaceae) when seeds have not been hand-cleaned. In this case, it seems unlikely that introduced rats could be effective secondary dispersers regarding the recruitment of this large-seeded shrub on Mauritius (chapter 6; but see Shiels and Drake, 2011).

Here, we used a field experiment to test whether hand cleaning of seeds increases the recruitment of seedlings in a tropical rainforest on La Réunion (Mascarenes), an oceanic island where all native large-bodied frugivores went extinct (Albert et al., 2020a; Cheke, 1987b; **Fig.7.1**). To test this hypothesis, we chose *Labourdonnaisia calophylloides* Bojer and *Mimusops balata* (Aubl.) C.F. Gaertn, two native large fleshy-fruited tree species typical of the Sapotaceae family, *i.e.* species that play an important role in mature tropical rainforest as long-lived shade-tolerant trees (Cadet, 1977; Dafreville, 2013). The experiment was realized with no conspecific tree nearby, which allowed to control seed rain due to the loss of all large native frugivorous vertebrates and to avoid possible Janzen-Connell effects. Because focal shade-tolerant tree species should normally be dispersed in different spatio-temporal contexts, we tested the effect of seed cleaning under two canopy closure levels and two years apart. Finally, we monitored the interactions with the fauna of Mare Longue, whose protagonists are today mainly introduced (*e.g.* tanrec, rats, snails).

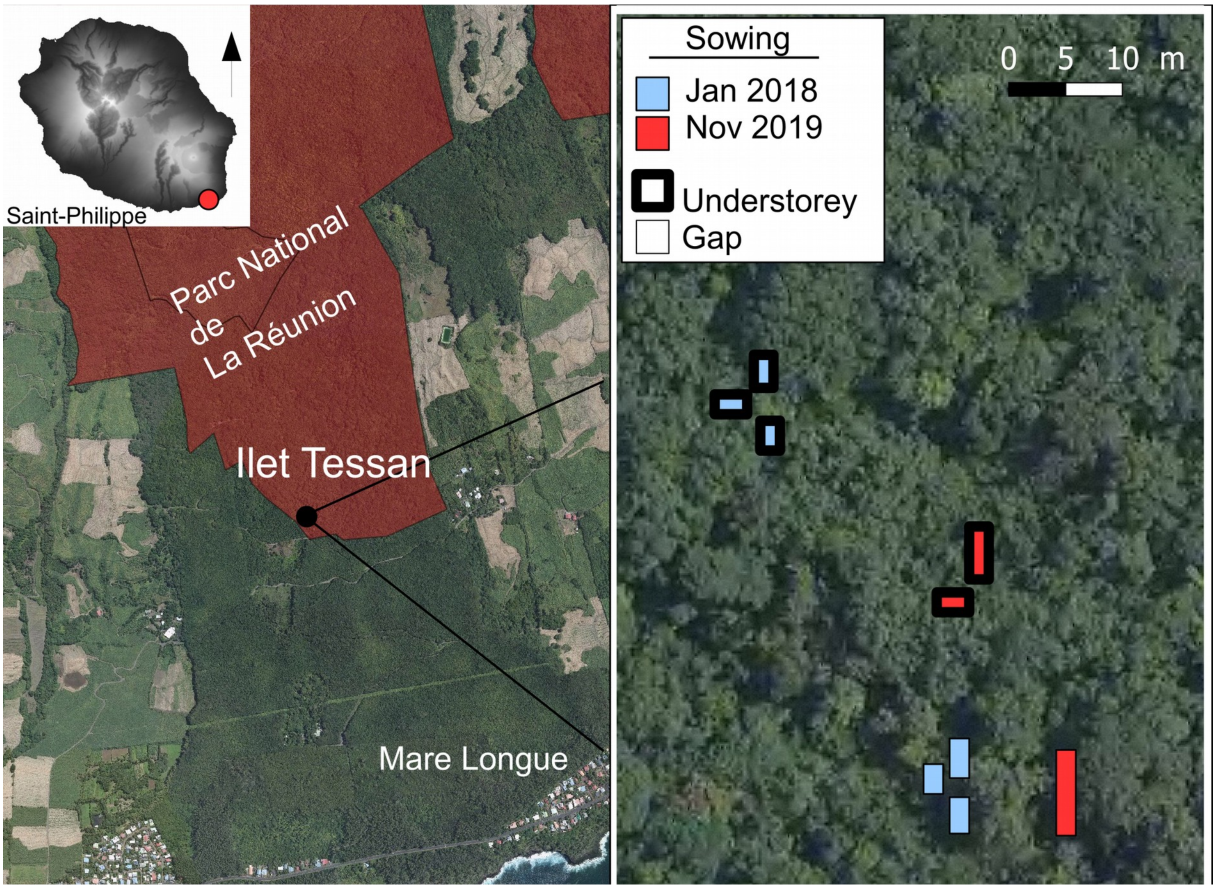

Fig.7.1 Study site. *The forest corridor of Mare Longue, municipality of Saint-Philippe, is the most preserved corridor of native forests from sea level to high elevations (>2200 m asl) in the Mascarenes. The field experiment is located at Ilet Tessan around 150 m asl, at the edge of the National Park of La Réunion. In order to adapt to rugged terrain on a recent pāhoehoe lava flow, quadrats of varying size were delineated for each of the four sowing areas (combination of factors "year of sowing" & "canopy closure"). In each sowing area and for both focal species,* Labourdonnaisia calophylloides *and* Mimusops balata*, "hand cleaning of seeds" and "flesh persistence" modalities were replicated 12 times at a rate of 20 seeds per modality. For a detailed view of the sowing, please report to* ***App.7.1***.

METHODS

Study area

This study site was located in the South-East of La Réunion (Mascarene archipelago) on the wet windward at Mare Longue (mean annual precipitation: ca 4300 mm, Réchou et al., 2019) (**Fig.7.1**). At low elevations, the corridor of Mare Longue materializes a recent pāhoehoe lava flow (age = *ca* 430 years old) which probably explains why this area has not been cleared (Albert et al., 2020b). This corridor shelters one of the best-preserved tropical rainforests on La Réunion (Cadet, 1977; Strasberg, 1996), because community assembly occurred before the beginning of human colonization, leading to rapid extirpation of all large native frugivores (Albert et al., 2020a). This lava flow displays a very thin soil on continuous rock (Meunier et al., 2010) where mature trees of *L. calophylloides* and *M. balata* may be common (Strasberg, 1996). The forest corridor of Mare Longue is quite heterogeneous regarding vegetation types, with native species-rich habitats alternating with plantations of native trees and invaded areas (**Fig.7.1**).

Our field experiment took place in the native forest at Ilet Tessan where selective logging on *L. calophylloides* and *M. balata* probably occurred and where the relative scarcity of focal species allowed to avoid conspecific tree in the vicinity of the sowing areas (**Fig.7.1**). We also chose sowing areas to avoid temporary streams that occur during heavy rains and that could strongly impact the distribution of seeds and fruits within the experimental design. Sowing areas were a maximum of 50 m apart (**Fig.7.1**). Sowing areas in the understorey showed a shrub stratum dominated by *Syzygium jambos* (Myrtaceae), well-known since a long time as a highly invasive species on La Reunion (Macdonald et al., 1991). Sowing areas in gaps were mostly invaded by the exotic shrub *Clidemia hirta* (Melastomataceae) (Mandon-Dalger et al., 2004). Both invasive species were uprooted before sowing and controlled all along the experiment.

Experimental design

We collected freshly fallen ripe fruits of *L. calophylloides* and of *M. balata* at the foot of parent trees in the forest of Mare Longue in late December 2017 and November 2020. For each species, we hand-cleaned 500 seeds and kept an equivalent number of seeds within intact fruits: for the single-seeded *L. calophylloides,* 500 fruits and for *M. balata,* 168 fruits in January 2018 (mean of 2,9 seeds per fruit) and 250 fruits in November 2019 (mean of 2 seeds per fruit). Fruits and seeds were stored in a cold-room during maximum three weeks before sowing.

Ex-situ tests

To test whether there was an intrinsic limitation prior to the field experiment, we hand-cleaned 500 additional seeds in January, and realized viability and germination tests. We used the colorimetric test of tetrazolium chloride (0,1% *i.e.* 0,1 g of powder / 100 ml of filtered water), which leads to a pink coloration of the living tissues after six hours of soaking. We performed five repetitions on 20 seeds for each viability test. Seeds of *L. calophylloides* and *M. balata* showed a viability of respectively 93% +/- 2,7 and 86% +/- 4,2. These results indicated that seeds used for the experiment showed a very high viability rate.

Field experiment

The effect of seed cleaning was tested under two levels of canopy closure, resulting in four combinations with 12 repetitions per combination. At the rate of 20 seeds per repetition, we thus sowed a total of 960 seeds for each species in January 2018 and in November 2019. The experimental design was materialized to the ground with a 0,4 m x 0,4 m wire mesh (**App.7.1**).

Rigorous evaluation of germination in this experiment was not possible because early stages of root development could not be observed when it took place within the fruit (**Fig.7.2**). We therefore monitored the seedling recruitment by counting the number of rooted seedlings from the first emergence two months after sowing. La Réunion was subject to several tropical depressions during the first months of the experiment in 2018 (Berguitta and Dumazile cyclones in January and March 2018, respectively), we therefore controlled the number of fruits and seeds after cyclones, which was made possible by the large size of seeds of *L. calophylloides* (mean seed diameter: 12 mm) and *M. balata* (seed diameter: 24 mm) (**Fig.7.2** & **App.7.1**). Cyclones had no impact on the experimental design.

Fig.7.2 *Germination five weeks after sowing of* Mimusops balata *(left) and* Labourdonnaisia calophylloides *(right). In this case,* i.e. *"hand-cleaning of seeds", germination can be seen, but in the case of "flesh persistence" modality, only the emergence of seedlings from the fruit can be properly assessed. Photos: A. Gorissen*

Seed and fruit predation by *Rattus rattus* have already been reported for Sapotaceae seeds in the Mascarenes (Baider and Florens, 2006; Eric Rivière, pers. comm.), that is why we took into account the potential impact of this introduced seed predator. Due to the difficulty to use predator exclosure on rug substrates of Ilet Tessan, we controlled the number of seeds and fruits in each replicate during six months after sowing. We also used two Bushnell Trophy Cam HD to monitor potential seed and fruit predators. These digital camera traps were set up in the understorey at *ca* 1,5 meter from seeds and fruits, and set to operate during the day and night with a movement trigger.

Statistical analyses

The proportion of seedlings relative to number of seeds was analyzed at the time when all seedling emergences were assumed to have occurred. We modeled the proportion of seedlings depending on four factors with two levels: hand cleaning of seeds (yes *versus* no), canopy closure (gap *versus* understory), year (Jan. 2018 *versus* Nov. 2019) and species (*L. calophylloides versus M. balata*) using a generalized linear model (GLM) with a binomial distribution. The proportion of seedlings was assessed using the number of rooted seedlings and the number of seeds or fruits after potential removal from the experiment. We tested all possible models with predictors as well as their interactions and eventually retained the full model that displayed the lowest AIC.

RESULTS

Temporal monitoring showed a rapid emergence of seedlings two months after sowing in January 2018 (**Fig.7.3**). The emergence was especially massive for hand-cleaned seeds and median proportions peaked in May 2018. This demonstrated that seedlings of focal species were quite capable of establishing despite the very thin soil on continuous rock (**App.7.2**). Field observations showed that all emergences occurred in the first six months after sowing. Trends have been relatively stable since then despite the unusual drought that struck the area between December 2018 and April 2019. Such a temporal monitoring could not be performed after the second sowing in November 2019, but based on these results (**Fig.7.3**), recruitment between the two years of the experiment was compared approximately 6.5 months after sowing.

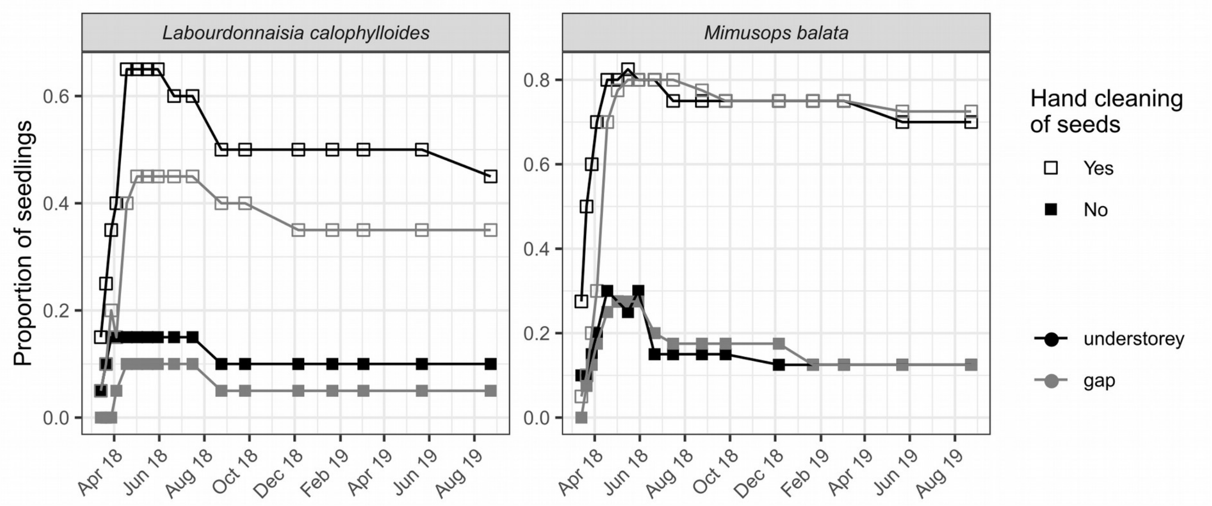

Fig.7.3 Temporal monitoring of seedling recruitment of* Labourdonnaisia calophylloides *and* Mimusops balata *after the first sowing in January 2018. *Full and empty squares respectively display "flesh persistence" and "Hand cleaning of seeds" treatments, black and grey squares respectively display "understorey" and "gap" treatments. For each date, squares display the median of observed values.*

In 2018, we did not detect any noticeable interaction between introduced vertebrates and fruits & seeds of *Labourdonnaisia calophylloides* and *Mimusops balata*, but the same year, tests in the vicinity at Ilet Tessan revealed potential high levels of seed predation or secondary dispersal by *Rattus rattus* (**App.7.3**). On the contrary, in November 2019, 22 fruits of *L. calophylloides* and four seeds of *M. balata* were removed and predated by *Rattus rattus,* respectively (**App.7.3**). The statistical response was controlled accordingly. Likewise, although invertebrates were seen eating the pulp of focal species in January 2018, the phenomenon was much more massive in November 2019, and *Achatina immaculata* sometimes performed a very effective seed cleaning especially in the understorey (**App.7.3**).

The best fitting GLM included the four factors ("hand cleaning of seeds", "canopy closure", "year of sowing", "species") with all possible interactions (pseudo-R^2_{glm} = 0,697, **App.7.4**). Hand cleaning of seeds was by far the best predictors and had a strong positive impact on seedling recruitment (estimated value= x 3,2, **Fig.7.4** & **App.7.4**). Field observations showed that seeds of *L. calophylloides* often remained trapped within unconsumed pericarp (**App.7.5**). Likewise, germination of *M. balata* often occurred but seedlings have difficulties rooting in the soil due to the thickness of the exocarp and to the fleshy environment which promoted the development of a root system that remained in the open air after flesh disappearance (**App.7.6**). The instability of the exocarp which generally persisted after the disappearance of the mesocarp often resulted in tilting movements of seedlings (**App.7.6**). The positive impact of hand cleaning of seeds was stronger in the first year of the experiment, as illustrated by the interaction between both factors which was highly significant (**Fig.7.4** & **App.7.4**). As already mentionned, *Achatina immaculata* fed heavily on fleshy fruits of focal species in the understorey in November 2019 (**App.7.3**), which probably explains why the impact of hand-cleaning of seeds was much less marked the second year, especially for *L. calophylloides*. The same year, the positive impact of hand cleaning of seeds remained nevertheless very strong in the gap where few *Achatina immaculata* were observed feeding on the flesh of focal species. Over the two years of the experiment, *M. balata* showed an overall higher estimated recruitment than *L. calophylloides* (0,46 *versus* 0,37) and a stronger positive effect of hand cleaning of seeds (x 3,7 *versus* x 2,4) resulting in high recruitment rates for *M. balata* (0,72) and *L. calophylloides* (0,52) (**Fig.7.4** & **App.7.4**). Finally, *M. balata* showed a higher recruitment than *L. calophylloides* in the gap.

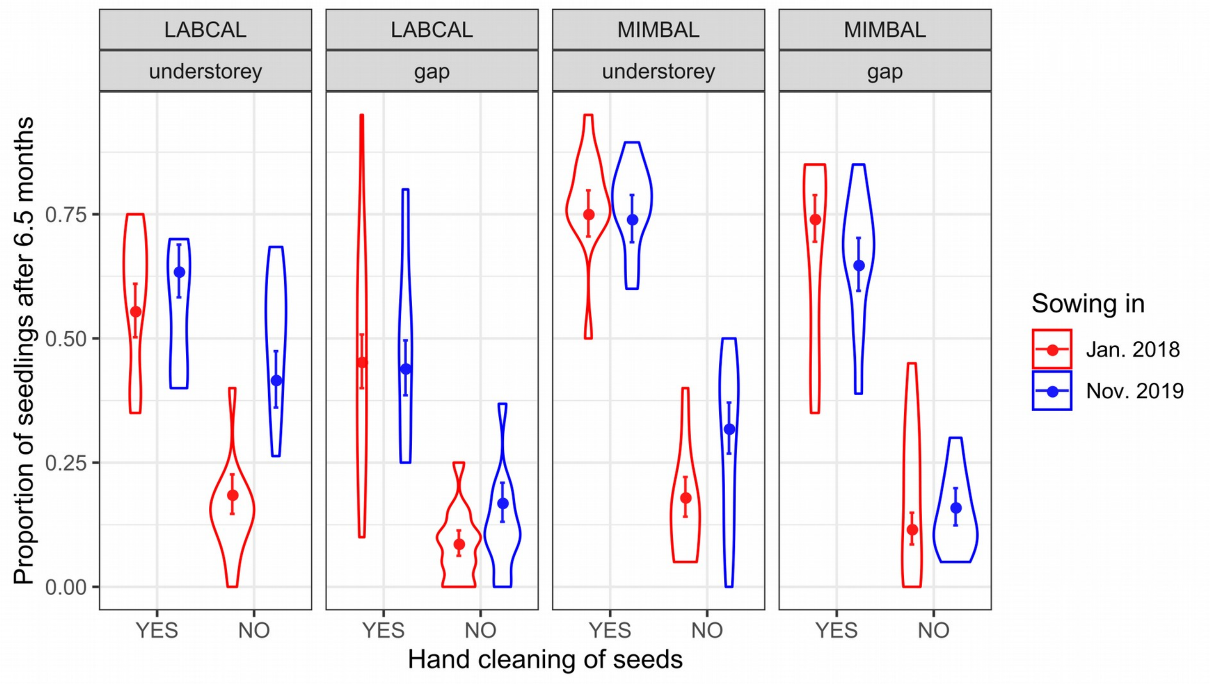

Fig.7.4 Seedling recruitment of* Labourdonnaisia calophylloides *(LABCAL) and* Mimusops balata *(MIMBAL) 6,5 months after sowing. *Violin plots show raw data, points and error bars respectively display mean values and confidence intervals predicted by the best fitting GLM.*

DISCUSSION

Most studies exploring the consequences of frugivore loss on tree recruitment focused on the Janzen-Connell hypothesis (Comita et al., 2014; Hansen et al., 2008; Terborgh, 2012; Terborgh et al., 2008). In contrast, few field studies have investigated the impact of pervasive flesh persistence around seeds resulting from the non-consumption of fruits after the extirpation of frugivores (but see Levi and Peres, 2013). We show using a field experiment without conspecific trees in the very vicinity of sowing areas that the role of flesh persistence has probably been underestimated and that it may be alone a primary cause of recruitment loss of *Labourdonnaisia calophylloides* and *Mimusops balata,* two large-seeded trees of the Sapotaceae family, as already demonstrated by Levi and Peres (2013) in Mata Atlantica for *Manilkara bidentata* (Sapotaceae). Thus, the reward that has been selected to effectively disperse large seeds in a highly competitive environment via frugivory (Eriksson et al., 2000), may become alone a major handicap for large-seeded plants when mutualist partners disappear from the ecosystem. However, our results are not in line with those of Baider and Florens (2006) that claim seed cleaning to have no effect on the germination rate of *Sideroxylon grandiflorum* (Sapotaceae) on Mauritius. Even if their weak sampling (only 32 fruits) may considerably limit the scope of their results, the negative impact of flesh persistence might be all the more important as the ratio of pulp to seed is high. Indeed, this ratio is much higher in *L. calophylloides* and *M. balata* than in *S. grandiflorum*. Our study also emphasizes significant inter-annual fluctuations in recruitment resulting from the complex role played by invasive seed predators and giant snails. This shows the difficulty of understanding the consequences of the extinction of native frugivores in ecosystems that have been largely refaunated by invasive animals since the beginning of human colonization (Meyer and Shiels, 2009; Shiels and Drake, 2011; Vizentin-Bugoni et al., 2019).

Processes by which flesh persistence may strongly limit recruitment

Several possible processes are involved in the negative effect of flesh persistence on tree recruitment. We distinguish here between those which act (i) before and (ii) after germination. (i) Before germination, flesh persistence induces a “no innate dormancy” for focal species, *i.e.* seeds are able to germinate quickly as soon as the flesh is removed (Baskin and Baskin, 2004), as demonstrated at Ilet Tessan. It is actually difficult to unravel the types of exogenous dormancy with our experiment.

Indeed, the hardness of the exocarp, especially for *M. balata* (**App.7.6**) and the presence of hydrophobic compounds in the latex-rich flesh of *L. calophylloides* (**App.7.5**)*,* might lead to a decrease in water level, preventing the induction of germination. Likewise, germination might be directly inhibited by chemical dormancy or mechanical resistance whatever the water potential (Baskin and Baskin, 2004). Pre-germination limitations might also be enhanced by the presence of pathogenic organisms, as suggested by Wyse Jackson et al. (1988) and noted by Levi and Peres (2013) in the same botanical family. Unfortunately, we have no new elements to contribute to a better understanding of this phenomenon. (ii) We show that flesh persistence may limit the survival of seedlings after germination. The hardness of the exocarp results in a major handicap for many seedlings because the root system not only has difficulty crossing the exocarp, but also tends to develop in the flesh (**App.7.6**). Many seedlings thus show secondary roots that remain in the open air once the flesh has disappeared. Most seedlings are subsequently badly anchored and much less armed to face all the biotic and abiotic hazards in the understory. As simple as this may seem, we did not find any studies documenting this type of recruitment limitation.

The negative impact of flesh persistence on recruitment and the relative commonness of focal species: a paradox?

Focal species have been chosen because they are still common in old-growth forests and generally produce a great amount of fruits easy to sample (Albert et al., 2020a; Cadet, 1977; Strasberg, 1996). Although these species have not been able to recolonize historical lava flows of the Piton de la Fournaise for more than two centuries (Albert et al., 2020a), they sometimes reach high levels of recruitment in old-growth forests, especially *L. calophylloides* which is dominant at all stages of growth in permanent plots at Mare Longue (Strasberg, 1996; chapter 6). This might seem paradoxical in view of the results following sowing in January 2018. However, our experiment reveals strong inter-annual differences in terms of seedling recruitment due to introduced giant snails and secondary dispersal & seed predation due to ship rats. The ability of these introduced animals to modulate the recruitment at Ilet Tessan shows that focal tree species may have benefited from complex interactions with introduced animals since the extirpation of native frugivores. In fact, poachers themselves may have played a significant role in supporting tree recruitment. These results may have important implications for understanding the dynamics of focal tree species in native forests.

At Ilet Tessan, the invasive giant snail *Achatina immaculata* usually known for its negative impact on native plants on islands (Tillier, 1992) can partially support the recruitment of focal species by cleaning the seed of *L. calophylloides* (**App.7.3**). While the role of these invertebrate should not be overestimated because they do not have the capacity to move away large seeds from mother trees, they are usually seen feeding on large fleshy fruits of other tree species such as *Hyophorbe indica* and might consequently support their recruitment in the understory of old-growth forests.

Rattus rattus shows surprising behavioural variability at Ilet Tessan. Fruits and seeds of focal species have not been attractive in 2018, but camera trap monitoring revealed the same year the high palatability of large fruits such as those of the endemic palm tree *Hyophorbe indica* (**App.7.3**) and the relative palatability of focal species in November 2019. The reasons for such variability remain unclear and might be related to environmental context (Loayza et al., 2020). *Rattus rattus* actually plays an ambivalent role as seed predator & secondary disperser (Shiels and Drake, 2011). It undeniably destroyed some seeds of *M. balata* at study site as already demonstrated for other large-seeded plants elsewhere on La Réunion (chapitre 5), but it behaves mainly as a secondary disperser of *L. calophylloides.* However, *Rattus rattus* may be a low-effective disperser of *L. calophylloides* in comparison with extinct large-bodied frugivores due to flesh persistence induced by its food wasting behaviour and its limited range (chapitre 5). A similar conclusion can be drawn on Mauritius for *Syzygium mamillatum*, a large-fruited endemic shrub of which *Rattus rattus* is a secondary disperser (Hansen et al., 2008). While the recruitment of this shrub is experimentally restored by the action of frugivore giant tortoises (Hansen et al., 2008), it remains very low in permanent plots of Brise Fer where many ship rats are present (chapitre 6).

Poachers have been using the latex of *L. calophylloides* fruits to catch birds all around the island (Cheke, 1987b). Indeed, they might have partially replaced extinct large-bodied frugivores by cleaning a great number of seeds and giving them mobility. Field observations show numerous seedlings near areas where poachers remove the flesh from fruits with an elaborated technique. Hence, *L. calophylloides* might be one of the large-seeded tree species that has suffered least from the loss of native frugivores and the *Labourdonnaisia* climax stage described by Cadet (1977) may be this signature. According to this hypothesis, canopies of tropical rainforest have become progressively richer in *L. calophylloides* since frugivore extinction to the detriment of many large-seeded species whose recruitment has been altered.

Regarding the other focal species, *M. balata*, the situation is more contrasted in terms of sapling recruitment. For example, this species does not regenerate well in the two best-preserved permanent plots where are encountered very large mother trees (Strasberg, 1996; chapitre 6). One may argue that this species is more light-demanding than *L. calophylloides* (Sarrailh et al., 2007) which ultimately explains this lack of recruitment, but the present experiment shows that this species regenerates also very well in the understory once the seeds have been hand-cleaned. Direct sowing could show whether *M. balata* is able to recruit in these permanent plots and ultimately demonstrate whether the disruption of frugivory interactions is the main limiting factor. In this case, the difference in recruitment currently observed in native forests might be due to differential behaviour of the introduced fauna depending on environmental contexts (Loayza et al., 2020).

Lastly, our field experiment shows that large-seeded trees can reach high recruitment rates in previously weeded areas notwithstanding the hyperskelitic soil (Meunier et al., 2010). If these recalcitrant species are quickly sown, seedling recruitment rates can be higher on the field than germination rates in *ex situ* nursery reported by Sarrailh et al. (2007). This demonstrates that plant-soil interactions which remain not well understood in the tropics (Camenzind et al., 2018) work well at Ilet Tessan. Thus, coupling invasive species control protocols with direct sowing is likely to be relevant for considering restoration actions in the long term, especially since native species that are still well dispersed will probably benefit from alien plant weeding (Baider and Florens, 2011; chapitre 6), as observed for several tree species such as *Antirhea borbonica* (Rubiaceae) and *Ficus mauritiana* (Moraceae) at Ilet Tessan (**App.7.7**).

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DISCUSSION GÉNÉRALE

Au cours de cette thèse, nous cherchons à comprendre quelles sont les conséquences écologiques des ruptures d'interactions entre les plantes à fruits charnus et les vertébrés frugivores dans les Mascareignes. L'archipel est tristement célèbre pour avoir abrité jusqu'au $18^{ème}$ siècle une faune de vertébrés originale et pléthorique aujourd'hui largement éteinte dont le Dodo, mais il abrite encore des écosystèmes indigènes à forts enjeux de conservation et protégés au sein de parcs nationaux à La Réunion et à Maurice. Les inventaires historiques et relativement exhaustifs des faune et flore indigènes des Mascareignes, l'existence d'ouvrages taxonomiques et de collections depuis le $18^{ème}$ siècle et les récentes archives subfossiles, permettent de reconstruire avec précision la composition des communautés animales et végétales dans les forêts tropicales de l'archipel. De plus, les disparités entre les îles concernant les niveaux de défaunation et la chronoséquence offerte par un des volcans les plus actifs au monde, font des Mascareignes un système d'étude particulièrement pertinent pour analyser les conséquences des changements d'interactions de frugivorie depuis la colonisation humaine récente.

Nous étudions d'abord la distribution spatiale des traits de dispersion dans l'archipel et explorons dans quelle mesure la rupture d'interactions de frugivorie a pu influencer la cinétique d'extinction des vertébrés frugivores via la destruction des habitats favorables (partie I). Ensuite, via l'extinction des frugivores, nous examinons les conséquences des ruptures d'interactions de frugivorie sur la dynamique forestière le long de la chronoséquence des coulées du Piton de la Fournaise (partie II) et sur le maintien de la diversité des ligneux dans les forêts anciennes et protégées de l'archipel (partie III). Cette discussion générale s'organise en sept points qui visent à rappeler les principales conclusions et revenir sur un certain nombre de questions qui n'ont pu être suffisamment développées dans les chapitres précédents. Si chacune des grandes parties se voit consacrée un point, quatre points supplémentaires s'attachent à discuter thématiquement les résultats pour élargir la réflexion : les enseignements concernant l'étude de la succession, les limites des protocoles mis en œuvre pour comprendre la faune, les enseignements concernant les invasions de plantes exotiques, et le besoin urgent d'action de conservation et de restauration pour soutenir la dynamique forestière. Cette discussion générale ouvre ainsi plusieurs perspectives de recherche dans le champ de l'écologie, la biogéographie, l'évolution et la biologie de la conservation des écosystèmes forestiers en s'appuyant notamment sur des expérimentations annexes et en proposant des exemples d'actions de conservation *in situ*.

Distributions présente et passée des plantes à fruits charnus et des frugivores

La diversité biologique des forêts de basse altitude dans les Mascareignes est très largement dominée par les espèces ligneuses à fruits charnus parmi lesquelles les espèces à gros fruits (diamètre >1,2 cm) sont particulièrement structurantes dans les canopées de ces forêts (Albert et al., 2018 ; chapitres 1 et 2). Si, avant l'arrivée de l'Homme, les forêts mauriciennes présentaient probablement peu de variations dans leur diversité des traits de dispersion en raison de l'altitude limitée de cette île, il en va très différemment à La Réunion où un des gradients d'altitude les plus puissants au niveau mondial a été mis en évidence concernant les changements dans les proportions de plantes à fruits charnus (de plus de 80 % des plantes ligneuses au niveau de la mer à zéro % au dessus de 2400 m). La décroissance des proportions de plantes à gros fruits charnus le long des gradients d'altitude est en réalité encore plus forte et ces espèces sont essentiellement confinées dans une étroite bande de végétation de basse altitude comme l'avaient déjà remarqué Cheke et Dahl (1981). Ces patterns ont d'importantes implications. Tout d'abord, les habitats les plus vulnérables suite à la perte des vertébrés frugivores à La Réunion sont ceux de basse altitude qui sont aujourd'hui largement transformés et fragmentés (Strasberg et al., 2005), ce qui nous a conduit dans les parties II et III de cette thèse à nous concentrer sur la forêt tropicale humide dont les vestiges représentent d'importants enjeux de conservation (*cf* les six points suivants de cette discussion générale). Ensuite, la destruction précoce de la ceinture d'habitats de basse altitude à La Réunion est probablement le facteur principal qui explique l'étonnant paradoxe quand on compare aujourd'hui La Réunion et Maurice avec respectivement « les forêts indigènes sans les grands vertébrés frugivores » et « les vertébrés frugivores sans les forêts » (chapitre 2). Cette hypothèse s'appuie largement sur ce que la distribution actuelle des plantes à fruits charnus peut nous enseigner sur la distribution passée des vertébrés frugivores largement éteints. Enfin, la modélisation statistique associée aux patterns de distribution des plantes à fruits charnus suggère la présence d'habitats diversifiés dans les zones les plus sèches de basse altitude où plus aucun témoin de végétation indigène ne subsiste à l'échelle des Mascareignes.

Le puissant gradient d'altitude comme facteur de vulnérabilité des vertébrés frugivores

Si l'ensemble de la faune des Mascareignes a subi une extinction massive à l’échelle de tout l’archipel, la faune de vertébrés frugivores de La Réunion présente dès l’origine une vulnérabilité accrue face à la colonisation humaine en raison de facteurs climatiques et biogéographiques. En effet, les autres facteurs habituellement associés aux extinctions dans les îles (introduction de prédateurs, chasse ou surface absolue des habitats indigènes détruits) ne peuvent expliquer seuls pourquoi La Réunion a perdu si rapidement sa faune en comparaison avec l'île sœur, Maurice (chapitre 2). La destruction quasi-totale et précoce des habitats favorables de basse altitude à La Réunion constitue un cas d'école qui s’inscrit dans un cadre plus général où les îles océaniques de haute altitude ont des taux d'extinction de frugivores plus élevés que les autres îles à l'échelle globale (Heinen et al., 2017).

Les facteurs climato-topographiques et biogéographiques qui déterminent la distribution spatiale des traits des fruits influençaient la distribution des vertébrés frugivores qui dépendaient de ces habitats au moins pour leur alimentation (chapitres 1 et 2). Les transitions brutales dans les communautés de plantes à La Réunion s'accompagnaient probablement de changements tout aussi forts dans les assemblages de frugivores comme cela a été montré dans divers systèmes montagneux continentaux (Dehling et al., 2014; Ferger et al., 2014; Hazell, 2019). Par exemple, les plantes à gros fruits charnus deviennent très rares dès le niveau supérieur de l'étage submontagnard (>1200 m) où l'ennuagement très important pourrait entraîner une forte baisse de la production primaire nette (Malhi et al., 2017), et la plupart des lignages de plantes à fruits charnus sont fortement limités par leur tropicalité au dessus de la zone d'apparition du gel (Kerkhoff et al., 2014). De plus, les proportions beaucoup plus importantes de plantes à fruits charnus dans les écosystèmes subalpins des Andes et de Papouasie (Buitrón-Jurado et Ramírez, 2014; Turner, 2001) suggèrent qu'il existe un important forçage régional (*sensu* Ibanez et al., 2018) qui pré-déterminerait les habitats de montagne à être moins favorables aux vertébrés frugivores dans l'écozone afrotropicale par rapport à d'autres régions du monde.

Si la destruction précoce des habitats de basse altitude prodiguant de grandes quantités de nourriture a pu jouer un rôle déterminant dans la disparition rapide des frugivores à La Réunion (chapitre 2), cela n'exclut pas pour autant que des limitations physiologiques se soient exercées directement sur ces vertébrés dans les habitats relictuels moins favorables en termes de température et de précipitations (McCain, 2009). Ce dernier mécanisme pourrait d'ailleurs être davantage satisfaisant pour expliquer les difficultés de vertébrés forestiers appartenant à d'autres guildes (*e.g.* insectivores) à survivre dans des habitats suboptimaux (*cf* Thiollay et Probst, 1999) voire défavorables.

Certains récits de voyageurs relatent au 17ème siècle des migrations saisonnières avec des éléments de l'avifaune « descendant des montagnes » (Cheke et Hume, 2008; Lougnon, 2005), laissant entendre que cette faune pourrait avoir utilisé temporairement les habitats de montagne (*sensu* chapitre 2). Mais il faut rester prudent dans l'interprétation des récits d'une époque où ces voyageurs fréquentaient essentiellement une étroite bande littorale de l'île, généralement sous-le-vent : ces migrations saisonnières intervenaient probablement entre les basses et moyennes altitudes (Hume, 2011). Les ceintures de forêts de basse altitude ayant été rapidement détruites et celles de moyenne altitude soumises à de multiples et fortes perturbations anthropiques, les habitats de montagne n'ont probablement pas agi comme des refuges pour la majeure partie des vertébrés car ils n'étaient pas adaptés pour y survivre (chapitre 2).

Le rôle du filtre de dispersion sur la répartition des plantes à fruits charnus sous-estimé ?

La dispersion des plantes à fruits charnus reposant sur les vertébrés frugivores, ces derniers jouent un rôle primordial dans l'assemblage des communautés de plantes ligneuses (*cf* Cadotte et Tucker, 2017). Dans le chapitre 1, nous considérons que les conditions environnementales contrôlaient directement la distribution de types de fruits à La Réunion avant l'extinction massive de la faune, avec une barrière à la dispersion assumée très faible. Pourtant, si nous connaissons bien l'aire de distribution des petits frugivores relictuels à La Réunion (*Hypsipetes borbonicus, Zosterops* spp.), les choses sont plus complexes concernant les grands frugivores éteints et la discussion passe assez vite sur le fait que certaines corrélations pourraient refléter leur aire de distribution passée (aux Baléares, *cf* Riera et al., 2002). Certaines plantes ligneuses pourraient par exemple être absentes des zones les plus orientales de La Réunion parce que le filtre environnemental se serait exercé sur leur disperseur potentiel, *e.g. Cylindraspis indica*. Pour tester cette hypothèse, nous pouvons d'abord nous appuyer sur les récits des pionniers qui ont parfois longuement décrit la faune éteinte. Il apparaît que les mentions de la tortue géante de Bourbon sont rares sur la côte-au-vent : « quelques tortues » et « quelques captures » sont respectivement relatées en 1671 au « pays qu'on nomme Brûlé » et « à l'embouchure de la rivière Saint-Jean » (Lougnon, 2005). Cependant, les récits évoquent surtout les zones sous-le-vent précocement colonisées, et leur rareté dans le Sud-Est pourrait provenir du fait que le front pionnier n'y est parvenu que tardivement, quand *C. indica* était déjà presque éteinte dans les écosystèmes. La paléontologie pourrait apporter des éléments déterminants, mais les vestiges subfossiles de *C. indica* très abondants sur la côte-sous-le-vent (Mourer-Chauviré et al., 1999) sont rares sur la côte-au-vent où une carapace aurait été retrouvée dans la Mare d'Arzule d'après Bory de Saint Vincent (1804). Il serait pourtant précipité d'en déduire que cette espèce était originellement absente ou très rare dans la zone. Le même dilemme existe en effet à Madagascar où l'absence d'ossements subfossiles d'*Aldabrachelys abrupta* sur la côte Est pourrait provenir d'une combinaison de facteurs : les conditions climatiques rendent difficile la conservation des ossements sur la façade orientale où sont de plus absents des environnements propices au piégeage accidentel de la faune (Goodman et Jungers, 2014).

Pour mieux comprendre la distribution passée de la faune éteinte et démêler les mécanismes d'assemblages des communautés de plantes, un changement d'échelle pourrait être entrepris au niveau des îles du Sud-Ouest de l'océan Indien. Plusieurs de celles-ci possèdent encore de grands frugivores qui sont éteints dans les Mascareignes (e.g *Alectroenas* spp. à Madagascar, aux Comores et aux Seychelles) et suffisamment de contrastes environnementaux dans les différentes îles pour mieux comprendre dans quelle mesure les frugivores contraignent la distribution des plantes à fruits charnus et *vice versa* (*cf* Correa et al., 2015). Enfin, des semis expérimentaux permettraient de tester si certains ligneux à grosses graines sont capables de s'établir dans des habitats où ils sont actuellement absents dans l'Est de l'île (*e.g. Latania lontaroides*, *Terminalia bentzoë*).

De la nature des habitats de basse altitude les plus secs

Les habitats originels de basse altitude sous-le-vent étaient peut-être les plus favorables aux grands vertébrés forestiers des Mascareignes comme cela a déjà été suggéré dans les Antilles et à Hawai‘i (Olson et James, 1989). Pourtant, la nature de ces habitats insulaires reste très mal connue car ils ont été précocement soumis à de sévères perturbations et complètement transformés. Si le débat sur leur nature originelle reste ouvert à La Réunion (*cf* Boullet, 2020; Cadet, 1977; Strasberg et al., 2005), nous avons néanmoins de bonnes raisons de croire que les bas de l'Ouest étaient au moins parsemés de forêts galeries là où les conditions environnementales étaient plus favorables, voire dominés par un habitat diversifié avec une structure forestière potentiellement semi-ouverte en raison des hautes densités de *Cylindraspis indica* (*cf* Bakker et al., 2016). Pour étayer cette hypothèse, nous pouvons nous appuyer sur (1) la modélisation des traits de dispersion basés sur des variables climato-topographiques, (2) les récits des pionniers et (3) les travaux paléoécologiques.

Fig.d.1 *Graines de* Terminalia bentzoë *issues des fouilles de Mourer-Chauviré* et al. *dans les marais de l'Ermitage. Photo : D. Strasberg.*

(1) La modélisation de la distribution des traits de dispersion n'est guère compatible avec l'existence de savanes indigènes dominées par des Poaceae défendue par Boullet (2020), et ces habitats où *Latania lontaroides* et *Terminalia bentzoë* sont supposés avoir joué un rôle important (Cadet, 1977; Strasberg et al., 2005) pourraient avoir été relativement riches en espèces ligneuses, notamment à fruits charnus (chapitres 1 & 2). Néanmoins, du fait de la destruction intégrale de la végétation dans les zones les plus sèches, nos modélisations sont basées sur une extrapolation des coefficients dans ce secteur et doivent être prises avec prudence (**App.2.3**). (2) Certains récits au début de la colonisation humaine évoquent de véritables forêts au niveau de la mer. Houssaye décrit par exemple très clairement que la Pointe des Galets est boisée en 1689, et qu'une grande partie de la végétation sous-le-vent a déjà été largement incendiée (Lougnon, 2005). (3) Les études paléoécologiques offrent un fort potentiel d'investigation. Si les

premiers travaux palynologiques à l'étang de Saint-Paul n'ont pas permis de mettre en évidence l'existence d'une savane indigène avant la colonisation humaine, de nombreuses graines ont en revanche été excavées parmi une quantité prodigieuse d'ossements de *Cylindraspis indica* par Mourer-Chauviré et al. (1999) dans les marais de l'Ermitage (D. Strasberg, données non-publiées, **Fig.d.1**). Parmi ces graines témoignant de l'existence de diverses espèces d'arbres à gros fruits de la forêt de basse altitude, on peut identifier les attendues *L. lontaroides* et *T. bentzoe*, mais aussi *Cassine orientalis*, *Pandanus sylvestris, Foetidia mauritiana* ou encore *Sideroxylon majus*. Néanmoins, ces graines ne peuvent être rigoureusement associées à une séquence stratigraphique pour comprendre dans quel contexte elles se sont précisément déposées et la proximité des semenciers demeure spéculative. Cela invite à reprendre les travaux paléoécologiques à l'Ermitage d'autant qu'il existe de multiples méthodes pour étudier les restes subfossiles de la flore (*e.g.* bois morts, pollens ou graines), de la faune (*e.g.* os, élytres) voire des microfossiles (*cf* la très belle étude de Rijsdijk et al. (2009) à la Mare aux Songes à Maurice). L'existence de nombreux sites potentiellement favorables tout autour de l'île invite plus globalement à poursuivre les investigations paléoécologiques à La Réunion (chapitre 2).

La dynamique de colonisation des forêts indigènes profondément altérée à La Réunion

Après avoir étoffé la chronoséquence des coulées de lave du Piton de la Fournaise à basse altitude (Albert et al., 2020b ; chapitre 3), nous montrons une perte dramatique de la diversité des plantes ligneuses sur les coulées historiques, *i.e.* qui se sont produites après le début de la colonisation humaine permanente en 1665 (Albert et al., 2020a ; chapitre 4). L'ampleur de cet effondrement est telle que la diversité *alpha* à tous les stades de croissance est plus élevée dans 1000 m² de forêt ancienne que la diversité *gamma* sur les coulées du 20ème siècle où le même cortège d'espèces indigènes est rencontré de manière récurrente. Si diverses études ont montré à l'échelle des communautés l'impact négatif de plusieurs décennies de rupture d'interactions de frugivorie sur les forêts continentales (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010) ou insulaire (Wandrag et al., 2017), le système d'étude des coulées du Piton de la Fournaise révèle pour la première fois les conséquences à long terme de la défaunation sur la capacité d'une forêt tropicale humide à se reconstruire. Cela montre aussi que la défaunation peut impacter le fonctionnement des écosystèmes de manière comparable aux principaux déterminants des changements globaux (Dirzo et al., 2014; Young et al., 2016).

Des études observationnelle et expérimentale couplées dans un système unique

Seule une longue chronoséquence comme celle des coulées de lave du Piton de la Fournaise peut permettre de comprendre les conséquences de la perte des vertébrés frugivores sur plus de trois siècles (Albert et al., 2020a ; chapitre 4). S'appuyant sur une combinaison de facteurs unique au monde, *i.e.* un des volcans terrestres les plus actifs dans un des derniers territoires tropicaux à avoir été colonisés par l'Homme, cette expérience naturelle nous offre une sorte de machine à remonter le temps et illustre le potentiel des îles pour tester des questions en écologie qui ne peuvent être explorées ailleurs (Warren et al., 2015). Il n'est cependant pas possible de démontrer formellement que c'est bien la rupture de la dispersion des plantes à fruits charnus à partir du 18ème siècle qui explique l'effondrement de leur diversité sur les coulées historiques, il aurait fallu pour cela mesurer la pluie de graines en continu depuis le 17ème siècle. A ce jour, le plus ancien suivi diachronique de la reconstruction d'une forêt tropicale ne dépasse d'ailleurs pas 130 ans (Thornton, 1997). Mesurer la pluie de graines et tester l'impact d'autres limitations étaient en revanche réalisables lors de cette thèse, et l'expérimentation mise en place au

Tremblet (chapitre 5) est venue corroborer les conclusions du chapitre 4, tout en apportant de nouveaux éclairages.

Les chapitres 4 et 5 combinés permettent de mieux discuter les mécanismes à l'œuvre derrière l'effondrement de la diversité sur les coulées de lave historiques. La pluie de graine très appauvrie en 2019-2020 ne laisse que peu de doutes sur l'impact très négatif de la disparition des frugivores indigènes sur la dynamique de colonisation des plantes. Cela est d'autant plus marquant que les populations de frugivores en 2020 sont à des niveaux supérieurs à ce qu'ils étaient à l'époque des relevés botaniques de Cadet sur lesquels s'appuie le chapitre 4 : *Hypsipetes borbonicus* était alors peu commun en raison du braconnage intense et *Pycnonotus jocosus* venait d'être introduit et ne jouait pas encore le rôle qu'il joue aujourd'hui du fait de l'explosion de ses populations en quarante ans (Cheke et Hume, 2008). Pourtant, aucune graine de plus de 8 mm de diamètre n'a pu être piégée malgré une disponibilité importante en grosses graines à proximité. Et même si des événements rares de dispersion peuvent probablement intervenir (*cf* le point « faunes »), on comprend bien pourquoi les plantes à gros fruits sont si rares sur les coulées historiques. Cela est particulièrement problématique pour les plantes pionnières à fruits charnus qui ont de grandes difficultés à se maintenir dans le sous-bois des forêts anciennes (Wandrag et al., 2017).

Dans les *kipukas* très isolés, la diversité est plus faible que dans les forêts moins fragmentées, mais ce phénomène est surtout observé sur les coulées historiques car les derniers *kipukas* de forêt ancienne au Grand Brûlé abritent souvent une remarquable diversité malgré des surfaces parfois très réduites (chapitre 4). La perte des grands vertébrés frugivores n'a en effet pas seulement entraîné la perte de la dispersion des plantes à grosses graines, mais aussi la fin de la dispersion à longue distance pour la plupart des plantes à fruits charnus indigènes (*cf* Naniwadekar et al., 2019; Wotton et Kelly, 2012). Même sur la coulée de 1800 qui présente pourtant une largeur modeste d'environ 100 m, le bulbul de la Réunion ne disperse que peu de graines de taille moyenne au centre de la coulée du fait de son comportement essentiellement forestier (chapitre 5). Il ne faut donc pas s'attendre à ce que ce passereau qui est le dernier frugivore indigène depuis plus de 150 ans, ait pu participer de manière efficace à la reconstruction des écosystèmes forestiers dans la caldeira où dominent de vastes zones ouvertes. De nombreuses espèces emblématiques de la forêt tropicale humide ont localement disparu avec la destruction de la dernière forêt littorale de l'île en 2007 ou sont confinées à de rares *kipukas* au Sud de la caldeira (chapitre 4). Si rien n'est fait avant leur inexorable destruction, la diversité des plantes indigènes se réduira à une vingtaine d'espèces avec une diversité fonctionnelle très faible.

Pour démontrer que l'absence de nombreuses plantes indigènes est d'abord la conséquence d'une limitation de la dispersion suite à la perte des frugivores, nous avons semé diverses espèces à grosses graines (chapitre 5). Au Tremblet, nous montrons sans équivoque que trois espèces d'arbre à grosses graines sont tout à fait capables de s'établir jusqu'au centre de la coulée de 1800 et que la prédation des graines n'est qu'une limitation secondaire comme dans d'autres îles où la dispersion reste le mécanisme le plus limitant (Hansen et al., 2008; Wotton et Kelly, 2011). Nous avons de même semé diverses espèces indigènes à fruits charnus au Grand Brûlé sur la coulée de 1943 (**Fig.d.2**). Le semis a été réalisé dans une zone incendiée en 2019 où on note de fortes abondances de plantes exotiques et une diversité de plantules indigènes très faible malgré la présence de nombreux semenciers indigènes et de bulbuls de la Réunion dans le *kipuka* contigu (Thébaud et Strasberg, 1997). Les nombreuses levées de plantules observées après les semis sur la coulée de 1943 malgré des conditions environnementales difficiles montrent encore une fois que l'extrême pauvreté des ligneux indigènes sur ces coulées récentes est avant tout la conséquence d'une forte limitation de la dispersion.

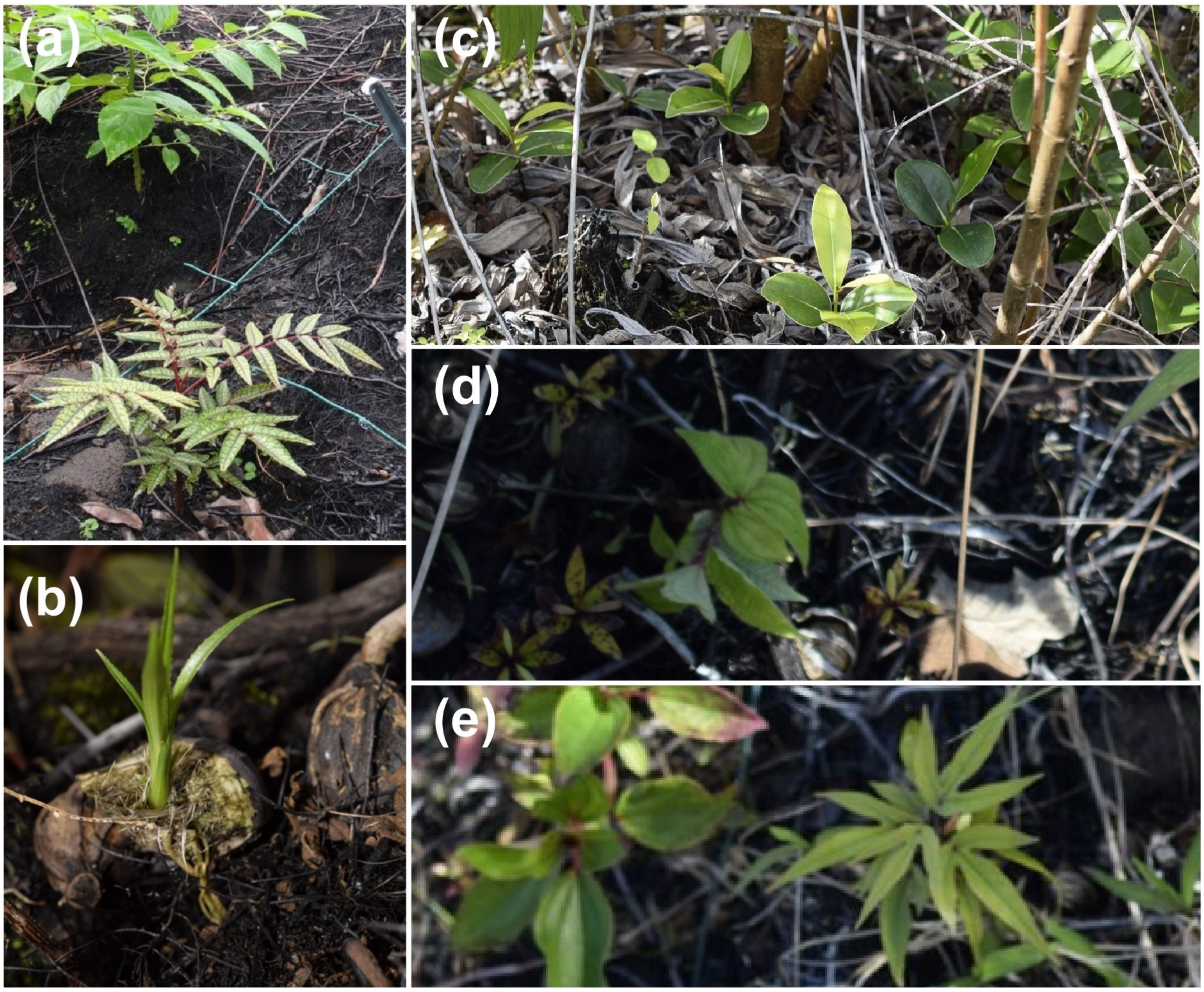

***Fig.d.2** Plantules issues de semis sur la coulée de 1943 incendiée en janvier 2019. La zone de semis est très ouverte et les conditions environnementales difficiles comme l'attestent les dimensions modestes de la flore exotique envahissante à proximité. Pourtant, l'établissement au moins sous forme de plantules de la plupart des espèces semées montre que leur absence sur les coulées du 20ème siècle est bien la conséquence d'une très forte limitation de la dispersion. (a)* Poupartia borbonica *(Anacardiaceae); (b)* Pandanus purpurascens *(Pandanaceae); (c)* Mimusops balata *(Sapotaceae); (d)* Syzygium borbonicum *(Myrtaceae); (e)* Hernandia mascarensis *(Hernandiaceae). Photos : A. Gorissen.*

Les frugivores indigènes ont probablement joué un rôle qui allait au-delà de la vection des diaspores dépulpées sur les coulées de lave du Piton de la Fournaise. La faune d'origine décrite comme pléthorique par les pionniers (Cheke et Hume, 2008; Lougnon, 2005) l'était peut-être tout autant dans les *kipukas* où les ressources étaient abondantes, et a probablement contribué à un apport important de nutriments via leurs fèces, mais aussi de micro-organismes facilitateurs (Cázares et al., 2005; Correia et al., 2019; Walker et Moral, 2003). Vu le regain d'intérêt pour le rôle des vertébrés dans le recyclage des nutriments dans les écosystèmes (Andriuzzi et Wall, 2018; Dirzo et al., 2014; Falcón et Hansen, 2018; Young et al., 2016), ces hypothèses qui ont été très peu étudiées dans le cadre de la succession primaire offrent d'intéressantes perspectives expérimentales à La Réunion.

Recolonisation des plantes post-glissement de terrain et dans les déprises agricoles

La forte perte de résilience des écosystèmes forestiers mise en évidence sur les coulées historiques du Piton de la Fournaise s'exprime partout où les écosystèmes indigènes ont été sévèrement perturbés. Cela peut concerner la recolonisation des plantes après d'autres phénomènes naturels tels les glissements de terrain, mais aussi dans d'anciennes cultures à l'abandon qui concernent d'importantes surfaces à La Réunion (Cheke et Hume, 2008).

La Réunion présente un relief particulièrement accidenté (**Fig.1.1c**) dont les impressionnants remparts qui sont classés au patrimoine mondial de l'humanité et sujets à de fréquents glissement de terrain (Raucoules et al., 2006). Ces derniers entraînent généralement une succession primaire, avec la perte des banques de graines et de plantules sur un substrat souvent mis à nu ou très appauvri (Walker et Moral, 2003). La dispersion joue dès lors un rôle central dans la recolonisation des plantes (Shiels et Walker, 2003). Nous avons de bonnes raisons de penser que la fréquence importante des glissements de terrain à La Réunion et la non-capacité des écosystèmes à se reconstruire depuis des siècles (chapitres 4 et 5) entraînent une forte perte de diversité dans toute l'île. Cela est d'autant plus dommageable que ces remparts abritent souvent des vestiges de forêt ancienne qui n'ont pas été défrichés en raison de l'impossibilité de mettre ces surfaces en culture (Cadet, 1977; Strasberg et al., 2005). De nombreuses observations dans les remparts montrent en effet que la végétation est souvent structurée en bandes perpendiculaires aux courbes de niveau, avec une diversité des traits de dispersion très faible là où la végétation semble plus jeune. Si le suivi 40 ans après Cadet (1977) de plusieurs relevés post-glissement de terrain suggère clairement une succession très perturbée, la forte hétérogénéité des traits de dispersion n'a cependant pu être reliée à l'âge des communautés à large échelle comme dans le chapitre 4.

La recolonisation des plantes est encore davantage perturbée dans les cultures abandonnées à La Réunion comme l'avait déjà remarqué Cadet (1977). Les vastes surfaces de déprise agricole peuvent se trouver à proximité de riches reliques de forêt indigène mais montrent souvent un fort niveau d'envahissement (Strasberg et al., 2005) associé à une faible diversité des traits de dispersion. Parmi les ligneux indigènes avec les plus grosses graines, on y rencontre souvent *Molinaea alternifolia* et *Doratoxylon apetalum* comme au Tremblet (chapitre 5), mais aussi *Olea lancea* (5,5 mm) sous-le-vent. Ces espèces s'accompagnent d'un nombre restreint de plantes indigènes généralement à petites graines. Le cortège de plantes capables de recoloniser les déprises agricoles à basse et moyenne altitude est en réalité proche de celui observé sur les coulées du 20ème siècle (chapitre 4), auquel s'ajoutent quelques ligneux qui semblent relativement bien dispersés sous-le-vent comme *Pleurostylia pachyphloea* ou *Turraea thouarsiana*. Au final, la baisse de la diversité fonctionnelle indigène dans ce cadre est généralement comparable à ce qui est observé dans celui de la succession primaire à La Réunion, comme ailleurs (Caves et al., 2013; Franklin et Rey, 2007). Ces déprises agricoles montrent des niveaux d'invasion souvent élevés, probablement encore davantage que sur les coulées historiques où la situation est déjà très préoccupante (chapitre 5 ; Potgieter et al., 2014; Strasberg, 1994). Cela provient probablement de la propagation massive *in situ* par l'Homme de plantes cultivées à fruits charnus comme *Psidium cattleianum, Syzygium jambos*, *Rubus alceifolius* ou *Lantana camara* sur lesquelles se nourrissent ensuite les frugivores indigènes et introduits (*cf* point « invasions »).

Dispersion et reconstruction des écosystèmes montagnards et subalpins

Les expérimentations réalisées au cours de cette thèse se sont concentrées en forêt tropicale humide sur des plantes à fruits charnus, mais la question des conséquences de la défaunation sur des habitats parfois pauvres en espèces à fruits charnus se pose également. *Sophora denudata* (Fabaceae) est par exemple un des arbres les plus abondants et structurants à La Réunion aux hautes altitudes où il joue un rôle majeur dans le fonctionnement des écosystèmes, mais présente des difficultés de régénération en particulier quand le sous-bois est dominé par des Poacées exotiques (Gabriel et Jauze, 2008). Cet arbre est apparenté à Hawai'i avec *Sophora chrysophylla* avec lequel il partage une niche écologique proche. Ces deux espèces appartiennent en fait à un lignage de plantes dont les ratites et rallidés peuvent avaler les graines et lever la forte dormance par la même occasion (Kildisheva et al., 2013; Levey et al., 2002). Si le disperseur potentiel de *S. chrysophylla* demeure inconnu à ce jour à Hawai'i (Don Drake, comm. pers.), il est troublant de constater que la Réunion abritait un énigmatique râle endémique, « l'oiseau bleu » ('*Porphyrio coerulescens*'), qui vivait en altitude et dont la distribution pourrait avoir été beaucoup plus étendue que la seule Plaine des Cafres où il a souvent été relaté (Hume, 2019). *S. denudata* pourrait ainsi avoir perdu son vertébré disperseur, ce qui expliquerait pourquoi cet arbre qui peut encore être localement abondant, présente une telle agrégation spatiale de la régénération et reste parfois absent de vastes surfaces aux hautes altitudes. Les rares forêts à *Sophora* rencontrées jusqu'à 2400 m d'altitude ne sont que les vestiges de forêts beaucoup plus étendues avant la colonisation humaine (Strasberg et al., 2005). Une part importante des fourrés éricoïdes subalpins pourrait d'ailleurs être secondaire et provenir de la recolonisation massive des habitats détruits grâce à la grande capacité de dispersion des Ericaceae et Asteraceae (chapitre 1). Dans les zones où *S. denudata* ne peut être dispersée par les eaux de ruissellement, il ne faut pas escompter que cet arbre participe au retour de la forêt dont la limite altitudinale est normalement donnée à La Réunion à 2450 m par Irl et al. (2016).

La question se pose également pour les nombreuses espèces du genre *Dombeya* (Malvaceae) qui jouent un rôle capital dans les canopées des forêt de montagne. De nombreux travaux ont été menés sur les traits floraux et la pollinisation des Dombeyoideae dans la région, mais les modalités de dispersion dans ce groupe demeurent très mal connues. Pourtant, certaines études en Afrique mentionnant le rôle de mammifères (Lambert, 1999) et oiseaux (Seyani et White, 1991) comme disperseurs de ces plantes à fruits secs invitent à la réflexion.

Perspectives micro-évolutives chez un palmier endémique

L'étude de la pluie de graines sur la coulée de 1800 montre que les fruits d'*Acanthophoenix crinita,* palmier avec des graines de taille moyenne, sont attractifs pour les frugivores relictuels (chapitre 5). Ce palmier qui jouait un rôle majeur dans les écosystèmes d'origine (Cheke et Hume, 2008), offre une remarquable opportunité de tester un scénario micro-évolutif. En effet, une sélection directionnelle entraînant une forte diminution de la taille de graine a peut-être été exercée par les petits frugivores relictuels depuis trois siècles. Cela ne serait pas une première chez les palmiers où ce phénomène a été montré sur des pas de temps très variables allant de plusieurs milliers d'années (Lim et al., 2020) à moins de 150 ans (Galetti et al., 2013), avec une perte potentiellement rapide de la diversité génétique (Carvalho et al., 2016; Giombini et al., 2017). *Acanthophoenix crinita* qui montre une bonne dynamique de régénération sur les coulées récentes dès lors qu'il n'est pas braconné pour son «chou» très prisé (**Fig.d.3**), est considéré comme endémique de la Réunion et distinct d'*Acanthophoenix rubra* qui n'existerait plus que dans les zones cultivées à La Réunion (Ludwig, 2006). Les principaux caractères qui permettent de distinguer les deux taxa sont les tailles des fruits et graines, les autres critères y compris les aires de distribution présentés par Ludwig (2006) s'avérant en réalité peu discriminants. Selon notre hypothèse, ces deux taxa pourraient appartenir à la même espèce, et leurs diaspores auraient divergé depuis trois siècles, avec d'un côté les cultivateurs maintenant la taille prédéfaunation, et de l'autre la frugivorie du bulbul de la Réunion ayant entraîné une forte diminution de celle-ci. Seule une étude couplant des analyses morphologique et génétique chez *Acanthophoenix* dans les Mascareignes permettrait de tester si la défaunation sévère des écosystèmes a rapidement eu de drastiques conséquences évolutives à La Réunion.

***Fig.d.3** Vue aérienne de la canopée d'un* kipuka *au pied des Grandes Pentes vers 500 m d'altitude. Le palmier* Acanthophoenix crinita qui *est particulièrement structurant sur cette coulée datée du 18ème siècle s'établit aussi sur les coulées adjacentes plus récentes. Photo de drone : H. Santacreu.*

La difficile étude de la succession dans les forêts tropicales via les chronoséquences

Depuis quelques années déjà, l'emploi des chronoséquences pour étudier la succession des écosystèmes forestiers tropicaux soumis à diverses perturbations a été vivement critiqué (Johnson et Miyanishi, 2008; Walker et al., 2010). L'effondrement de la diversité de traits de dispersion fortement corrélé à la disponibilité des frugivores sur les coulées historiques du Piton de la fournaise apporte peut-être la plus frappante des démonstrations du caractère problématique des longues chronoséquences pour étudier la succession en milieu tropical (Albert et al., 2020a ; chapitre 4).

A La Réunion, les types de végétation interprétés comme des stades successionnels précoces par Cadet (1977) sont en réalité caractéristiques de la capacité des écosystèmes à se reconstruire depuis le début de la colonisation humaine permanente. La résilience des écosystèmes n'ayant cessé de se dégrader en particulier en raison de la disparition des agents de dispersion, les communautés sur les coulées historiques (ne) s'enrichissent peu (plus) en ligneux indigènes à fruits charnus, mais sont en revanche petit à petit envahies par des plantes exotiques (Potgieter et al., 2014; Strasberg, 1994; chapitre 5). Ainsi, la *forêt à Agarista* de Cadet (1977) ne deviendra jamais une *forêt à Sideroxylon* qui ne deviendra jamais à son tour une *forêt à Labourdonnaisia*, parce que *Labourdonnaisia* n'atteint pas les coulées post-1800 et que *Sideroxylon* n'est pas (ou est très peu) dispersé sur les coulées dominées par *Agarista* (Albert et al., 2020a ; chapitres 4 et 5). Et ce constat était déjà valable bien avant que les invasions végétales perturbent davantage la dynamique de la colonisation des plantes. Le même problème est posé par l'interprétation faite par Potgieter et al. (2014) de la chronoséquence du Piton de la Fournaise. Selon ces auteurs, l'invasion de *Casuarina* aurait accéléré le taux de la succession végétale d'un facteur 7, mais le temps que mettait une forêt indigène à se structurer quand les ligneux indigènes n'étaient pas fortement limités par la dispersion demeure en réalité inconnu. Si connaître la succession qui permettait de bâtir la forêt tropicale humide d'origine à La Réunion pourrait bien être inatteignable, l'étude de la chronoséquence suggère néanmoins que les écosystèmes forestiers étaient très résilients avant le début de la colonisation humaine permanente. Par exemple, la coulée de lave de Mare Longue avait 220 ans environ en 1800 quand la grande faune est déjà éteinte, en d'autres termes, elle avait l'âge de la coulée de 1800 aujourd'hui (étudiée dans le chapitre 5). La forêt de Mare Longue présente pourtant une diversité des traits de dispersion très forte sur l'ensemble de la largeur de la coulée, cette diversité étant comparable à ce qui est observé dans les plus belles forêts anciennes sur sol (Albert et al., 2020a ; chapitre 4). Cela suggère que les nombreuses espèces ligneuses ont été capables d'atteindre et de s'établir sur cette coulée en moins de deux siècles, ce qui semble tout à fait crédible quand on voit la capacité de certains écosystèmes tropicaux isolés à se développer et se diversifier rapidement sur des volcans neufs (Thornton, 1997). La forêt de Mare Longue qui est considérée comme l'un des plus beaux vestiges de forêt tropicale humide des Mascareignes est pourtant en cours d'appauvrissement, et pas uniquement parce que certaines espèces pionnières disparaissent petit à petit du système (chapitres 6). L'incapacité de nombreux ligneux à grosses graines à se régénérer dans le sous-bois laisse même entendre que le stade dit « préclimacique à *Labourdonnaisia »* (Cadet, 1977) pourrait bien être la signature d'un relâchement de compétition qui profite essentiellement à une espèce indigène (chapitres 7).

Les types de végétation à la Réunion qui sont avant tout marqués par la limitation de la dispersion montrent que toute tentative de description de la succession est hasardeuse en l'absence d'une excellente connaissance de l'histoire naturelle attachée à une chronoséquence. Car dans une Réunion hypothétique précocement colonisée, que seraient devenues les forêts du Grand Brûlé si la forêt à *Agarista* s'était développée partout avec la destruction progressive de tous les *kipukas* de forêt ancienne ? Qui aurait pu imaginer la magnifique forêt littorale de la Ravine Criais avec de nombreuses espèces ligneuses à grosses graines poussant dans la caldeira du Piton de la Fournaise ? Probablement personne. Certains travaux historiques menés à Hawai‘i sur la succession végétale continuent à être cités sans réserve dans des livres de référence en écologie (*cf* Chazdon, 2014) malgré les mises en garde de Johnson et Miyanishi (2008). Dans cet archipel où l'Homme est installé depuis plus de 1500 ans, nul doute que les extinctions pré-européennes massives et longtemps sous-estimées (Heinen et al., 2017; Kirch, 1982; Olson et James, 1989) ont eu des conséquences désastreuses sur la dynamique de la végétation. Cela interdit de prétendre retracer la succession végétale sur les coulées de cet archipel en utilisant des chronoséquences allant parfois jusqu'à plusieurs milliers d'années (*cf* Atkinson, 1970; Drake et Mueller-Dombois, 1993; Kinney et al., 2015).

La diversité indigène en sursis dans les forêts anciennes défaunées

Les plus beaux témoignages de forêt tropicale humide des Mascareignes, comme les forêts de Mare Longue (La Réunion) et de Brise Fer (Maurice), sont protégées par des parcs nationaux. Mais ces forêts sont en cours de transformation même si l'ampleur de celle-ci est largement modulée par le niveau de défaunation des grands vertébrés frugivores (chapitre 6). Malgré le faible niveau d'invasion, la plupart des espèces ligneuses indigènes à fruits charnus se régénèrent mal à Mare Longue, tandis que la situation est beaucoup plus encourageante à Brise Fer où seules les espèces à grosses graines sont impactées négativement. La différence de recrutement entre les sites est d'autant plus marquante que la richesse spécifique est le double à Brise Fer de celle de Mare Longue. Ainsi, la forêt de Mare Longue devrait connaître un appauvrissement majeur de sa canopée et celle de Brise Fer un *shift* vers une canopée moins riche en espèces à grosses graines (chapitre 6). Ce constat est particulièrement troublant car la forêt hautement fragmentée de Brise Fer est beaucoup plus résiliente que celle de Mare Longue pourtant considérée comme un écosystème de référence dans l'écozone. Mais ce paradoxe a une explication principale : l'importante population de roussettes qui maintient une dispersion efficace de nombreuses plantes à fruits charnus à Maurice comme ailleurs dans l'Ancien Monde (Bollen et Elsacker, 2002; Florens et al., 2017b; McConkey et Drake, 2006; Oleksy et al., 2017; van Toor et al., 2019), contrairement au bulbul à La Réunion dont les niveaux populationnels et la rayon d'action en font un disperseur d'efficacité moindre (chapitres 4 et 5). La roussette noire qui contribue à maintenir de hauts niveaux de diversité de juvéniles depuis le contrôle de *Psidium cattleianum* dans les années 1990, ne semble pas pour autant disperser efficacement les plantes à grosses graines et la disparition des frugivores avec une grande ouverture de bec/bouche dans cette île impacte négativement nombre d'espèces ligneuses appartenant aux plus grandes radiations (Ahmad et al., 2016; Linan et al., 2019; Malcomber, 2002). Ces patterns de régénération inquiétants, en particulier à La Réunion, sont conformes à ce qui a été montré dans les grandes forêts continentales où le recrutement est partout altéré en à peine quelques décennies de défaunation (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010). En l'absence de la faune mutualiste, il est ainsi illusoire de prétendre protéger efficacement une forêt tropicale ancienne et cela est valable sur les continents comme dans les îles.

Les processus à l'œuvre

De nombreuses plantes à fruits charnus ont de grandes difficultés pour se maintenir dans les forêts tropicales anciennes, mais parmi les processus potentiellement multiples (*cf* Wang et Smith, 2002), les limitations post-dispersion du recrutement induites par la perte (ou la faiblesse) de la dispersion jouent un rôle majeur (chapitre 6).

Le principal processus post-dispersion est généralement associé à l'hypothèse de Janzen-Connell où les ennemis naturels empêchent l'installation des conspécifiques à proximité des arbres mères (Carson et al., 2008; Terborgh, 2012; Fig.i.1) Si nos résultats ne permettent pas de démêler les diverses limitations possibles du recrutement dans les six hectares de Mare Longue et Brise Fer (chapitre 6), cette limitation pourrait être souvent impliquée car Hansen et al. (2008) ont déjà montré son rôle dans le défaut de recrutement de l'arbuste à grosses graines *Syzygium mamillatum* à Brise Fer. Pourtant, l'importante méta-analyse de Comita et al. (2014) a montré que le recrutement est fortement réduit à proximité des pieds mères où la densité des conspécifiques est importante, sans que l'hypothèse de Janzen-Connell ne soit impliquée pour autant. Le rôle de la compétition intra-spécifique pourrait par exemple être sous-estimé (Comita et al., 2014). De plus, Levi et Peres (2013) ont montré que l'extirpation des frugivores entraîne une forte limitation du recrutement d'un arbre appartenant aux Sapotaceae en raison de la simple persistance de la pulpe et que l'hypothèse de Janzen-Connell n'intervient que secondairement. Levi et Peres (2013) suggérant ce processus transposable à de nombreuses espèces avec une pulpe abondante, nous avons testé l'impact de la persistance de celle-ci sur deux arbres de la même famille et avons montré également un fort impact négatif sur le recrutement de *Labourdonnaisia calophylloides* et *Mimusops balata* (même si certains animaux introduits peuvent jouer un rôle complexe dans le rétablissement partiel du recrutement, chapitre 7). D'autres ligneux pourraient pâtir encore plus sévèrement de la persistance systématique du péricarpe dans les Mascareignes, *e.g. Foetidia mauritiana* (Lecythidaceae) qui montre de rares levées de plantules si les graines ne sont pas extraites du péricarpe ligneux (*cf* Cuénin et al., 2019). Tout ceci montre la difficulté de démêler les différentes limitations induites par la perte des frugivores, d'autant que d'autres processus sont également à l'œuvre.

Les limitations du recrutement peuvent également être de nature environnementale. Les plantes pionnières anémochores comme *Agarista salicifolia* ont par exemple des difficultés à se régénérer dans le sous-bois sombre, ce qui mène à sa quasi-disparition au sein des jeunes cohortes (chapitre 6). A l'inverse, les plantes à grosses graines sont généralement adaptées aux sous-bois sombres (Leishman et al., 2000), il paraît donc difficile d'invoquer des conditions de lumière inadaptées pour expliquer un tel défaut de recrutement pour la plupart des espèces dans les Mascareignes. Pour les plantes à fruits charnus potentiellement plus demandeuses en lumière, une dispersion efficace leur permet normalement d'atteindre des conditions favorables à leur établissement, ce qui n'arrive généralement pas ou se produit peu en particulier à La Réunion (**Fig.d.2**, chapitres 4, 5 et 6). Si les plantes zoochores pionnières à fruits charnus sont particulièrement vulnérables en cas de rupture d'interactions de frugivorie (Wandrag et al., 2017), nous montrons de même que des espèces communes tolérantes à l'ombre, devraient être capables de s'installer massivement dans des trouées où elles demeurent pourtant absentes si nous ne rétablissons pas expérimentalement la fonction de dispersion (chapitre 7).

Le principal processus pré-dispersion à l'origine de graves difficultés de recrutement est à l'échelle globale la rupture des interactions de pollinisation (Neuschulz et al., 2016). Dans les Mascareignes, de rares cas ont été montrés (Bissessur et al., 2020), et la principale limitation pré-dispersion à l'échelle des communautés pourrait plutôt concerner la difficulté à fructifier massivement en raison du détournement des ressources par des plantes envahissantes (Krivek et al., 2020). Depuis le contrôle de l'invasion de *Psidium cattleianum* à Camizard, Krivek et al. (2020) ont par exemple montré que deux arbres indigènes à grosses graines fructifient beaucoup plus, entraînant une forte hausse des interactions de frugivorie avec la roussette noire. La disponibilité en fruits a probablement augmenté à Brise Fer depuis la lutte intensive contre *P. cattleianum* dans les années 1990, mais les espèces à grosses graines ne se régénèrent pas bien pour autant (chapitre 6). A La Réunion, nous montrons que de nombreuses espèces produisent une quantité importante de fruits et graines mais ne sont pas dispersées, ce qui exclut probablement une rupture de pollinisation pour la majorité des ligneux (chapitre 5 ; *cf* aussi Albert et al., 2017). Cependant, quelques espèces qui ont abondamment fleuri au Tremblet n'ont pas produit de fruits, *e.g. Noronhia broomeana, Ocotea obtusata, Tabernaemontana mauritiana* (chapitre 5). Il peut exister une grande variabilité spatiale ou temporelle dans les patterns phénologiques de floraison et de fructification (D. Strasberg, comm. pers.) et les 18 mois de suivi au Tremblet restent insuffisants pour tirer des conclusions quant à une éventuelle rupture de pollinisation. Des observations récurrentes de terrain montrent tout de même que *T. mauritiana* fructifie rarement malgré des floraisons fréquentes et massives. Vu les hauts niveaux de destruction et de fragmentation des habitats de basse altitude (Neuschulz et al., 2016) et l'introduction d'animaux connus pour leur potentiel impact négatif (Bissessur et al., 2020; Dupont et al., 2004), d'éventuelles ruptures d'interactions de pollinisation pourraient être impliquées et mériteraient une investigation.

Vers des études de la dynamique forestière à proprement parler

Pour comprendre les conséquences de la défaunation en frugivores plus importante à Mare Longue par rapport à Brise Fer, nous avons comparé les structures diamétriques des deux forêts au début des années 2010 (chapitre 6). Si les conclusions accablantes ne laissent guère de doutes sur les problèmes de régénération de nombreuses espèces en particulier à Mare Longue, cela ne remplace pas pour autant une véritable étude la dynamique forestière (Condit et al., 1998). Les données qui continuent à être collectées dans les Mascareignes permettront de comparer la dynamique des deux systèmes et de revisiter nos conclusions dans un futur proche. De même, une approche inductive (*e.g.* Hubbell, 2001) sur les distribution diamétriques pourrait permettre de prédire des changements dans la diversité des cohortes et de comparer ces prédictions avec les observations. Divers scénarios pourraient être testés dans les hectares permanents avec par exemple le semis direct de plantes à grosses graines simulant le rôle des grands frugivores et des zones témoins qui conserveraient leur trajectoire actuelle.

Fig.d.4 *Mise en collection aux Colimaçons de la plante hémiparasite à fruits charnus* Bakerella hoyifolia *qui était présumée éteinte à La Réunion jusqu'à 2017. La plante installée sur* Aphloia theiformis *a produit des fleurs en 21 mois et des fruits sont actuellement en maturation. Photos : A. Rhumeur & A. Gorissen.*

Les plantes aériennes à fruits charnus très vulnérables face à la perte des frugivores

Parmi les plantes ligneuses non-suivies dans les hectares permanents des Mascareignes, les plantes aériennes à fruits charnus doivent impérativement être dispersées par les frugivores pour se maintenir sur les arbres hôtes (Benzing, 2012). Les Mascareignes comptent diverses plantes épiphytes et parasites à fruits charnus dont plusieurs sont gravement menacées. A La Réunion, deux d'entres elles présentent d'étonnantes convergences qui ont été inscrites dans la taxonomie, la peu commune épiphyte *Medinilla loranthoides* (Melastomataceae) ressemblant au rarissime gui endémique, *Bakerella hoyifolia* (Loranthaceae), avec une présentation analogue des fleurs et fruits sur la partie défeuillée des rameaux (Albert et al., 2017). Il est surprenant de rencontrer des espèces apparentées sur presque chaque grand arbre dans les forêts tropicales humides à Madagascar où les fruits de ces plantes sont particulièrement consommés par des lémuriens, roussettes, pigeons, perroquets et autres passereaux (Atsalis, 1999; Bollen et Elsacker, 2002; Bollen et al., 2003; Hemingway, 1998). La quasi disparition de *Bakerella hoyifolia* à La Réunion alors qu'elle était commune dans les forêts d'origine, pourrait donc être la conséquence d'une rupture des interactions de frugivorie (pour une revue des autres facteurs potentiellement impliqués, *cf* Albert et al. (2017)). Les deux patchs découverts fleurissent et fructifient abondamment, et si l'utilisation de pièges caméras a pu montrer un haut niveau de fréquentation par le pollinisateur *Zosterops borbonicus*, elle n'a en revanche révélé aucune interaction de frugivorie avec la faune relictuelle (Albert et al., 2017). Ainsi, la petite population découverte dans les hauts de Saint-Philippe pourrait avoir survécu dans une forêt submontagnarde qui a été un des derniers sanctuaires de la rougette à La Réunion (*cf* Cheke et Hume, 2008). Quoi qu'il en soit, il y a urgence à multiplier cette plante dont la population se résume pour l'instant à deux patchs distants de 50 m, et les agents du CBNM l'ont d'ores et déjà mis en collection avec succès aux Colimaçons (**Fig.d.4**). Ce qui est bien la preuve que *Bakerella hoyifolia* est tout à fait capable de s'établir facilement dès lors qu'on la disperse sur un arbre hôte, ici *Aphloia theiformis*, pourtant très commun autour de la population d'origine. Si le grand nombre de fruits produit par *B. hoyifolia* doit dans un premier temps faire l'objet de multiplications tous azimuts, il pourrait permettre prochainement de lancer de nouvelles expérimentations de semis directs pour mieux démêler les limitations à l'œuvre derrière la quasi disparition de cette magnifique plante à La Réunion.

Réchauffement climatique et échappatoire altitudinale dans une île défaunée

Le réchauffement climatique en cours entamera davantage la capacité des plantes mal dispersées à se maintenir dans les forêts anciennes (Wiens, 2016). En effet, même si la hausse de la température devrait moins impacter les Mascareignes que les continents et les hautes latitudes (Boucher et al., 2019), on peut s'attendre à un déplacement vertical des limites thermiques des habitats de 300 m d'ici la fin du $21^{\text{ème}}$ siècle avec une hausse de deux degrés minimum et un gradient thermique moyen de 0°65 C pour 100 m de dénivellation (mais *cf* Pouteau et al., 2018). Ainsi, la limite de la forêt tropicale humide riche en plantes à grosses graines pourrait bien coïncider à la fin du $21^{\text{ème}}$ siècle avec celle de la forêt submontagnarde de Strasberg et al. (2005). A La Réunion comme ailleurs sous les Tropiques, les plantes avec une spécialisation thermique auront donc besoin de migrer le long des pentes pour s'adapter (Colwell et al., 2008; Laurance et al., 2011), mais à moins que du ré-ensauvagement n'intervienne entre temps (*cf* González-Varo et al., 2017), de nombreuses espèces ne le pourront ou y arriveront très mal (McConkey et O'Farrill, 2016). Pour les populations qui seront contraintes dans leur distribution actuelle, il va sans dire que les perturbations induites par le réchauffement climatique (*e.g.* stress thermiques, hydriques) contribueront à augmenter le risque d'extinction locale car elles peinent déjà à se maintenir pour nombre d'entre elles (chapitre 6). Enfin, étant donné que de nombreuses espèces avec une forte limitation de la dispersion ne participeront pas ou peu à la migration des habitats le long des pentes, les projets de restauration devront prendre en compte ce *shift* altitudinal en s'appuyant sur une actualisation des enveloppes climatiques des différents habitats.

Le rôle des faunes indigène et introduite demeure difficile à appréhender

Le rôle des faunes indigène et introduite a surtout été étudié de manière indirecte au cours de cette thèse. Pour comprendre le rôle des frugivores, nous avons par exemple largement étudié les traits de dispersion des plantes en les associant aux traits de la faune (chapitres 1, 2, 4, 5 et 6), mais aussi la localisation des relevés de végétation et trappes à graines pour comprendre les déplacements de la faune dans des paysages hétérogènes (chapitres 4 et 5) ou encore l'impact du nettoyage des graines via la consommation de la pulpe en réalisant manuellement cette opération (chapitre 7). Pour comprendre l'impact des prédateurs de graines, nous avons de même contrôlé le nombre de graines semées (chapitre 7) et utilisé des cages d'exclusion (chapitre 5). Pour aller plus loin lors de nos expérimentations, ces méthodes indirectes ont été couplées à de nombreuses observations directes et divers dispositifs permettant de suivre la faune (quatre pièges caméras et deux enregistreurs acoustiques). Il persiste néanmoins de nombreuses limites à notre compréhension fine de son rôle.

Utiliser les tailles de fruits et de graines pour comprendre les conséquences de rupture d'interaction de frugivorie (chapitres 4 et 6) peut révéler un pattern de recrutement similaire suivant des limitations pré- ou post-dispersion : les plantes à grosses graines sont par exemple souvent la cible de vertébrés prédateurs de graine (Forget et al., 2005). Même si nous montrons expérimentalement que la prédation des graines est une limitation secondaire pour les ligneux à grosses graines au Tremblet (chapitre 5), nous ne pouvons rigoureusement démêler les causes derrière le défaut de recrutement de nombreuses espèces dans la comparaison entre les forêts de Mare Longue et Brise Fer (chapitre 6). Pour la plupart des ligneux à grosses graines ayant des difficultés de régénération, la forte limitation de la dispersion est probablement le principal facteur à l'œuvre. Si cela semble aller de soi à la Réunion où le plus gros frugivore indigène pèse 55 g en moyenne, cela est également valable à Maurice où la roussette pourrait disperser peu efficacement les grosses diaspores en raison de sa taille de bouche limitée par rapport à d'autres vertébrés, tels les pigeons (Meehan et al., 2002; Whittaker et Jones, 1994; Wotton et Kelly, 2011) et tortues (Hansen et al., 2008). A Maurice, plusieurs lignages de plantes à grosses graines pourraient néanmoins avoir des traits végétatifs qui rendent ces plantes très attractives pour les cerfs et macaques qui sont absents à La Réunion (Cheke et Hume, 2008), ce qui pourrait aggraver le défaut de recrutement de ces plantes, et par exemple expliquer pourquoi *Labourdonnaisia* spp. s'y régénèrent si mal en comparaison avec La Réunion.

Piéger des oiseaux frugivores était initialement prévu au Tremblet pour comprendre rigoureusement « qui disperse quoi », mais les difficultés technico-légales de mise en œuvre nous ont conduit à mesurer la pluie de graine avec des trappes pour nous concentrer sur « qui est dispersé » (chapitre 5). Nous avons ainsi opté pour une méthode permettant de collecter en continu les diaspores dispersées par tous les vertébrés arboricoles et d'accumuler une grande quantité de graines pour mieux comprendre les limitations qui pèsent sur le recrutement des plantes (Muller-Landau et al., 2002). Même si la structure spatiale de la pluie de graine suggère des comportements sensiblement différents entre *Hypsipetes borbonicus* et *Pycnonotus jocosus* et que les quatre pièges caméras couplés aux observations directes ont permis d'apporter de nombreux enseignements, il reste que nous ne savons pas exactement quels sont les frugivores qui ont dispersé les graines identifiées dans les différentes trappes (chapitre 5). Pour tenter de mieux comprendre le comportement des frugivores au Tremblet, nous avons également utilisé des enregistreurs acoustiques (*cf* Katz et al., 2016a, 2016b). Cependant, la méthode s'est révélée inadaptée, principalement en raison de la petitesse du site d'étude et de la difficulté à optimiser les vraies détections (taux de faux positifs et faux négatifs importants, Maigné et al., 2019). Une approche basée sur des points de comptage a été envisagée durant la dernière partie de l'expérimentation au Tremblet, mais le confinement lié à l'épidémie de covid-19 n'a pas rendu possible sa mise en œuvre. Pour aller véritablement plus loin dans la compréhension de « qui fait quoi », le metabarcoding pourrait permettre d'identifier aussi bien les plantes que les vertébrés qui les ont dispersées (González-Varo et al., 2014). L'intérêt apparaît limité au Tremblet pour les premières qui montrent une surdispersion phylogénétique (Albert et al., 2018) et sont de ce fait relativement faciles à discriminer d'un point de vue morphologique (Leishman et al., 2000). Le fort conservatisme des traits des graines rendrait en revanche une étude comparable beaucoup plus délicate dans une communauté où coexistent de nombreuses plantes apparentées (*cf* à Maurice la tentative de discriminer *Diospyros* spp. dans les fèces de tortues en utilisant le marqueur ITS (Tatayah et al., 2018)). Au Tremblet, le metabarcoding permettrait surtout d'aller vers l'identification des disperseurs à partir d'échantillons collectés dans des trappes (González-Varo et al., 2018).

Les îles océaniques ont été particulièrement touchées par les extinctions de vertébrés indigènes (Heinen et al., 2017), mais elles connaissent un processus de refaunation depuis le début de la colonisation humaine (chapitre 2). Une question importante consiste à comprendre dans quelle mesure les frugivores introduits pourraient disperser les plantes indigènes (Loayza et al., 2020). Nos résultats montrent que les nouvelles interactions de frugivorie profitent essentiellement aux plantes exotiques à fruits charnus (chapitre 5), comme cela a déjà été montré à Hawai‘i (Vizentin-Bugoni et al., 2019). Nous détectons en effet un nombre limité d'interactions de frugivorie entre le principal frugivore introduit, *Pycnonotus jocosus*, et les espèces indigènes au Tremblet (chapitre 5). Par exemple, ce passereau consomme fréquemment diverses plantes exotiques envahissantes dans le sous-bois des forêts indigènes en délaissant des arbustes voisins comme *Gaertnera vaginata* ou *Chassalia corallioides* qui sont en revanche fréquemment visités par *Hypsipetes borbonicus*. Des observations en milieu (péri-) urbain montrent pourtant que *Pycnonotus jocosus* consomme les fruits de diverses espèces indigènes plantées, ce qui suggère que le comportement de ce passereau pourrait être fortement modulé par la disponibilité en fruits à l'échelle du paysage (Vizentin-Bugoni et al., 2019).

Fig.d.5 Tenrec ecaudatus *mangeant l'intérieur d'une figue de* Ficus mauritiana *au Tremblet en février 2019. La plupart des détections s'est en réalité produite durant la nuit. Photo : S. Albert.*

Les animaux introduits peuvent également jouer un rôle très ambigu et difficile à appréhender. Chez les mammifères, *Tenrec ecaudatus* peut par exemple déchausser de nombreuses plantules au Tremblet en fouillant dans la litière et consommer massivement certaines plantes indigènes comme *Ficus mauritiana* (**Fig.d.5**) et exotiques comme déjà rapporté ailleurs (Cheke et Hume, 2008). Cependant, notre dispositif conçu pour mesurer la pluie de graines issue des vertébrés volants et arboricoles n'a pas permis d'inclure ses fèces dans les résultats. Les rats remportent la palme de la complexité (Abe, 2007; Campbell et Atkinson, 2002; Shiels, 2011; Shiels et Drake, 2011) : omnivores et prédateurs de graine, disperseurs de plantes envahissantes et indigènes parfois à grosses graines (malgré un rayon d'action limité), le tout avec une remarquable variabilité dans l'espace (chapitre 5) et le temps (chapitre 7). Si l'on ajoute la quasi restauration en 2020 du recrutement de *Labourdonnaisia calophylloides* après le dépulpage massif opéré par *Achatina immaculata* (chapitre 7), la variabilité de certains comportements mis en évidence invite à la prudence quant à la portée d'expérimentations souvent très limitées dans l'espace et le temps. Quoi qu'il en soit, ces animaux introduits sont aujourd'hui des acteurs incontournables des nouveaux écosystèmes insulaires et méritent d'être davantage étudiés pour mieux comprendre leur impact sur le fonctionnement des forêts.

Les invasions végétales résultent aussi de victoires par forfait

Les Mascareignes sont sévèrement impactées par les invasions végétales comme nombre d'archipels (Kueffer et al., 2010; Strasberg, 1994). Si les processus impliqués sont divers, la capacité d'une plante à exercer une forte pression de propagules est primordiale dans son potentiel invasif (*invasiveness*). De même, la résilience des écosystèmes tropicaux qui implique une dispersion efficace module également la propension de ces écosystèmes à être envahis (*invasibility*) (Richardson et al., 2011). L'évaluation au Tremblet de la disponibilité en fruits/graines, de la pluie de graines et du recrutement des plantes indigènes et exotiques à l'échelle des communautés apporte donc d'intéressants éclairages pour comprendre les invasions de plantes à La Réunion (chapitre 5).

Nos résultats montrent que certaines plantes à fruits charnus exotiques bénéficient d'un très haut niveau de dispersion à La Réunion en accaparant les interactions de frugivorie en particulier avec la faune introduite (chapitre 5). Plusieurs de ces plantes produisent une grande quantité de fruits et de graines qui sont massivement dispersées, *e.g*. *Clidemia hirta* et dans une moindre mesure *Rubus alceifolius* (Baret et al., 2008; Mandon-Dalger et al., 2004). D'autres espèces dont les semenciers peuvent être peu présents (*Trema orientalis*) voire absents (*Litsea glutinosa*) sur le site étudié, n'ont cependant pas de difficultés à y être dispersées. Cela montre qu'à disponibilité équivalente en fruits avec de nombreuses espèces indigènes, ces plantes envahissantes présentent souvent une attractivité supérieure pour les frugivores du site (Kueffer et al., 2009) et ce, dans toutes les classes de taille de graines qui sont encore dispersées.

Les plantes exotiques envahissantes à fruits charnus bénéficient sans surprise de hauts niveaux de dispersion, mais dans le même temps d'un relâchement de compétition qui peut être observé aussi bien dans le sous-bois des forêts anciennes, que sur les coulées récentes du Piton de la Fournaise. Nos analyses révèlent que les hauts niveaux de dispersion dont bénéficient les plantes indigènes à Brise Fer, permet probablement leur relatif maintien dans la parcelle permanente envahie par *Psidium cattleianum* (non discuté dans le chapitre 6 ; ***A*****pp.6.9**). Il ne s'agit pas ici de nier l'impact négatif de *P. cattleianum* (Baider et Florens, 2011; Lamarque et al., 2011) qui justifie de nombreuses opérations de lutte dans l'archipel (Florens et al., 2012; Roussel et Triolo, 2016). Il est néanmoins surprenant que le recrutement de la plupart des plantes à fruits charnus soit supérieur dans cette parcelle de Brise Fer par rapport aux parcelles permanentes non-envahies de Mare Longue. De plus, la grande majorité des espèces indigènes a de grandes difficultés à atteindre les écosystèmes en cours de reconstruction sur les coulées historiques du Piton de la Fournaise (chapitre 5). Nous montrons pourtant que les espèces à grosses graines semées ont été tout à fait capables de s'établir sur cette coulée historique, y compris là où les plantes les plus problématiques comme *Dicranopteris linearis, Psidium cattleianum* ou *Clidemia hirta* n'ont pas été contrôlées (***A*****pp.5.12**). Si ces semis expérimentaux sont encore trop récents pour que l'on puisse tirer de solides conclusions quant à l'impact de la compétition avec les plantes envahissantes, cela suggère que les traits de dispersion des plantes indigènes jouent un rôle dans la réponse des communautés aux invasions (Fried et al., 2019). Il est donc primordial de questionner la forte limitation de la dispersion des plantes indigènes induite par la défaunation pour comprendre la sévérité des invasions végétales. Dès lors, la défaunation importante et souvent ancienne des îles océaniques pourrait être le participe d'une forte susceptibilité insulaire (*cf* Jeschke et al., 2018).

La grande attractivité de certaines plantes exotiques à fruits charnus associée à une forte limitation de la dispersion de la plupart des ligneux indigènes peut avoir des conséquences spectaculaires à La Réunion. Suite à l'incendie des coulées récentes en janvier 2019 au Grand

Brûlé, la dynamique de colonisation des plantes est dominée par *Trema orientalis* alors que des prospections montrent que les semenciers de cette espèce sont relativement rares dans le paysage. Vu les densités de baliveaux observées (**Fig.d.6**), cette espèce a probablement accumulé une banque de graines prodigieuse (*cf* Archibald et al., 2017) en entretenant de hauts niveaux d'interactions avec les passereaux indigènes et introduits (chapitre 5). Le fait que les plantules indigènes soient si rares dans ce nouvel écosystème malgré leur capacité à s'y installer dès lors qu'elles y sont dispersées (**Fig.d.2**) suggère là encore qu'il y a victoire par forfait des plantes exotiques envahissantes.

La compétition induite par les plantes exotiques envahissantes entraîne probablement l'inhibition de la germination et/ou une forte mortalité des plantules de nombreuses espèces indigènes à fruits charnus qui sont pourtant dispersées. Cela est démontré à Maurice par la spectaculaire hausse du recrutement dans les hectares permanents où *P. cattleianum* a été contrôlée (chapitre 6 ; ***A*pp.6.9**), mais également à La Réunion par les difficultés de plusieurs espèces d'arbres à atteindre le stade baliveau au centre de la coulée de 1800 (chapitre 5), empêchant la structuration de l'écosystème par des arbres qui sont encore tant soit peu dispersés. Dans ce dernier cas de figure, si *P. cattleianum* a probablement un impact très négatif (Huenneke et Vitousek, 1990), la fougère *Dicranopteris linearis* pose elle-aussi problème en constituant un matelas racinaire inhibiteur (**App.5.18**) comme déjà montré ailleurs (Cohen et al., 1995; Slocum et al., 2004). De même, la fougère *Nephrolepis biserrata* connue pour son potentiel impact négatif (Cleary et Eichhorn, 2018), entraîne à Mare Longue un recrutement encore plus faible dans la parcelle permanente où elle atteint un fort taux de recouvrement en comparaison avec les deux autres parcelles suivies (non discuté dans le chapitre 6 ; **App.6.6**).

Fig.d.6 *Régénération massive de* Trema orientalis *(au second plan) en juillet 2020 au Grand Brûlé après l'incendie de Janvier 2019. Sur de vastes superficies, ce petit arbre est en train de devenir dominant et pourrait bien supplanter l'autre espèce envahissante qui a aussi largement profité de l'incendie,* Boehmeria penduliflora *(au premier plan). Photo: A. Gorissen.*

Ces réflexions autour de la perte de la dispersion des plantes indigènes dans des habitats envahis invite à poursuivre les expérimentations de terrain pour mieux comprendre les limitations du recrutement et explorer dans quelle mesure la dispersion pourrait qualitativement et quantitativement moduler la résistance aux invasions (*cf* Fried et al., 2019). A ce titre, des espèces d'arbres à petites, moyennes et grosses graines pourraient être semées à des densités variables dans un plan d'expérimentation testant l'impact de la compétition avec une plante envahissante, *e.g. Psidium cattleianum* (modalités invasion/éradication/contrôle). En parallèle, un suivi des changements potentiellement induits au niveau du sol s'impose pour mieux comprendre les processus de compétition à l'œuvre (*e.g.* allélopathie, détournement des ressources, compétition apparente). L'étude des microbes du sol dont l'influence demeure globalement mal comprise dans les forêts tropicales (Camenzind et al., 2018) pourrait apporter des éléments déterminants (Pinzone et al., 2018).

Semer à large échelle et ré-ensauvager pour soutenir la dynamique forestière

Les semis réalisés au cours de cette thèse montrent qu'en nous substituant à la faune éteinte, le recrutement de diverses espèces ligneuses est possible y compris sur des coulées récentes où elles ont toujours été absentes (chapitres 5 et 7 ; **Fig.d.2**). Ces semis pourraient être entrepris dans des actions de restauration écologique de grande envergure. Mais parce que ces dernières sont intrinsèquement limitées dans l'espace et surtout le temps, elles ne remplaceront jamais de grands frugivores dont nous devrions favoriser le retour.

Se substituer à la faune éteinte en semant massivement

Les semis expérimentaux avaient également l'ambition d'ouvrir des perspectives de restauration écologique en proposant des protocoles plus légers à mettre en œuvre que les traditionnelles plantations. Ces dernières nécessitent en effet une logistique lourde depuis la production des plants en pépinière jusqu'à la plantation, ce qui contraint considérablement le rayon d'intervention (Shaw et al., 2020) et coûte cher (Meli et al., 2018). Les plantations peuvent de plus propager des maladies depuis les pépinières vers les milieux naturels (Sims et Garbelotto, 2018), mais elles sont largement privilégiées à La Réunion au motif que les semis directs ne fonctionneraient pas (ou très mal). Au cours de cette thèse, nous montrons pourtant qu'en nous substituant à la faune éteinte, le semis direct de plantes à grosses graines peut enrichir assez facilement certaines coulées récentes à basse altitude et que d'autres limitations comme la prédation des graines sont secondaires (chapitres 5 et 7).

Ces protocoles se résument en quatre étapes principales : récolte, dépulpage, stockage et semis. (1) Les récoltes massives sont relativement aisées dans les corridors forestiers (*e.g.* Mare Longue, Basse Vallée) pour les espèces communes à gros fruits, mais de nombreuses espèces en danger comme *Diospyros borbonica* ne sont pas en reste certaines années et pourraient également donner lieu à des semis massifs (chapitre 5). La difficulté tient à ne pas râter les fructifications ce qui nécessite un effort de prospection non-négligeable qui pourrait s'appuyer sur les réseaux naturalistes et des agents de terrain du Parc national et de l'ONF. Il va sans dire toute récolte en coeur de Parc et sur le domaine ONF nécessite les autorisations délivrées par les autorités compétentes. (2) Le dépulpage des fruits mûrs est généralement facile pour la plupart des espèces, mais certaines à latex comme *Labourdonnaisia calophylloides* mériteraient une investigation pour optimiser le procédé d'extraction de la pulpe qui demeure particulièrement fastidieux. (3) Les modalités de stockage des semences dépendent de leur type, nous avons surtout travaillé avec des espèces dont les graines sont récalcitrantes, leurs semences devant être conservées au maximum un mois en chambre froide dans des bacs étanches afin de préserver au mieux le potentiel germinatif (Baskin et Baskin, 2014). La plupart des autres espèces ne nécessitent pas de telles précautions dès lors que les graines ont été dépulpées. (4) Définir la densité des semis est plus délicat. Nous avons semé à des densités très élevées lors de nos expérimentations pour limiter l'espace à dégager et optimiser la récolte des données. Dans les systèmes forestiers préservés, la pluie de graine générée par l'activité des grands frugivores atteint 1 graine. m^{-2}. an^{-1} environ pour les plantes à grosses graines (Levi et

Peres, 2013; Terborgh et al., 2011). Les densités étaient probablement plus importantes à La Réunion quand la faune était pléthorique et pourraient être ajustées en fonction de la disponibilité en graines ou de l'échelle considérée, mais il faut garder en tête que le recrutement des plantules croît linéairement avec la densité des semis (Meli et al., 2018).

Les conditions d'accès aux écosystèmes indigènes sont souvent difficiles et interrogent sur les moyens à mettre en œuvre pour les semis directs (Novikov et Ersson, 2019). La modeste expérimentation du Tremblet montre la difficulté de procéder au sol dans des fourrés perturbés avec des claies de portage (chapitre 5). Un semoir rotatif monté sur un hélicoptère pourrait permettre d'ensemencer assez rapidement de vastes surfaces inaccessibles (*cf* Novikov et Ersson, 2019; Shaw et al., 2020), par exemple au Grand Brûlé avec une densité de semis de 5000 graines.ha^{-1} (*cf* Meli et al., 2018). Des arbres très productifs entre novembre à janvier permettraient de récolter le nombre de graines nécessaire et serviraient de fer de lance à ce semis multi-espèces : *Calophyllum tacamahaca* (30 kg.ha^{-1}), *Labourdonnaisia calophylloides* (7,5 kg.ha^{-1}), *Mimusops balata* (33 kg.ha^{-1}) ou *Syzygium cymosum* (3,3 kg.ha^{-1}). Ensemencer massivement la caldeira devient dès lors possible à vaste échelle, par exemple dans une zone pilote de 50 hectares où une canopée de *Trema orientalis* est en train de se constituer (**Fig.d.6**). Cela montre que nous ne devons pas nous résoudre à voir disparaître des coulées historiques les espèces les plus emblématiques de la forêt tropicale humide, d'autant que nous devrions veiller à conserver des écosystèmes attractifs en prévision du possible retour des grands frugivores.

Ré-ensauvager les écosystèmes avec des vertébrés clés de voûte

Si les protocoles de semis direct offrent d'intéressantes perspectives dans une île défaunée comme La Réunion, ils n'ont pour autant pas la prétention de se substituer efficacement aux frugivores de grande taille. D'abord parce qu'ils ne peuvent être entrepris qu'à des échelles spatiale et temporelle limitées en comparaison avec les capacités de dispersion de la grande faune. Rien ne peut remplacer des frugivores en grand nombre en quête perpétuelle de nourriture et dotés d'un grand rayon d'action. Mais aussi parce que les frugivores permettent aux graines de certaines espèces d'échapper à une prédation précoce en mangeant les fruits sur les arbres (Benítez-Malvido et al., 2016), tandis que les protocoles de semis s'appuient essentiellement sur du ramassage de diaspore au sol ou dans des filets où peut s'exercer une très forte pression d'ennemis naturels (comme cela a été observé chez *Poupartia borbonica* lors de cette thèse). Quoi qu'il en soit, le retour des grands frugivores est souhaitable à La Réunion et ne doit pas être opposé à des actions de semis à grande échelle menées par l'Homme. Ces perspectives sont même complémentaires dans la mesure où la dispersion à longue distance des plantes à grosses graines n'est guère envisageable par la faune susceptible de ré-ensauvager (*rewilding*) prochainement les écosystèmes. Il reste que si une politique de semis direct pourrait être assez facilement déployée par les gestionnaires d'espaces naturels, le ré-ensauvagement des écosystèmes soulève de nombreuses questions socio-économiques (Cybèle, 2018) ou écologiques (Vizentin-Bugoni et al., 2019) qui rendent sa mise en œuvre plus complexe.

Le ré-ensauvagement avec des grands frugivores peut être envisagé à différentes échelles et avec des objectifs variables en fonction des contextes qui sont disparates. Il est par exemple plus aisé de ré-ensauvager les îlots de Maurice avec les tortues terrestres *Aldabrachelys gigantea* et *Astrochelys radiata* (Cole, 2012; Griffiths et al., 2011) que La Réunion : ces îlots sont des réserves naturelles isolées tandis que les problèmes de sécurisation des animaux sont prégnants à La Réunion où le braconnage est à redouter. Pourtant, le lancement du projet de réintroduction de tortues à la réserve d'*Ebony Forest* à Chamarel (Maurice) montre qu'une initiative analogue pourrait voir le jour à La Réunion (*cf* https://www.ebonyforest.com). Cette possibilité qui a d'ailleurs été longtemps envisagée par les acteurs du LIFE + forêt sèche et discutée lors d'un symposium consacré à la question au congrès IB2019 (Juvik, 2019), n'a malheureusement pas été mise à exécution. S'il ne faut pas attendre d'un tel projet qu'il ait un impact significatif sur la restauration de la dispersion à l'échelle d'un écosystème à La Réunion, il reste qu'une réserve avec des tortues terrestres pourrait non seulement être une passionnante expérience de restauration écologique (Hansen et al., 2010), mais aussi et surtout avoir une importante vocation pédagogique. Elle contribuerait notamment à montrer au public, touristes et élèves, que les grands vertébrés ont un rôle essentiel à jouer dans les forêts tropicales indigènes.

Fig.d.7 Dortoir de la roussette noire* (Pteropus niger) *dans l'Est de La Réunion. *La roussette noire a recolonisé La Réunion depuis Maurice au début des années 2000 plus de deux siècles après en avoir disparu. Photo : Gildas Monnier.*

Le retour de la roussette noire (*Pteropus niger*) à la Réunion constitue une remarquable opportunité pour les écosystèmes forestiers (**Fig.d.7**), car cette grande chauve-souris frugivore endémique de l'archipel joue un rôle doublement mutualiste en tant que pollinisateur et disperseur (Florens et al., 2017a; Nyhagen et al., 2005). Les premiers travaux sur cette espèce à La Réunion montrent que les individus suivis sont capables de parcourir une vingtaine de kms au cours d'une seule nuit (GCOI, 2019), ce qui corrobore les travaux de Oleksy et Ayady (2019) à Maurice. Ainsi, elles assurent déjà une continuité géographique entre les dortoirs situés à basse altitude dans des habitats totalement transformés et la végétation indigène de l'Est de l'île où elles vont probablement se nourrir (GCOI, 2019). Si elles propageront peut-être de nouvelles plantes exotiques (Rouget et al., 2016), ces potentiels effets néfastes seront probablement contrebalancés par la restauration d'interactions mutualistes de pollinisation et de dispersion qui étaient éteintes depuis des siècles (*cf* van Toor et al., 2019). Pour s'en convaincre, il suffit de constater la remarquable régénération de la plupart des plantes indigènes à Brise Fer malgré la persistance de nombreuses plantes exotiques à l'échelle du paysage (chapitre 6). A La Réunion, les reliques de forêts indigènes aux basses et moyennes altitudes riches en arbres à gros fruits (chapitre 2) sont sans surprise les plus attractives pour la roussette (GCOI, 2019). Ces reliques sont souvent très fragmentées et à proximité directe des activités humaines, tandis que les plus grandes zones en coeur de Parc national se trouvent entre Saint-Philippe et Sainte-Rose, notamment au Grand Brûlé qui voit malheureusement les *kipukas* riches en espèce à gros fruits charnus disparaître depuis des siècles sans possibilité de se reconstruire (chapitres 3 et 4). Pour que cette zone qui constitue la plus grande aire de basse altitude à distance des activités humaines soit réellement attractive pour les roussettes, il est non seulement possible (chapitre 5 ; **Fig.d.2**), mais il y a surtout urgence à ramener des semenciers indigènes dont se nourrit cette espèce (Florens et al., 2017a). Il y a d'autant plus de raisons d'envisager de vastes zones favorables et protégées pour les roussettes qu'avec la croissance exponentielle de la population de l'Est (GCOI, 2019), le risque de conflit d’intérêt avec les arboriculteurs doit être anticipé. Le défi est grand comme le montre la situation à Maurice où cette espèce qui joue pourtant un rôle clé de voûte dans les forêts indigènes est décimée à des fins démagogiques (Florens, 2015). Par conséquent, les acteurs locaux de la conservation devraient veiller à créer les conditions de l’acceptation de cette espèce endémique de l'archipel et inclure un important volet socio-écologique dans les prochains travaux de recherche (*cf* Cybèle, 2018).

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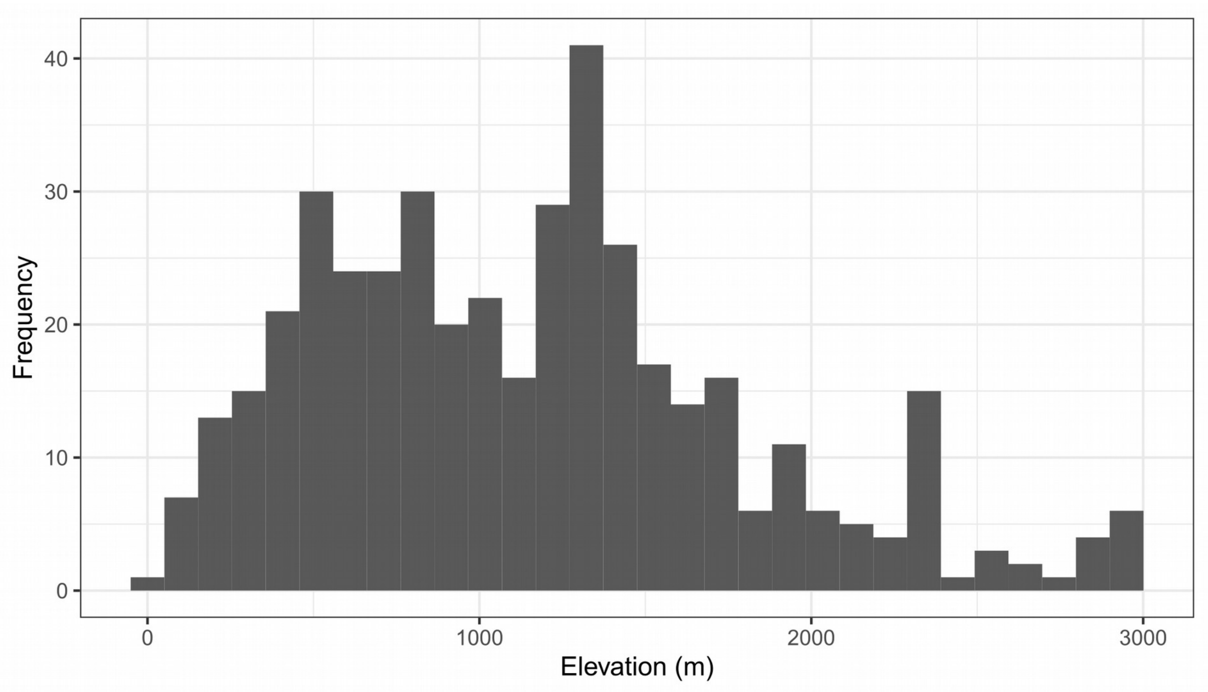
APPENDICES



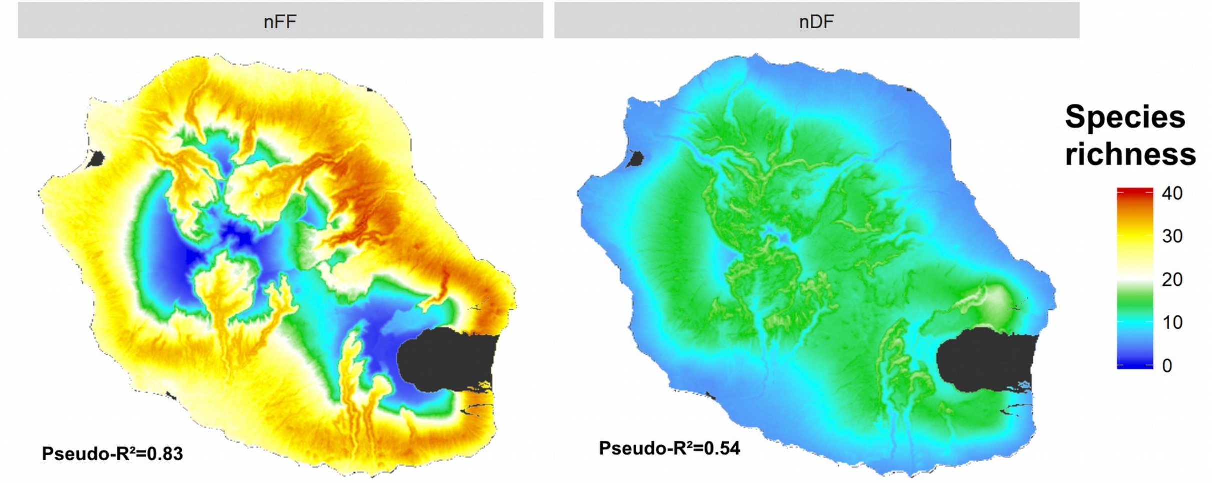
App.1.1 *Histogram of plot elevation (n=429). There were only four plots of well-preserved forest between 0-100 m a.s.l because almost all native forests have been destroyed/transformed in the very lowlands (most plots of native vegetation in this elevational range were on recent lava flows and excluded from our analyses). At high elevations, there were 43 plots above 2000 m a.s.l, 13 plots above 2500 m a.s.l.*

App.1.2 *Summary of species richness according to fruit type (DF: dry-fruited, FF: fleshy-fruited), geographical distribution (SIE: single-island endemic of Réunion, Mascarene-shared: Mascarene endemic species shared by Réunion and Mauritius and/or Rodrigues, Widespread: indigenous species with a wider distribution) and growth form of woody species sampled in the 429 historical plots.*

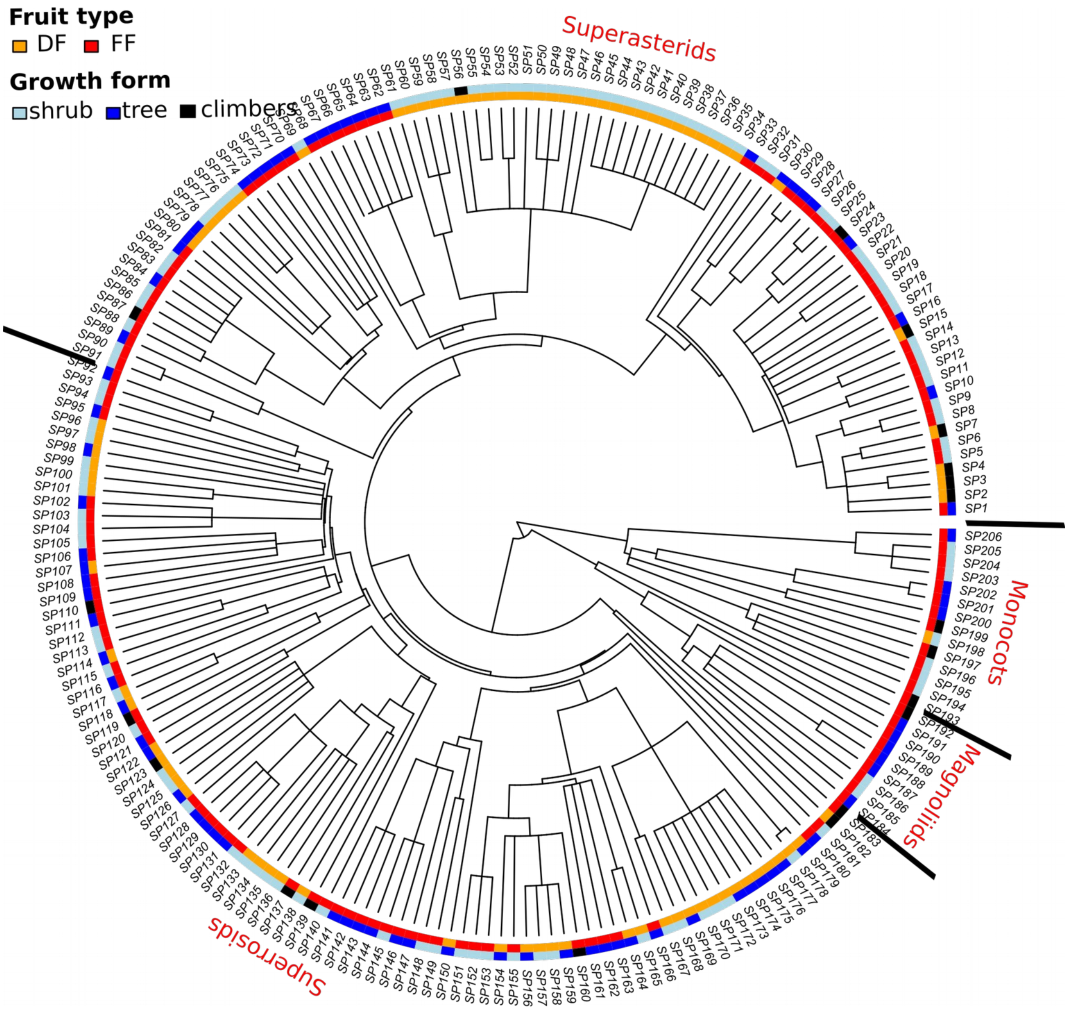
Fruit type	Status	Shrub	Tree	Climber	Woody species
DF	SIE	37	10	1	48
	Mascarene-shared	11	11	2	24
	Widespread	10	2	5	17
FF	SIE	27	21	0	48
	Mascarene-shared	19	27	3	49
	Widespread	7	11	9	27
		111	82	20	213

App.1.3 *Comparison of pseudo-R² and spatial autocorrelation Moran's index of E-GLM (GLM with environment predictors only), ES-GLM (GLM with environment predictors and spatial filtering) and S-GLM (GLM with only spatial filtering). PFF : fleshy-fruited species proportion, pFFtree : fleshy-fruited tree species proportion ; pFFshr : fleshy-fruited shrub species proportion.*

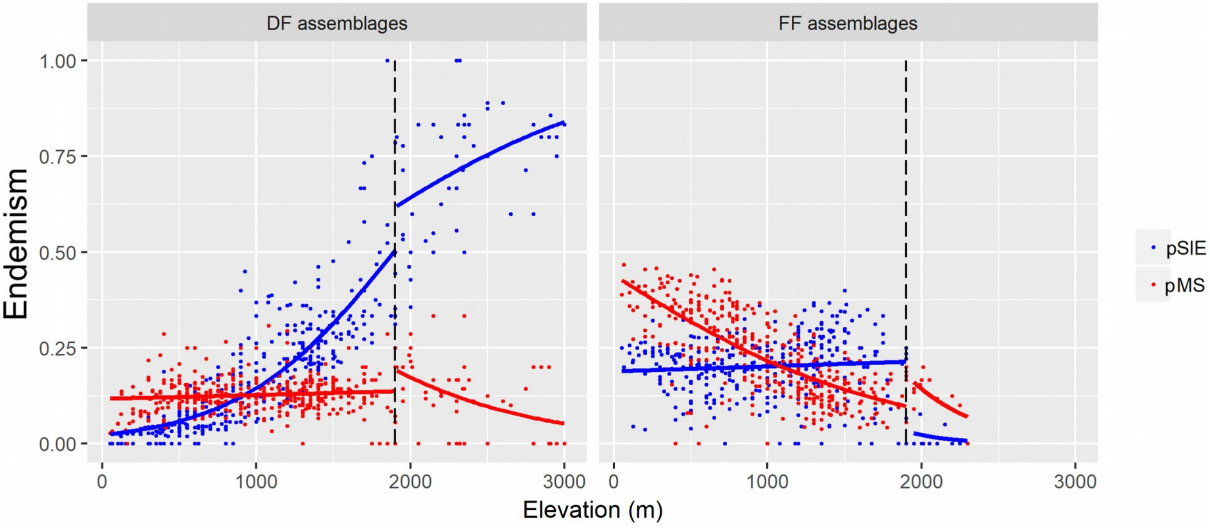
Response	pFF			pFFtree			pFFshr		
GLM	E	ES	S	E	ES	S	E	ES	S
Pseudo-R²	0,73	0,78	0,07	0,64	0,74	0,1	0.41	0,50	0,06
Moran's I	0,31 ***	0,08 NS	-	0,37 ***	0,07 NS	-	0,23 ***	0,06 NS	-



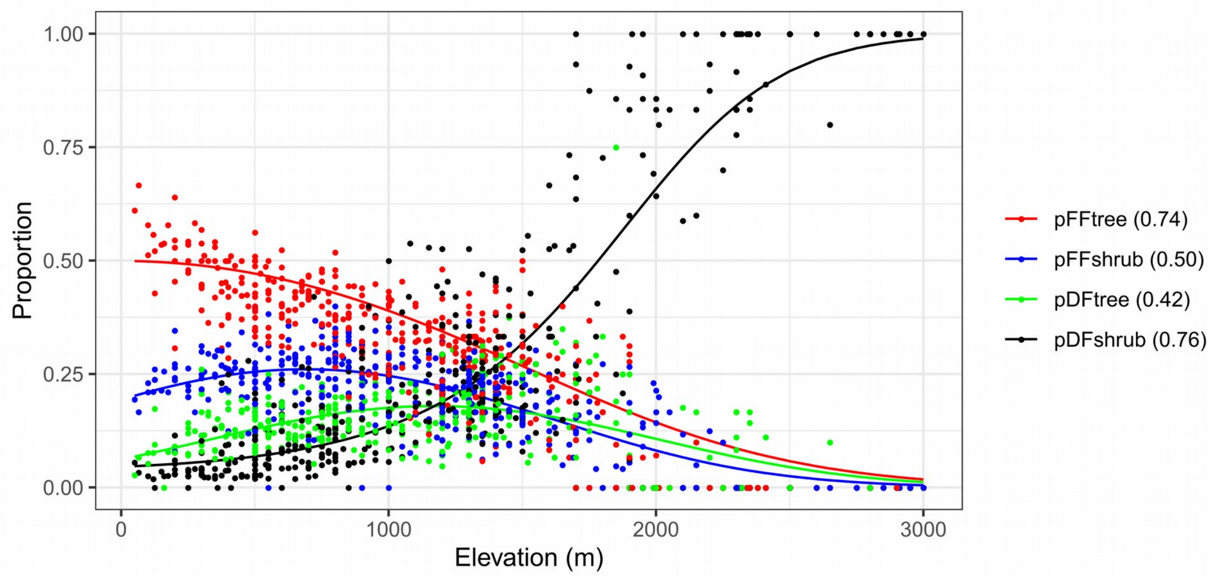
App.1.4 *Spatial modeling of nFF (fleshy-fruited species richness) and nDF (dry-fruited species richness) for an area of 1000 m² by interpolation of ES-GLM coefficients (same methods as for pFF + surface as an additional predictor). High and low species richnesses are respectively shown in warm and cool colors. A mask is applied on recent lava flows and wetlands.*



App.1.5. *Phylogenetic tree of native woody angiosperms recorded in the 429 historical plots based on the phylogeny from Zanne et al (2013). For each species, fruit type (DF: dry-druited, FF: fleshy-fruited) and growth form are shown.*



App.1.6 *Observed relationships between elevation and endemism according to fruit type assemblages. Woody species communities were split into DF and FF assemblages. We calculated for both the proportion of single-island endemic species from Réunion (pSIE in blue) and the proportion of Mascarene-shared species (pMS in red), i.e. archipelago endemic species shared by Réunion and Mauritius and/or Rodrigues. Dashed lines symbolize the transition between montane forest and subalpine shrubland. For each assemblage, logistic regressions were performed on these two ranges of elevation.*

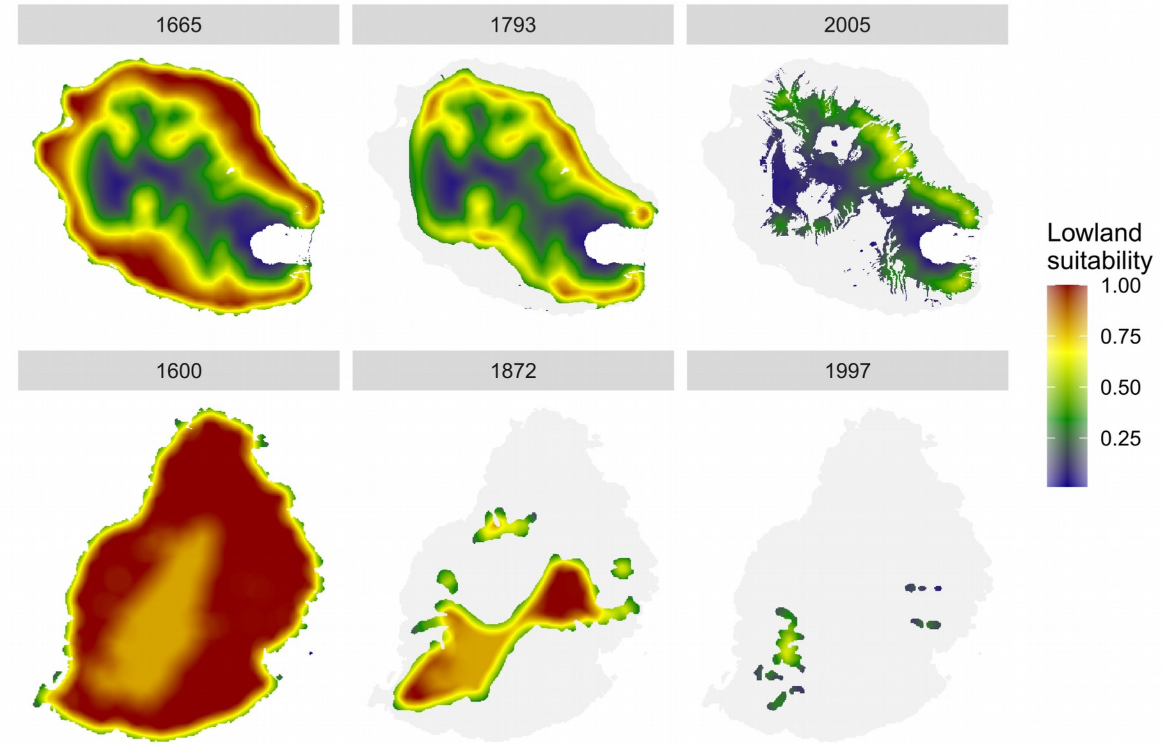


App.1.7 *Relationships between proportions of different functional growth forms and elevation. pFFtree, pFFshrub, pDFtree and pDFshrub are respectively the fleshy-fruited tree species proportion, fleshy-fruited shrub species proportion, dry-fruited tree species proportion and dry-fruited shrub species proportion. Climbers are excluded from our analyses. Predicted probabilities as fit by glm with analyses based on binary data are displayed by the lines. Pseudo-R² of ES-GLMs are in parentheses.* ***Main results****: pFFtree decreases sharply with elevation whereas pDFtree showes a mid-elevation peak around 1250 m a.s.l. The canopy in the lowlands is dominated by FF trees and is increasingly enriched with DF trees. However, ES-GLM showes a weak explanatory power for pDFtree and poorly fitted above 1500 m a.s.l. Empirical data actually show that DF trees are much more present subalpine shrubland (up to 2600 m a.s.l) than FF trees. DF shrubs strongly dominate woody species communities in subalpine shrubland on Réunion.*

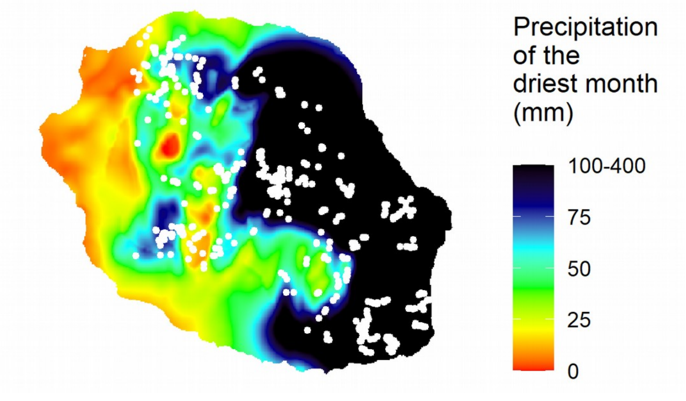
***App.2.1 Overview of main introduced vertebrates established in native land ecosystems** on La Réunion, Mauritius mainland and Mauritius northern islets ("FI" Flat Island", "GI" Gabriel Island, "GQ" Gunner's Quoin, "RI" Round Island, "SI" Serpent Island). Diet: "F" frugivore, "G" granivorous, "H", herbivore, "I" diet mostly composed of invertebrates, "O" omnivore including vertebrates, "P+" mostly predator, "P-" diet that sometimes includes vertebrates; "*" several species in the same genus; "#" species introduced as taxon substitutes. Dates in red symbolize the introduced species that went extinct in the meantime. Date: "<" before, ">" after, "?" attested presence but unknown date of introduction. References: "1" (Cheke, 2010), "2" (Cheke and Hume, 2008), "3" (Bissessur and Probst, 2018), "4" (Barré et al., 2005), "5" (Hume, 2013), "6" (Griffiths et al., 2011), "7" (Cole, 2012), "8" (Cheke, 2013), "9" (Cole, 2009), "10" (Guillermet et al., 1998).*

Taxon		Diet	Réunion	Mauritius	Mauritius islets	Ref
Amphibia **(b)**						
Guttural toad	*Amietophrynus gutturalis*	I	1927	1922	-	1,2
Malagasy grass frog	*Ptychadena mascaren.*	I	1790	1760	-	2
Aves						
Common myna	*Acridotheres tristis*	F I P-	1759	1762	1965 GQ	1,2
Grey-headed lovebird	*Agapornis canus*	F G	1840	1730	-	2
Red avadavat	*Amandava amandava*	G	1750	1745	-	2
Feral pigeon	*Columba livia*	G I	1800	1830	-	2
Black parrot	*Coracopsis sp*	F	1790	-	-	2
House crow	*Corvus splendens*	O	-	1880	-	1-3
Common quail	*Coturnix coturnix*	G	1860	1885	-	2
Common waxbilll	*Estrilda astrild*	G	1820	1810	1900 FI, 1990 GQ	2
Painted quail	*Excalfactoria chinensis*	G	1820	1775	-	2
Cardinal fody	*Foudia madagascariensis*	G	1765	1765	1965 FI	2
Grey francolin	*Francolinus pondicerianus*	G	1845	1740	20th FI GQ	2,3
Red junglefowl	*Gallus gallus*	F G H I	1892	1705	-	2
Zebra dove	*Geopelia striata*	I H	1790	1760	19th RI FI, 20th GI GQ	2
Common hill myna	*Gracula religiosa*	F I P-	>1970	-	-	4
Helmeted Guineafowl	*Numida meleagris*	F G H I	1710	1720	1905 FI	2
Red-billed leiothrix	*Leiothrix lutea*	F	1980	-	-	4
Finches (2-3 species)	*Lonchura spp**	G	1770	1740	Late 20th GQ RI	2
Malagasy partridge	*Margaroperdix madagascar.*	G I	1840	1740	-	2
Madagascar turtle-dove	*Nesoenas picturatus*	F G I	1660	1800	-	5
House sparrow	*Passer domesticus*	G	1845	1850	1965 FI, 1990 RI GI	2
Jungle bush quail	*Perdicula asiatica*	G I	1845	1855	-	2
Village weaver	*Ploceus cucullatus*	G I	1880	1885	-	2
Ring-necked parakeet	*Psittacula krameri*	F	-	1885	-	2
Red-whiskered bulbul	*Pycnonotus jocosus*	F	1970	1892	Late 20th FI GI GQ	1,2
Canaries (2 species)	*Serinus spp**	G	1770	1755	1965 FI	2
Doves (2 species)	*Spilopelia spp**	G H	-	1765	1950 GQ	2
Mammalia						
Cattle	*Bos taurus*	H	1629	1606	1800	1,2
Goat	*Capra hircus*	H	1612	1606	19th	1,2
Deer	*Cervus timorensis*	H	1758	1639	20th	1,2
Horse	*Equus ferus*	H	-	1670	-	1,2
Lemur	*Eulemur fulvus*	F H	1820	-	-	1,2
Cat	*Felis catus*	P+	1680	1680s	19th	1,2
Palm squirrel	*Funambulus palmarum*	F G	1858	-	-	2
Mongoose	*Herpestes auropunctatus*	P+	-	1900	-	1,2
Hare	*Lepus nigricollis*	H	1777	1735	19th	1,2
Macaque	*Macaca fascicularis*	O	-	1602	-	1,2
Mouse	*Mus musculus*	O	<1754	<1750	19th	1,2
Rabbit	*Oryctolagus cuniculus*	H	-	1755	19th	1,2
Brown rat	*Rattus norvegicus*	O	1735	1735	19th	1,2
Ship rat	*Rattus rattus*	O	1674	14th	19th	5
Greater Tenrec	*Setifer setosus*	I	-	1790	-	1,2
Musk shrew	*Suncus murinus*	I	1730s	1765	-	1,2
Pig	*Sus scrofa*	O	1629	1606	-	1,2
Tenrec	*Tenrec ecaudatus*	F I	1801	1785	-	1,2
Chelonii						
Aldabra giant tortoise #	*Aldabrachelys gigantea* **#**	F H	-	-	1880 FI; 21st RI	2,6,7
Radiated tortoise #	*Astrochelys radiata* **#**	F H	-	-	21st RI	7
Wattle-necked Softshell Turtle	*Palea steindachneri*	O	-	1920	-	8
Red-eared slider	*Trachemys scripta*	H I	-	1980	-	9
Squamata						
Rainbow agama	*Agama agama*	I P-	1997	-	-	10
Oriental garden lizard	*Calotes versicolor*	I P-	1870	1900	-	2,9
Square-toed gecko	*Ebenavia inunguis*	I	-	1880	-	9
Panther Cameleon	*Furcifer pardalis*	I	1830	1825	-	2
Asian geckos (2 species)	*Hemidactylus spp**	I	1860	1760	1990 FI GI	2
Common worm gecko	*Hemiphyllodactylus typus*	I	1965	1880	-	2
Indian wolf snake	*Lycodon aulicus*	P+	1835	1870	-	2,9
Mada. Geckos (2 species)	*Phelsuma spp**	I P-	1980	1980	-	1,2,9

(a) Island	Sea	Transformed habitats	0 - 400 m	400 - 800 m	800 - 1200 m	1200 - 1600 m	1600 - 2000 m	2000 - 2400 m	2400 - 3000 m
Mauritius	0	0	1	0,8	-	-	-	-	-
La Réunion	0	0	1	0,8	0,4	0,2	0,1	0,05	0,025



App.2.2 Assessment of lowland suitability since first human settlements taking into account the fragmentation of native habitats on La Réunion and Mauritius. *For each island, we used a Digital Elevation Model of 150 m resolution.* ***(a)*** *Suitability values were assigned to pixels of native forests from 1 at sea level to 0,025 for high elevations using a simple elevational typology. In order to account for habitability of adjacent areas, we calculated for each pixel the average of pixel values within a radius of 2.5 km. A value of zero was assigned to the ocean and transformed habitats. While in the latter case this value might seem exaggerated, it takes into account the fact that native vertebrates were subject to very strong anthropogenic pressures there.* ***(b)*** *Habitat suitability is displayed by a color gradient: warm and cool colors respectively show high and low quality of habitats for forest vertebrates. Top, La Réunion; bottom, Mauritius.*



App.2.3 Location of vegetation surveys in relation with precipitation of the driest month on La Réunion. *The 430 historical plots used for analyses are shown in white and values of precipitation derived from 30-year averages. The colour gradient is deliberately saturated above 100 mm.*

App.3.1 *Available radiocarbon ages and location of the recent (<1000 yr) eruptions of Piton de la Fournaise. Calibrated ages have been computed with Calib 7.1 online version (Stuiver et al., 2019). For the current work, we determined the calibrated radiocarbon ages with SHCal13 (Hogg et al., 2013), calibration specifically determined for the southern hemisphere, instead of the IntCal13 (Reimer et al., 2013) calibration curve. Eruptions highlighted in grey are used for calibrating the* Agarista *model. EF cald: Enclos Fouqué caldera; Age BP: Before Present; CE: Common Era*

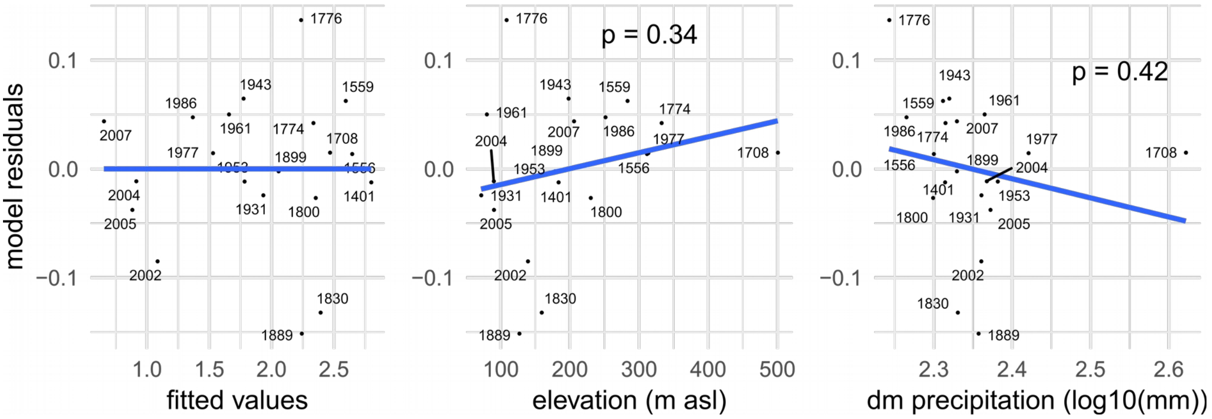
Eruption	Location	^{14}C age (BP)	±	SHCal13 calibration			IntCal13 calibration			X (UTM, WGS 84 40S)	Y (UTM, WGS 84 40S)
				Median probability (CE)	Calibrated min (CE) 2σ	Calibrated max (CE) 2σ	Median probability (CE)	Calibrated max (CE) 2σ	Calibrated min (CE) 2σ		
Langevin plateau 1 fall	W of EF cald	868	30	1218	1162	1271	1177	1046	1251	360177	7650158
Langevin plateau 2 fall	W of EF cald	620	30	1354	1312	1422	1349	1292	1399	360177	7650158
Le Baril 1 lava flow	S flank	575	75	1401	1287	1491	1358	1281	1444	365841	7638410
Petit Cratère cone	NW of EF cald	420	25	1488	1448	1622	1455	1431	1615	361290	7655172
Ravine Ango lava flow	SE flank	455	70	1493	1408	1632	1457	1318	1635	374810	7638926
Piton Indivis cone	NE flank	420	80	1532	1410	1655	1500	1327	1649	376296	7655301
Ravine Citrons Galets lava flow	SE flank	385	25	1556	1462	1627	1486	1443	1626	374463	7644286
Plaine des Sables fall	W of EF cald	380	25	1558	1464	1628	1493	1446	1630	361199	7651747
Mare Longue lava flow	South flank	364	25	1559	1484	1636	1517	1451	1632	369289	7637962
Partage cliff 1 fall	N of EF cald	340	30	1560	1497	1649	1559	1470	1639	366110	7653616
Piton Taipoul cone	S of EF cald	355	75	1567	1443	1798	1549	1427	1794	366431	7645459
Piton Nelson cone	NE flank	260	80	1707	1497	1950	1643	1450	1950	376296	7655597
Partage cliff 2 fall	N of EF cald	255	30	1743	1633	1802	1650	1521	1950	365582	7653225
Piton Rampe 14 lava flow	NW of EF cald	140	90	1812	1655	1950	1791	1528	1950	363034	7654507
Partage cliff 3 fall	N of EF cald	160	30	1838	1673	1950	1773	1664	1950	364087	7653099
Partage cliff 4 fall	N of EF cald	130	30	1856	1690	1950	1821	1675	1941	365582	7653225

App.3.2 *Comparison of calibrated models: Model 1 with intercept only, Model 2 with maximal distribution of* Agarista *(D_{95}, see main text for definition), Model 3 with an additional quadratic term ($I(D_{95}^2)$). Adding a quadratic term has a weak effect (increase of R-squared = 1.75%), but the difference is nevertheless highly significant. Rse.Df: Residual Degrees of Freedom; RSS: Residual sum of squares; Df: degrees of freedom; Pr(>F): P-value.*

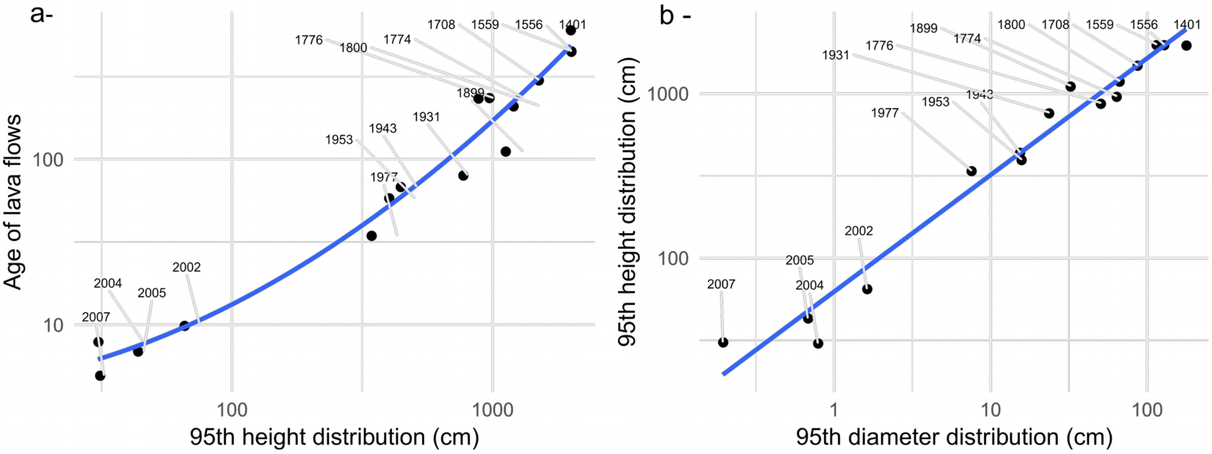
Model	Res.Df	RSS	Df	Sum of Squares	F value	Pr(>F)	R²
1: age ~ 1	19	7.8681					
2: age ~ D_{95}	18	0.2242	1	7.6439	1499.746	< 2.2 E-16	0.971
3: age ~ D_{95} + I(D_{95}^2)	17	0.0866	1	0.1376	26.997	7.289E-05	0.988

App.3.3 *Calibrated model of the functional relationship between the 95th percentile of the diameter distribution of* Agarista *(D_{95}) and the age of lava flows. The best model includes a hump-shaped transformation. Residual standard error: 0.07509 on 17 degrees of freedom. Multiple R-squared: 0.9881, Adjusted R-squared: 0.9867. F-statistic: 708.5 on 2 and 17 DF, p-value: < 2.2e-16.*

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.9686	0.0284	34.0886	4.31E-17
Log(D_{95})^2	0.1260	0.0243	5.1958	7.29E-05
Log(D_{95})	0.5301	0.0461	11.4892	1.95E-09



App.3.4 *Study of calibrated model residuals depending on fitted values, elevation and precipitation of driest month (dm precipitation) of sampled plots. The test of Spearman's rank correlation coefficients shows there is no significant relationship between model residuals and elevation/precipitation.*



App.3.5 a- *Relationship between 95th percentile of height distribution and age of lava flows.* ***b-*** *Relationship between 95th percentile of diameter distribution and 95th percentile of height distribution. Note the log-log scale for both relationships and that height measurements are not available for four lava flows that have been used in the model calibration based on the 95th percentile of diameter distribution (1986, 1961, 1889, 1830).*

App.4.1. *Overview of the frugivore vertebrate of La Réunion with indication of the body mass (g) and conservation UICN status (EX: extinct, EN: endangered, LC: least concern). "*" occasionally frugivore; "1" Data related to extinct frugivore species without any available measurement were inferred from subfossils archives and/or from extant closely related species; "2" rough approximate value because substantial differences were found depending on the sources. "3" A small population has been occurring in the East of La Réunion since the beginning of the 21st century.*

Taxonomy	Species name	Body mass (g)	IUCN status	Source
Aves				
Columbiformes	*Alectroenas* sp Blue pigeon	[1]170	**EX**	1–3
	**Nesoenas duboisi* Réunion pink pigeon	[1]300	**EX**	4
Passeriformes	**Foudia delloni* Réunion fody	[1]15	**EX**	4
	Fregilupus varius Hoopoe starling	110	**EX**	6
	Hypsipetes borbonicus Réunion bulbul	55	LC	4
	Zosterops borbonicus Réunion grey white-eye	9	LC	4
	Zosterops olivaceus Réunion olive white-eye	10	LC	4
Psittaciformes	*Mascarinus mascarin* Mascarin parrot	[1]250	**EX**	5,7
	Psittacula (?) borbonicus Réunion red & green parrot	[1]180	**EX**	5,7
	Psittacula eques Ring-necked parakeet	180	**EX**	5,7
	Psittacula bensoni Thirioux's grey parrot	[1]250	**EX**	5,7
Chelonii				
	Cylindraspis indica Réunion giant tortoise	[1,2]50 000	**EX**	5,8
Mammalia				
Chiroptera	*Pteropus niger* Black-spined flying fox	450	**[3]EX**	9
	Pteropus subniger Rougette	[1,2]250	**EX**	5,10
Squamata				
	Leiolopisma ceciliae Arnold's Skink	[1,2]130	**EX**	5,8
	**Phelsuma borbonica* Reunion day gecko	10	EN	12

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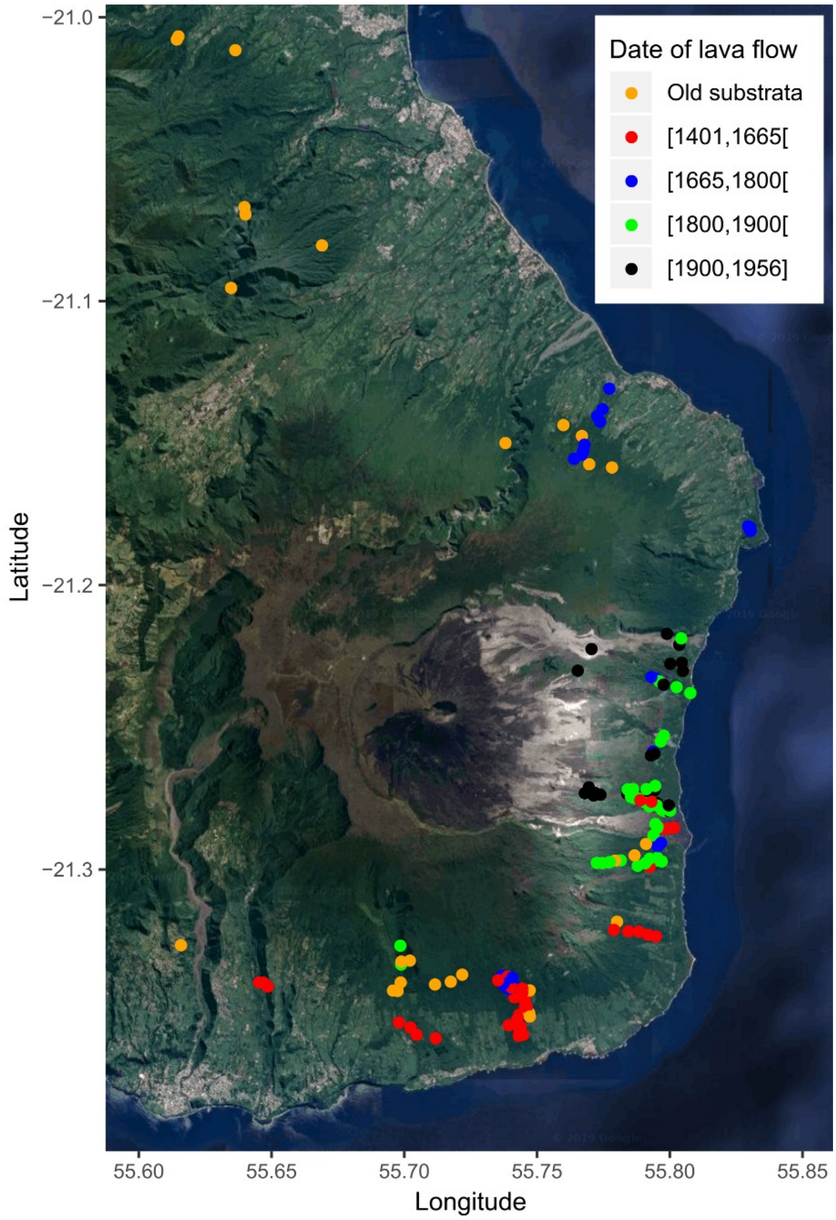

App.4.2 *Spatial distribution of the 151 vegetation plots in the Piton de la Fournaise area. On this satellite view, forests currently found below 500 m asl can be seen on recent lava flows that are not arable, while forests on old substrata no longer exist at very low elevations (see **Fig.4.2**). Here, Cadet's historical sampling is projected on a recent satellite view (R package ggmap), which reveals the vegetation plots that have subsequently been destroyed. For example, numerous plots are now below the huge lava flow that occurred in 2007 (red, blue, green and black dots in the centre right ca 21.28S, 55.79E).*

Reference

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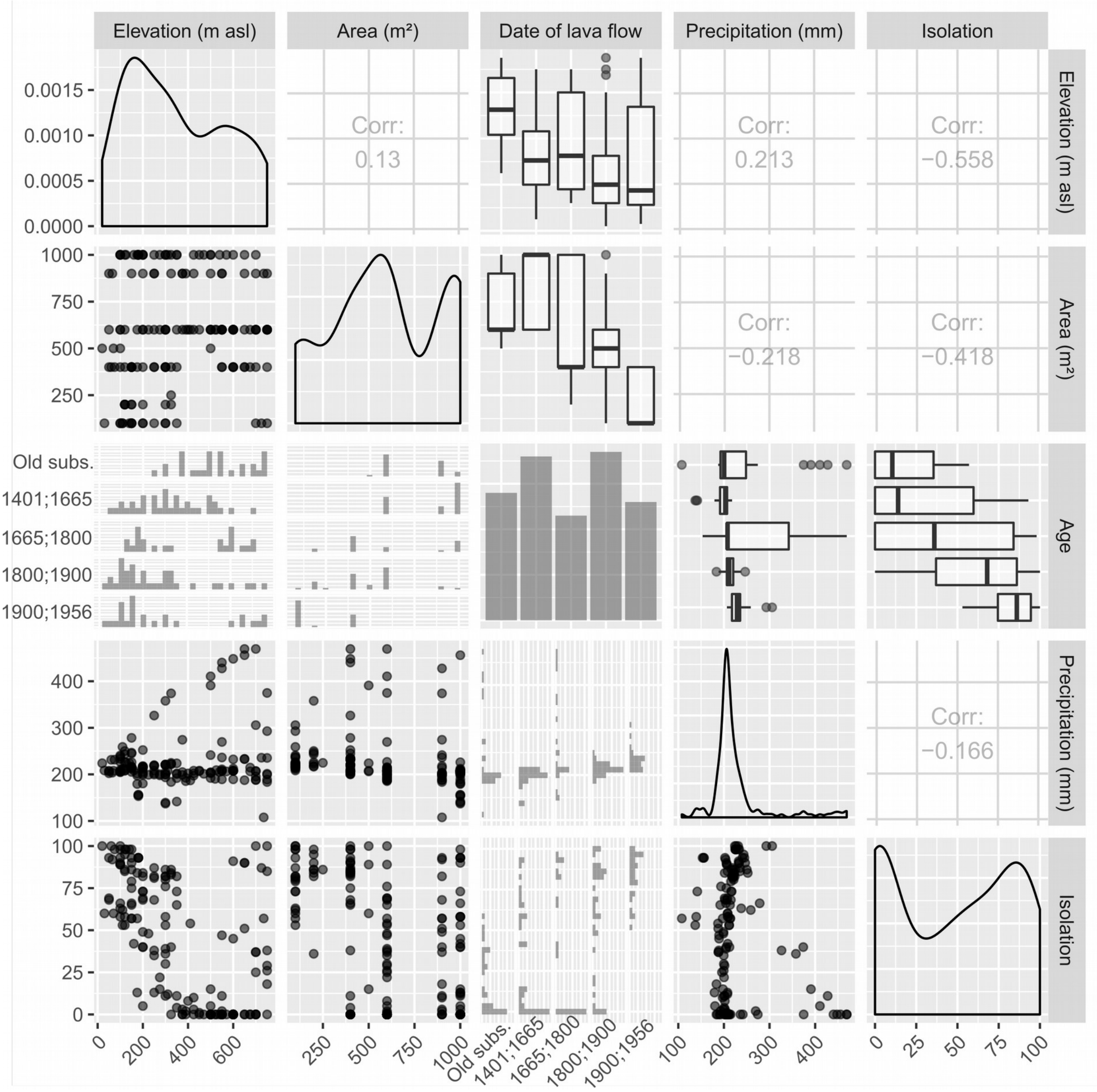
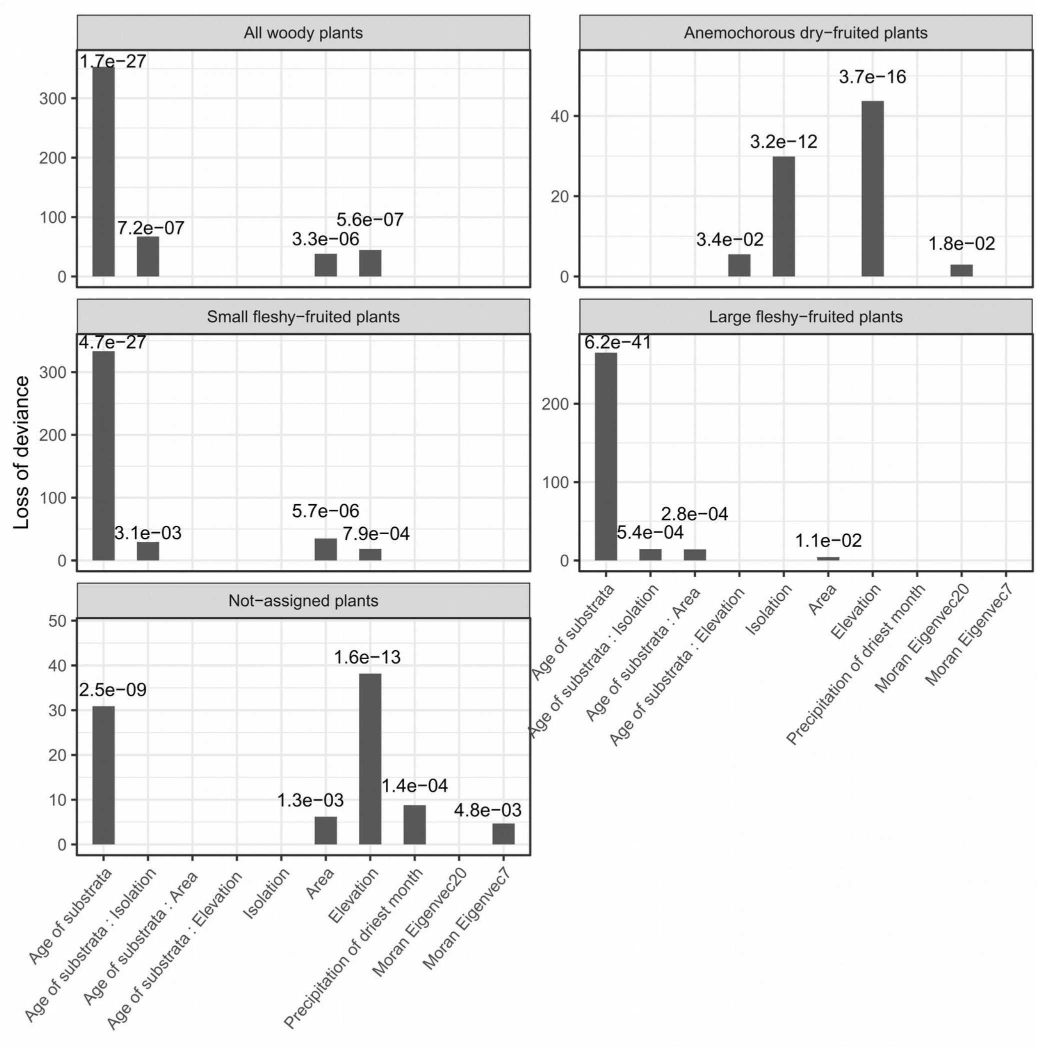


App.4.3 *Scatterplot showing the univariate and bivariate distributions of "elevation", "area", "age of substrata", "precipitation of driest month" and "isolation".*

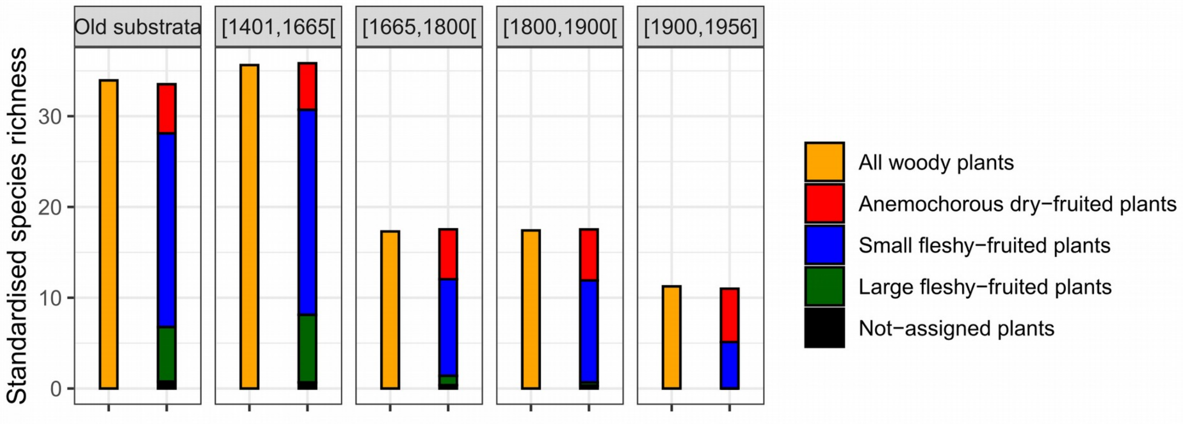
App.4.4 *Summary of Poisson GLMs for woody plants overall and each dispersal trait group. The species richness is estimated according to five variables, i.e. age of substrata (factor with five levels), sampling area, elevation, precipitation of driest month, isolation, and several interaction terms, e.g. age : isolation. Moran eigenvectors are used to control spatial autocorrelation.*

Dispersal trait group	Variable	Estimate	Std Error	Z value	P value
All woody plants	(Intercept)	2.98E+00	1.05E-01	2.85E+01	4.41E-178
All woody plants	Elevation	8.37E-04	1.25E-04	6.68E+00	2.38E-11
All woody plants	Area	5.28E-04	8.54E-05	6.19E+00	6.20E-10
All woody plants	Age [1401,1665[	-7.16E-02	5.45E-02	-1.31E+00	1.90E-01
All woody plants	Age [1665,1800[	-3.22E-01	6.67E-02	-4.83E+00	1.39E-06
All woody plants	Age [1800,1900[	-4.53E-01	7.88E-02	-5.75E+00	8.81E-09
All woody plants	Age [1900,1956]	-6.29E-01	5.00E-01	-1.26E+00	2.09E-01
All woody plants	Age Old substrata : isolation	-1.99E-03	1.52E-03	-1.31E+00	1.91E-01

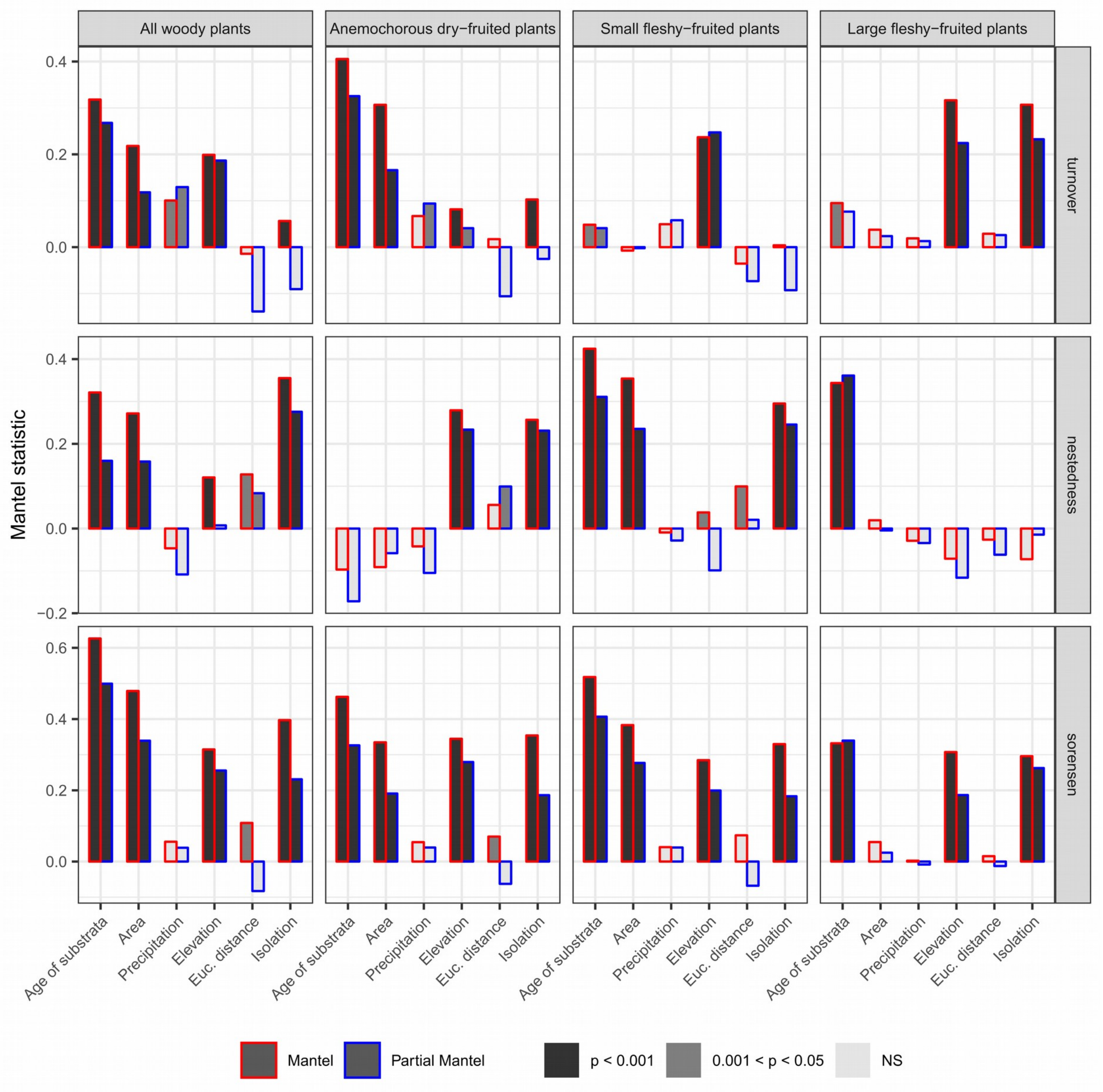
All woody plants	Age [1401,1665[: isolation	1.15E-03	9.22E-04	1.24E+00	2.14E-01
All woody plants	Age [1665,1800[: isolation	-8.50E-03	1.44E-03	-5.89E+00	3.88E-09
All woody plants	Age [1800,1900[: isolation	-5.65E-03	1.32E-03	-4.28E+00	1.91E-05
All woody plants	Age [1900,1956] : isolation	-1.11E-02	5.85E-03	-1.89E+00	5.84E-02
Anemochorous dry-fruited plants	(Intercept)	1.72E+00	1.35E-01	1.27E+01	3.52E-37
Anemochorous dry-fruited plants	Elevation	1.01E-03	2.25E-04	4.51E+00	6.58E-06
Anemochorous dry-fruited plants	Isolation	-8.24E-03	1.52E-03	-5.42E+00	5.89E-08
Anemochorous dry-fruited plants	Moran Eigenvec20	-6.83E-01	3.97E-01	-1.72E+00	8.57E-02
Anemochorous dry-fruited plants	Age [1401,1665[: Elevation	-3.69E-04	2.26E-04	-1.64E+00	1.02E-01
Anemochorous dry-fruited plants	Age [1665,1800[: Elevation	2.08E-05	1.89E-04	1.10E-01	9.12E-01
Anemochorous dry-fruited plants	Age [1800,1900[: Elevation	1.12E-04	2.11E-04	5.32E-01	5.95E-01
Anemochorous dry-fruited plants	Age [1900,1956] : Elevation	3.84E-04	2.91E-04	1.32E+00	1.86E-01
Small fleshy-fruited plants	(Intercept)	2.47E+00	1.36E-01	1.82E+01	1.20E-73
Small fleshy-fruited plants	Elevation	7.09E-04	1.65E-04	4.30E+00	1.72E-05
Small fleshy-fruited plants	Area	6.46E-04	1.09E-04	5.92E+00	3.20E-09
Small fleshy-fruited plants	Age [1401,1665[	-3.96E-02	6.85E-02	-5.78E-01	5.63E-01
Small fleshy-fruited plants	Age [1665,1800[	-4.02E-01	8.75E-02	-4.59E+00	4.39E-06
Small fleshy-fruited plants	Age [1800,1900[	-5.09E-01	1.02E-01	-4.98E+00	6.23E-07
Small fleshy-fruited plants	Age [1900,1956]	-3.14E-01	8.48E-01	-3.70E-01	7.11E-01
Small fleshy-fruited plants	Age Old substrata : isolation	-1.38E-03	1.92E-03	-7.16E-01	4.74E-01
Small fleshy-fruited plants	Age [1401,1665[: isolation	1.03E-03	1.15E-03	8.98E-01	3.69E-01
Small fleshy-fruited plants	Age [1665,1800[: isolation	-6.98E-03	1.81E-03	-3.85E+00	1.20E-04
Small fleshy-fruited plants	Age [1800,1900[: isolation	-3.63E-03	1.68E-03	-2.16E+00	3.10E-02
Small fleshy-fruited plants	Age [1900,1956] : isolation	-2.39E-02	1.03E-02	-2.32E+00	2.03E-02
Large fleshy-fruited plants	(Intercept)	1.29E+00	3.66E-01	3.52E+00	4.35E-04
Large fleshy-fruited plants	Area	6.21E-04	4.53E-04	1.37E+00	1.70E-01
Large fleshy-fruited plants	Age [1401,1665[	7.42E-01	4.82E-01	1.54E+00	1.24E-01
Large fleshy-fruited plants	Age [1665,1800[	-1.38E+00	5.79E-01	-2.38E+00	1.72E-02
Large fleshy-fruited plants	Age [1800,1900[	-4.50E+00	1.13E+00	-3.99E+00	6.60E-05
Large fleshy-fruited plants	Age [1900,1956]	-2.06E+01	1.11E+04	-1.85E-03	9.99E-01
Large fleshy-fruited plants	Age [1401,1665[: Area	-8.38E-04	5.82E-04	-1.44E+00	1.50E-01
Large fleshy-fruited plants	Age [1665,1800[: Area	9.04E-04	7.39E-04	1.22E+00	2.21E-01
Large fleshy-fruited plants	Age [1800,1900[: Area	3.55E-03	1.38E-03	2.57E+00	1.01E-02
Large fleshy-fruited plants	Age [1900,1956] : Area	-6.21E-04	1.41E+01	-4.41E-05	1.00E+00
Large fleshy-fruited plants	Age Old substrata : isolation	3.22E-03	3.92E-03	8.21E-01	4.12E-01
Large fleshy-fruited plants	Age [1401,1665[: isolation	2.12E-03	1.96E-03	1.08E+00	2.80E-01
Large fleshy-fruited plants	Age [1665,1800[: isolation	-1.59E-02	4.98E-03	-3.19E+00	1.43E-03
Large fleshy-fruited plants	Age [1800,1900[: isolation	-5.39E-03	9.05E-03	-5.96E-01	5.51E-01
Large fleshy-fruited plants	Age [1900,1956] : isolation	7.57E-13	1.39E+02	5.44E-15	1.00E+00
Not-assigned plants	(Intercept)	-2.97E+00	6.55E-01	-4.54E+00	5.67E-06
Not-assigned plants	Elevation	3.61E-03	6.03E-04	5.98E+00	2.21E-09
Not-assigned plants	Age [1401,1665[	-1.31E-01	2.61E-01	-5.01E-01	6.16E-01
Not-assigned plants	Age [1665,1800[	-7.38E-01	2.84E-01	-2.60E+00	9.43E-03
Not-assigned plants	Age [1800,1900[	-9.17E-01	3.72E-01	-2.47E+00	1.36E-02
Not-assigned plants	Age [1900,1956]	-1.86E+01	1.52E+03	-1.23E-02	9.90E-01
Not-assigned plants	Area	1.20E-03	4.80E-04	2.50E+00	1.23E-02
Not-assigned plants	Precipitation of driest month	3.17E-03	1.04E-03	3.06E+00	2.21E-03
Not-assigned plants	Moran Eigenvec7	1.94E+00	8.95E-01	2.16E+00	3.04E-02



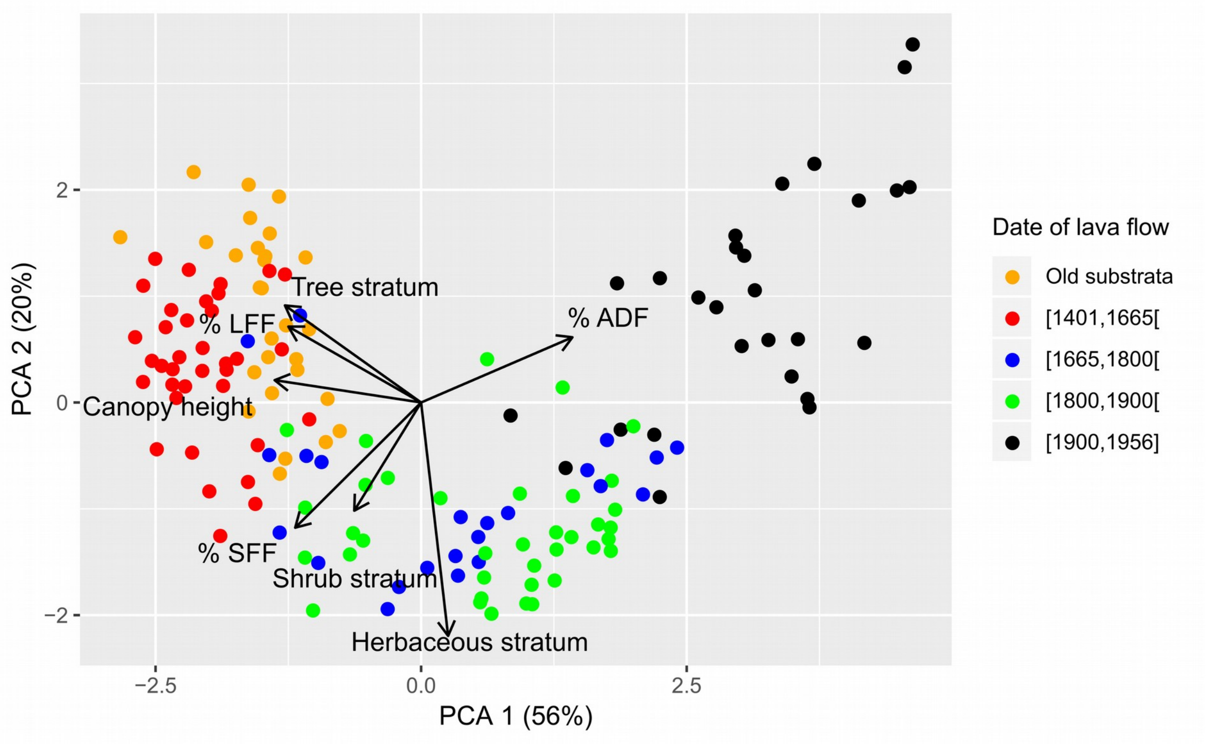
App.4.5 *Loss of GLM deviance when each variable is removed from the full model (including interaction terms and Moran eigenvectors). Significance of anova type-II test is given.*



App.4.6 *Comparison of total standardised richness ("All woody plants") with the sum of standardised richness estimated separately for each dispersal trait group. Note that we include plants that were not assigned to a specific group because their dispersal strategy is unclear. The standardised richness of not-assigned plants was estimated with same methods. Overall the sum of separate values provides a similar estimate to the total standardised richness, with a low average relative difference of 0.5%.*

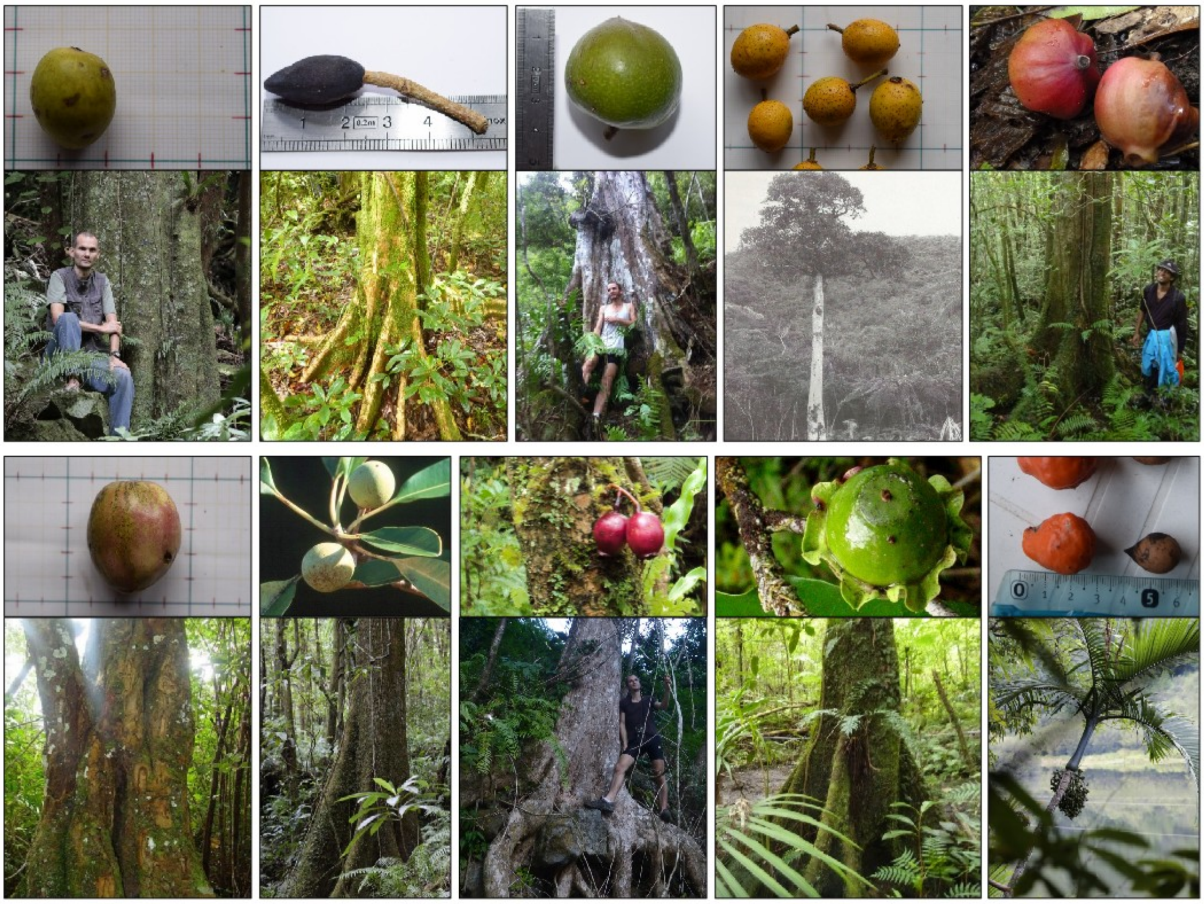


***App.4.7** Results of simple (red) and partial (blue) Mantel tests on relationships between six environmental and spatial distance matrices (age of substrata, sampling area, precipitation of driest month, elevation, Euclidean distance, isolation) and pairwise dissimilarities (Sorensen, turnover and nestedness) for each dispersal trait group. The significance of tests is presented in shades of grey.*

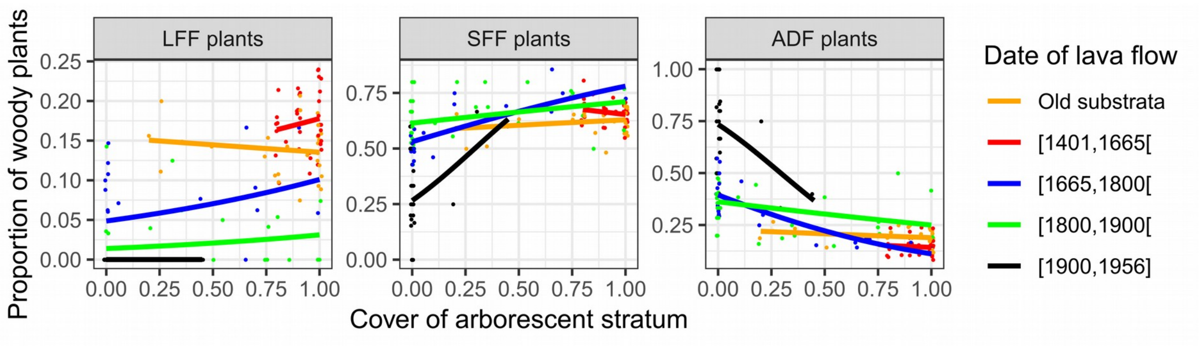


App.4.8 *PCA ordination plot showing the distribution of 151 historical plots along major PCA components and their association with four descriptors of vegetation structure and three descriptors of dispersal trait diversity. Tree, shrub and herbaceous stratum cover (%) and maximum canopy height (m) were assessed for each plot. Dispersal trait diversity is here based on dispersal trait proportions: % ADF = number of anemochorous dry-fruited species / number of woody plant species; % LFF = number of large fleshy-fruited species / number of woody plant species; % SFF = number of small fleshy-fruited species / number of woody plant species. Proportions account for the strong heterogeneity of plot area. Age class of vegetation plots is shown in different colors. The proportion of explained variance is given for each component.*

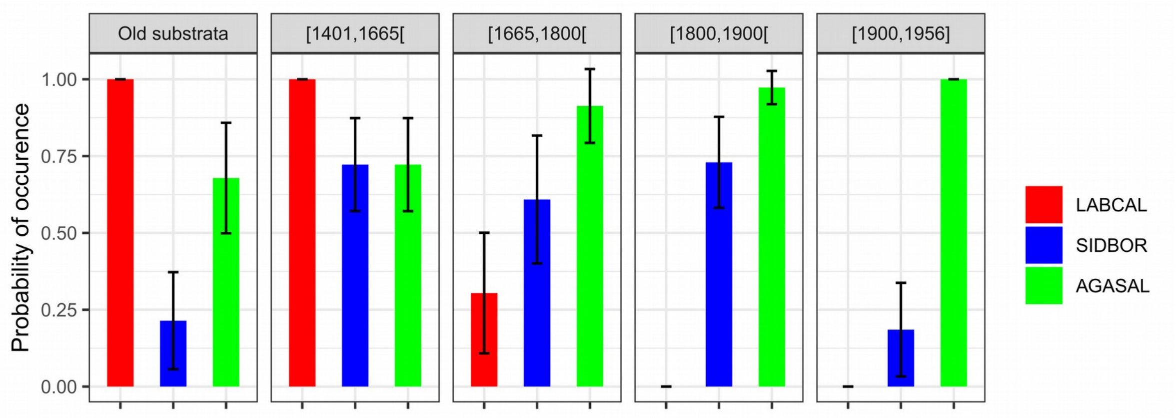
A high proportion of total variance (76%) is explained. There is a strong relationship between dispersal trait diversity and vegetation structure across the chronosequence (temporal gradient is clearly visible). Plots on lava flows that occurred before 1665 usually show a high proportion of large and small fleshy-fruited species, in addition to a well closed tree stratum with tall trees. Plots on lava flows that occurred between 1665 and 1800 show a more heterogeneous distribution: several plots have well-structured vegetation, while many have an open canopy, like most plots on lava flows after 1800.



***App.4.9** Examples of native large fleshy-fruited trees that play a structural role in canopies of tropical rainforests on Réunion. Top, from left to right:* Cassine orientalis *(Celastraceae),* Chionanthus broomeana *(Oleaceae),* Sideroxylon majus *(Sapotaceae),* Drypetes caustica *(Putranjivaceae),* Hernandia mascarensis *(Hernandiaceae). Bottom, from left to right:* Ochrosia borbonica *(Apocynaceae),* Labourdonnaisia calophylloides *(Sapotaceae),* Syzygium cymosum *(Myrtaceae),* Diospyros borbonica *(Ebenaceae),* Hyophorbe indica *(Arecaceae). Photo montage: S. Albert*



***App.4.10** Relationship across the chronosequence between the cover of arborescent stratum and the proportion of large fleshy-fruited (LFF), small fleshy-fruited (SFF) and anemochorous dry-fruited (ADF) plants among woody plants. Points and lines, respectively, display vegetation plots and predicted probabilities as fit by binomial glm. The proportions used account for the strong heterogeneity of plot area.*



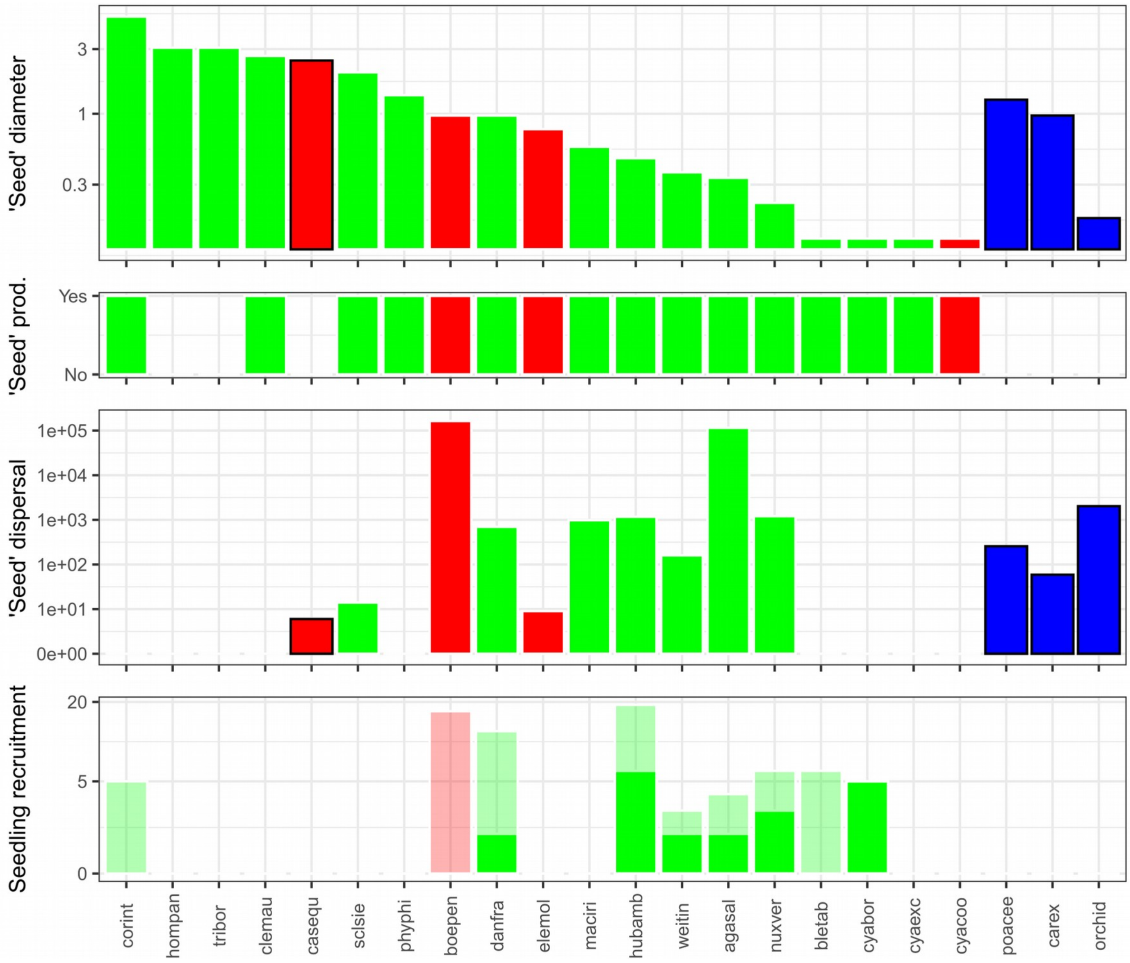
App.4.11 *Probability of occurrence across the chronosequence of three large common tree species: AGASAL,* Agarista salicifolia *(Ericaceae), an anemochorous long-lived pioneer tree; SIDBOR,* Sideroxylon borbonicum *(Sapotaceae), a small fleshy-fruited long-lived pioneer tree; LABCAL,* Labourdonnaisia calophylloides *(Sapotaceae), a large fleshy-fruited shade-tolerant tree. Bars and error bars, respectively, display mean of occurrence within plots and confidence intervals. Long-lived pioneer trees live over 500 years. LABCAL is always present on substrata before 1665, rare on lava flows dating from [1665,1800] and totally absent on lava flows that occurred after the extinction of every large-bodied frugivore, regardless of the level of canopy closure. SIDBOR is well represented on lava flows until 1900, but is rare on lava flows that occurred in the 20th century, despite the fact that it should be able to grow there. On the contrary, AGASAL is always present on recent lava flows. Hence, by taking into account the differences in shade tolerance of common species, we show the same strong correlation between the age of substrata as a proxy of disperser availability and the presence of plants in plots.*

App.4.12 *Examples of large fleshy-fruited tree species settled on lava flows of the 16th century at Marelongue. These trees can have buttresses and reach 20 m high despite the hyperskeletic abruptic Leptosol on continuous rock (see Meunier et al., 2010). On each photo,* Labourdonnaisia calophylloides *(Sapotaceae) and* Syzygium borbonicum *(Myrtaceae) are respectively to the left and to the right. Photos: Alexis Gorissen.*

***App.5.1 View towards the East above the study site**. Most of the 1800 lava flow shows an open low canopy, whereas the closed canopy of the old-growth forest is dominated by trees that exceed 20 m high. Drone image: H. Santacreu.*

***App.5.2 Overview of the four tree species used for the sowing on the 1800 flow**. From left to right,* Calophyllum tacamahaca, Syzygium cymosum, Diospyros borbonica, Sideroxylon borbonicum*. Top, seeds on graph paper; in the middle, fruits; bottom, trunk base. Photos: S. Albert & A. Gorissen.*

App.5.3 Test of exclosure effectiveness*. Left, rat eating waxtag hanging outside the cage (dashed arrow). Right, rat trying to get the waxtag hanging inside the cage (solid arrow), without success.*



App.5.4 Assesment over 18 months of active seed rain and seedling recuitment in relation to mean seed (or spore) diameter (mm) for dry-fruited plants and fern trees*. Plants are presented and ranked-ordered by estimated seed (or spore) diameter. Green, red and blue bars are native, alien and unidentified plant species, respectively. Dry-fruited plants are all anemochorous, except SCLSIE & PHYPHI (probably ornithochorous), and CORINT (autochorous). Recruitment of dry-fruited plants was estimated only for woody plants, as herbs often have a cespitose habit. Species abbreviations: AGASAL,* Agarista salicifolia*; BOEPEN,* Boehmeria penduliflora; *CASEQU*, Casuarina equisetifolia*; CLEMAU,* Clematis mauritiana; CORINT, Hancea integrifolia; *DANFRA*, Danais fragrans; *ELEMOL,* Elephantopus mollis; *HOMPAN*, Homalium paniculatum; *HUBAMB,* Hubertia ambavilla*; MACIRI,* Machaerina iridifolia*; NUXVER,* Nuxia verticillata*; ORCHID,* Orchidaceae*; POACEE, Poaceae; PHYPHI,* Phyllanthus phillyreifolius*; SCLSIE,* Scleria sieberi*; TRIBOR,* Trichosandra borbonica*;*

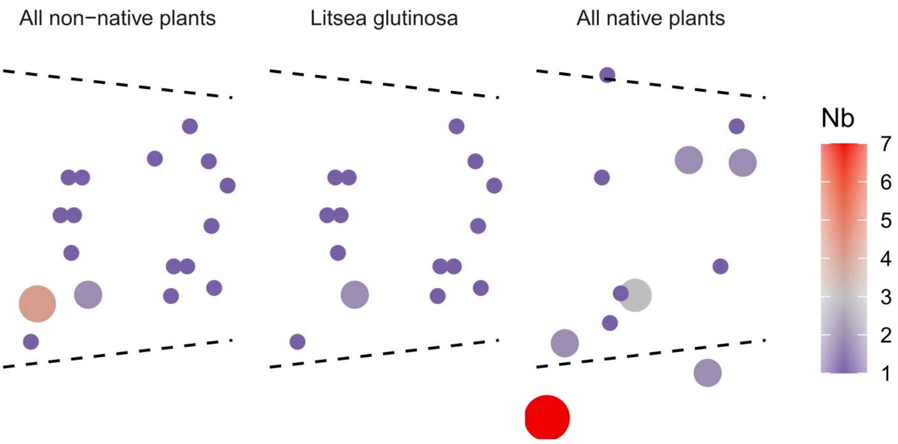
WEITIN, Weinmannia tinctoria*. Fern trees: BLETAB,* Blechnum tabulare*; CYABOR,* Cyathea borbonica*; CYACOO,* Cyathea cooperi*; CYAEXC,* Cyathea excelsa.

App.5.5 Summary of univariate GLMMs that assess the relationship with the cumulative number of seeds per species per trap. *Models are ranked-ordered by decreasing AIC. R: "Random effect", Df: "Degrees of freedom", AIC: "Akaike information criterion".*

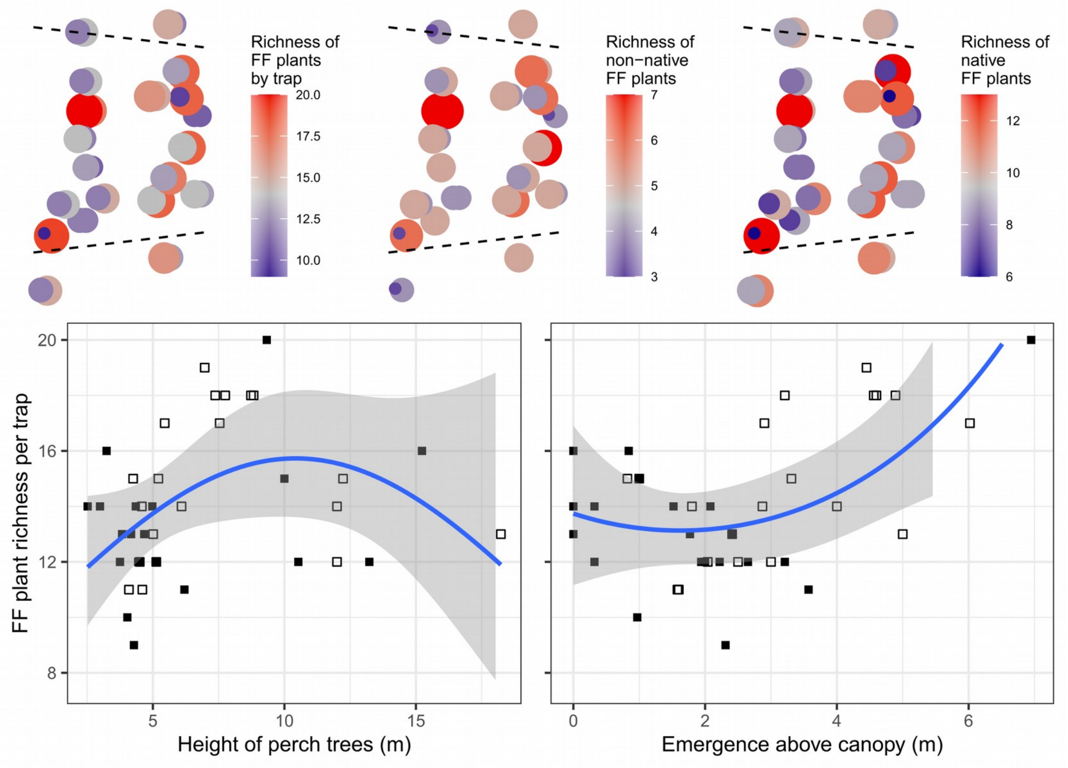
Predictor	Transformation	Df	AIC	Delta AIC	Delta AIC fixed
1		2	8621,2	8621,2	
(1 | placette)		3	8607,1	14,1	
R = (1 | placette) + (1 | code)		4	6632,8	1988,4	0,0
Distance to OGF margin + R		9	6598,4	2022,8	34,4
Status + R		7	6595,1	2026,1	37,7
Height + R	Poly, 2	8	6591,2	2030,0	41,6
Production of fleshy fruits + R		7	6586,6	2034,6	46,2
Emergence + R		7	6580,4	2040,8	52,4
Lfruit mass + R	Poly, 2	9	6574,6	2046,6	58,2
Lfruit diameter + R	Poly, 2	9	6570,1	2051,1	62,7
Lseed number + R	Poly, 2	9	6569,8	2051,4	63,0
Seed availability + R		9	6553,6	2067,6	79,2
Distance to the closest mother plant + R		9	6551,1	2070,1	81,7
Lseed mass + R	Poly, 2	9	6536,6	2084,6	96,2
Lseed diameter + R	Poly, 2	9	6516,9	2104,3	115,9
Fruit availability + R		9	6482,9	2138,3	149,9

App.5.6 Analyses of deviance of the best fitting multivariate GLMM that assess the relative influence of five predictors with the cumulative number of seeds per species per trap*. "P": p value, "NS": p > 0.1, "QS": 0.05 < p < 0.1, "*": 0.01 < p < 0.05, "**": 0.001 < p < 0.01, "***": p < 0.001, "****":* $p < 10^{-6}$.

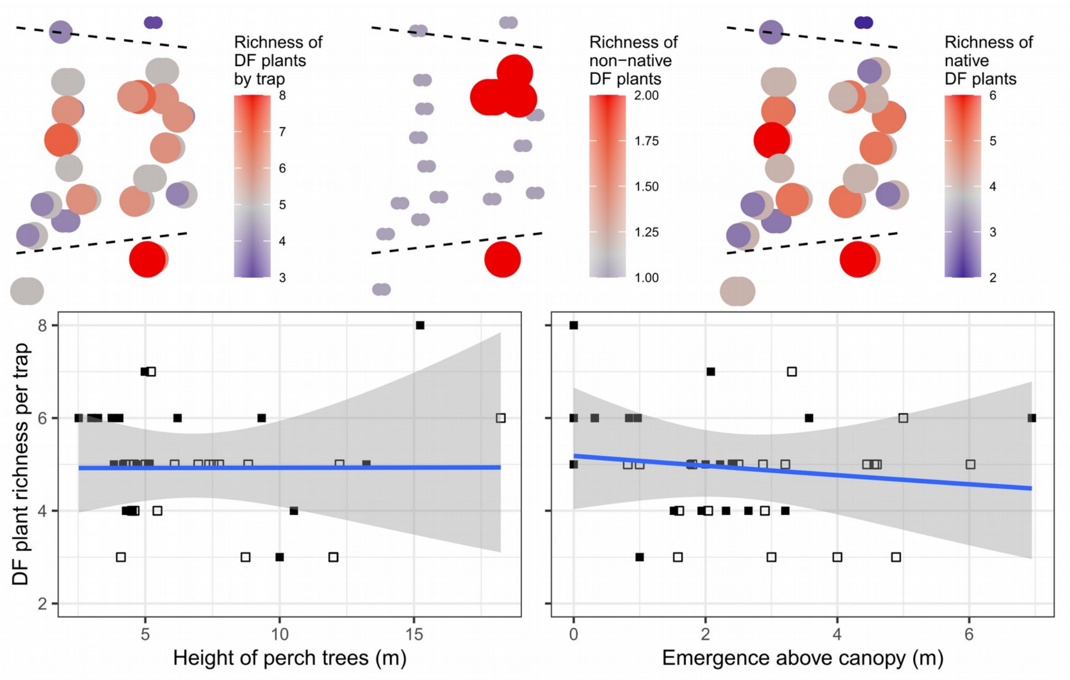
	Conditional model			Zero-inflated model	
Predictor	Chisq	Df	P	Chisq	P
Fruit availability	23,07	2	***	63,00	****
Status	2,19	1	NS	0,08	NS
Distance to OGF margin	2,36	2	NS	0,83	NS
poly(Lseed diameter), 2)	97,20	2	****	5,86	QS
Emergence	8,23	1	**	9,16	**
Fruit availability : Status	4,71	2	QS	21,82	***
Distance to OGF : poly(Lseed diameter), 2)	21,22	4	***	17,47	**



App.5.7 Spatial distribution of trapped seeds of which diameter > 5 mm. *The northern and southern limits of the 1800 flow are materialized by dashed lines. The six native species that participate in the seed rain are not shown unlike* Litsea glutinosa *which is the main contributor for non-native plants in spite of the absence of mother trees at study site.*



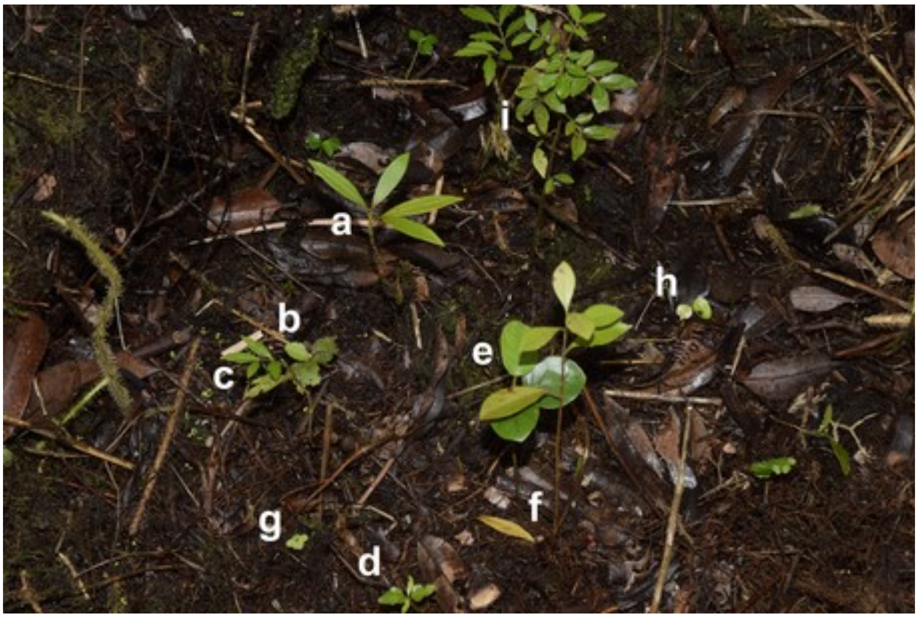
App.5.8 Spatial distribution of fleshy-fruited species richness per trap. *Top: spatial distribution of species richness by trap. The northern and southern limits of the 1800 flow are materialized by dashed lines. Bottom: relationships between richness by trap and height / emergence of perch trees. Full and empty squares are respectively fleshy-fruited and dry-fruited perch trees.*



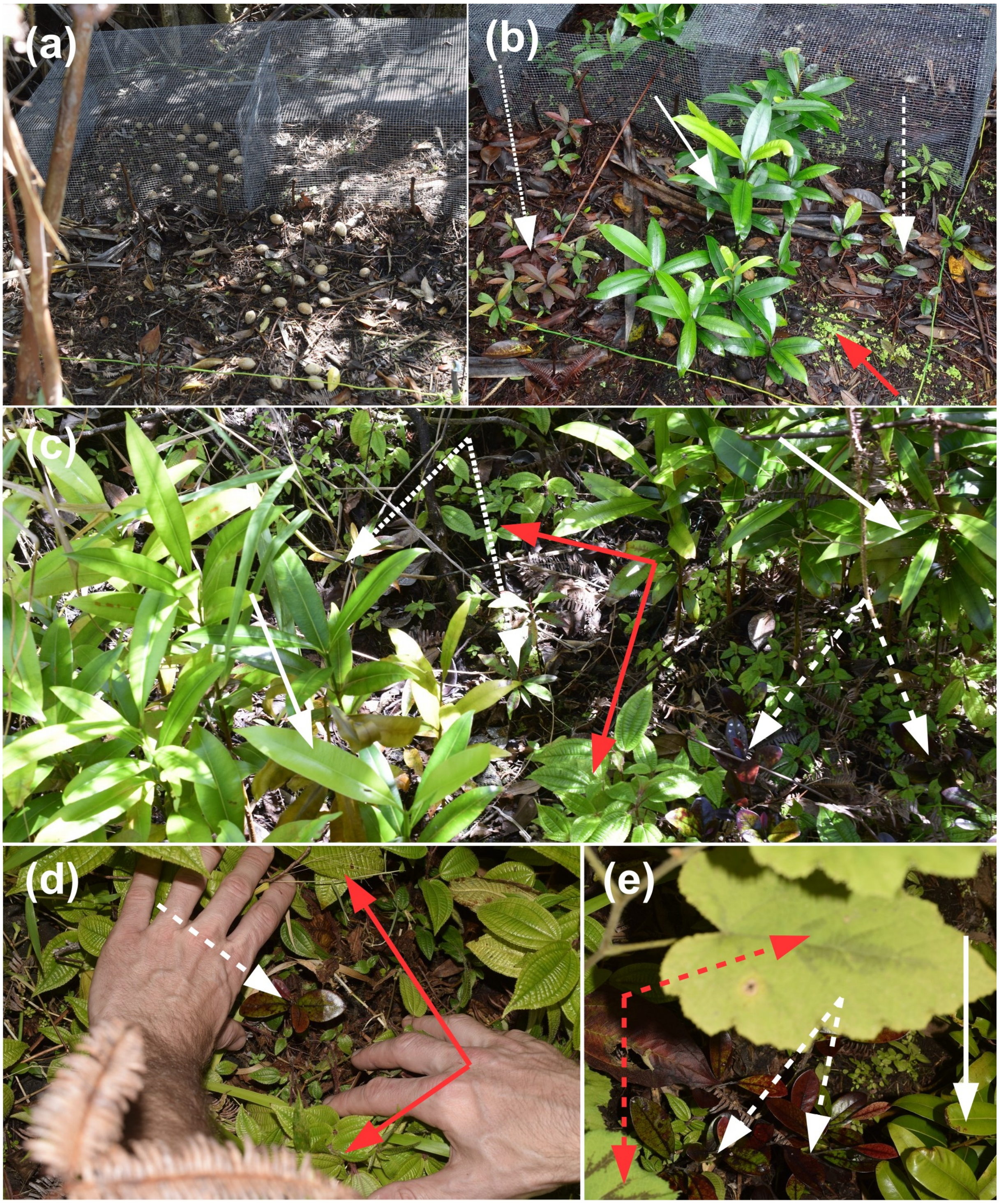
App.5.9 Spatial distribution of dry-fruited species richness per trap. *Top: spatial distribution of species richness by trap. The northern and southern limits of the 1800 flow are materialized by dashed lines. Bottom: relationships between richness by trap and height / emergence of perch trees. Full and empty squares are respectively fleshy-fruited and dry-fruited perch trees.*

App.5.10 Summary of observed frugivory interactions at Le Tremblet*. Plants in bold are non-native. “*”, Mother trees absent from study site and observations made at Saint-Philippe. Abbrevations for detection methods: “Bino”, binoculars; “Cam”, camera-trap; “****Cam****”, camera-trap on the ground; “Fec”, feces in seed traps; “+”, numerous events; “-”, few events; “/”, destroyed seeds. Abbreviations for frugivores: ZOSBOR,* Zosterops borbonicus*; ZOSOLI,* Zosterops olivaceus*; HYPBOR,* Hypsipetes borbonicus*; LEILUT,* Leiothrix lutea*; PYCJOC,* Pycnonotus jocosus; *ACRTRI*, Acridotheres tristis*; RATRAT,* Rattus rattus*; TENECA,* Tenrec ecaudatus*. For plant abbreviations, see* ***Fig.5.3****.*

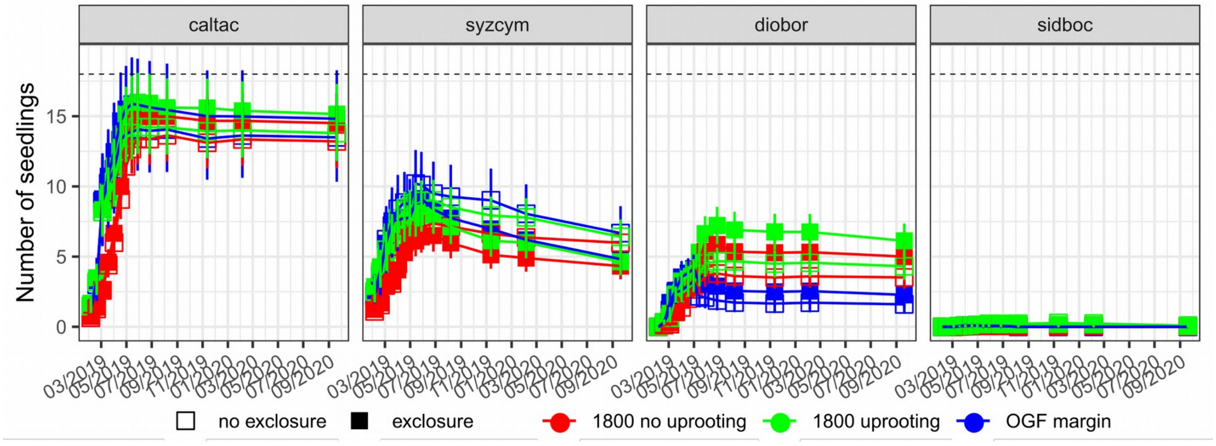
	Frugivorous vertebrates							
Plants	ZOSBOR	ZOSOLI	HYPBOR	LEILUT	PYCJOC	ACRTRI	RATRAT	TENECA
ARDCRE			Bino -		Bino -			
CLIHIR			Cam -		Cam +		Fec +	
CITAUR					**Cam** +		**Cam** +	
LITGLU*			Bino -		Bino +	Bino +		
LIVCHI*					Bino +	Bino +		
PSICAT			Bino +		Bino +		**Cam** + Fec /	
RUBALC					Cam +		Fec + Fec /	
TREORI	Cam +		Cam -		Cam +		Cam -	
ALLBOR			Bino -					
ANTBOR			Bino +		Bino -		Fec /	
APHTHE			Bino +		Bino -		Fec - Fec /	
CALTAC							**Cam** -	
CHACOR			Cam +					
DORAPE			Bino +					
FICDEN			Bino +		Bino +		**Cam** +	
FICLAT			Bino -					
FICMAU			Bino -					**Cam** +
FICREF	Bino -		Bino +		Bino +		**Cam** +	
GAEVAG			Cam +					
GENBOR		Bino +						
HYOIND							**Cam** +	
LABCAL							**Cam** -	
MOLALT			Bino +					
POLREP			Bino +				Fec - Fec /	
PSIMAU			Cam -					
SIDBOR			Bino -					



App.5.11 Seedlings at the foot of a perch tree on the 1800 flow. *“a”,* Gaertnera vaginata*; “b”,* Ardisia crenata*; “c”,* Molinaea alternifolia*; “d”,* Chassalia corallioides*; “e”,* Litsea glutinosa*; “f”,* Psidium cattleianum*; “g”,* Rubus alceifolius*; “h”,* Piper borbonense*; “i”,* Doratoxylon apetalum*. Photo: S. Albert.*



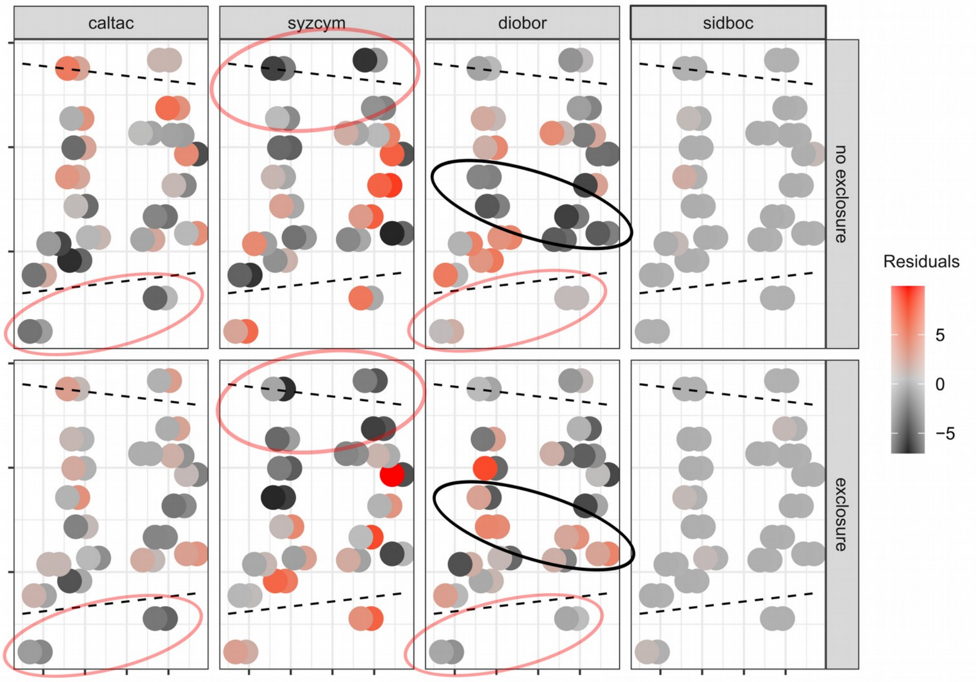
***App.5.12 View of the sowing experiment on the 1800 lava flow*. *(a)* Two weeks after sowing in January 2019. *(b)* Six months after sowing during exclosure removal in early July 2019. *(c : e)* 21 months after sowing in late September 2020. Numerous seedlings of sown large-seeded species are visible, sometimes in the middle of a large number of seedlings belonging to invasive alien species.* Calophyllum tacamahaca *(white arrow),* Syzygium cymosum *(white dotted arrow) and* Diospyros borbonica *(white dashed arrow). Invasive plants:* Clidemia hirta *(red arrow),* Rubus alceifolius *(red dashed arrow). Photos: Alexis Gorissen.*



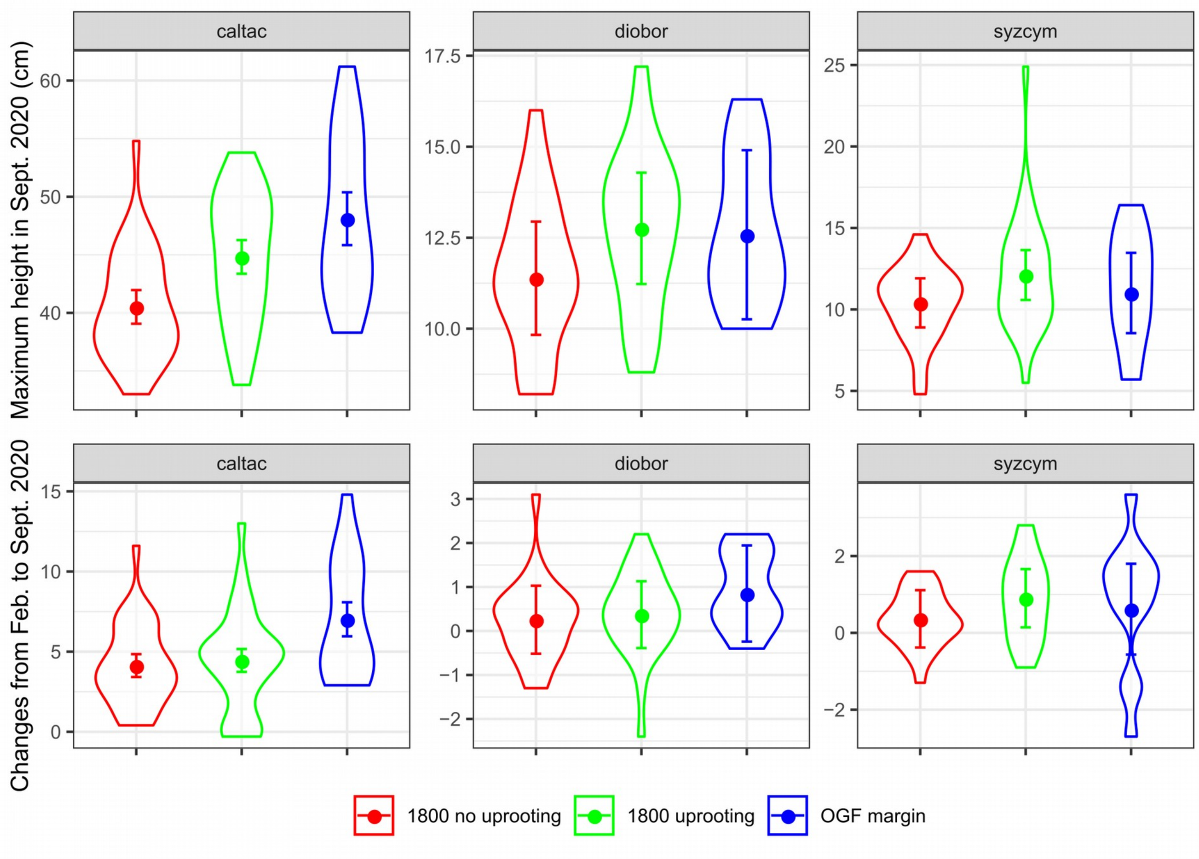
App.5.13 Temporal monitoring of seedling recruitment (sowing the 30/12/2018). *Three factors were tested (1) sown species: ("caltac":* Calophyllum tacamahaca*; "diobor":* Diospyros borbonica*; "syzcym":* Syzygium cymosum*; "sidboc":* Sideroxylon borbonicum*); (2) plant competition (levels in colors, "OGF": old-growth forest); (3) seed predation (empty or full squares). 18 seeds per modality were sown (dashed lines). Squares and error bars displayed estimates and confidence intervals.*

App.5.14 Analysis of deviance of the best fitting GLMM that assesses the influence of three experimental factors on seedling recruitment six months after sowing*. "NS": $p > 0.1$, "QS": $0.05 < p < 0.1$, "*": $0.01 < p < 0.05$, "**": $0.001 < p < 0.01$, "***": $p < 0.001$, "****": $p < 10^{-6}$.*

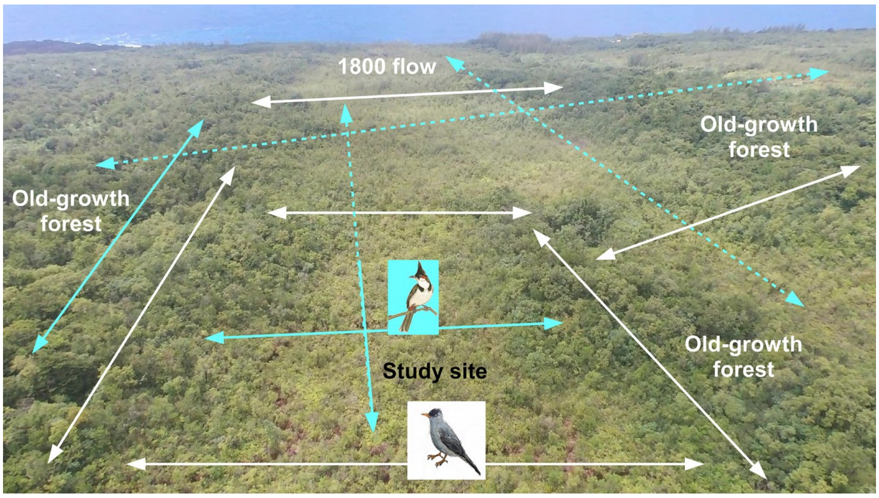
Predictor	Chisq	Df	P value
Seed predation	5,14	1	*
Competition with invasive plants	7,97	2	*
Sown species	557,94	3	****
Sown species : Seed predation	18,75	3	***
Sown species : Competition with invasive plants	29,67	6	***



App.5.15 Spatial distribution of GLMM residuals estimating the number of seedlings six months after sowing*. The northern and southern limits of the 1800 flow are materialized by dashed lines. The red ellipses illustrate patches of model overestimation for both modalities, while the black ellipses show a patch of model overestimation only for the "no exclosure" modality.*

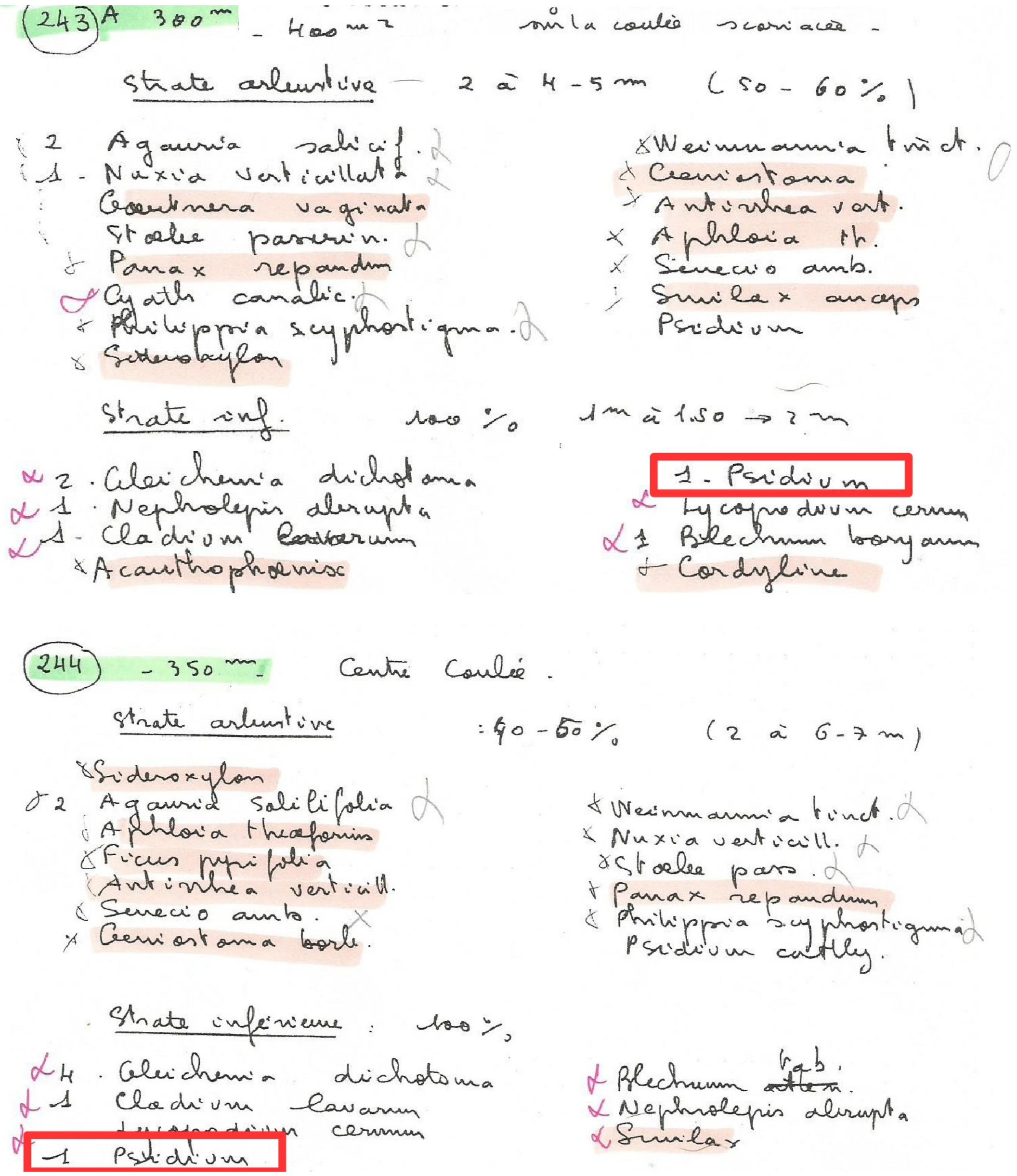


App.5.16 Relationships between growth of seedlings from sowing experiment and the three factors tested: *(1) sown species: ("caltac":* Calophyllum tacamahaca*; "diobor":* Diospyros borbonica*; "syzcym":* Syzygium cymosum*;* Sideroxylon borbonicum *was excluded from analyses because the number of seedlings is much too small, see App.5.13); (2) competition with invasive plants (levels displayed by colors, "OGF": old-growth forest); (3) seed predation (not shown because not significant). Two statistical responses are presented:* ***Above****, maximum height of seedlings 21 months after sowing (see App.5.12).* ***Below****, differences observed in the maximum height of seedlings between February and September 2020. Violins, squares and error bars respectively displayed raw data, estimates and confidence intervals predicted by GLMMs. Note the different scale for the y-axis. The results were obtained using the same methods as described in the eponymous section, except that GLMMs were performed with a Gaussian distribution.*



App.5.17 Observed (solid lines) and putative (dotted lines) movements of main frugivores. *Movements of* Hypsipetes borbonicus and Pycnonotus jocosus *are displayed in white and cyan. Drone image: Hugo Santacreu.*

App.5.18 Root mat that covers a large part of the soil on the 1800 flow. *It is mainly constituted by rhizomes and roots of* Dicranopteris linearis *and* Psidium cattleainum. *The red circles show the base of* Sideroxylon borbonicum *trunk before removal of the root mat (red arrows). It is striking to note that this tree has bark as in the open air under 15 cm of root mat and that no roots are prospecting it. This root mat probably prevents the establishment of several species in spite of their dispersal by current frugivores at study site. Photos: A. Gorissen.*



(243) A 300 m – 400 m² sur la coulée scoriacée –

Strate arbustive — 2 à 4-5 m (50-60 %)

2 Agauria salicif.
1 - Nuxia verticillata
Cordemoya vaginata
Stoebe passerin.
Panax repandum
Cyath. canalic.
Philippia scyphostigma.
Sideroxylon

Weinmannia tinct.
Ceriostoma
Antirhea vert.
Aphloia th.
Senecio amb.
Smilax anceps
Psidium

Strate inf. 100 % 1 m à 1.50 → 2 m

2. Gleichenia dichotoma
1. Nephrolepis abrupta
1 - Cladium Lavarum
Acanthophoenix

1 - Psidium
Lycopodium cernuum
1 Blechnum boryanum
Cordyline

(244) – 350 m – Centre Coulée.

Strate arbustive : 40-50 % (2 à 6-7 m)

Sideroxylon
2 Agauria salicifolia
Aphloia theaeformis
Ficus populifolia
Antirhea verticill.
Senecio amb.
Ceriostoma borb.

Weinmannia tinct.
Nuxia verticill.
Stoebe pass.
Panax repandum
Philippia scyphostigma
Psidium cattley.

Strate inférieure : 100 %

4. Gleichenia dichotoma
1 Cladium Lavarum
Lycopodium cernuum
1 Psidium

Blechnum ~~atten.~~ tab.
Nephrolepis abrupta
Smilax

App.5.19 Cadet's phytosociological surveys conducted in 1972 on the 1800 lava flow near the current study site. *Only the woody strata are presented with the semi-quantitative Braun-Blanquet coefficients (range of cover: "+": <5% few individuals, "1": <5% numerous individuals, "2": 5-25%, "3": 25-50%, "4": 50-75%).The native species composition is almost identical to that observed today, but notable phenomena over the last forty years are the considerable increase of* Psidium cattleianum *and the massive recruitment of* Clidemia hirta *which was absent at Cadet's time in the low stratum (see* ***Fig.5.3*** *for comparison purposes).*

App.6.1. Overview of the frugivore vertebrate of Mauritius (M) and La Réunion (R) *with indication of the body mass (g) and conservation UICN status (EX: extinct, EN: endangered, LC: least concern). "*" occasionally frugivore; "1" Data related to extinct frugivore species without any available measurement were inferred from subfossils archives and/or from extant closely related species; "2" rough approximate value because substantial differences were found depending on the sources. "3" A small population has been occurring in the East of La Réunion since the beginning of the 21st century. "4" Species locally extinct at Brise Fer, but present on the Mauritius islets.*

Taxonomy	Species name	Island	Mass (g)	IUCN status	Source
Aves					
Columbiformes	*Alectroenas nitidissima* Pigeon hollandais	M	[1]170	**EX**	1–3
	Alectroenas sp Blue pigeon	R	[1]170	**EX**	1–3
	**Nesoenas duboisi* Réunion pink pigeon	R	[1]300	**EX**	4
	**Nesoenas mayeri* Mauritius pink pigeon	M	300	VU	4
	Raphus cucullatus Dodo	M	[1]16 000	**EX**	5
Passeriformes	**Foudia delloni* Réunion fody	R	[1]15	**EX**	4
	**Foudia rubra* Mauritius fody	M	15	EN	4
	Fregilupus varius Hoopoe starling	R	110	**EX**	6
	Hypsipetes olivaceus Mauritius bulbul	M	55	LC	4
	Hypsipetes borbonicus Réunion bulbul	R	55	LC	4
	Zosterops borbonicus Réunion grey white-eye	R	9	LC	4
	Zosterops chloronothos Mauritius olive white-eye	M	10	CR	4
	Zosterops mauritianus Mauritius grey white-eye	M	9	LC	4
	Zosterops olivaceus Réunion olive white-eye	R	10	LC	4
Psittaciformes	*Lophopsittacus mauritianus* Raven parrot	M	[1]1697	**EX**	5,7
	Mascarinus mascarin Mascarin parrot	R	[1]250	**EX**	5,7
	Psittacula (?) borbonicus Réunion red & green parrot	R	[1]180	**EX**	5,7
	Psittacula eques Ring-necked parakeet	M - R	180	**R:EX** – M:VU	5,7
	Psittacula bensoni Thirioux's grey parrot	M - R	[1]250	**EX**	5,7
Chelonii					
	Cylindraspis inepta Mauritius domed tortoise	M	[1,2]50 000	**EX**	5,8
	Cylindraspis triserrata Mauritius high-backed tortoise	M	[1,2]50 000	**EX**	5,8
	Cylindraspis indica Réunion giant tortoise	R	[1,2]50 000	**EX**	5,8
Mammalia					
Chiroptera	*Pteropus niger* Black-spined flying fox	M - R	450	**R:**[3]**EX**; M: EN	9
	Pteropus rodricensis Golden bat	M	254		5
	Pteropus subniger Rougette	M - R	[1,2]250	**EX**	5,10
Squamata					
	Leiolopisma ceciliae Arnold's Skink	R	[1,2]130	**EX**	5,8
	Leiolopisma mauritiana Didosaurus	M	1 120	**EX**	5,8
	Leiolopisma telfairii Telfair's skink	M	68	[4]**EX**	11
	**Phelsuma borbonica* Reunion day gecko	R	10	EN	12
	**Phelsuma guentheri* Günther's day-gecko	M	75	[4]**EX**	5
	**Phelsuma rosagularis* Upland forest day-gecko	M	4	DD	5

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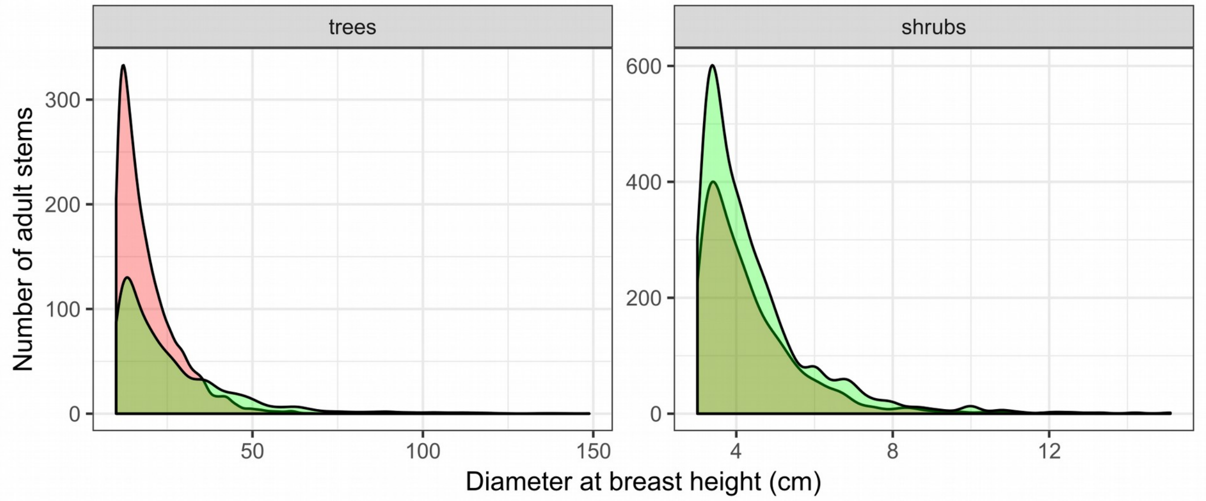
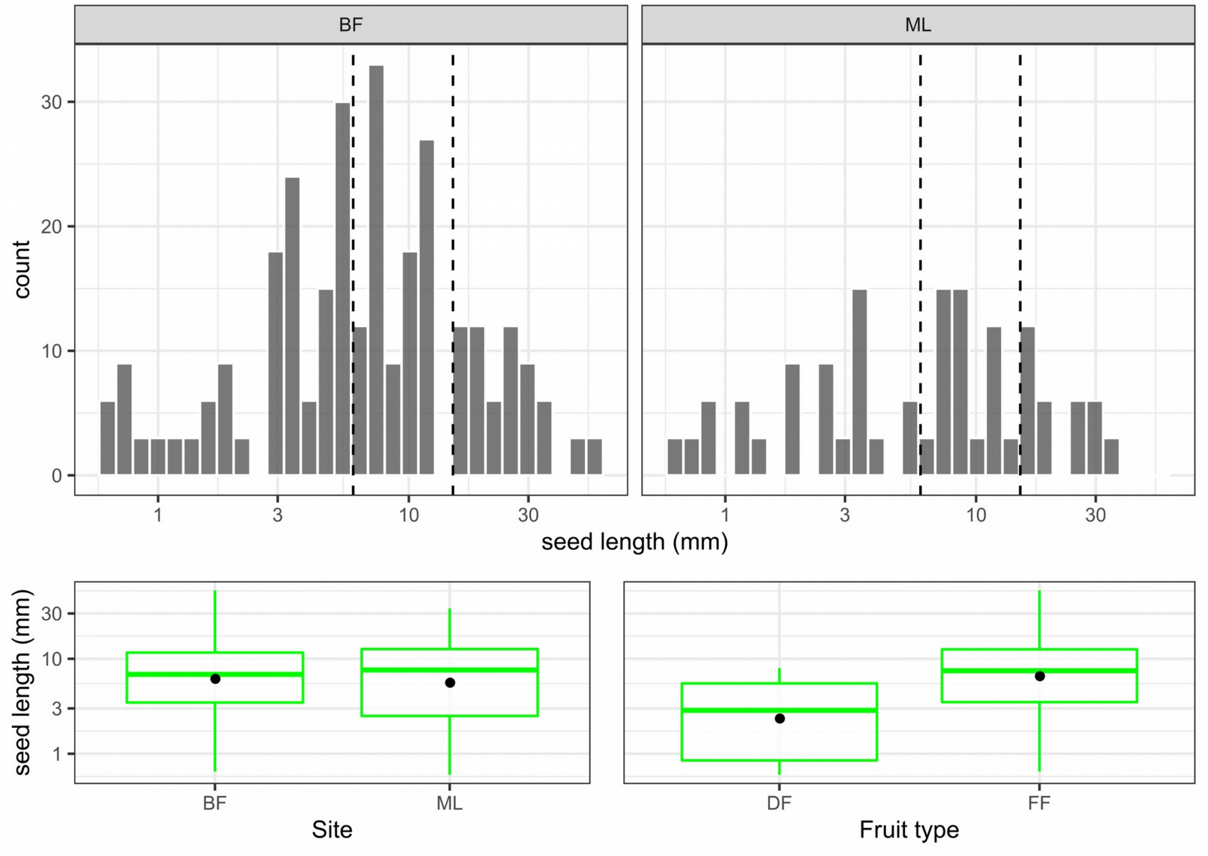
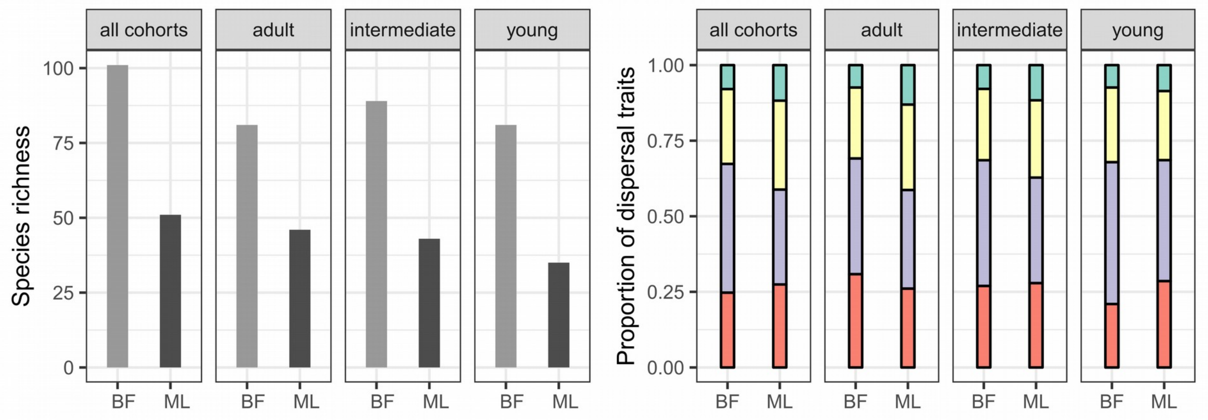


App.6.2 Diameter structure of adult cohorts in the permanent plots at Brise Fer (red) and Mare Longue (green). *Woody species without secondary growth were excluded from analyses.*



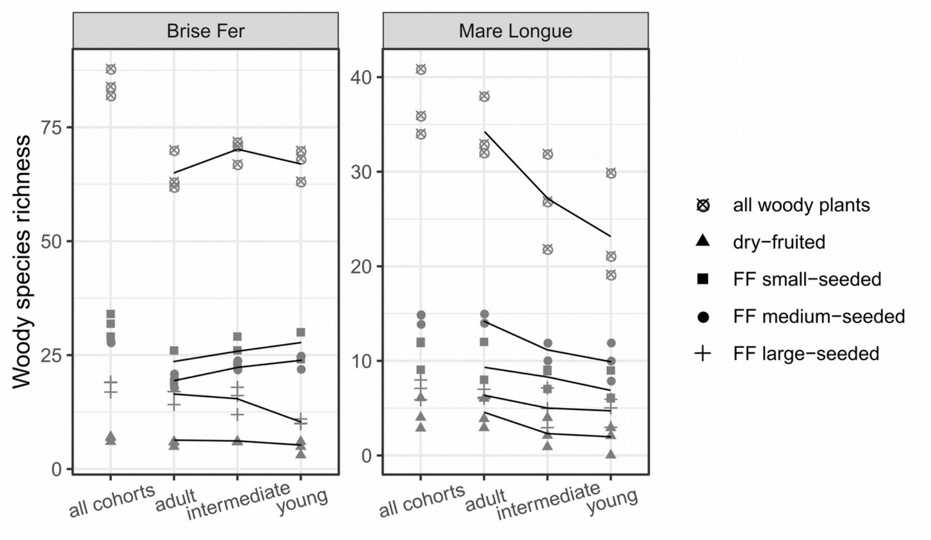
App.6.3 Distribution of explanatory variables. *Above, univariate distribution of mean seed length of woody species at Brise Fer (MAU-BF) and Mare Longue (REU-ML); dashed lines represent size class limits (6 and 15 mm). Below, relationship between mean seed length and site, and between mean seed length and fruit type*



App.6.4 Assessment of global woody species richness and dispersal trait proportion for different diametric cohorts *(young, intermediate and adult) at Brise Fer (MAU-BF) and Mare Longue (REU-ML).* ***Left****, for each site (Brise Fer: grey; Mare Longue: dark grey), the total species richness within permanent plots is given.* ***Right****, dispersal trait proportions are given relative to the total richness at Brise Fer and Mare Longue. Dispersal traits are displayed by colors: red, fleshy-fruited large-seeded plants; purple, fleshy-fruited medium-seeded plants; yellow, fleshy-fruited small-seeded plants; cyan, dry-fruited plants. Woody species without secondary growth were excluded from analyses.*

App.6.5 Overview of woody plant genera occurring at Brise Fer and Mare Longue. *For each island, it is shown whether the genus is present in permanent plot ("Brise Fer" or "Mare Longue"), absent from permanent plot but present on the island ("Present") or totally absent from the island ("Absent").*

	Mauritius			La Réunion		
Genus	Brise Fer	Present	Absent	Mare Longue	Present	Absent
Agarista	0	1	0	1	1	0
Allophylus	1	1	0	1	1	0
Antidesma	1	1	0	1	1	0
Antirhea	1	1	0	1	1	0
Aphloia	1	1	0	1	1	0
Apodytes	1	1	0	0	1	0
Badula	1	1	0	0	1	0
Bertiera	1	1	0	1	1	0
Bremeria	1	1	0	0	1	0
Calophyllum	1	1	0	1	1	0
Canarium	1	1	0	0	0	1
Casearia	1	1	0	1	1	0
Cassine	1	1	0	1	1	0
Chassalia	1	1	0	1	1	0
Chionanthus	0	1	0	1	1	0
Cnestis	1	1	0	1	1	0
Coffea	1	1	0	1	1	0
Colea	1	1	0	0	0	1
Coptosperma	1	1	0	0	1	0
Cossinia	1	1	0	0	1	0
Diospyros	1	1	0	1	1	0
Dodonea	1	1	0	0	1	0
Dombeya	0	1	0	1	1	0
Doratoxylon	1	1	0	1	1	0
Drypetes	0	1	0	1	1	0
Elaeocarpus	1	1	0	0	0	1
Embelia	1	1	0	0	1	0
Erythrospermum	1	1	0	0	0	1
Erythroxylum	1	1	0	1	1	0
Eugenia	1	1	0	0	1	0
Fernelia	1	1	0	1	1	0
Ficus	1	1	0	1	1	0
Gaertnera	1	1	0	1	1	0
Geniostoma	1	1	0	0	1	0
Grangeria	1	1	0	0	1	0
Gymnosporia	1	1	0	0	0	1
Hancea	1	1	0	1	1	0
Harungana	1	1	0	0	0	1
Hilsenbergia	1	1	0	0	0	1
Homalium	1	1	0	1	1	0
Ixora	1	1	0	1	1	0
Labourdonnaisia	1	1	0	1	1	0
Leea	1	1	0	1	1	0
Ludia	1	1	0	0	0	1
Macaranga	1	1	0	0	0	1
Margaritaria	1	1	0	0	0	1
Memecylon	1	1	0	1	1	0
Mimusops	1	1	0	1	1	0
Molinaea	1	1	0	1	1	0
Mussaenda	1	1	0	1	1	0
Nuxia	1	1	0	1	1	0
Ochna	1	1	0	0	0	1
Ochrosia	0	1	0	1	1	0
Ocotea	1	1	0	1	1	0
Olea	1	1	0	0	1	0
Orfilea	1	1	0	0	0	1
Pittosporum	1	1	0	1	1	0
Pleurostylia	1	1	0	0	1	0
Polyscias	0	1	0	1	1	0
Poupartia	0	1	0	1	1	0
Premna	1	1	0	0	1	0
Protium	1	1	0	0	0	1
Psiloxylon	1	1	0	1	1	0
Psychotria	1	1	0	0	1	0
Pyrostria	1	1	0	0	1	0
Scutia	1	1	0	0	1	0
Securinega	1	1	0	0	1	0
Sideroxylon	1	1	0	1	1	0
Syzygium	1	1	0	1	1	0
Tabernaemontana	1	1	0	1	1	0
Tambourissa	1	1	0	1	1	0
Terminalia	0	1	0	1	1	0
Turraea	1	1	0	0	1	0
Vepris	1	1	0	0	1	0
Warneckea	1	1	0	0	0	1
Weinmannia	1	1	0	1	1	0
Xylopia	1	1	0	1	1	0
Total	69	77	0	44	63	14



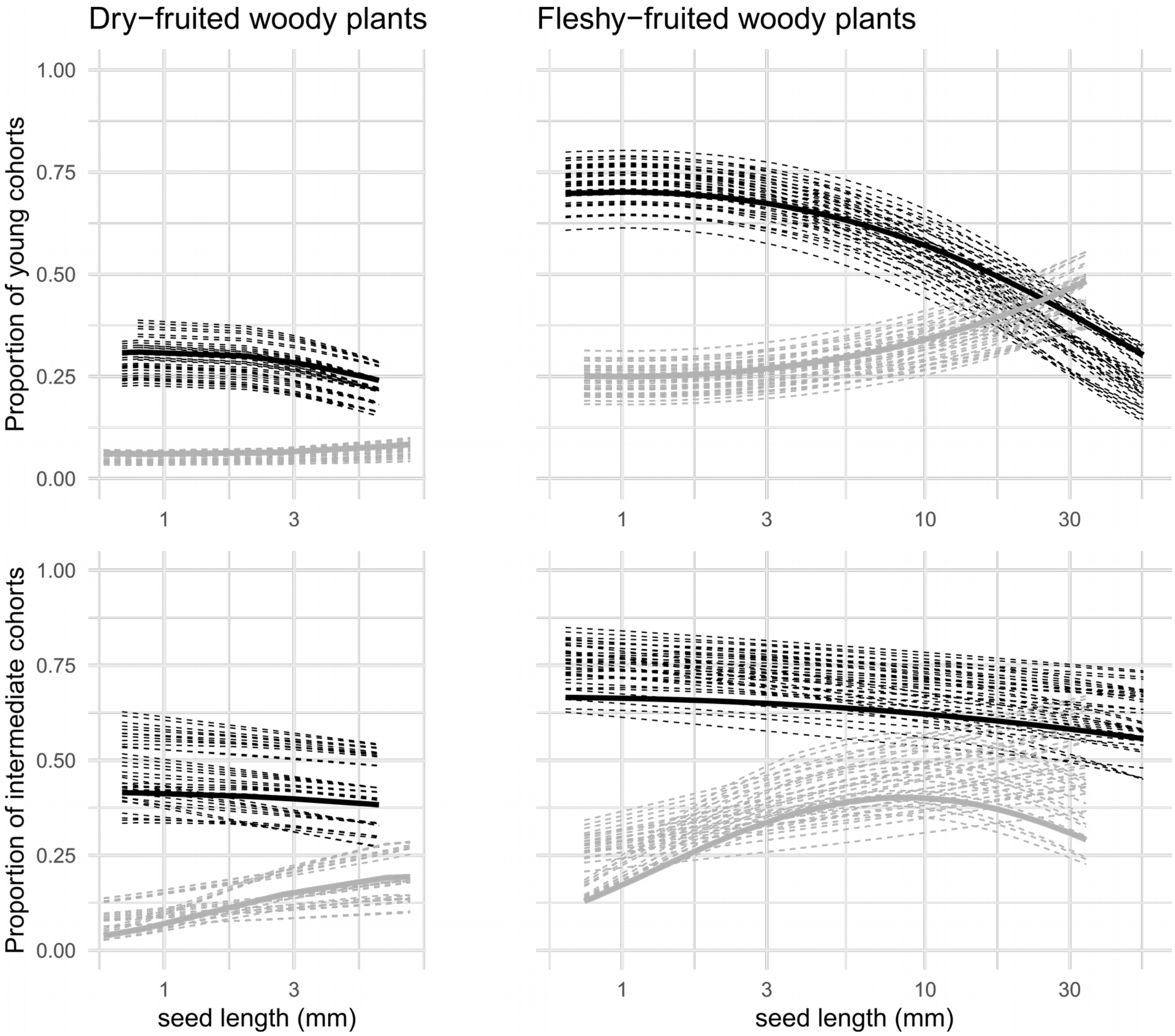
App.6.6 Assessment of woody species richness across diameter cohorts at Brise Fer and Mare Longue in relation to dispersal traits *(dry-fruited; fleshy-fruited small-seeded plants: 0,06 < seed length < 0,5 cm; fleshy-fruited medium-seeded plants: 0,6 < seed length < 1,5 cm; fleshy-fruited large-seeded plants: 1,5 < seed length < 5,3 cm). Richness by plot is displayed by grey points and changes in mean richness by site across diameter cohorts by black lines. Note the different scale for the y-axis.*

App.6.7 Analysis of deviance table and summary of the best fitting GLMMs*. Type III and Type II Wald chi square tests were respectively performed for "proportion of young cohorts" and "proportion of intermediate cohorts" GLMMs. P: p value, QS: 0.05 < p < 0.1, **: 0.001 < p < 0.01, ***: p < 0.001.*

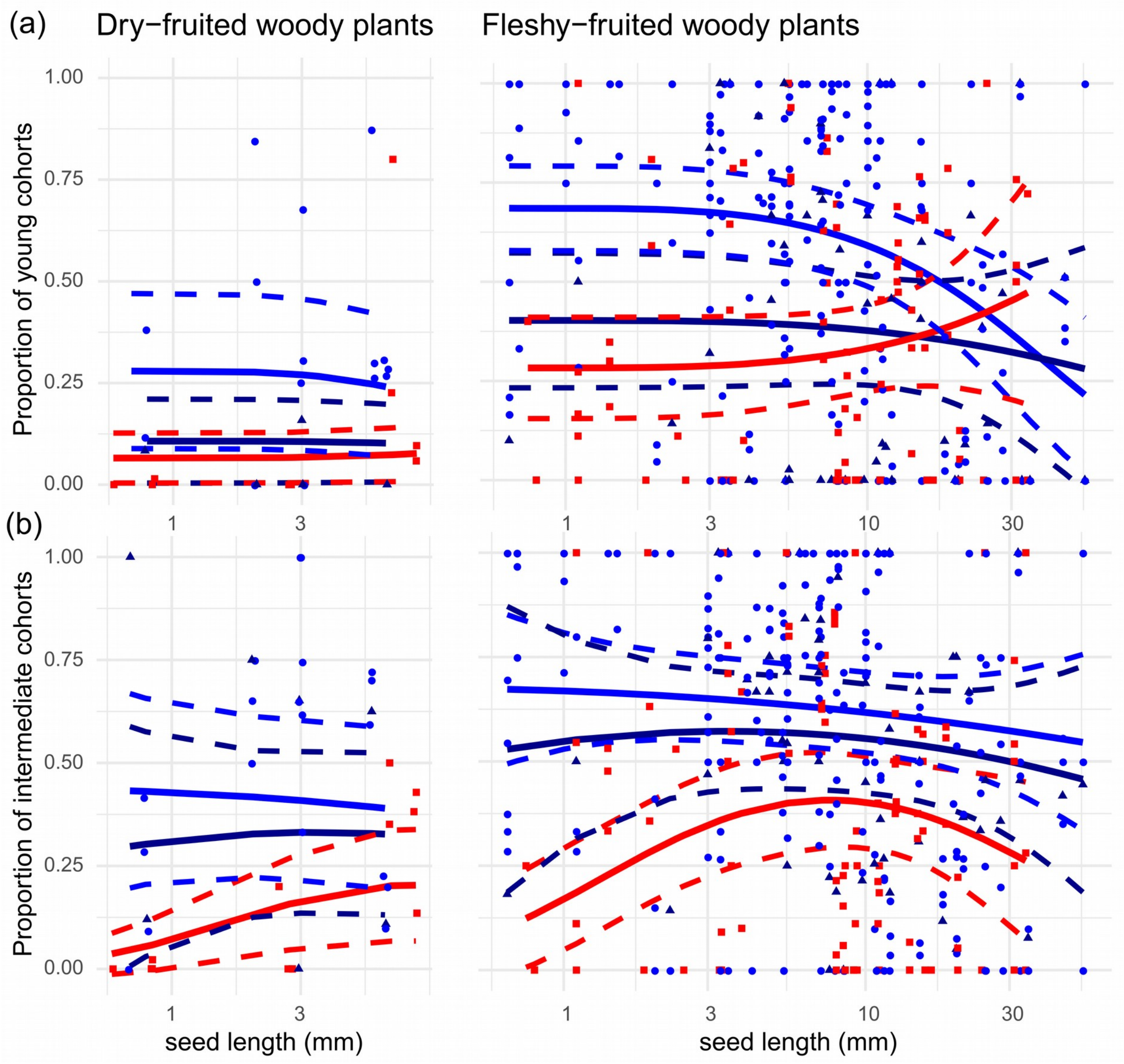
	Proportion of young cohorts			Proportion of intermediate cohorts		
	Chisq	Df	P	Chisq	Df	P
(intercept)	2,81	1	QS	1,72	1	NS
poly(log10(seed length), 2)	8,15	1	**	0,92	2	NS
site	33,17	1	***	41,40	1	***
fruit type	14,02	1	***	7,28	1	**
poly(log10(seed length), 2) : site	12,31	1	***	9,59	2	**

Summary of best fitting GLMMs*. "Disp": dispersal trait; "ML": Réunion - Mare Longue; ":": interaction terms. "P": p value, "NS": p > 0.1, "QS": 0.05 < p < 0.1, "*": 0.01 < p < 0.05, "**": 0.001 < p < 0.01, "***": p < 0.001. Overdispersion parameters for betabinomial family: 2,79 and 5,98.*

	Proportion of young cohorts			**Proportion of intermediate cohorts**		
Fixed effects	Estimate	Std. Error	P	Estimate	Std. Error	P
Intercept	-0,78	0,46	QS	-0,51	0,39	NS
poly(log10(seed length), 2)1	-	-	-	-1,89	2,02	NS
poly(log10(seed length), 2)2	-0,57	0,20	**	-0,46	1,74	NS
Site, ML	-1,98	0,34	***	-1,20	0,19	***
Pulpe, FF	1,66	0,44	***	1,02	0,38	**
poly(log10(seed length),2)1 : site, ML	-	-	-	6,42	2,88	*
poly(log10(seed length),2)2 : site, ML	1,01	0,29	***	-5,68	3,14	QS
Random effects	Variance			Variance		
genus:(family: order)	3,21E-01			1,88E-01		
family: order	2,88E-01			3,57E-01		
order	1,09E-01			1,01E-01		
plot: site	3,61E-02			2,03E-02		
site	2,67E-09			2,63E-09		

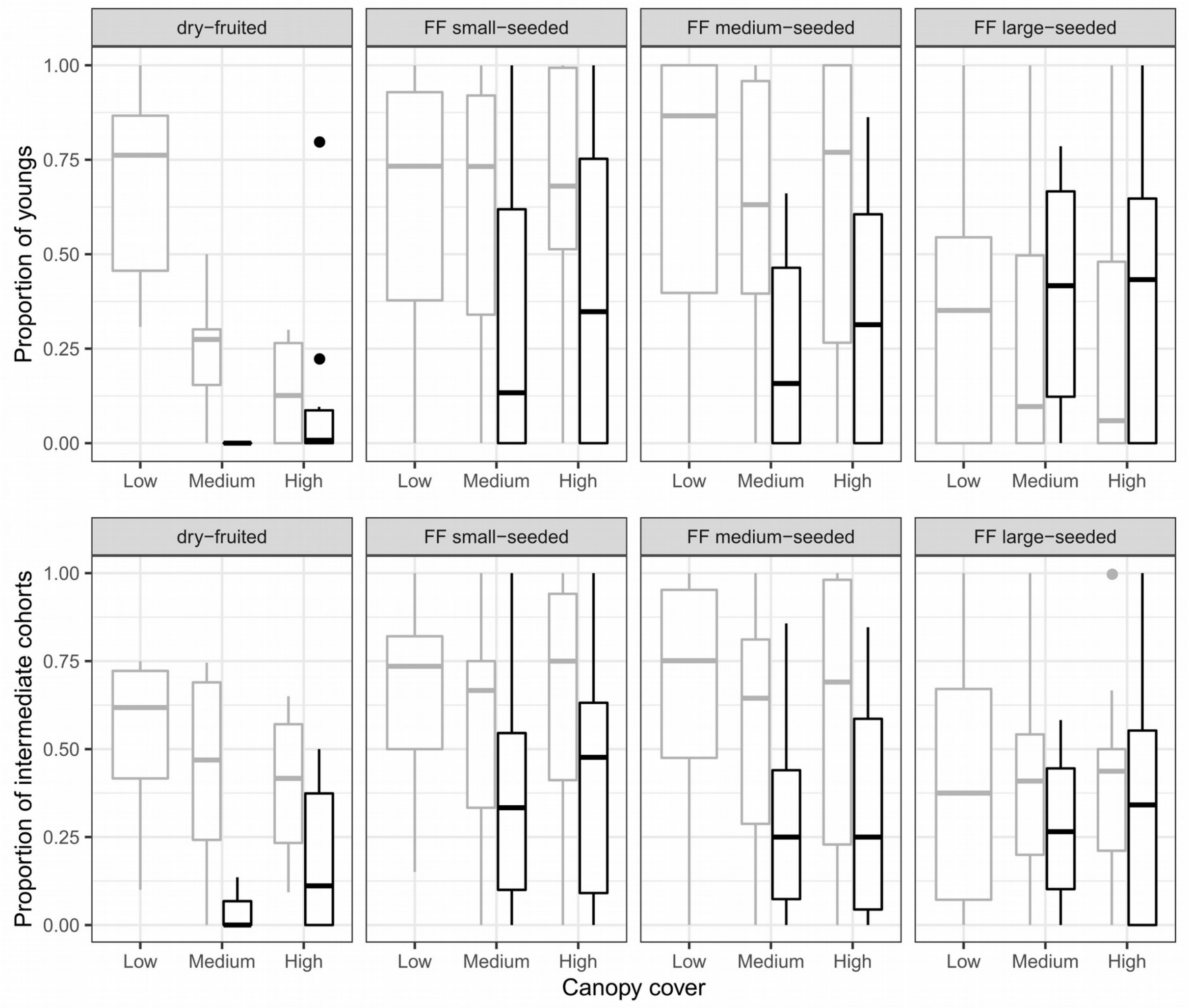


App.6.8 Sensitivity analyses to evaluate the influence of cohort definition on demographic status assessment in Mascarene plots. *Mean estimates by GLMMs for each of the 36 cohort definitions are displayed by dotted lines. Estimated proportions presented in the paper (Fig.6.5) are displayed by solid lines. (a) Proportion of young cohorts, i.e.* $n_{young} / (n_{young} + n_{adult})$*; (b) Proportion of intermediate cohorts,* $n_{int.} / (n_{int.} + n_{adult})$*.*



App.6.9 Same results as those presented in Fig.6.5 but taking into account the 1-ha unweeded permanent plot at MAU-BF to show the different recruitment trajectories with or without weeding of* Psidium cattleianum *at MAU-BF. *Proportion of young and intermediate cohorts of woody plants in relation to site (weeded MAU-BF: blue; unweeded MAU-BF: deep blue; REU-ML: red), fruit type (fleshy versus dry) and mean seed length (mm). Points, solid lines and dashed lines display proportions of juveniles for each woody species in each permanent plot, estimates and confidence intervals from GLMMs, respectively. (a) Proportion of young cohorts, i.e.* $n_{young}/(n_{young}+n_{adult})$*; (b) Proportion of intermediate cohorts,* $n_{int.}/(n_{int.}+n_{adult})$*. A value of 0.5 means that a species has as many juveniles as adults. A value of 0.25 means that a species has three times as many adults as juveniles.*

The weeding of three permanent plots of MAU-BF has significantly increased the recruitment of juveniles of small-seeded and medium-seeded fleshy-fruited species compared to the permanent hectare that remains invaded to date by Psidium cattleianum. *The strong increase of recruitment is especially visible for young cohorts. Surprisingly, however, recruitment still tends to be higher in the invaded hectare at MAU-BF than at REU-ML understory, which is generally considered to be in a good state of conservation. This shows that the effective dispersal of many woody species may allow their relative maintenance in invaded vegetation.*



App.6.10 Relationship between juveniles proportions of woody species and canopy cover within permanent plots at MAU-BF (grey) and REU-ML (black)*. Here, basal area of trees (> 10 cm in dbh) was used as a proxy of canopy cover and defined as a three level factor: low cover (BF1 with 34.8 m².ha^{-1}); medium cover (BF2 with 48.7; ML3 with 57.9 m².ha^{-1}); high cover (BF3 with 58.4; ML1 with 69.6; ML2 with 76.7 m².ha^{-1}). Boxplots display raw data for each dispersal trait group. Changes in canopy cover at plot level mainly impacts the recruitment of dry-fruited plants.*

App.7.1 Sowing experiment of* Labourdonnaisia calophylloides *(black arrows) and* Mimusops balata *(red arrows), in the gap in January 2018. *Arrows and unfilled arrows illustrate “flesh persistence” and “hand cleaning of seeds” modalities, respectively. For more details about the seeds of focal species, please see **Fig.7.2**. Photo: F. Guilhabert.*

App.7.2 *Seedlings of* Mimusops balata *(**left**, 4,5 months after sowing in January 2018) and* Labourdonnaisia calophylloides *(**right**, 6 months after sowing). Photos: F. Guilhabert & S. Albert*

App.7.3 Monitoring of plant-animal interactions at Ilet Tessan. Left, *no evidence of seed predation or secondary dispersal was noted after first sowing of focal species in January 2018, in spite of the strong presence of* Rattus rattus *in the vicinity. Indeed, between the 20th and 27th of July 2018,* Rattus *removed 39 out of 40 fruits of* Hyophorbe indica, *a large-seeded endemic and endangered palm tree.* ***Centre****, several seeds of* M. balata *were predated* in situ *after sowing in November 2019*, as well as *numerous fruits of* L. calophylloides that were removed from the experiment *(image not shown for the latter).* ***Right****, the giant snail* Achatina immaculata *fed largely on fruits of* L. calophylloides *in November 2019. Note the effective seed cleaning with the hilum clearly visible (red arrow). Photos: A. Gorissen & S. Albert*

App.7.4 Summary of the best fitting GLM *that includes four factors "hand cleaning of seeds", "canopy closure", "Date" and "species" with the six possible interactions. "MIMBAL", "Mimusops balata; ":", interaction terms.*

Predictor	Estimate	Std.Error	z.value	P
(Intercept)	0,225	0,109	2,070	0,038
Hand cleaning of seeds, no	-1,697	0,149	-11,370	6E-30
Canopy closure, gap	-0,411	0,138	-2,980	0,003
Date, Nov. 2019	0,331	0,139	2,378	0,017
Species, MIMBAL	0,882	0,145	6,095	1E-09
Hand cleaning of seeds, no : Canopy closure, gap	-0,457	0,155	-2,947	0,003
Hand cleaning of seeds, no : Date, Nov. 2019	0,808	0,154	5,229	2E-07
Hand cleaning of seeds, no : Species, MIMBAL	-0,918	0,154	-5,967	2E-09
Canopy closure, gap : Species, MIMBAL	0,357	0,151	2,367	0,018
Date, Nov. 2019 : Species, MIMBAL	-0,386	0,150	-2,570	0,010
Canopy closure, gap : Date, Nov. 2019	-0,384	0,151	-2,540	0,011

App.7.5 Fruit of **Labourdonnaisia calophylloides** *with the seed trapped in the pericarp rich in latex.* ***Left****: 5 weeks after sowing;* ***Right****: 6,5 months after sowing. Photos: A. Gorissen & S.Albert*

App.7.6 Seedling development *of* Labourdonnaisia calophylloides *(left) and* Mimusops balata *(centre & right) within the pericarp. Right, roots that developed within the pericarp have remained in the air after flesh disappearance 3,5 months after sowing. Photos: F. Guilhabert & A. Gorissen*

App.7.7 View of the experiment in the gap in July 2020, 2,5 years after sowing *(for the comparison, see App.7.1). The largest native saplings are the result of spontaneous regeneration,* Antirhea borbonica *(white arrows),* Ficus mauritiana *(white unfilled arrow),* Ocotea obtusata *(white line arrow), but numerous seedlings of* L. calophylloides *(red arrows) and* M. balata *(red unfilled arrows) are visible and reach 45 cm high. Photos: A. Gorissen*

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Résumé

Les forêts tropicales sont largement dominées par les plantes à fruits charnus dont la dispersion est assurée par les vertébrés frugivores. L'effondrement global des grands vertébrés interroge donc quant à la résilience de ces écosystèmes, en particulier dans les îles qui concentrent l'essentiel des extinctions documentées. Les Mascareignes sont un remarquable système d'étude des ruptures d'interactions de frugivorie car la faune d'origine, pléthorique jusqu'à la colonisation humaine au 17ème siècle et aujourd'hui largement éteinte, est bien connue tout comme sa flore diversifiée qui compte parmi les plus menacées. La Réunion abrite encore des forêts indigènes le long de puissants gradients environnementaux et un volcanisme actif offrant l'opportunité d'explorer sur le long terme les conséquences de la défaunation. De plus, les niveaux variables d'extinction de vertébrés forestiers entre La Réunion (principal frugivore relictuel, masse $_{\text{bulbul}}$ = 55 g) et Maurice (masse $_{\text{roussette}}$ = 450 g) permet d'utiliser ces îles comme pseudo-réplicats pour tester diverses hypothèses. Cette thèse s'organise en trois parties qui visent à **(1)** décrire les patrons de distribution spatiale des traits de dispersion à La Réunion et Maurice, et comprendre les implications pour l'extinction de la faune qui a été fulgurante à La Réunion ; **(2)** évaluer les conséquences de la rupture des interactions de frugivorie sur la reconstruction des écosystèmes forestiers sur les coulées de lave du Piton de la Fournaise ; **(3)** évaluer les conséquences de la rupture des interactions de frugivorie sur le maintien de la diversité dans les forêts de l'archipel établies avant la colonisation humaine. **(1)** Les proportions de plantes à fruits charnus dans les communautés de plantes ligneuses chutent avec l'altitude et cette diminution est d'autant plus forte que les fruits sont gros. En comparant les principaux facteurs d'extinction de vertébrés entre La Réunion et Maurice, nous montrons que la destruction précoce des habitats favorables de basse altitude à La Réunion a probablement joué un rôle central dans la fulgurance des extinctions. **(2)** Après avoir étoffé la chronoséquence des coulées du Piton de la Fournaise, nous montrons que la disparition des populations de frugivores a profondément altéré la capacité des forêts de basse altitude à se rebâtir dès le 18ème siècle et que la refaunation des écosystèmes avec des frugivores introduits profite essentiellement aux plantes exotiques à fruits charnus. Néanmoins, en restaurant la dispersion, les plantes à grosses graines sont capables de s'installer sur les coulées historiques où recrutent très majoritairement des plantes envahissantes. **(3)** En comparant les forêts de référence de La Réunion et Maurice, nous montrons que la roussette noire permet un bien meilleur recrutement de nombreuses espèces ligneuses à Brise-Fer que le bulbul de La Réunion à Mare-Longue, excepté pour les plantes à grosses graines qui se régénèrent assez mal dans les deux îles. Une expérimentation à Mare-Longue montre enfin comment la persistance de la pulpe seule peut limiter fortement le recrutement, mais que ce dernier peut être notablement influencé par la faune introduite. Nos résultats inquiétants montrent l'urgence de protéger les grands frugivores indigènes où ils existent encore et de favoriser leur retour quand ils ont disparu. Parallèlement, des semis à large échelle devraient être envisagés dans les aires protégées où le maintien, voire le retour de la dynamique forestière indigène sont impératifs.

Abstract

Tropical forests are mostly dominated by fleshy-fruited plants, which are dispersed by frugivorous vertebrates. The global collapse of large vertebrates therefore raises questions about the resilience of these ecosystems, particularly on islands, which concentrate the bulk of extinctions. The Mascarenes are a remarkable system to study disruption of frugivory interactions because the pristine fauna, plethoric until human colonization in the 17th century and now largely extinct, is well known as well as its diverse flora which is particularly at risk. La Réunion is still home to indigenous forests along strong environmental gradients and active volcanism that offers the opportunity to explore the long-term consequences of defaunation. In addition, the varying levels of vertebrate extinctions between La Réunion (main extant frugivore, mass = 55 g) and Mauritius (450 g) makes it possible to use these islands as pseudo-replicates to test various hypotheses. This thesis is organised in three parts which aim to **(1)** describe the spatial distribution patterns of dispersal traits on La Réunion and Mauritius, and understand the implications for vertebrate extinctions which have been particularly rapid on La Réunion; **(2)** evaluate the consequences of frugivory disruption on the reconstruction of forest ecosystems on the lava flows of the Piton de la Fournaise; **(3)** assess the consequences of frugivory disruption on the maintenance of diversity in forests established before human colonisation. **(1)** Proportions of fleshy-fruited plants strongly decrease with elevation and this decrease is all the more pronounced the larger the fruit are. By comparing the main factors of vertebrate extinctions between La Réunion and Mauritius, we show that the early destruction of favorable lowland habitats on La Réunion probably played a central role in the rapidity of frugivore extinctions. **(2)** After expanding the chronosequence of the Piton de la Fournaise flows, we show that frugivore extinctions have profoundly altered the capacity of lowland forests to rebuild since the 18th century and that the refaunation of ecosystems with alien frugivores mainly benefits alien fleshy-fruited plants. Reinstating dispersal, native large-seeded plants are nevertheless capable of settling on historical flows where recruitment is overwhelmingly dominated by invasive plants. **(3)** By comparing two reference forests of La Réunion and Mauritius, we show that the Mauritian flying fox allows a much better recruitment of many plant species at Brise-Fer than the Réunion bulbul at Mare-Longue, except for large-seeded plants which regenerate poorly in both islands. An experiment finally shows how the persistence of fruit flesh alone can strongly limit tree recruitment, but that the latter can be modulated by introduced fauna. Our overall worrying results show the urgency to protect large native frugivores wherever they still exist and of encouraging their return where they had disappeared. At the same time, large-scale sowing should be envisaged in protected areas where the maintenance or even the return of native forest dynamics are imperative.