

# Characterization and evolution of the lowland tropical rain forest of the smallest oceanic Gondwana fragments, with implications for restoration and invasion ecology

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## ABSTRACT

The Seychelles granitic islands have been small, mid-oceanic, equatorial, mountainous and moist islands for at least 50 million years, with an uninterrupted vegetation cover since their separation from Gondwana. Therefore, unlike hotspot oceanic islands that drastically vary in environmental heterogeneity according to their age, the Seychelles can provide observational data where evolutionary time is de-correlated from habitat heterogeneity. In this paper, we aim to describe for the first time its most widespread, least known, and most threatened ecosystem type: the lowland rain forest. Surprisingly, this had never been done before and the reason is simply that only 6.5 % of those forests have survived untouched by the 2.5 centuries of human presence on these islands. We set six permanent vegetation plots within the largest (ca. 50 ha) and best-preserved relict of this forest, plus four permanent plots in a nearby site (1 km away) that is ecologically homologous but has been intensively modified, abandoned for the last 40 years and which is now a structurally mature late secondary forest. Each plot covered 500 m<sup>2</sup> and all vascular plants were inventoried in a series of subplots corresponding to different strata. Within the 0.5 ha of surveyed forest, we observed 35 native species (17 canopy/under-canopy trees, 8 shrubs or small understorey trees, and 10 herbs), of which 11 are endemic (31 %). All plots within the natural forest site were floristically and structurally very similar. Their flora (within just 500 m<sup>2</sup>) represented about 87 to 92 % of the total flora of the Seychelles lowland mesic forests (defined as an ecological group). In addition, the three most dominant under-canopy trees corresponded to paleo-endemic species having the particularity to be both climax and pioneer trees, which is very unusual. Our study also shows that exotic species were hardly present in undisturbed natural forests but, in disturbed forests, on the other hand, native species were re-colonizing so-called novel ecosystems. Based on these results, we present a list of native species which are appropriate for restoration programs in the Seychelles lowland rain forests, including one that was previously considered as an exotic invasive but which could greatly improve restoration work. Finally, our study sets the basis for long term monitoring of natural ecosystem resilience to invasions on the one hand, and biotic novelty of novel ecosystems on the other.

## 1. Introduction

The Seychelles forests have been impacted to a large extent by human disturbances and subsequent biological invasions (Fock-heng, 1965; Sauer, 1967; Carlstroem, 1996; Rocamora and Henriette, 2015). Senterre and colleagues (Senterre and Wagner, 2014; Senterre and

Henriette, 2015) have estimated that only 12.5 % of the land area of the main Seychelles granitic islands is still in a natural state (never clear cut or burnt). The remaining land area is made up of semi-natural landscapes (i.e. regenerating after past anthropic disturbances) at different successional stages (58.8 %) and anthropic ecosystems such as cities, agricultural land, active forestry plantations, etc. (28.7 %). The

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currently semi-natural land areas were deforested throughout the 19th century and reforested with exotic tree species (along with some indirect species invasions) until the end of the 20th century (Senterre and Henriette, 2015, p. 12). During this process, *Cinnamomum verum*, one of the first introduced tree species ecologically adapted to Seychelles' forests, became the most dominant tree in most of these landscapes (Kueffer et al., 2013). The other introduced species which locally co-dominate the current vegetation include *Falcataria moluccana* (in lowland and submontane areas with deep soils), *Tabebuia heterophylla* (on topographically drier landforms of the lowland), *Psidium cattleianum* (especially in the montane belt), *Sandoricum koetjape* (in ancient lowland and submontane forest plantations on deep soils), and *Syzygium jambos* (mostly in the montane belt). In addition to deforestation, forest fires and subsequent soil degradation have affected large areas, mostly on lowland ridges of Mahé, Praslin and a few more small islands (Senterre, 2009a, 2009b). Exotic species such as *Chrysobalanus icaco* were planted to control soil erosion in those areas and this shrub is now the dominant species, forming dense thickets.

Today, these vast areas of semi-natural landscapes provide many opportunities for restoration projects. Based on Senterre and Wagner (2014: 67), current semi-natural landscapes corresponding to a forest climax (see definition in Senterre et al., 2021) represent 12,086 ha (excluding here beach forests and mangroves), most of which are located in the lowland bioclimatic belt (9,143 ha, or 76 % of all semi-natural areas). Although these vast lowland semi-natural areas are the most accessible for restoration projects in collaboration with local communities, they correspond to the least known and least studied ecosystem of the Seychelles granitic islands. This is simply because most botanical surveys in Seychelles have focused on the highest altitudes where natural remains are more frequent and endemism richness is higher. Due to this lack of data, most restoration programs currently taking place in the lowland belt consist of planting endemic species (often submontane and montane ones) without necessarily considering their ecology.

In this paper, we study two sites – firstly, the best-known natural remains of the Seychelles lowland mesic forest, still largely dominated by native species, located at Pointe Civine (Silhouette Island). Secondly, a site located at Anse Lascars separated from Pointe Civine by about 1 km of rocky slopes and cliffs, which is a typical Cinnamon-dominated semi-natural forest with similar ecological conditions to those of Pointe Civine. The two selected sites have been studied in order to:

- Describe quantitatively the plant community of Seychelles' natural lowland mesic forest,
- Quantitatively monitor the hypothetical future invasion of exotic species into the natural area at Pointe Civine (i.e. resilience of the natural ecosystem),
- Quantitatively monitor the hypothetical irreversible biotic novelty of the semi-natural area at Anse Lascars, currently dominated by exotic species (i.e. resilience of supposedly novel ecosystem),
- Provide basic data to guide restoration and conservation projects in Seychelles.

## 2. Material and methods

### 2.1. Study area

The Republic of Seychelles includes the only mid-oceanic archipelago of continental origin in the world, containing 41 small islands (24,713 ha) separated from each other by up to 35 km. Located near the equator, at 4° 37' S and 55° 27' E, and culminating at 909 m a.s.l., the climate is tropical perhumid with ca. 2300 mm of annual rainfall and 0–2 dry months in the lowland, and up to more than 4000 mm in the montane belt (Cazes-Duvat and Robert, 2001, p. 13). This granitic land mass formed long before the appearance of modern floras, ca. 750 Ma ago (Torsvik et al., 2013), and started drifting after the breakup of Gondwana (130 Ma), at the very beginning of the evolution of flowering

plants. They became isolated from Madagascar at ca. 73 Ma and, at last, separated from India at ca. 62 Ma, which corresponds to the formation of the two youngest islands of the group: Silhouette and North Island (Torsvik et al., 2013; Shellnutt et al., 2017). Ever since, the granitic islands of Seychelles have formed a microcontinent isolated in the middle of the Indian Ocean (Dahl, 2004; Weigelt and Kref, 2013), leading to the evolution of a unique biodiversity characterized by a high degree of endemism and especially of paleo-endemism, considering its relatively poor flora (Kier et al., 2009, p. 9324; Caujapé-Castells et al., 2010).

Among the granitic islands, Silhouette has a remarkable conservation value. It is the third largest island of the group (2,000 ha), the second highest (760 m), and the only one along with Mahé to reach the montane belt, resulting in a high ecosystem richness (Senterre et al. 2009; Senterre and Wagner 2014). Most importantly, Silhouette island has been much less impacted by humans compared to Mahé (Gardiner, 1907, pp. 158, 160; Vesey-Fitzgerald, 1940; Jeffrey, 1962). Senterre and Wagner (2014: p.67) estimated that ca. 51.4 % of its land area remains natural (never clear cut, intensively cut or planted), as opposed to 7.8 % for Mahé. As for the other islands, untouched forests remain mostly in the mountains, but a large lowland area has been mentioned by various recent explorers as being still preserved on the south slopes of the island, near Pointe Civine (Vesey-Fitzgerald, 1940; Jeffrey, 1962, pp. 21, 27; Friedmann, 1987; Senterre and Henriette, 2015).

From January to June 2019, we explored extensively the southern slopes of Silhouette, as well as other lowland areas which represented gaps in exploration such as the area near Casse Tonnère (north slopes) (Fig. 1). We used Android Smartphones rather than traditional GPS devices for improved exploration capacities (Senterre et al., 2019; Nowak et al., 2020), which allowed us to map precisely the extent of the natural forest of Pointe Civine and to confirm its typical climax stage (old growth, mature) with a near absence of exotic species. This forest, which seems to have been unchanged for at least 80 years (Vesey-Fitzgerald, 1940, pp. 475, 477), is located on gentle slopes with well-developed soil (although not deep), spread with rock boulders and a few intermittent streams. The bed rock is a syenite, i.e. an alkaline igneous rock of magmatic origin, similar to granite and rich in Sodium (Stephens, 1996). It is bordered to the east by a large area of rocky slopes (inselberg flank) sparsely vegetated and extending from the top of Mont Coco Marron downward into the ocean. To the east of that rocky stretch, there is a vast area of forest ecologically homologous to the forest of Pointe Civine but which was completely clear cut, transformed into Cinnamon (*Cinnamomum verum*) plantations and then abandoned for the last 40 years (Gerlach, 2011; also confirmed by local inhabitants: Therese Malbrook, pers. comm., 2018). This second site is located near Anse Lascars and Anse Patates and the area is hereafter referred to as "Anse Lascars".

### 2.2. Sampling design and species inventory methods

Ten plots have been established and distributed over the two studied areas (six at Pointe Civine and four at Anse Lascars) (Fig. 1), each of them placed within ecologically homogeneous stands of lowland mesic forest (i.e. excluding coastal influences, ravines, swamps and saxicolous forests near the rocky outcrops). The ten plots were set permanently using PVC pipes, aluminum tags, and painting on rocks. Sampled trees were also permanently tagged using paint and a within-plot x/y coordinate system.

Each plot consisted of three nested subplots representing three different forest strata: (1) subplot "T" for the tree community, on a 50 × 10 m area (all trees with diameter at breast height, DBH ≥ 5 cm); (2) subplot "S" for the understorey shrubs and tree saplings community, on a 50 × 4 m area (DBH < 5 cm and total plant height greater than 1 m); and (3) subplot "H" for the herbaceous understorey and regeneration of the upper forest strata, on a 50 × 4 m area (vascular terrestrial herbaceous plants, tree trunk epiphytes and tree/shrub seedlings smaller than

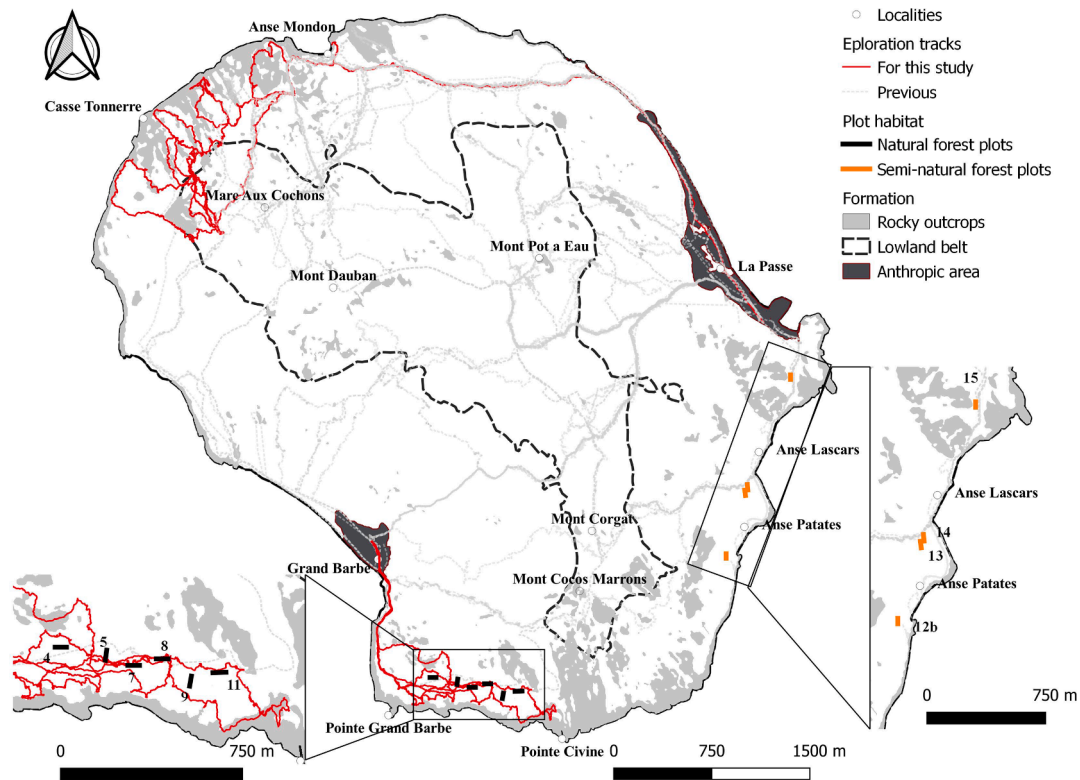


Fig. 1. Map of Silhouette island showing the lowland belt, anthropic areas, rock surfaces, exploration tracks of this study (representing ca. 59 km of exploration) and plot locations (distinguishing the natural and semi-natural sites).

1 m). Considering the extremely reduced flora of Seychelles, especially for lowlands, each plot although relatively small was large enough to provide a representative sampling of the local tree community.

For the T subplots (trees), all individuals were marked with a number on the trunk using outdoor paint. The DBH was measured at 1.3 m above ground, following usual specifications and exceptions (see White and Edwards, 2000, p. 15), and the exact height of the DBH measure was marked using paint. In the case of individual trees with multiple trunks (e.g. typically some coppiced Cinnamon trees at the Anse Lascars site), we measured and marked only the dominant trunk. For each tree, we also recorded the position in the x/y plot coordinate system, the total height, and the position relative to canopy (under-canopy, canopy, or emergent tree: Queensland Government, 2014, p. 12). In the shrub subplots (S), we only recorded the number of individuals per species per plot sections of  $10 \times 2$  m (Appendix A). Finally, for the H understory subplots, we recorded a coefficient of abundance-dominance (Appendix B) for each species in each plot section of  $10 \times 2$  m. The semi-quantitative data from H subplots were integrated with the quantitative data from the T and S subplots by converting the abundance-dominance index into the average cover value. All data were then normalized to relative abundances, compiled, and converted back to the abundance-dominance coefficient value (corresponding to a logarithmic scale).

This multistrata method is similar to Gentry's (1982) and has been used in previous vegetation studies in Seychelles (Senterre et al., 2009; Elzein, 2011; Senterre and Chong-Seng, 2016; Cesar and Zehnder, 2020). The permanent marking of trees and the exact height at which the DBH was measured will provide high quality data on growth rates. Ecosystemic and floristic data were collected using a Smartphone Application designed using Open Foris Collect and which is integrated into a National database managed by the Seychelles National Herbarium (Senterre et al., 2019, 2021).

### 2.3. Data analysis

Floristic similarities and plant communities were analyzed using Detrended Correspondence Analysis (DCA) and Bray-Curtis distance (coupled with UPGMA grouping method) using the R packages *vegan* and *labdsv* (Legendre, 2014; De Cáceres et al., 2019; Oksanen et al., 2019; Roberts, 2019). Based on DCA and floristic distance analysis, we established a consensus typology for the studied plots, and we used the R package *indicpecies* (De Cáceres et al., 2020) to evaluate the indicator value of species for each of the recognized plant communities in the typology. For the indicator value analysis, floristic data were compiled from the nested subplot series by extracting the 'set of the present' (Hallé et al., 1978; Oldeman et al., 1990), i.e. all observations of adult individuals, therefore excluding the tree seedling community observed in subplots S and H.

Floristic diversity has been analyzed using the Fisher alpha index (Condit et al., 1998) calculated on the tree subplots and various additional indicators commonly used in the literature have also been computed (Appendix C).

Structural variables such as stem density ( $N$ , trees  $\text{ha}^{-1}$ ) and basal area ( $G$ ,  $\text{m}^2 \text{ha}^{-1}$ ) were also computed. Tree density was calculated as the average number of trees per hectare, and basal area as the sum of the cross-sectional area 1.3 m above the ground using the following equation:

$$G = \frac{\pi}{4s} \sum_{i=1}^n 0.0001 \cdot d_i^2$$

where  $G$  is the cumulated basal areas of trees per plot, expressed in  $\text{m}^2 \text{ha}^{-1}$ ;  $d_i$  is the diameter in cm of the  $i^{\text{th}}$  tree in the plot and  $s$  is the unit area of the plot expressed in  $\text{m}^2$ .

Stem diameter structures (or diameter distributions) were established by pooling data from all plots inventoried within a given site (natural vs. semi-natural site). To better depict the size class distribution

patterns (SCD), we used the method of Condit et al. (1998). For forest community, we used the number of individuals as a dependent variable and the break points between each size class as an independent variable. Each size class had 15 cm width, starting from 5 cm DBH (e.g. 5 cm ≤ DBH ≤ 20 cm, 20 cm < DBH ≤ 35 cm, 35 cm < DBH ≤ 50 cm, etc.). Since some size classes were not recorded, the number of individual species in each class was transformed by 'ln (1 + number of individuals)', as suggested by Obiri et al. (2002). Diameter distributions were analyzed for both sites. Reverse-J SCD curves indicate good recruitment, with more individuals in smaller size classes and fewer in larger classes (Obiri et al., 2002; Martins and Shackleton, 2017). Unimodal SCD curves indicate populations with a limited recruitment, with more individuals in larger size classes and fewer in smaller size classes (Mensah et al., 2020).

### 3. Results

In total, 49 species from 49 genera and 34 families have been recorded during this study. Among them, 11 species were endemic, 24 indigenous and 14 considered exotic. Within the T sublots (trees), 489 individual plants from 25 species, 25 genera and 17 families have been surveyed. All individuals have been identified to species level and no voucher specimen has been collected during this survey considering that the lowland flora is well known by the authors.

#### 3.1. Floristic distinction between natural and semi-natural lowland mesic forest

The analysis of floristic data clearly recognizes the contrast between natural vs. semi-natural lowland mesic forests, at Pointe Cive and Anse Lascars sites respectively (Figs. 2 & 3). For the Detrended Correspondence Analysis (DCA) in Fig. 2, the main axis corresponds to the gradient of naturalness, while the second axis reflects the higher inter-plots floristic variability in semi-natural areas, which is possibly due to the complex history of human intervention with fine grain spatial patterns at Anse Lascars. The biotic difference between the Pointe Cive and Anse Lascars sites is unlikely to be due to spatial auto-correlations for two reasons. Firstly, the easternmost plot of Pointe Cive is almost as far away from the westernmost plot of Pointe Cive (ca. 1 km) as it is from the westernmost plot of Anse Lascars (ca. 1.2 km). Secondly, the authors have a good field knowledge of the small forest patches located between the rocky outcrops separating Pointe Cive from Anse Lascars. Those natural forest patches, some of which are geographically closer to Anse

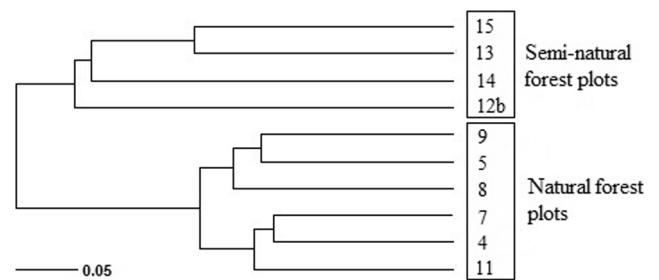


Fig. 3. Classification of the studied plots based on their Bray-Curtis floristic distance (UPGMA grouping method).

Lascars, are biotically and structurally similar to the Pointe Cive forest. They were not included in our sampling design due to access difficulties. Finally, as we will explain in the discussion, the literature supports the interpretation of the Pointe Cive forest as a natural forest site.

#### 3.2. Floristic description of the Seychelles natural lowland mesic forest

The natural lowland mesic forest surveyed at Pointe Cive was particularly homogenous in composition. The frequency observed among the most abundant tree species ranged from 67 % to 100 %, with an average of 90 %. The “indval” analysis (R package labdsv) supports the DCA and floristic dissimilarity analysis, providing several significant indicator species for natural forests (Table 1). Natural lowland mesic forests are characterized by the abundance and constancy of *Calophyllum inophyllum* (relative abundance: 19 %), *Adenantha pavonina* (23.2 %) and *Phoenicophorium borsigianum* (25.1 %) in the tree stratum, *Allophylus pervillei* (32 %) in the shrub stratum, and *Nephrolepis biserrata* (12.6 %) and *Phymatosorus scolopendria* (45.1 %) in the understorey, combined with the rarity of the exotic species *Cinnamomum verum* (5.5 %) and *Cocos nucifera* (0.3 %) (Fig. 4). Note that, although *Cocos nucifera* is considered a native species of the Seychelles granitic islands (see Vesey-Fitzgerald, 1940), it is native to the coastal fringe vegetation only and its presence inland is due to the human propagation of native and imported nuts. In the Pointe Cive forest (which is non-coastal, located at 100 to 500 m from the shore), *Cocos nucifera* was recorded in only one clump in one plot, most likely due to an accidental introduction.

Within the tree stratum (subplots T), 94.2 % of all individuals were native, representing 88.9 % of all species inventoried in the natural

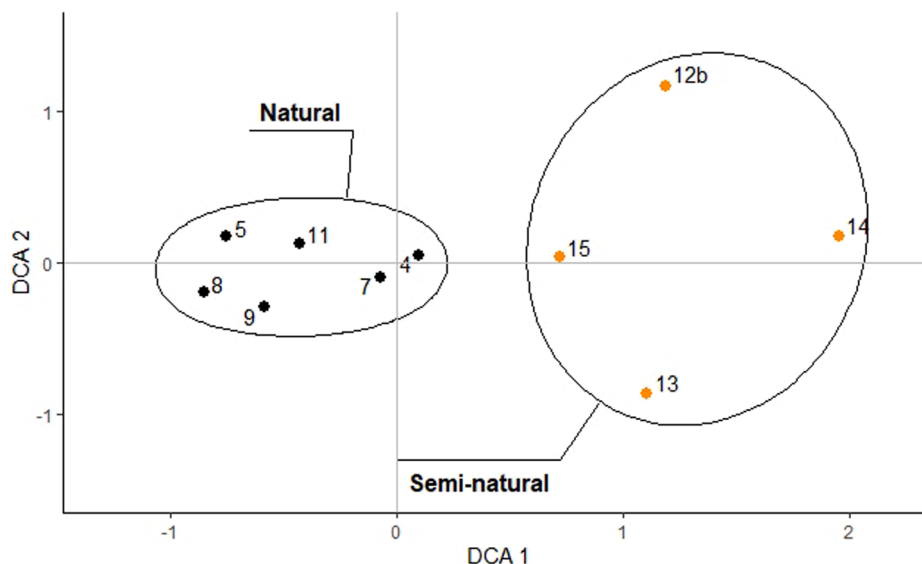


Fig. 2. Detrended Correspondence Analysis of the ten plots of the study area (using floristic data of the set of the present).

**Table 1**

List of species inventoried in plots located in natural forests ('N': Pointe Civine) and semi-natural forests ('SN': Anse Lascars), ordered alphabetically. For each species, observed in each series of subplots ('s-Plot'), we indicate the frequency (F), relative abundance (A<sub>r</sub>) and IndVal value (multiplied by 100). Basic species metadata are also indicated such as the biological type ('BT': T, tree species; S, shrub species, H, herbaceous species) and the origin status in the Seychelles granitic islands ('Orig.': Pend, palaeo-endemic species; End, endemic species; Ind, indigeneous, non-endemic native species; Exo, exotic/introduced species).

Species	Family	Orig.	BT	s-Plot	F		A <sub>r</sub>		Indval	
					N	SN	N	SN	N	SN
<i>Adenantha pavonina</i> L.	Fabaceae	Ind	T	T	100	50	23.2	1.2	91.7	4.2
				S	67	0	2.2			
				H	100	100	6.9	14.0		
<i>Allophylus pervillei</i> Blume	Sapindaceae	Ind	S	S	83	0	32.0		83.3	0
				H	100	75	6.8	4.0		
<i>Alocasia macrorrhizos</i> (L.) G.Don	Araceae	Exo	H	H	0	25		1.0	0	25
<i>Anacardium occidentale</i> L.	Anacardiaceae	Exo	T	T	0	25		0.6	0	25
<i>Artocarpus altilis</i> (Parkinson) Fosberg	Moraceae	Exo	T	T	0	50		2.5	0	50
				S	0	25		0.7		
				H	0	25		1.0		
<i>Averrhoa bilimbi</i> L.	Oxalidaceae	Exo	T	T	0	25		1.2	0	25
				S	0	25		2.1		
<i>Calophyllum inophyllum</i> L.	Clusiaceae	Ind	T	T	100	75	19.0	3.1	76.9	17.3
				H	100	50	2.1	1.0		
<i>Cenchrus polystachios</i> (L.) Morrone	Poaceae	Ind	H	H	17	0	0.3		16.7	0.0
<i>Cerbera manghas</i> L.	Apocynaceae	Ind	T	T	50	0	0.9		50	0
				S	50	0	4.0			
				H	33	0	0.3			
<i>Cinnamomum verum</i> J.Presl	Lauraceae	Exo	T	T	67	100	5.5	58.0	14.6	78.2
				S	67	100	11.1	12.0		
				H	100	100	6.0	27.4		
<i>Clidemia hirta</i> (L.) D.Don	Melastomataceae	Exo	H	H	33	25	0.2	0.4		
<i>Cocos nucifera</i> L.	Arecaceae	Exo	T	T	17	100	0.3	8.6	0.8	95.5
				S	17	100	3.6	57.7		
				H	17	75	0.0	5.2		
<i>Cyperus</i> sp.	Cyperaceae	Ind	H	H	0	25		0.2		
<i>Davallia denticulata</i> (Burm.f.) Mett. ex Kuhn	Davalliaceae	Ind	H	H	33	0	0.1		33.3	0.0
<i>Deckenia nobilis</i> H.Wendl. ex Seem.	Arecaceae	PEnd	T	T	67	75	3.7	8.0	29.9	41.3
				S	17	50	0.4	1.4		
				H	0	100		4.8		
<i>Dichanthium aristatum</i> (Poir.) C.E.Hubb.	Poaceae	Exo	H	H	17	0	0.3		16.7	0.0
<i>Diospyros boiviniana</i> (Baill.) G.E.Schatz & Lowry	Ebenaceae	End	T	T	33	0	0.9		33.3	0.0
				S	33	0	1.3			
				H	33	0	0.2			
<i>Dracaena floribunda</i> Baker	Ruscaceae	Ind	S	T	33	25	0.6	0.6		
				S	50	50	2.7	4.2	32.5	25.6
				H	100	100	0.9	4.8		
<i>Falcataria moluccana</i> (Miq.) Barneby & J.W.Grimes	Fabaceae	Exo	T	T	0	25		0.6	0.0	25.0
				H	0	50		0.7		
<i>Ficus lutea</i> Vahl	Moraceae	Ind	T	T	(+)	(+)	(+)	(+)	(+)	(+)
<i>Furcraea foetida</i> (L.) Haw.	Agavaceae	Exo	H	H	0	25		1.4	0.0	25.0
<i>Haplopteris ensiformis</i> (Sw.) E.H.Crane	Pteridaceae	Ind	H	H	33	0	0.1		33.3	0.0
<i>Intsia bijuga</i> (Colebr.) Kuntze	Fabaceae	Ind	T	T	17	0	0.3		16.7	0.0
				H	33	0	0.1			
<i>Jasminum fluminense</i> Vell. subsp. <i>mauritanium</i> (Bojer ex DC.) Turrill	Oleaceae	Ind	S	S	33	0	4.0			
				H	33	25	0.7	0.2	22.2	8.3
<i>Ludia mauritiana</i> J.F.Gmel. var. <i>sechellensis</i> F.Friedmann	Salicaceae	End	T	T	17	0	0.3		16.7	0.0
				H	17	0	0.2			
<i>Mangifera indica</i> L.	Anacardiaceae	Exo	T	T	0	25		0.6	0.0	25.0
				S	0	25		0.7		
				H	0	25		0.6		
<i>Mapania floribunda</i> (Nees ex Steud.) T.Koyama	Cyperaceae	End	H	H	17	0	0.3		16.7	0.0
<i>Memecylon elaeagni</i> Blume	Melastomataceae	End	S	S	33	0	0.9		33.3	0.0
				H	17	25	0.0	0.2		
<i>Mimusops sechellarum</i> (Oliv.) Hemsl.	Sapotaceae	End	T	S	17	0	0.9			
				H	50	25	0.4	0.2		
<i>Morinda citrifolia</i> L.	Rubiaceae	Ind	T	T	33	0	0.6		33.3	0.0
				H	0	75		1.3		
<i>Nephrolepis biserrata</i> (Sw.) Schott	Nephrolepidaceae	Ind	H	H	100	50	12.6	1.0	73.5	13.2
				T	83	75	11.0	3.1	63.5	17.9
<i>Nephrosperma vanhoutteana</i> Balf.f.	Arecaceae	Pend	T	S	67	50	9.3	7.7		
				H	100	100	8.7	12.7		
				H	100	100	8.7	12.7		
<i>Oplismenus compositus</i> (L.) P.Beauv.	Poaceae	Ind	H	H	33	25	0.4	0.4	17.5	11.8
<i>Pandanus balfourii</i> Martelli	Pandanaeae	End	T	T	33	0	1.2		33.3	0.0
				H	17	0	0.0			
<i>Paragenipa wrightii</i> (Baker) F.Friedmann	Rubiaceae	End	S	S	67	0	1.8		66.7	0.0
				H	50	25	0.2	0.2		
<i>Phoenicophorium borsigianum</i> (K.Koch.) Stuntz	Arecaceae	Pend	T	T	100	25	25.1	2.5	82.8	4.3
				S	100	75	7.6	12.7		

(continued on next page)

Table 1 (continued)

Species	Family	Orig.	BT	s-Plot	F		A <sub>r</sub>		Indval	
					N	SN	N	SN	N	SN
<i>Phyllanthus pervilleanus</i> (Baill.) Müll.Arg.	Euphorbiaceae	Ind	S	H	100	100	4.3	8.4		
<i>Phymatosorus scolopendria</i> (Burm.f) Pic.Serm.	Polypodiaceae	Ind	H	H	17	0	0.0			
<i>Planchonella obovata</i> (R.Br.) Pierre	Sapotaceae	Ind	T	H	33	0	0.1			
<i>Premna serratifolia</i> L.	Lamiaceae	Ind	T	T	17	0	0.6		16.7	0.0
				S	33	25	1.3	0.7		
<i>Psidium cattleianum</i> Sabine	Myrtaceae	Exo	T	S	17	0	0.4			
<i>Psilotum nudum</i> (L.) P.Beauv.	Psilotaceae	Ind	H	H	50	50	0.2	2.1	21.9	28.1
<i>Psychotria pervillei</i> Baker	Rubiaceae	End	S	S	33	0	2.7		33.3	0.0
				H	50	0	0.5			
<i>Pyrostria bibracteata</i> (Baker) Cavaco	Rubiaceae	Ind	T	T	67	0	3.7		66.7	0.0
				S	50	0	6.7			
				H	67	50	1.4	0.4		
<i>Spondias cytherea</i> Sonn.	Anacardiaceae	Exo	T	T	0	25		1.9	0.0	25.0
<i>Tabebuia heterophylla</i> (DC.) Britton	Bignoniaceae	Exo	T	T	0	50		6.2	0.0	50.0
				H	0	50		3.3		
<i>Tacca leontopetaloides</i> (L.) Kuntze	Dioscoreaceae	Ind	H	H	0	25		0.2	0.0	25.0
<i>Tarennia sechellensis</i> (Baker) Summerh.	Rubiaceae	Ind	S	T	33	0	2.8			
				S	50	0	7.1		50.0	0.0
				H	67	0	0.6			
<i>Terminalia catappa</i> L.	Combretaceae	Ind	T	T	17	50	0.3	1.2	4.2	37.5
				H	0	25		0.2		



Fig. 4. Illustrations of the natural lowland mesic forest typically found at Pointe Civine (Silhouette Island): (A) View of the forest landscape, showing the island of Mahé in the background; (B) Typical view of the forest understorey (photographs by B. Senterre).

forest at Pointe Civine, as opposed to 19.8 % and 43.8 % respectively in the semi-natural forest at Anse Lascars. Apart from the three most characteristic tree species mentioned above, the other native trees are more or less sparsely distributed in the natural forest site: *Nephrosperma vanhoutteana* (relative abundance: 11 %), *Deckenia nobilis* (3.7 %), *Pyrostria bibracteata* (3.7 %), *Tarennia sechellensis* (2.8 %), *Pandanus balfourii* (1.2 %), *Cerbera manghas* (0.9 %), *Diospyros boiviniana* (0.9 %), *Memecylon elaeagni* (0.9 %), *Dracaena floribunda* (0.6 %), *Morinda citrifolia* (0.6 %), *Premna serratifolia* (0.6 %), *Intsia bijuga* (0.3 %), *Ludia mauritiana* var. *sechellensis* (0.3 %), *Terminalia catappa* (0.3 %), *Planchonella obovata* (0.1 %), *Mimusops sechellarum* and *Ficus lutea* (the last two tree species were only seen nearby the plots).

Within the understorey of the natural forest, we encountered 19 species in the shrub stratum, of which 16 are native. The abundance of *Allophylus pervillei* (32 % of all shrubs) is a strong indicator of natural lowland mesic forests. The remaining and most dominant species of the shrub layer were *Cinnamomum verum* (relative abundance: 11.1 %), *Nephrosperma vanhoutteana* (9.3 %), *Phoenicophorium borsigianum* (7.6 %), and *Tarennia sechellensis* (7.1 %), all representing the regeneration of the canopy and under-canopy trees, or ephemeral dispersal attempts (as it seems that most Cinnamon seedlings do not make it to the canopy). Again, native species largely dominated over exotic ones, and only one exotic species (*Cinnamomum verum*) ranked in the top 5 most dominant species in the shrub layer (Table 1). *Cinnamomum verum* was also the most widespread exotic species in the shrub stratum of natural lowland mesic forests, occurring in 4 plots.

Dominant ground cover in the understorey herbaceous stratum (subplot H) was also overwhelmingly native in natural lowland mesic forests. Out of 33 species recorded, only 3 exotic species were found at Pointe Civine and none of them dominated the ground cover. The best indicator species of Seychelles natural lowland mesic forests were *Phymatosorus scolopendria* (relative abundance: 45.1 %) and *Nephrolepis biserrata* (12.6 %), which are both common fern species but are dominant typically in natural lowland forests. Most of the remaining species in the herbaceous layer of natural lowland mesic forests were seedlings of native trees and shrubs such as *Nephrosperma vanhoutteana* (relative abundance: 8.7 %), *Adenantha pavonina* (6.9 %) and *Allophylus pervillei* (6.8 %). The most abundant exotic species found in the herbaceous layer was *Cinnamomum verum* (relative abundance: 6 %).

### 3.3. Vegetation structure and inferred ecosystem dynamics

The overall size class distribution shows an inverted-J shaped curve (straight line in logarithmic scale) in both natural and semi-natural lowland mesic forests (Fig. 5). For  $DBH \geq 5$  cm and  $DBH \geq 10$  cm (two common thresholds used in other studies), the stem densities in natural forests were respectively  $1090 \pm 106$  and  $703.3 \pm 81$  stems  $ha^{-1}$ , and basal areas were respectively  $45.4$  and  $43.4$   $m^2$   $ha^{-1}$ . In comparison, semi-natural forests had stem densities of  $810 \pm 136$  and  $615 \pm 78$  stems  $ha^{-1}$  respectively for  $DBH \geq 5$  cm and  $DBH \geq 10$  cm, and basal areas of  $36.4$  and  $35.5$   $m^2$   $ha^{-1}$  respectively for the same two thresholds. Therefore, the natural forest of Pointe Civine appears to have a slightly larger biomass compared to the semi-natural forest of Anse Lascars, while canopy height (about 20–25 m high) and the maximum tree DBH observed are similar in the two forests. These results suggest that the semi-natural forest of Anse Lascars corresponds to a late secondary stage of development (i.e. structurally almost mature but not yet floristically mature).

If we look in more detail at the species contributions to the canopy (trees with  $DBH \geq 20$  cm) and under-canopy strata (trees with a DBH from 5 to 20 cm), greater differences between the natural and semi-natural forests appear. While canopy trees are purely native in natural forests (*Calophyllum inophyllum*, 160 stems  $ha^{-1}$ , and *Adenanthera pavonina*, 146.7 stems  $ha^{-1}$ ) and purely exotic in semi-natural forests (*Cinnamomum verum*, 115 stems  $ha^{-1}$ , *Cocos nucifera*, 70 stems  $ha^{-1}$ , and *Tabebuia heterophylla*, 45 stems  $ha^{-1}$ ), the main under-canopy trees include native species in both situations. Although the under-canopy of semi-natural forest was largely dominated by *Cinnamomum verum* (355 stems  $ha^{-1}$ , 74.7 % of all under-canopy stems), the presence of a native species 're-colonization' was clear with *Deckenia nobilis* (40 stems  $ha^{-1}$ , 8.4 %), *Nephrosperma vanhouetteana* (25 stems  $ha^{-1}$ , 5.3 %) and *Phoenicophorium borsigianum* (20 stems  $ha^{-1}$ , 4.2 %).

In the natural forest, the most abundant species within the DBH class 5–20 cm were *Phoenicophorium borsigianum* (273.3 stems  $ha^{-1}$ ), *Nephrosperma vanhouetteana* (120 stems  $ha^{-1}$ ), *Adenanthera pavonina* (106.7 stems  $ha^{-1}$ ), *Calophyllum inophyllum* (46.7 stems  $ha^{-1}$ ), and *Deckenia nobilis* (13.3 stems  $ha^{-1}$ ). Interestingly, the same dominant under-

canopy tree species (i.e. the three paleo-endemic palm genera *Deckenia*, *Nephrosperma* and *Phoenicophorium*) were also an important component of the understorey vegetation (representing 17.3 % of all observed individuals of the shrub stratum), while the two main canopy tree species (*Adenanthera pavonina* and *Calophyllum inophyllum*) were poorly represented. Therefore, it seems that, unlike in many continental tropical rain forests, some important components of the canopy and sub-canopy are able to regenerate even within a forest stand at climax, i.e. without the need for disturbance or tree-fall gap. Nevertheless, the two most important canopy trees have a more limited recruitment in climax stands (although not null, based on observations made outside the plots) and might therefore benefit from restoration programs.

## 4. Discussion

### 4.1. Biogeography of the Seychelles lowland mesic forest

The two main components of the Seychelles lowland mesic forest are widespread non-endemic species. The first one, *Calophyllum inophyllum*, is a native tree from the east coast of tropical Africa, Western Indian Ocean islands, India, Southeast Asia, all the way to Taiwan, the Ryukyu and Line islands, and New Caledonia. Throughout its range, this tree typically forms part of the narrow coastal forest fringe, also known as "beach forest" (Stevens, 1980, pp. 328, 331), extending only up to 20–40 m inland. This species is dispersed via sea-drift seeds (Hanaoka et al., 2014) and it only rarely forms a constituent of non-coastal lowland forests, as is typically the case in Seychelles (on developed soils derived from granite) and a few other small islands within its range (mostly on sandy soils). The second one, *Adenanthera pavonina*, is native to Sri Lanka and Southeast Asia, where it is generally a typical constituent of the non-coastal lowland mesic forests, along with a much larger diversity of tree species compared to the diversity observed in Seychelles.

Apart from these two non-endemic native components of the lowland forest, the other main component tree species are endemic to the granitic Seychelles, including the 3 palm species, all of which represent monotypic genera (Lewis, 2002; Baker et al., 2011) and indicate paleo-endemism. We suggest that these paleo-endemic elements have achieved long term resilience to the extreme small-island situation of Seychelles by adapting to become dominant elements of both climax stage and pioneer or secondary stages of forest rejuvenation, while at the same time maintaining their ability to regenerate within climax stands. In addition, these species have a wide ecological range, from lowland to montane belts and from ravines to ridges. Overall, within our plots, the native flora of the lowland mesic forest contains 31 % endemism (of which 27 % represents paleo-endemism). Because of this endemic singularity, these lowland mesic forests can be considered as a type of ecosystem endemic to the granitic Seychelles (Senterre et al., 2020, 2021).

### 4.2. Species diversity and representativity of the ecosystem's biota

The native lowland mesic forest of the granitic Seychelles has a very low species richness and species diversity. Within the 0.5 ha of surveyed forest, only 35 native species were observed (17 canopy/under-canopy trees, 8 shrubs or small understorey trees, 10 herbs). Based on expert knowledge and the National Biodiversity database developed in Seychelles, the native community sampled in the Pointe Civine natural forest represents at least 86.8 % of the entire native flora found in Seychelles for that particular ecosystem (up to 92 % depending on the species considered as part of that ecological group). This observation is also supported by the few descriptions of the pre-human state of lowland mesic forests available (e.g. Fauvel, 1909; Vesey-Fitzgerald, 1940: 473–476; Jeffrey, 1962; Lionnet, 1972, 1984). On the other hand, the representativity of the natural community is much lower in the studied semi-natural forest but still considerable with about 55 % of the lowland mesic forest community observed within the 0.2 ha surveyed. The

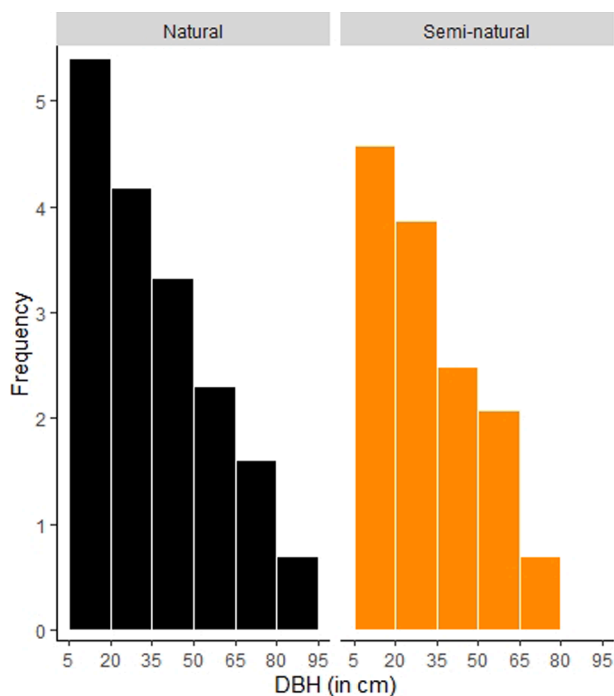


Fig. 5. Size-class distribution for all plots located in natural forests compared with plots located in semi-natural forests.

increasing relative abundance of native species like *Deckenia nobilis* (40 stems ha<sup>-1</sup>, 8.4 %), *Nephrosperma vanhouetteana* (25 stems ha<sup>-1</sup>, 5.3 %) and *Phoenixophorium borsigianum* (20 stems ha<sup>-1</sup>, 4.2 %) in the understorey of the semi-natural forest (compared to the canopy and under-canopy; see section 3.3 and Table 2) indicates that it is a re-colonization and not a relictual presence (relative abundance increasing rather than stable). Therefore, although some semi-natural forests are currently dominated by exotic species, they do not seem to have been irreversibly modified into “novel ecosystems” and might in fact be better interpreted as “novel stands” (i.e. biotic divergence of an individual stand that may or may not be passed on to the next ecosystemic generation and may or may not be able to extirpate native characteristic biota in the long term).

Also, it seems that in the natural (and pre-human) Seychelles lowland mesic forests, everything was everywhere, as if only few solutions existed to ensure a long-term stability in an extremely remote and spatially restricted island life. Nevertheless, from the authors' field experience, ecology remains a strong driver because the flora of lowland ravines and inselbergs still contrasts with that of mesic landforms, but again, with the same species composition found across the islands, in ravines and inselbergs, respectively. Thus, all the main biotic communities in Seychelles are clearly correlated with ecological gradients; a situation unlike hyper diverse continental rain forests (where such correlation is just harder to see, with too many opportunities for too many species), and unlike small oceanic islands with a more active or recent disturbance pattern (volcanism, tectonic movements, etc.). This can probably be explained by the fact that, compared to most other small oceanic islands, the Seychelles have always been covered with

vegetation, with limited opportunities for colonisation by long distance newcomers. Indeed, the Seychelles have been isolated from other Gondwana fragments for the last 50 Ma, without volcanism or major hurricanes. Although Seychelles must have been through the same climate change episodes during the Quaternary as everywhere else, its oceanic subequatorial position might have made it less catastrophic. Hence, these factors resulted in the relative rarity of evolutive radiations in Seychelles and the high biotic homogeneity across space, within contrasted ecosystem types. We suggest that these ecosystems became biotically contrasted because they had a long time to fine-tune their adaptations and because species extinctions-replacements have been based on ecological skills within a particularly stable environment rather than on opportunities or environmental changes.

Based on the T subplots (trees), we evaluated the Fisher alpha index of diversity to 4.09 in natural forest and 4.4 in semi-natural forest, i.e. far from values normally observed in tropical rain forests and more similar to values observed in temperate forests (Leigh, 1999) or, in the tropics, on other isolated oceanic islands (Itow, 1988). Compared with lowland forests found in Mauritius or Reunion Island (Strasberg, 1996; Florens et al., 2012), tree density is much lower in Seychelles, but comparable with densities found in high-diversity rainforests in the Southwest Pacific (Ibanez et al., 2018). However, paleo-endemism in Seychelles is a lot more frequent than in Reunion and Mauritius. Out of the 14 endemic plant genera of Seychelles (Friedmann, 1994; Larridon et al., 2018; Razafimandimbison et al., 2020), 4 monotypic palm genera (28.6 %) occur in the lowland belt indicating that it has been extremely isolated for an exceptionally long time in Seychelles, as have the sub-montane and montane belts. A similar pattern of paleo-endemism is

Table 2

Summary of plant community indicators of nativeness, invasion, and ecosystem structure and functioning (see Appendix C).

Indicators [unit]	Strata / Subplot dataset	Natural forest			Semi-Natural forest		
		Native species	Exotic species	All	Native species	Exotic species	All
Density [stems/ha]	T, DBH ≥ 20 cm	340	13.3	353.3	60	275	335
	T, DBH 5–20 cm	326.7	26.7	353.3	55	230	285
	T, DBH ≥ 5 cm	1026.7	63.3	1090	160	650	810
	T, DBH ≥ 10 cm	663.3	40	703.3	115	500	615
	S	1591.7	283.3	1875	475	1300	1775
Abundance [individuals]	T, DBH ≥ 5 cm	308	19	327	32	130	162
	T, DBH ≥ 10 cm	199	12	211	23	100	123
	S	191	34	225	38	104	142
	H	4426	325	4751	675	467.5	1142.5
	S, set of the present	106	0	106	6	0	6
Inventoried area [ha]	H, set of the present	2837	16	2853	79	27	106
	T	0.30			0.2		
	S	0.12			0.08		
Stand basal area [m <sup>2</sup> /ha]	H	0.12			0.08		
	T, DBH ≥ 5 cm			45.42			36.4
DBH max [cm]	T, DBH ≥ 10 cm			43.4			35.5
	T, DBH ≥ 5 cm	81.5	27.8	81.5	52.1	77.3	77.3
Species Richness	T, DBH ≥ 5 cm	16	2	18	7	9	16
	T, DBH ≥ 10 cm	10	2	12	5	9	14
	S	16	3	19	5	5	10
	H	29	4	33	20	9	29
	S, set of the present	6	0	6	1	0	1
	H, set of the present	9	1	10	6	2	8
	T, DBH ≥ 5 cm	3.58	0.22	4.09	2.79	1.95	4.4
Fisher α	T, DBH ≥ 10 cm	2.21	0.68	2.75	1.96	2.39	4.06
	S	4.15	0.79	4.94	1.54	1.09	2.45
	T	16.66	5.55	22.22	6.25	18.75	25
Rarity Index							
Dominance Index	T			1.61			4.69
Endemism rate [%]	All	30.3			28.57		
Native community representativity	All	86.84			55.26		
Bray Curtis dissimilarity to primeval	All, set of the present	0.025			0.35		
Overall Nativeness	All	86.8			63.6		
Canopy Nativeness	T, DBH ≥ 5 cm	88.9			43.8		
Canopy Weighted Nativeness	T, DBH ≥ 5 cm	94.2			19.8		
Canopy Functional Nativeness	T, DBH ≥ 5 cm	96.1			62.7		
Understorey Nativeness	H (all data)	86.1			61.3		
Tree sapling nativeness	S (tree species data)	69.1			23.3		
Tree seedling nativeness	H (tree species data)	80.3			52.9		



found on Lord Howe Island, Australia (Conn and Green, 1996; Sheringham et al., 2016), which also has a monotypic endemic genus of palm dominant in lowland mesic forests. Other small, mountainous, moist, highly isolated islands with poor flora and strong paleo-endemism are very rare worldwide and include the subtropical islands of Rapa, French Polynesia (Meyer, 2011) and Robinson Crusoe, eastern Pacific Ocean (Hobohm, 2014). High endemism and paleo-endemism are more common on larger and more diverse tropical islands, e.g. Borneo, Sumatra, Cuba, Hispaniola, Puerto Rico, Tasmania, Sri Lanka, Madagascar, Socotra (Veron et al., 2019, p. 7).

#### 4.3. Origin status of *Adenanthera pavonina* in Seychelles

The origin status of *Adenanthera pavonina* in Seychelles has been debated since the 1990s (Gerlach, 1996), when conservation and invasion ecology gained momentum in Seychelles. The species was considered “probably native” until 1940 (Baker, 1877; Summerhayes, 1931, p. 276), but then came to be considered as “exotic and invasive” by Vesey-Fitzgerald (1940: 31) based on the gregarious behavior he observed in secondary forests (as if being a pioneer was the exclusivity of invasive alien species). He was then followed by others and most importantly by Friedmann in his flora of Seychelles (Friedmann, 1994), which resulted in the current dominant view of restoration ecologists in Seychelles. Nevertheless, we present here strong evidence supporting its native origin.

Firstly, Dufresne, in 1768, described this species in Seychelles without any possible ambiguity (“tree bearing pods, each having 7–8 red seeds”: Lionnet, 1984, pp. 32, 67). A few years later, Malavois (1787 in Fauvel 1909: 269–275) and Brayer du Barré (1775 in Fauvel, 1909, p. 219) also made mention of a “Bois Noir” being constitutive of native forests and a good native timber resource. Although they did not describe unambiguously *Adenanthera pavonina*, we know that in the 19th century *Adenanthera pavonina* was called “Bois Noir” (Baker 1877: 91). The only other species called “Bois Noir” at that time, i.e. *Albizia lebeck*, was introduced to the Mascarenes only in 1767 (Baker, 1877, p. 94) and therefore these early mentions of a widespread Bois Noir in Seychelles can only be referring to *Adenanthera pavonina*. In addition, we have shown in this study that *Adenanthera pavonina* is a co-dominant canopy tree in the best-known remnant of undisturbed lowland forest of Seychelles which has remained floristically stable for at least 80 years (Vesey-Fitzgerald, 1940: 477). Based on these observations, we conclude that *Adenanthera pavonina* was present in Seychelles before the introduction of exotic timber species (and especially their widespread naturalization), and that it was not only present but formed an important constituent of the lowland forests that were logged during the end of the 18th century and the 19th century. However, it was most likely introduced to the outer islands of Seychelles and is therefore both native and exotic to the Seychelles as a country. This observation could have a major impact on restoration ecology, since on one hand, some organizations are currently using resources for the control of this supposedly Invasive Alien Species, and on the other hand, *Adenanthera pavonina* is currently blacklisted from restoration programs although seeds are widely available and can be stored easily. It is also N-fixing, it provides good timber and can be both a pioneer and climax species.

#### 5. Conclusions

In this study, we described quantitatively for the first time the plant community, diversity and vegetation structure of the native lowland mesic forests of the Seychelles granitic islands. These lowland mesic forests are believed to have covered about 53 % of those islands (13,250 ha) before the arrival of humans, and today they represent 76 % of the restoration opportunities (Senterre and Wagner, 2014). The results obtained here are key for Seychelles conservation as: (1) they improve knowledge on the best adapted local species for restoration of lowland forests, (2) they provide useful indicators to monitor restoration

projects, and (3) they provide baseline data to evaluate on the one hand the resilience of natural vegetation to biological invasions, and on the other hand the permanence of novel ecosystems’ novelty. In addition, (4) this paper provides a precise description of a type of ecosystem that is unique and could contribute to a better understanding of island biogeography theories.

#### 5.1. Improved knowledge on native species ecologically adapted for restoration programs

Although a lot of focus has been put on the use of the beloved palms of Seychelles for restoration (all representing endemic monotypic genera), our study shows that these species are mainly under-canopy components, therefore able to mitigate understorey invasion but not to fully mitigate canopy invasion. Our study also shows that the most abundant native canopy tree species have been neglected for restoration, typically *Calophyllum inophyllum*, *Adenanthera pavonina*, *Mimusops sechellarum*, *Intsia bijuga* and *Ficus lutea*. In particular, *Adenanthera pavonina* appears to be a good species for restoration as it has unlimited availability of seeds (like *Calophyllum* and *Ficus*), is fast growing and is adapted to both understorey and gap colonization. It is therefore a species that could improve considerably the restoration of lowland mesic forests, by facilitating the propagation of a canopy competitor in Cinnamon-dominated forests. It could also reduce the propagule pressure of Cinnamon within a relatively short period of time (maybe 20 years). By providing evidence for the native origin of that species and by explaining its potential keystone function in restoration of lowland mesic forests of Seychelles, we hope that resources will be allocated to develop more lowland restoration programs based on this species, as well as the other native trees emphasized in this study, instead of controlling it as an IAS and prohibiting its use for restoration purposes.

#### 5.2. Compilation of indicators and baseline data for ecosystem monitoring

Another important factor for efficient restoration programs is the establishment of metrics to quantify restoration success (Ruiz-Jaén and Aide, 2005; Ruiz-Jaén and Mitchell Aide, 2005; Suding, 2011; Sansvervo and Garbin, 2015), habitat quality (Queensland Government, 2014), and disturbance (Watt, 1998). In this study, we provide baseline data and measurements for a detailed set of such indicators. Also, we hope that these indicators will be useful to trigger additional research on the invasibility of ecosystems in Seychelles (Guo et al., 2015; Hui et al., 2016).

#### 5.3. Permanent plots are an important asset to monitor ecosystem resilience vs. Novelty

Additionally, the set of permanent plots established constitutes an important asset to pursue the study of ecosystem dynamics. In the Pointe Civine area, exotic species have penetrated the natural forest but only to a limited extent. The permanent plots set up during the current study will allow the precise monitoring of the resilience or invasibility of these forests (Guo et al., 2015; Hui et al., 2016). On the other hand, the permanent plots in the degraded forests of Anse Lascars will allow for the testing of the potential permanence of novel ecosystems’ novelty, i.e. the long term extirpation of characteristic native biota (Kueffer et al., 2013, pp. 233, 234). Just a few decades after man abandoned those lands, and just a century after it was last deforested, we observe an abundant regeneration of native species in the understorey and the under-canopy (Cesar and Zehnder, 2020). Exotic species do penetrate undisturbed native ecosystems and will surely result in some extinctions (e.g. for threatened species), but even in places where humans have helped those exotic species a lot, they do not appear to extirpate completely the characteristic native components. Cinnamon-invaded forests should then be better seen as ‘novel stands’, rather than novel ecosystem types. More studies are needed to find out what they will become at climax and

after a few centuries of maturation or ecosystemic cycles, and we cannot exclude the re-colonization by the native species (see [Crouzeilles et al., 2017](#)).

#### 5.4. Detailed description of a unique ecosystem with potential use in island biogeography studies

Although it was known that Seychelles have a very reduced flora and high endemism, including paleo-endemism, so far nobody had described the endemism pattern at the scale of plant communities. We show here for the first time that the lowland rain forest in Seychelles is a further depauperate flora (compared to the submontane and montane belts), but maintaining the same endemism pattern (ca. 31 %) and the same paleo-endemism as that observed for the overall flora. In other words, the endemism rate is not much smaller in the lowland rain forest compared to montane forests, although native species richness increases with elevation. We hope that this paper can bring more attention to the Seychelles as a potential key site for the study of island biogeography theories. The extremely small size and remoteness of this archipelago combines with a particularly stable habitat heterogeneity for about 50 million years and could therefore complement studies made on hotspot islands, where island age is correlated with habitat heterogeneity (Sarmiento [Cabral et al. 2017](#); [Borregaard et al. 2017](#)). In addition, comparisons between the three main altitudinal belts (lowland, submontane and montane) could still provide an important insight into the effects of land area (decreasing from lowland to montane).

#### CRedit authorship contribution statement

**François Baguette:** Conceptualization, Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Said Harryba:** Investigation. **Teesha Baboorun:** Investigation. **Pierre-André Adam:** Supervision, Funding acquisition, Writing – review & editing. **Bruno Senterre:** Conceptualization, Methodology, Investigation, Data curation, Writing – review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A, B and C. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119837>.

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