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Impacts of woody invasive species on tropical forests of the Seychelles

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Christoph Küffer

Dipl. Umwelt-Natw. ETH
born April 13, 1974
citizen of Täuffelen BE

Accepted on the recommendation of

Prof. Dr. Peter J. Edwards, examiner
Dr. Hansjörg Dietz, co-examiner
Prof. Dr. Andrew Hector, co-examiner

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Summary

1 A considerable body of recent research has focussed on why a small proportion of plant species spread rapidly when introduced into a new area. In this context, species invasiveness and habitat invasibility have been extensively studied, mostly in productive habitats, but information on how invasive plants affect ecosystem function remains scarce. In particular, there have been very few studies on the invasibility of and invasion impacts in very nutrient poor habitats, including many tropical forests. In this thesis, heavily invaded tropical rainforests on nutrient poor soils on one of the granitic islands of the Seychelles group were investigated. The aims of the study were: (i) to evaluate the invasiveness and persistence of woody invasive plants in these forests, (ii) to assess the impacts of the invaders on soil nutrient availability and forest development, and (iii) to derive conclusions relevant for forest management and rehabilitation.

2 Two main conclusions emerged from an expert-based evaluation of the state of plant invasion in the Seychelles. First, although many tree species have been introduced to the Seychelles, rather few are invasive in the mid-altitude and montane forests. Second, both local environmental conditions - in particular the very nutrient-poor soils - and land-use history, which included periods of nearly complete deforestation, were important factors determining which species became invasive.

3 Litter properties of the six most abundant native and invasive woody species in mid-altitude forests were compared. Leaf litter of the invasive species had markedly higher N and P contents but lower polyphenol concentrations. It also tended to decompose faster than the litter of native species. Soil nutrient availability was investigated under stands of three species that differed greatly in their litter properties - the N-fixing invasive species *Falcataria moluccana*, the very widespread invasive *Cinnamomum verum*, and the endemic *Northea hornei*. The results revealed only small differences in soil conditions. It appears that invasive species adapted to very nutrient poor soils are particularly effective in nutrient uptake which may have counterbalanced a fast release of nutrients from litter in established stands.

4 In a root trenching experiment, the dominant invasive canopy tree *Cinnamomum verum* showed strong belowground competitive effects; these were attributed to the dense root mat produced by this species which apparently suppresses tree regeneration. Release from belowground competition through trenching was stronger for seedlings than saplings, and for juveniles of invasive than for juveniles of native tree species. Thus, forest dominance by *C. verum* appears to shape tree regeneration not only by generally reducing rates of colonization but also by inhibiting the growth of small-seeded or invasive trees at the seedling stage. Undisturbed *C. verum* forests may, therefore, represent good nurse habitats for the regeneration of native trees.

5 In a comparative investigation of the nutritional quality of fleshy fruits for fruit-eating birds, invasive tree species were shown to produce fruits of higher quality (relative yield, energy content) than native species. The most abundant invasive tree, *C. verum,* produced fruits with a particularly high fat and protein content. As a consequence, the native tree species may suffer from limited dispersal due to strong competition from the invasive trees for frugivorous birds. However, if much higher bird densities are supported by the ample food resources provided by invasive trees, dispersal of native trees could also be promoted.

6 The results of this thesis suggest that invasive tree species have important impacts upon nutrient poor ecosystems, and that these are not only distinct from those in nutrient rich habitats but, as a result of variation in growth strategy amongst invasive tree species (i.e. stress-tolerators vs. competitors), are also more varied. Which strategy dominates in a particular patch is likely to influence both nutrient cycling and the long-term development of the vegetation.

7 This thesis formed part of a collaboration between the Geobotanical Institute and the Seychelles Ministry of Environment and Natural Resources (MENR), and was developed in close association with practitioners in nature conservation. Based on these experiences, a research strategy was identified that seeks to explain the complexity of specific field or real-world cases. This strategy, referred to here as ‘integrative ecological research’, is seen as being of particular relevance for problem solving in environmental management. The focus on the case of *C. verum* secondary forests, for instance, made it possible to develop a promising concept for habitat rehabilitation in the Seychelles. This concept, based directly on the research results presented here, involves increasing native propagule pressure at a landscape scale while taking advantage of *C. verum* secondary forests as nurse habitats for native species.

Zusammenfassung

1 In den letzten Jahrzehnten befasste sich eine umfangreiche Forschung mit invasiven Pflanzen, d.h. mit gebietsfremden (vom Menschen eingeführten) Arten, welche sich schnell ausbreiten und dabei zu problematischen Auswirkungen führen können. Insbesondere wurde, vor allem in nährstoffreichen Ökosystemen, untersucht, welche Eigenschaften der invasiven Arten (‚invasiveness') und der betroffenen Habitate (‚invasibility') die schnelle Ausbreitung dieser Arten erklären. Wenig bekannt ist hingegen, wie invasive Arten das Funktionieren von Ökosystemen beeinflussen. Zudem wurden Pflanzeninvasionen in nährstoffarmen Gebieten, wie zum Beispiel viele tropische Regenwälder, kaum erforscht. In dieser Dissertation wurden stark von Pflanzeninvasionen betroffene tropische Regenwälder auf einer ozeanischen Insel der Seychellen untersucht. Die Böden dieser Wälder zeichnen sich durch Granit als Muttergestein und Nährstoffarmut aus. Die übergeordneten Forschungsfragen waren: (i) wie lassen sich die Ausbreitung und langfristige Etablierung von invasiven Gehölzpflanzen in diesen Wäldern erklären, (ii) zu welchen Auswirkungen auf die Nährstoffverfügbarkeit im Boden und die Waldentwicklung führen die invasiven Gehölze, und (iii) welche Empfehlungen lassen sich aus den Forschungsresultaten für den Naturschutz in den tropischen Regenwäldern der Seychellen ableiten.

2 Eine Synthese von Expertenwissen zu Pflanzeninvasionen in den Seychellen ermöglichte insbesondere zwei wichtige Schlussfolgerungen. Erstens ist die Zahl der problematischen invasiven Pflanzenarten auf den Seychellen, abgesehen von den Küstengebieten, relativ klein, obwohl eine grosse Anzahl gebietsfremder Arten auf die Inseln eingeführt wurde. Zweitens sind sowohl die lokalen abiotischen Umweltfaktoren – insbesondere die nährstoffarmen Böden, als auch die Geschichte der Landnutzung – insbesondere die zeitweilige fast vollständige Abholzung der Wälder – von zentraler Bedeutung für das Verständnis von Pflanzeninvasionen auf den Seychellen.

3 Ein Vergleich der Eigenschaften von abgestorbenem Blattmaterial (Streu) der sechs häufigsten einheimischen und invasiven Gehölze der Wälder auf mittlerer Höhenstufe zeigte, dass invasive Gehölze im Mittel Streu mit höherem Stickstoff- und Phosphorgehalt aber tieferem Gehalt an Sekundärmetaboliten (Tannine, Phenole) produzieren. Die Streu der invasiven Pflanzen wurde im Mittel auch schneller abgebaut als diejenige der einheimischen Pflanzen.

Zusätzlich wurden zwischen Baumgruppen der Stickstoff fixierenden, invasiven Art *Falcataria moluccana*, des sehr häufigen, nicht fixierenden invasiven Baumes *Cinnamomum verum*, und der endemischen Art *Northea hornei*, entgegen der Erwartung aufgrund der unterschiedlichen Eigenschaften der Streu, nur geringe Unterschiede in der Nährstoffverfügbarkeit im Boden beobachtet. Es scheint, dass sich invasive Pflanzen, welche sich erfolgreich auf nährstoffarmen Böden etablieren können, durch besonders effektive Mechanismen für die Nährstoffaufnahme aus dem Boden auszeichnen. Eine schnelle Aufnahme von Nährstoffen wiegt möglicherweise die schnelle Abgabe der Nährstoffe beim Streuabbau auf, wodurch sich die Nährstoffreservoirs im Boden wenig ändern.

4 In einem Experiment zur Auswirkung der Wurzelkonkurrenz von adulten *Cinnamomum verum* (Zimt) Bäumen auf aufwachsende Jungpflanzen wurde die Wurzelkonkurrenz manipuliert, indem mit einer Machete um Jungpflanzen quadratförmig Schlitze in den Boden geschnitten wurden (trenching). Jungpflanzen, welche durch diese Behandlung von der Wurzelkonkurrenz von Zimt befreit wurden, wuchsen deutlich schneller. Dabei war der Effekt bei Setzlingen (seedling, < 50 cm Höhe) stärker als bei grösseren Jungpflanzen (sapling, > 50 cm), und bei Jungpflanzen von invasiven stärker als bei Jungpflanzen von einheimischen Pflanzen. Die starke Wurzelkonkurrenz von Zimt lässt sich wahrscheinlich durch die für diese Art typische, dichte Wurzelmasse in der obersten Bodenzone erklären. Es scheint, dass dadurch die Einwanderung von neuen Pflanzenarten in Zimtwälder beeinflusst wird: einerseits wird der Aufwuchs von Jungpflanzen insgesamt behindert, andererseits werden Pflanzen mit kleinen Samen gegenüber Pflanzen mit grossen Samen, und invasive Pflanzen gegenüber einheimischen Pflanzen benachteiligt. Zimtwälder, welche nicht anthropogen gestört werden, könnten daher ein geeignetes Habitat für den Aufwuchs von einheimischen Pflanzen darstellen.

5 Ein Vergleich des Nährwertes von Früchten für fruchtfressende Vögel zeigte, dass invasive Gehölze Früchte von besserer Qualität (tiefer Wassergehalt, hoher Energiewert) produzieren als einheimische Arten. Die Früchte des häufigsten invasiven Baumes (*Cinnamomum verum*) hatten einen speziell hohen Fett- und Proteingehalt. Dies könnte die einheimischen Pflanzen benachteiligen, wenn die Vögel bevorzugt Früchte von invasiven Arten fressen und verbreiten. Andererseits könnten die einheimischen Arten auch profitieren, wenn durch das zusätzliche Angebot an invasiven Früchten mit hohem Nährwert die Populationsdichte der Vögel zunimmt, und dadurch auch die einheimischen Pflanzen häufiger verbreitet werden.

6 Die Resultate dieser Dissertation zeigen, dass invasive Gehölze auch in Habitaten mit nährstoffarmen Böden zu bedeutenden Störungen von Ökosystem-Prozessen führen können, und dass sich Störungen invasiver Arten zwischen nährstoffarmen und –reichen Habitaten unterscheiden. Insbesondere scheint die Variabilität der Auswirkungen zwischen verschiedenen

Typen von invasiven Arten nährstoffarmer Habitate besonders hoch zu sein. Entweder sind die Arten durch einen tiefen Nährstoffbedarf (stress-tolerator) oder eine effektive Aufnahme von Nährstoffen aus dem Boden (competitor) an die Nährstoffknappheit angepasst. Für die langfristigen Auswirkungen invasiver Arten auf ein nährstoffarmes Ökosystem ist es von entscheidender Bedeutung, welcher Typ sich etabliert.

7 Diese Dissertation wurde durch eine Zusammenarbeit zwischen dem Geobotanischen Institut (ETH Zürich) und dem Umweltministerium der Seychellen ermöglicht, und entwickelte sich daher in kontinuierlicher Zusammenarbeit mit Naturschutzfachleuten auf den Seychellen. Aufgrund der dadurch gewonnenen Erfahrungen, diskutiere ich die Bedeutung von ökologischer Forschung, welche sich gezielt mit der Komplexität von konkreten Ökosystemen oder Managementproblemen befasst (integrative ecological research), für die Lösung von Umweltproblemen. In dieser Dissertation, zum Beispiel, wurden in allen Teilstudien Zimtwälder untersucht. Aufgrund einer Synthese der verschiedenen Resultate liess sich ein viel versprechendes Konzept für die zukünftige Renaturierung dieser Wälder entwickeln, welches sowohl die Förderung der Produktion und Verbreitung von Samen einheimischer Pflanzen auf der Landschaftsebene und das Potential der Zimtwälder als geeignetes Habitat für den Aufwuchs von einheimischen Pflanzen berücksichtigt.

General Introduction

For more than 10 years plant invasions on the oceanic islands of the granitic Seychelles (Indian Ocean, see Chapter 1) have been investigated by the Geobotanical Institute (ETH Zurich, now being part of the Institute of Integrative Biology) (Fleischmann 1997b). This doctoral thesis and a complementary thesis (E. Schumacher, in prep.) were initiated to improve the mechanistic understanding of the processes underlying the high abundance of alien woody plants in most habitats on the granitic islands (Fleischmann et al. 1996, Fleischmann 1997a, Kueffer and Vos 2004). While the work by E. Schumacher focuses on the role of species traits (invasiveness, see Schumacher et al. 2003) this thesis is particularly concerned with the importance of habitat characteristics for invasion success and impact of alien woody plants (see Kueffer et al. 2003).

In this thesis the impact of invasive woody species on habitat characteristics such as litter decomposition, root competition and seed dispersal in mid-altitude and montane secondary forests were studied. The term *invasive* refers to *alien* (non-native) species (i.e. species that are thought to have been introduced by man to the granitic Seychelles) that are spreading or abundant in semi-natural and natural habitats.

The scale of the problem of biotic invasions

On a global scale, invasive alien species have been identified as being one of the five most important direct causes of the worldwide decline in biodiversity and ecosystem services, and their impact is predicted to rapidly increase in tropical forests (Millennium Ecosystem Assessment 2005). In the USA alone, costs due to environmental damage by invasive species add up to some 120 billion US$ per year (Pimentel et al. 2005). The threat of invasive alien species is therefore recognized as a conservation priority by the UN Convention on Biological Diversity (CBD) and the World Conservation Union (IUCN) (cf. McNeely et al. 2001).

Environmental impacts of invasive alien plants

The study of impacts of invasive species is of high relevance for ecology in general by providing an opportunity to evaluate the significance of traits of particular species for shaping communities and ecosystems (cf. e.g. Jenny 1941, Crawley et al. 1999, Grime 2001, Wardle 2001, Lavorel and Garnier 2002, Vitousek 2004). Species from oceanic islands are particularly interesting in this regard because their adaptations to local environmental conditions, partly determined by biogeographical factors, may differ from mainland species (e.g. Kitayama and Itow 1999).

Invasive plant species, which form part of anthropogenic global change (Vitousek et al. 1997), are especially significant when they alter the functioning of ecosystems (e.g. Mack et al. 2000, Dukes and Mooney 2004, Mooney et al. 2005). Examples of such alteration include grass invasions that create positive feedbacks upon the fire regime, invasions of *Tamarix* spp. that alter the hydrology of large areas, and invasion by the nitrogen-fixing shrub *Myrica faya* that increase the ecosystem N accumulation in early-successional habitats in Hawaii (Vitousek and Walker 1989, D'Antonio and Vitousek 1992, Zavaleta 2000). In addition, direct impacts of invasive species on native plant diversity, e.g. through resource competition or allelopathy, have often been reported, but mechanistic studies on how an invasive plant affects regeneration and persistence of native species are rare (Levine et al. 2003). Furthermore, there is much debate to what extent invasive species have been involved in species extinctions (Gurevitch and Padilla 2004).

While the characteristics of successful invaders (invasiveness, e.g. Kolar and Lodge 2001, Grotkopp et al. 2002) and the vulnerability of ecosystems to invasions (invasibility, e.g. Lonsdale 1999, Davis et al. 2000, Levine et al. 2004) have been extensively studied, most information about how ecosystem functions are affected by invasive species is rather anecdotal. There is the need for more empirical case studies and a better conceptual framework for predicting the long-term impact of particular invasive species upon particular ecosystems (Parker et al. 1999, Williamson 2001, Levine et al. 2003). The distinction between 'strong' invaders that have a major impact on an ecosystem and 'weak' invaders that have little effect may help to reconcile conflicting results in invasion biology (Ortega and Pearson 2005). However, to date it is not even settled whether impacts form a legitimate dimension of a scientific definition of an invasive species (Richardson et al. 2000, Daehler 2001, Davis and Thompson 2001).

The effect of an invasive species on ecosystem processes is expected to depend on whether it differs functionally from native species (e.g. Vitousek 1990). But just how large these functional differences must be to have an effect is likely to depend upon both the ecosystem and the invading species. For example, an ecosystem may be resilient enough to absorb the changes induced by a new species (e.g. Knops et al. 2002), while the invading species may adjust its characteristics to those of the native vegetation either through phenotypic plasticity or through the formation of new ecotypes (Sexton et al. 2002). Especially, when invaded habitats are characterised by high abiotic stress or low anthropogenic disturbances an adjustment of the invader's properties can be expected (Dietz and Edwards 2006). In stressed habitats or in the long term after removal of a disturbance, the impacts of invasive species on ecosystems might thus be lower. Alternatively, after initial establishment invasive species may initiate a positive feedback that drives the ecosystem from one stable state into a new one that is more favourable to them (Simberloff and Von Holle 1999), for instance by increasing nutrient availability (e.g. Ehrenfeld et al. 2001, Ostertag and Verville 2002).

Plant invasions on oceanic islands

Tropical forests on oceanic islands are generally more heavily invaded by alien plants than mainland tropical forests (Loope and Mueller-Dombois 1989, Cronk and Fuller 1995, Lonsdale 1999, Denslow 2003). A number of hypotheses have been put forward to explain the extent of invasions on oceanic islands (Elton 1958, Loope and Mueller-Dombois 1989, Cronk and Fuller 1995, Mack et al. 2000, Denslow 2003).

Islands are often depauperate in certain taxonomic and functional groups of species (Carlquist 1965, Whittaker 1998). The resulting reduced diversity and 'disharmony' in island floras have been suggested to explain the higher vulnerability of oceanic islands, a hypothesis that goes back to Darwin (1859). More specifically, there may be more vacant niches on oceanic islands that may be readily filled by introduced species. For example, the species poverty of island ecosystems may result in a low intensity of the competition exerted by the native vegetation, reducing resistance to invasions. Related to this species diversity hypothesis are the propositions that island plants are poor competitors compared to invasive species, and that most invertebrate herbivores on oceanic islands are specialists that attack only particular native species, i.e. enemy release for alien species (Keane and Crawley 2002) may be enhanced on oceanic islands.

The intensity of anthropogenic disturbances on oceanic islands, that are often very densely populated, is another factor often proposed to explain their higher vulnerability to invasions. Most small oceanic islands were largely deforested within less than a century after colonization, which must have facilitated subsequent invasions by alien species. In most cases, over 95% of the forests are secondary and dominated by alien species (e.g. Kendle and Rose 2001, Kueffer and Mauremootoo 2004, Kueffer and Vos 2004, Lugo 2004, Vos 2004). In contrast, in La Réunion for instance, the remaining 20-30% primary forest consist still mainly of native species (Kueffer and Lavergne 2004). Additionally, introduction rates of alien plant and animal species were often particularly high relative to the size of the land mass and of the native species pool (Cronk and Fuller 1995). More indirectly, the introduction of larger mammalian grazers, a guild that is mostly absent from island faunas, may have facilitated the spread of introduced grazing-adapted plants relative to non-adapted native species (Courchamp et al. 2003). Recent studies (Simberloff 1995, Lonsdale 1999, Denslow 2003, Bellingham et al. 2005) suggest that these anthropogenic disturbances (and the particular vulnerability of oceanic islands to some of these disturbances) rather than the nature of isolated and species-poor island ecosystems *per se* are the most important causes of massive biological invasions on oceanic island.

Not surprisingly, impacts of invasive plants on oceanic islands are often discussed in the context of ecological restoration, and the positive impacts of invasive species on the native biodiversity are sometimes mentioned (Safford and Jones 1998, Zavaleta et al. 2001, Drake et al. 2002, Ewel and Putz 2004, Kueffer et al. 2004, Lugo 2004). In the case of heavily invaded and disturbed island ecosystems, invasive species may facilitate habitat rehabilitation by providing services such as restoration of eroded soils, nurse plants for native plant regeneration, or substitute habitat for native animals (e.g. Parrotta et al. 1997, Safford and Jones 1998, Kendle and Rose 2001, D'Antonio and Meyerson 2002, Kueffer 2003, Ewel and Putz 2004, Lugo 2004).

Woody invasive species in the tropics

Woody plant families show an overrepresentation of invasive taxa compared to other families (Daehler 1998), and include many of the most problematic invasive plants of tropical oceanic islands (Binggeli 1996, Weber 2003). In the subtropics and tropics these families are the *Rosaceae*, legume families, *Pinaceae*, and to a lesser degree the *Myrtaceae* (Binggeli 1996). Forestry and agroforestry species are often fast-growing and/or N-fixing species. Also, they are often selected or bred for a broad tolerance of environmental conditions and for the restoration of degraded sites. Hence, they have a high potential to become invasive (Richardson et al. 2004). Agroforestry species, i.e. species that are used for non-traditional forestry purposes such as windbreaks, shading trees, intercropping, fruits and other crops, and erosion control, pose a particularly high risk for nature conservation because they are often used in small rural communities in the buffer zones of natural areas (Richardson et al. 2004).

In the mainland tropics deforestation of native forests and introductions of alien trees began on a large scale only a few decades ago (Richardson 1998, Fine 2002, Wright 2005), which may explain why woody plant invasions in the tropics are mainly confined to oceanic islands where deforestation and introductions of alien species started earlier. It can be expected, however, that the problem of woody plant invasions will increase in the mainland tropics. Invasions of woody plants on oceanic islands may thus provide a model system of the impacts that alien species may cause in the mainland tropics in the future.

Outline of the thesis

There is a severe lack of empirical studies on plant invasions in the tropics from outside Hawaii (cf. Fine 2002). In this thesis, the case of the granitic Seychelles is used to study aspects of the interaction of invasive woody species with habitat characteristics to improve the understanding and predictions of woody plant invasions and their impacts in tropical forests. Two chapters (2, 3) investigate the impact of invasive species on soil factors, and one chapter (4) discusses the role of invasive woody species for seed dispersal by frugivorous birds. Thus these three studies address critical aspects of the two sets of factors often invoked to explain plant invasions, namely habitat invasibility and propagule pressure (the number of seeds or other propagules arriving at a site) (Lonsdale 1999, Kueffer et al. 2003).

In chapter 1 *Woody plant invasions on the granitic islands of the Seychelles* I describe the context of woody plant invasions on the oceanic islands of the granitic Seychelles. The main objective is to provide the background information necessary for the generalisation of the results gained in Seychelles to other ecosystems, and for their interpretation in terms of ecosystem and invasive plants management in the Seychelles.

In chapter 2 *Impacts of invasive trees on litter decomposition in phosphorus-poor tropical forests in the Seychelles* I compare leaf litter properties and decomposability of the six most abundant native and invasive woody species in upland habitats in Seychelles. I further discuss differences in the soil nutrient availability between stands of an N-fixing invasive, a non-fixing invasive and a native species. The objective of this study was to investigate if invasive species influence nutrient cycling through differences in litter decomposition rates in a very infertile ecosystem.

In chapter 3 *Strong belowground root competition shapes tree regeneration in invasive* Cinnamomum verum *forests* I use root trenching experiments to investigate the impact of root competition on tree regeneration in forests dominated by *Cinnamomum verum* (Cinnamon). The aim of this project was to develop a mechanistic understanding of the impacts of a dominant invasive tree species on native species diversity through resource competition.

In chapter 4 *The role of invasive woody plants in plant-frugivore interactions in the Seychelles* I compare the characteristics of fleshy fruits of native and invasive woody species. The aim of this study was to test the hypothesis that invasive species produce fruits of higher quality than native species, and to predict the possible consequences for the efficiency of the dispersal of native and invasive plants by fruit-eating birds.

In chapter 5 *Integrative ecological research: Case-specific validation of ecological knowledge for environmental problem solving* I reflect on the context in which this thesis was conducted.

The thesis formed part of a collaboration between the Geobotanical Institute and the Seychelles Ministry of Environment and Natural Resources (MENR), i.e. it was developed in constant collaboration with nature conservation practitioners. Based on these experiences, I intend to identify boundary conditions and research practices that enhance the relevance of ecological research for environmental management, and I present a research strategy for ecology that I call 'integrative ecological research'.

In *General conclusions and management implications* I synthesize the results of the thesis in two ways. First, I outline the relevance of the results for a general understanding of plant invasions and the use of the Seychelles as a model system for invasion biology in future research. Second, I outline the implications of my study for habitat rehabilitation and invasive species management in Seychelles.

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Chapter 1

Woody plant invasions on the granitic islands of the Seychelles: Background

Introduction

This chapter provides background information on the study system and is based on a review of literature and expert knowledge on woody invasive species and habitat rehabilitation on the oceanic islands of the Western Indian Ocean (Seychelles, Comoros Archipelago, Mascarenes) (Kueffer and Lavergne 2004, Kueffer and Mauremootoo 2004, Kueffer and Vos 2004, Kueffer et al. 2004a, 2004b, Vos 2004). The work was carried out within the scope of this thesis and funded by the Forestry Department of the Food and Agriculture Organization of the United Nations (FAO).

Geography

The Republic of Seychelles is formed by two types of oceanic islands, c. 70 coralline (or 'outer') and 40 granitic (or 'inner') islands, scattered over an area of 1.3 Mio km^2 of ocean (4°-10° S, 45°-56° E) (Fig. 1a). The granitic Seychelles (4°-5° S, 55°-56° E) consist of a group of c. 40 islands of a total land area of c. 235 km^2 (Fig. 1b). They are very isolated from continents, lying nearly 1600 km from the eastern coast of Africa, 930 km from Madagascar and 1700 km from India.

Mahé is the largest island, comprising an area of 155 km^2 or two thirds of the total land area of the granitic islands, and rising to 914 m asl. at its highest point (Morne Seychellois) (Fig. 1c). The other main islands are Praslin (28 km^2, 370 m asl.), Silhouette (20 km^2, 750 m asl.), and La Digue (10 km^2, 330 m asl.). A further six islands are between 100 and 300 ha in size, and the remaining c. 30 islands range from 100 to < 1 ha. The nearest distances between the islands are between 1 and 50 km. During glacial periods, the last time 10'000 years ago, most of the land between and around the islands (bank of Seychelles) was free of water, i.e. the granitic Seychelles formed a single landmass of several 10'000 km^2 (Cazes-Duvat and Robert 2001).

Biogeography

The granitic islands of the Seychelles are of continental origin, i.e. they formed part of the ancient Gondwana supercontinent (South America, Africa, Antarctica, Madagascar, India, Australasia). Some 130 Mio years ago Madagascar, India and the granitic Seychelles broke away from Africa as a single unit. India and Seychelles separated from Madagascar c. 85 Mio years ago, and c. 65 Mio years ago also India and Seychelles broke apart (Briggs 2003).

The Gondwanan origin of the granitic Seychelles has two important implications. First, in contrast to the comparatively young volcanic or coralline rocks of other oceanic islands, the granitic Seychelles are formed by ancient, metamorphic bedrock (several 100 Mio year old

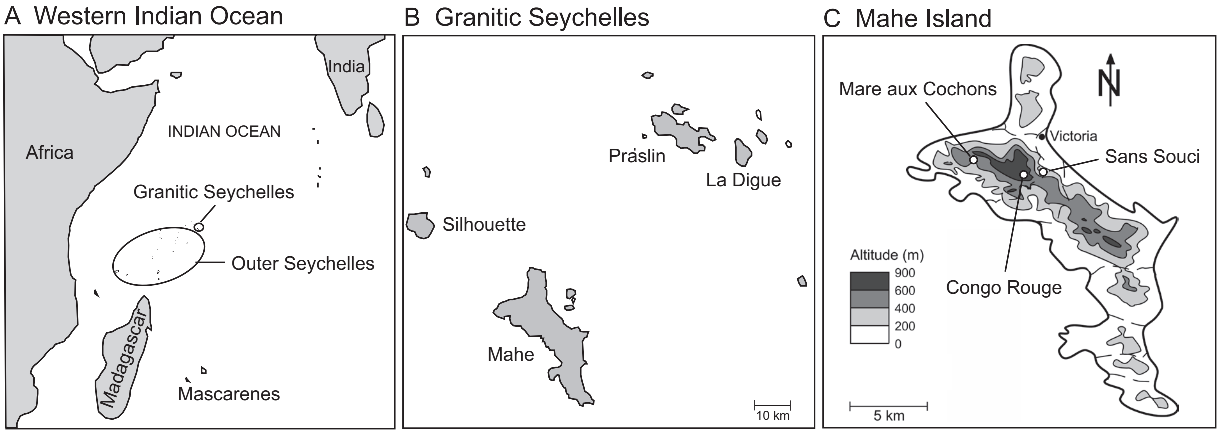

Fig. 1 The geography of the Seychelles. **A.** The territory of the republic of Seychelles in the Western Indian Ocean with the two principal island groups: the outer, coralline and the inner, granitic islands. **B.** The granitic Seychelles with the four principal islands Mahé, Praslin, Silhouette and La Digue. **C.** The largest island Mahé, where the study was carried out, with the capital of Seychelles Victoria, the two main field sites Mare aux Cochons and Congo Rouge, and the forestry station in Sans Souci, where the greenhouse and bird captivity experiments were performed (Figure: E. Schumacher).

granite) (Stoddart 1984). Only Silhouette and North island are of younger geologic origin, consisting of c. 60 Mio year old synite (Stoddart 1984).

Second, the species of the Seychelles evolved from an established fauna and flora. This led to a relatively harmonic flora and fauna, meaning that examples of prolific adaptive radiation are rare, and different guilds and taxonomic families are relatively homogeneously present, in contrast to volcanic oceanic islands (Carlquist 1965, Whittaker 1998, Silvertown 2004). It also explains the presence of species such as amphibians or the large seeded palm *Lodoicea maldivica* (Coco-de-Mer) that are not adapted to long-distance dispersal over the ocean. As a result of the former connection to both Africa-Madagacar and Asia the flora and fauna includes species of both African and Asian affinity (Stoddart 1984).

Climate

The climate of the Seychelles is equatorial with an annual rainfall of 1600 mm (at sea level on flat islands) to c. 3500 mm (on top of the highest peak, Morne Seychellois). Humidity is uniformly high, and mean temperatures at sea level range from 24°C to 30°C. The prevailing winds bring the wet northwest monsoon from December to March and the drier southeast monsoon from May to October (Stoddart 1984, Cazes-Duvat and Robert 2001).

History of anthropogenic land use and species introductions

Four main periods of human land use in the Seychelles can be distinguished (compare Lionnet 1961, Sauer 1967, Stoddart 1984):

- Period 1: early colonization (first permanent settlements, subsistence agriculture, c. 1750–1800);
- Period 2: colonial exploitation (rise of export agriculture, deforestation, species extinctions, c.1800–1900);
- Period 3: colonial administration (independent crown colony, reforestation, cinnamon industry, c. 1900-1970)
- Period 4: post-colonial era (independence, reorientation from primary to tertiary sector, rise of nature conservation; c. 1970 to present).

Period 1 (1750-1800)

The Seychelles were uninhabited before humans first settled between 1742 and 1770. Seychelles became a French colony until it was turned over to Britain in 1815. The main introductions in the first period were exotic animals (rats, pigs, goats, cattle), some spice and fruit trees (cloves (*Syzygium aromaticum*), nutmeg (*Myristica fragrans*) and cinnamon (*Cinnamomum verum*), rose apple (*Syzygium jambos*)), and crops such as maize, rice, and root crops. Only cinnamon, rose apple and rats became major invasive species; while there are no feral pigs and goats, that are together with feral deer and monkey often important invasive species on oceanic islands. For some of the possibly early introductions the status (native or alien) is not clarified (e.g. *Casuarina equisetifolia, Cocos nucifera*). The mangroves and lowland forest were mostly cleared in this period. By 1810, 3’500 people lived on the Seychelles which managed some 1000 ha as farmland.

Period 2 (1800-1900)

In the second period large-scale agriculture for export developed. The first important cash crop was cotton (*Gossypium* spp.) that was followed by coconut (*Cocos nucifera*) by the middle of the 19th century. Other crops, such as sugar cane (*Saccharum officinarum*), coffee (*Coffea* spp.), cloves, vanilla (*Vanilla planifolia*), or cacao (*Theobroma cacao*), were respectively produced for a few decades depending on the demand on the world market. The inland forest was cleared for shipbuilding and agriculture. As early as in the 1820s, most of Mahé was cleared of its original forest. By the 1870s, the native vegetation remained only in the form of small patches on hill tops. The intensive anthropogenic land use and hunting during the 19th century led to the extinction of several species, among them a giant tortoise, a crocodile, a white-eye (*Zosterops* sp.), a parakeet (*Psittacula* sp.) and c. eight plant species (Carlstroem 1996). By 1900, 20’000 people lived in the Seychelles.

Period 3 (1900-1970)

Most of the agricultural products of the 19th century lost their importance for the economy of the Seychelles early in the 20th century; an exception was coconut, though the marketed product shifted from oil and nuts to copra (dried coconut kernel). The independence from Maritius in 1903, which occurred when Seychelles gained the status of a British Crown Colony, increased the presence of British administrators and advisors in Seychelles and had an important influence on land management. For instance, throughout the 20th century alien tree species were planted for reforestation and timber production based on the consultancy of colonial advisors. Commonly used species were legume species such as *Adenanthera pavonina, Falcataria moluccana,* and *Pterocarpus indicus,* or *Eucalyptus robusta* (*Myrtaceae*)*, Tabebuia pallida (Bignoniaceae), Sandoricum koetjape (Meliaceae)*, and *Swietenia macrophylla (Meliaceae)*; and some coastal native species such as *Calophyllum inophyllum (Guttiferae)* or *Heritiera littoralis (Sterculiaceae)*. The most important change in land use practices, however, was the rise of the cinnamon industry.

The history of cinnamon in Seychelles is a curious one, as the plant was introduced deliberately at an early stage, but exploitation was long delayed and then involved feral rather than cultivated stands. By the late 19th century, cinnamon commonly dominated the secondary vegetation. A small amount of the cinnamon products had been exported in the early 19th century, and a small factory was distilling cinnamon oil before 1900. However, the cinnamon cultivar on Mahé was believed to be of inferior quality and was consequently almost not exploited until 1907.

After 1908, cinnamon became the main export after copra (Fig. 2). With the beginning of the cinnamon industry, an intensive and extraordinarily rapid second phase of forest destruction began. Cinnamon was cropped for its bark and leaves and the other woody plants were felled to provide firewood to operate the distilleries. An urgent need for reforestation was noted as early as 1910. After 1915, because shoot regrowth was too slow to yield sufficient bark, exploitation shifted by necessity to distilling leaf oil. As the mountain areas were deforested, the distilleries became concentrated along the coast where there was abundant coconut trash for fuel.

Cinnamon was mainly cropped on Mahé and to a lesser degree on Silhouette (where the topography was more difficult, and the secondary forests where dominated by *Adenanthera pavonina* rather than cinnamon, Vesey-Fitzgerald 1940) and on Praslin and La Digue (where the climate was too dry for an optimal yield). The average annual yield in the Seychelles in the

1960s was c. 13 litres cinnamon leaf oil per hectare. Hence, when annual leaf oil production of the Seychelles peaked at 110 tons during the middle of the twentieth century, there must have been over 80 km^2 of forest under cultivation (see also Lionnet 1961).

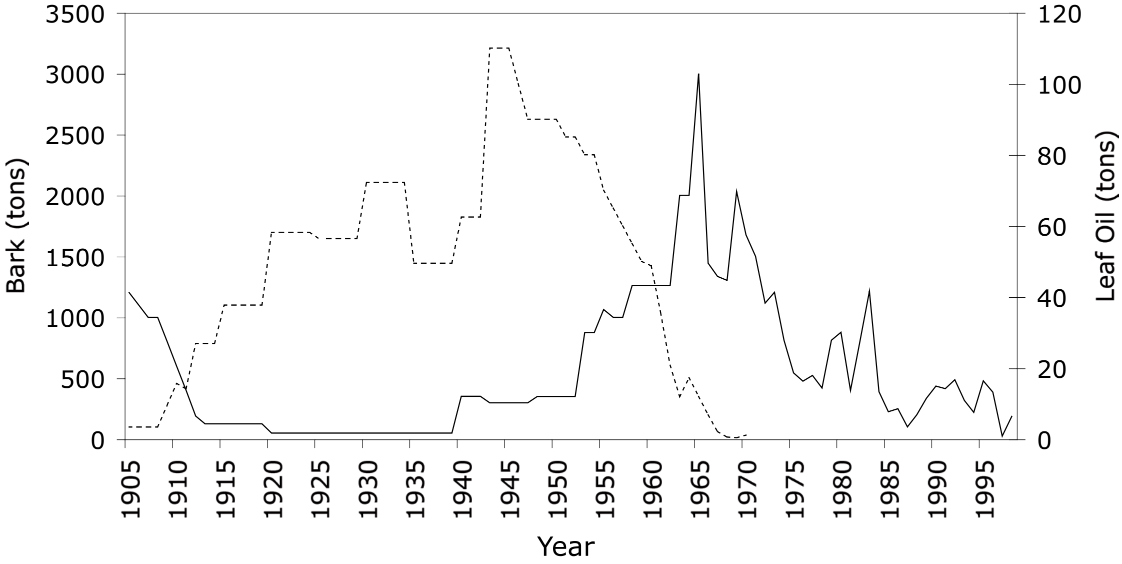

Fig. 2 The cinnamon (*Cinnamomum verum*) oil (dashed line) and bark (full line) production in the granitic Seychelles during the 20th century (data estimated by S. Zemp based on Lionnet (1961), Stoddart (1984), and annual reports of the Seychelles Department of Agriculture and the Seychelles Bureau of Information and Statistics).

Period 4 (1970-)

The end of the cinnamon industry coincided with the opening of the international airport in 1971 and the subsequent development of the tourist industry; this was strongly promoted by the Seychelles government after independence in 1976. In parallel to the reorientation of the economy from the primary to tertiary sector, nature conservation rapidly increased in importance. A nature conservation white paper to the Seychelles government in 1971 laid the foundation for the establishment of the national parks on Mahé (Morne Sechellois National Park, 3090 ha) and Praslin (Praslin National Park, 330 ha), and in 1983 the Vallee de Mai (20 ha, Praslin) was declared a UNESCO World Heritage Site.

Today, fisheries and tourism each contributes c. 50% of the foreign exchange income, while the cinnamon industry no longer plays an important part in the Seychelles economy (in recent years annual production of Seychelles cinnamon bark was only 200-300 tons). Despite the rapid population growth (some 81 000 inhabitants in 2002) and housing development, about 70% of the total land area is still covered by forest, mostly secondary, and only some 400 ha plantation forest remain.

Invasions by woody plant species

Vegetation types and habitat invasibility

The present vegetation of the Seychelles can be classified into six main vegetation types: beach fringe and coastal vegetation (including mangroves), lowland forest, mid-altitude forest, palm forest, inselberg vegetation, and montane forest (adapted from Stoddart 1984, Carlstroem 1996, Fleischmann et al. 2003).

The coastal vegetation in the Seychelles is mostly composed of indigenous (native but not endemic) species common to the shores of many tropical oceanic islands such as *Callophyllum inophyllum, Cordia subcordata, Hibiscus tiliaceus, Pisonia grandis, Scaevola sericea* or *Terminalia catappa*; but only two endemic species (*Allophyllus sechellensis* (*Sapindaceae*) and *Pandanus balfourii* (*Pandanaceae*)). *Cocos nucifera* and *Casuarina equisetifolia* are sometimes interpreted as invasive species of this habitat. The mangroves are composed of eight indigenous trees. There are no relevant invasive woody species in this habitat. Most of the coastal plateau consists of housing development areas, with ruderal sites heavily invaded by typical pantropical invasive species; particularly *Lantana camara, Leucaena leucocephala* and *Tabebuia pallida*.

The lowland forests (at c. 50 to 300 m asl.) are mostly abandoned timber plantations, where c. 90% of all woody species are non-native, e.g. *Adenanthera pavonina, Artocarpus heterophyllus, Cinnamomum verum, Falcataria moluccana* or *Sandoricum koetjape*, with a few colonizing endemic palms in the understorey.

Mid-altitude forests (at c. 300 to 650 m asl.) are typically dominated by *Cinnamomum verum* (80-90% of the adult layer) (Fleischmann 1997a, and C. Kueffer, unpublished data), intermixed with patches of the invasive *Pentadesma butyracea* and *Syzygium jambos,* and the native *Pandanus hornei* and *Northea hornei*.

Palm forests occur in mid-altitude and are characterised by a canopy dominated by endemic palm species (*Deckenia nobilis, Phoenicophorium borsigianum, Roscheria melanochaetes, Verschaffeltia splendida,* plus *Lodoicea maldivica* in some forests on Praslin). Palm forests are more common on Praslin, and small remnants can usually be found along rivers in the lowland. They are mainly invaded by *Cinnamomum verum* and *Psidium cattleianum*, but to a lesser degree than broadleaf mid-altitude forests, i.e. 10-40% of the adult layer (Fleischmann 1997a, Fleischmann et al. 2005).

Inselbergs are more or less extensive granite rock outcrops that are covered by a patchy and stunted vegetation. Inselbergs are the most resistant habitat to invasions (2-10% of the adult layer), and are invaded mainly by *Alstonia macrophylla, Cinnamomum verum*, and *Psidium cattleianum* (Fleischmann et al. 1996).

Montane cloud forests (between c. 650 and 900 m asl.) are regularly covered in clouds, and are rich in mosses, lichens, ferns (including a tree fern species) and epiphytic orchids. They are mainly invaded by *Cinnamomum verum* and *Psidium cattleianum* (5-40% of the adult layer) (Fleischmann 1997a, and C. Kueffer, unpublished data).

Generally, the less anthropogenically disturbed habitats such as palm forests, montane forests and inselberg vegetation are less invaded. In the palm and montane forests lower light availability and a thicker litter layer may reduce invasibility while on inselbergs the harsher environmental conditions (dryness, shallow soils, sun and wind exposed) certainly play a role.

Species

In all, c. 370 woody plant species have been reported from the granitic islands (Robertson 1989, Friedmann 1994). Of these, about 100 are native (c. 50% of which are endemic) and 270 (about 75% of the total species) are introduced. Nine woody species are particularly invasive in inland habitats (Table 1). All except three species were introduced in the 20th century, three of them in the last few decades. Many of these species show adaptations to infertile soils or shade, conditions typical for inland habitats in the granitic Seychelles (Table 2). In contrast, a further 17 invasive woody species are mainly invasive in coastal or lowland habitats and are of less importance in inland habitats, or are very recent introductions (Table 3). The small proportion of species from the total alien species pool that became invasive in inland habitats indicates that these habitats exhibit a strong resistance against the invasion of most alien species, possibly through their very infertile soils.

Tree and shrub species are responsible for the bulk of plant invasions. However, recently invasions by some creepers (e.g. *Merremia peltata, Thunbergia grandiflora, Philodendron* spp., *Quisqualis indica*) and herbs (e.g. *Dieffenbachia seguine, Elettaria cardamomum*) have increased in importance.

Environmental impacts

Little is known about environmental impacts of woody invasive species in the granitic Seychelles, and there has been no significant research on this topic.

However, it seems clear that most surviving native animals have persisted for at least 150 years in forests mainly dominated by alien species. This suggests that alien plant species provide for these animals the habitat and food resources formerly provided by the native vegetation. For instance, we may suppose that the rapid colonization of deforested land by invasive species such as cinnamon was critical in maintaining suitable habitat conditions for many animals - for example, through accumulations of moist leaf litter or rotten logs for endemic amphibians, caecilians, insects or snails. The restoration of a closed canopy may also have played a role for the survival of native plants. Vesey-Fitzgerald (1940) observed that endemic trees showed higher mortality where the canopy was destructed.

Some native species depend on tall and/or old native trees that disappeared because of the deforestation. Nests of the rare endemic Seychelles Scops owl (*Otus insularis*) have been found only in cavities of old, large individuals of the endemic *Dillenia ferruginea* and the alien *Pterocarpus indicus* (Fanchette et al. 2000, Currie 2002b), suggesting the importance of old trees, whether endemic or alien, for this critically endangered bird. Or, the endemic Seychelles fruit bat (*Pteropus seychellensis* subsp. *seychellensis*) roosts in tall alien trees such as *Falcataria moluccana* and *Casuarina equisetifolia* (Stoddart 1984). In the case of slow-growing late-successional endemic species it may take up to a century for large, old adult trees to form.

Seeds or fruits of alien plant species probably make up an important portion of the diet of all native granivores, omnivores, and frugivores (Stoddart 1984, Skerrett et al. 2001). Also, some endemic insects are known to feed on alien species (Matyot 1998, 2004).

However, in coastal areas, native invertebrate diversity and abundance are higher in native than alien dominated vegetation and on native tree species (Rocamora and François 2000, Currie 2002a, Hill 2002); and native vegetation seems to be necessary for the survival of most native insectivorous bird species, e.g. for *Acrocephalus sechellensis, Copsychus sechellarum,* or *Terpsiphone corvina* (Komdeur 1996, Currie 2002a, Currie et al. 2003, Millett et al. 2004, Komdeur and Pels 2005).

Recognition of the problem of plant invasions

The widespread occurrence of alien species in the Seychelles was noted already during the 19th century (e.g. Baker 1877). However, the need to take active measures against invasive plants was not recognized before the early 1990s (but see Diels 1905, Penny 1974). The reference book on the ecology of the Seychelles, published in 1984, includes an extensive discussion of the introduction pathways and presence of naturalized alien plants, but invasive species were not covered even in the chapter on the impact of man (Stoddart 1984). Similarly, in a book on the plants of the Seychelles published in 1986 and intended for a general audience, Friedmann included a chapter dedicated to the beauty of alien species but did not address the invasive species problem (Friedmann 1986).

By the 1990s the problem of invasive plants had been recognized as a serious issue for nature conservation. For instance, the problem is addressed in the first Environmental Management Plan of the Seychelles (presented in 1990), in the Flora of Seychelles (Friedmann 1994), and in a report to the Seychelles government on the conservation of the threatened flora (Carlstroem

1996). The distribution of invasive species was documented in a quantitative manner (Gerlach 1993, Fleischmann et al. 1996, Fleischmann 1997a), and options for the management of invasive species were identified (Fleischmann 1997b, 1999, Dogley 2004).

Today, the invasive species issue is widely recognized by conservationists, the government and the public. For instance, in 2003 a regional workshop on invasive species management was held in Seychelles (Mauremootoo 2003), and the Seychelles' National Strategy for Plant Conservation lists invasive species management as one of its 14 main targets (Beaver and Kueffer 2005).

Table 1 Taxonomy, origin and invasiveness of the nine main woody invasive species in semi-natural to natural inland habitats of the granitic Seychelles. The date of introduction refers to the earliest known occurrence of the species in the Seychelles (Sauer 1967, Robertson 1989, Friedmann 1994). C: montane cloud forest, I: Inselberg, M: mid-altitude forest, P: palm forest.

Species	Introduction date	Family	Invaded habitats	Native range
Cinnamomum verum	1772	Lauraceae	C, I, M, P	Western Ghats of Sri Lanka & India
*Falcataria moluccana**	1910	Mimosaceae	M	Moluccas & region
Psidium cattleianum	1850	Myrtaceae	C, I, M, P	Tropical America
Syzygium jambos	1787	Myrtaceae	C, M	SE Asia
Alstonia macrophylla	1950-1960s	Apocynaceae	I, M, P	SE Asia
Pentadesma butyracea	1910	Guttiferae	M	Africa
Chrysobalanus icaco	1910	Chrysobalanaceae	I, M	Tropical America
Clidemia hirta	1987 (Silhouette) 1990s (Mahé)	Melastomataceae	C, M	Tropical America
Dillenia suffruticosa	1960	Dillenaceae	M	SE Asia

* *Paraserianthes falcataria*

Table 2 Characteristics of the main invasive woody species (shade tolerance, adaptation to infertile soils, and regeneration strategy) compiled from the literature or based on field observations (C. Kueffer).

Species are shade tolerant (ST) or light demanding (LD) .

Species characteristics in relation to growth in infertile soil: AL: aluminum accumulator; AM: arbuscular mycorrhiza; CR: cluster roots; D: known to grow on degraded or infertile soils (outside Seychelles); EC: used for erosion control (in the Seychelles or elsewhere); EM: Ecto-mycorrhiza; N: N-fixing, OAE: Organic anion exudation; PU: efficient P uptake, RM: surface or topsoil root mat / lateral root system.

Regeneration strategies: Ap: apomixis; B: bird-dispersed; JB: juvenile (seedling or sapling) bank; LS: large seeds; SB: seed bank; SR: intensive seed rain; V: vegetative growth or resprouting; W: wind-dispersed.

Species	**Adaption to shade**	**Adaption to infertile soils**	**Regeneration strategy**	**References**
C. verum	ST-LD	AM, D, RM	B, JB, SR, V	Lionnet 1961, Purseglove 1991, Feldmann et al. 1999, pers. obs.
F. moluccana§	LD	AM, CR§§, D, N, OAE, PU, RM	SB, SR, W	Binkley 1997, Otsamo 2000, Miyasaka and Habte 2001, Ryan et al. 2001, Adams et al. 2002, pers. obs.
P. cattleianum	ST	AM, D, RM	B, SR,V	Gerrish and Mueller-Dombois 1980, Huenneke and Vitousek 1990, Koske et al. 1992, Pattison et al. 1998, Weber 2003
S. jambos	ST	D, RM	Ap, JB, LS, V	Lughadha and Proenca 1996, Horvitz et al. 1998, Lugo 2004, P. Binggeli, pers. comm.°
A. macrophylla	LD	D, EC, RM	SB, SR, W	Horvitz et al. 1998, Nilaweera and Nutalaya 1999, Ingle 2003, pers. obs.
P. butyracea	ST	RM	JB, LS, V	pers. obs., W. André, pers. comm.
C. icaco	LD-(ST)	D, EC	LS	Prance and White 1988, pers. obs.
C. hirta	LD-ST	AM, D	B, SB, SR	Gerrish and Mueller-Dombois 1980, Koske et al. 1992, DeWalt 2003
D. suffruticosa	LD	D	B	Sim et al. 1992, Tan et al. 1994, Lim and Turner 1996, Turner 2001, Davies and Semui 2006
*Acacia mangium**	LD	AM, D, EC, EM, N	SB, W	Hopkins and Graham 1983, Vadez et al. 1995, Ribet and Drevon 1996, Miyasaka and Habte 2001, Duponnois et al. 2002
Melastoma malabathricum+	LD	AL, AM, D, OAE	B	Burslem et al. 1994, Tan et al. 1994, Turner et al. 1995, Turner 2001, Watanabe and Osaki 2002, Davies and Semui 2006

*recent introduction (see Table 3), + status (native, invasive) uncertain

° see also http://members.lycos.co.uk/WoodyPlantEcology/pitcairn/syzygium.htm

§ *Paraserianthes falcataria*; §§ *Paraserianthes lophanta*

Table 3 The additional main woody invasive species in the granitic Seychelles, that occur mainly in coastal and lowland human-dominated to semi-natural areas (L), are of less importance in inland habitats (R), or are recent introductions (N).

Species	Family	Species	Family	Species	Family
Acacia mangium^{N}	Mimosaceae	*Casuarina equisetifolia*^{L}	Casuarinaceae	*Ochna ciliata*^{R}	Ochnaceae
Adenanthera pavonina^{L}	Mimosaceae	*Hevea brasiliensis*^{R}	Euphorbiaceae	*Psidium guajava*^{L}	Myrtaceae
Ardisia crenata^{R}	Myrsinaceae	*Lantana camara*^{L}	Verbenaceae	*Sandoricum koetjape*^{L}	Meliaceae
Ardisia elliptica^{R}	Myrsinaceae	*Leucaena leucocephala*^{L}	Papilionaceae	*Syzygium aromaticum*^{R}	Myrtaceae
Anacardium occidentale^{R}	Anacardiaceae	*Litsea glutinosa*^{L}	Lauraceae	*Tabebuia pallida*^{L}	Bignoniaceae
Carica papaya^{L}	Caricaceae	*Memecylon caeruleum*^{R}	Melastomataceae		

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Chapter 2

Impacts of invasive trees on litter decomposition in phosphorus-poor tropical forests in the Seychelles

Abstract

We studied how woody invasive species influence the turnover of nutrients in very phosphorus-poor tropical forests in the Seychelles**.** We compared leaf litter characteristics of six native and six invasive woody species, and measured decomposition rates of these litter types in stands dominated by *Cinnamomum verum* (the commonest alien tree), *Falcataria moluccana* (an introduced N-fixing tree) and *Northea hornei* (an endemic tree). We also measured nutrient availability in the soil of these stands. To determine whether decomposition was nutrient-limited, we studied the decomposition of cellulose and *C. verum* and *N. hornei* litter in a microcosm experiment with different nutrient treatments.

There were marked differences between the average leaf litter properties of native and invasive species: litter of invasive species had higher specific leaf areas, higher N and P concentrations and lower polyphenol concentrations. The litters of invasive species also decomposed more rapidly than those of native species. These differences in average values were mainly due to the strongly contrasting litter properties of the dominant endemic tree, *N. hornei,* and two fast-growing invasive species; for most other species the differences associated with provenance were small, and the litter properties of two pantropical invaders *Psidium cattleianum* and *Syzygium jambos* were similar to those of most native species.

Despite considerable differences in litter properties and in the quantities of N and P in the falling litter, we found only small differences in soil nutrient availability among stands of three species.

The results suggest that, by producing readily decomposable litter, some invasive species have the potential to alter rates of nutrient turnover. However, because the root systems of species invasive on infertile soils are particularly effective at capturing nutrients, faster decomposition does not necessarily lead to larger soil nutrient pools; thus, these trees may have less impact on nutrient cycling than species invading more nutrient-rich tropical forests.

Introduction

Plant invasions can alter the functioning of an ecosystem dramatically, for example through increasing fire frequency, changing hydrology or accelerating the turnover of nutrients (e.g. Mack et al. 2000, Dukes and Mooney 2004). Although most of the examples are anecdotal, it seems clear that the way an invasive species affects ecosystem processes depends on the properties of both the invasive species and the system that is invaded (Stock et al. 1995, Ehrenfeld 2003, Chapuis-Lardy et al. 2006). More empirical studies and an improved conceptual framework will be needed to predict how particular invasive species are likely to affect a particular ecosystem (e.g. Parker et al. 1999, Levine et al. 2003).

The evidence relating to impacts of non-native species on nutrient turnover remains sketchy and inconsistent (Ehrenfeld 2003, Levine et al. 2003). Many invasive plants grow faster and accumulate more biomass than native plants in the same ecosystems; their leaves often have a higher specific leaf area (Daehler 2003), contain higher concentrations of nutrients (Ehrenfeld 2003), and decompose more rapidly (e.g. Allison and Vitousek 2004, Rothstein et al. 2004). However, for each of these generalisations there are exceptions (see Ehrenfeld 2003).

The plant invaders that most consistently influence ecosystem processes are those that fix atmospheric nitrogen, thereby increasing both the availability of N in the soil and its turnover in the ecosystem (e.g. Vitousek and Walker 1989, Witkowski 1991, Hughes and Denslow 2005). For other functional groups various outcomes have been reported, with particular species increasing or decreasing the availability of N, or leaving it unaffected (Ehrenfeld 2003). Much less is known about impacts on other nutrients, though some invasive plants have been shown to increase availabilities of potassium and phosphorus (Ehrenfeld 2003, Vanderhoeven et al. 2005, Chapuis-Lardy et al. 2006).

The capacity of an invasive species to alter nutrient cycling is likely to be strongly influenced by the availability of that nutrient in the soil. Plant species adapted to nutrient-poor conditions typically grow slowly and use nutrients efficiently; their leaves tend to be long-lived, unpalatable to herbivores, and slow to decompose (Hobbie 1992, Berendse 1998, Aerts and Chapin III 2000). Whereas species invading nutrient rich ecosystems may require properties that cause them to accelerate nutrient cycling, species invading nutrient-poor ecosystems may require the opposite traits, causing them to slow down nutrient cycling; and whereas alien N-fixing plants can dramatically alter P- rich ecosystems, they may have much less impact where P is limiting (compare Vitousek et al. 2002). However, the evidence for such contrasts is limited because most plant invasions have been studied in ecosystems that are either naturally rich in nutrients or have been enriched due to human activities (Lake and Leishman 2004).

The aim of this study was to investigate how invasive trees influence nutrient cycling in a nutrient-poor tropical forest ecosystem. We predicted that in a forest where P availability is extremely low, woody invaders would have a different impact on nutrient cycling from that in younger, more P-rich ecosystems such as those studied on the volcanic islands of Hawai’i (Rothstein et al. 2004, Hughes and Denslow 2005). Our study was carried out on the island of Mahé in the Indian Ocean; this island - the largest in the Seychelles group - is formed of ancient granite that has never been covered by the ocean, so that soils have been continuously weathered for over 500 Mio years (Braithwaite 1984). Based on available data (Varley 1971, Dobrovol’skiy 1986) and on models of long-term soil development (Walker and Syers 1976, Vitousek 2004, Wardle et al. 2004), we expected the soils to be very infertile and to contain extremely low levels of available phosphorus.

The specific questions addressed in this study are: (1) do invasive species produce litter that is more nutrient-rich and labile than that of native species?; (2) does the litter of invasive species decompose faster than that of native species?; and (3) is the soil in stands of invasive species more fertile and/or less nutrient-limited than in stands of native species? To answer the first two questions, we measured various properties of the litter of six native and six invasive tree species and studied the decomposition of the litter in the field and in microcosms. To answer the third question we compared litter production and soil nutrient conditions in stands of two invasive and one native species.

Methods

Study sites

The study was carried out at two sites in the Morne Seychellois National Park on the island of Mahé (154 km^2). The mid-altitude site (430 m asl.) was in an upland valley at Mare aux Cochons (MC). The soils here are ferrasols (FAO/ISRIC/ISSS 1998) with sandy A horizon (89% sand, 5% silt, 6% clay) and loamy B horizon (60% sand, 20% silt, 20% clay). The area was deforested in the early 20th century and used until the 1970s for the production of *Cinnamomum verum* (Cinnamon) bark and leaf oil; since then, a secondary forest vegetation 7-12 m tall has developed. In our study site, there were six invasive and nine native woody dicotyledonous species, as well as various native palms and pandans that accounted for c. 3% of canopy trees. 92 % of the dicotyledonous trees > 10 cm girth were of invasive species, mostly *C. verum*, while about half the native trees were *Northea hornei*. The basal stem area (bsa) was 33.7 m^2 ha^{-1}.

The montane site was situated on a small plateau above Mare aux Cochons known as Congo Rouge (CR; 730 m asl.). The soils are ferrasols tending towards pseudo-podzols (FAO/ISRIC/ISSS 1998): below the organic O horizon is an eluvial E-horizon composed of coarse quartz-sand (96% sand, 4% silt, 0% clay) and underlain at a depth of c. 70 cm by the parental granite. Although the vegetation is now a dense montane cloud forest, most of the area was probably heavily cut at the end of the 19th century. The height of the canopy is 10–12 m, and the density and basal area of woody plants are higher than at MC (bsa: 45.5 m^2 ha^{-1}). About 70% of these plants are invasive species, of which two thirds are *C. verum* and one third *Psidium cattleianum*. The site has 11 native woody species, of which *N. hornei* makes up around two thirds of all individuals; in addition there are patches of native palms and pandans that account for c. 20% of all canopy trees.

Rainfall (tipping bucket rain gauge), air temperature and humidity (HOBO Pro RH/Temp sensor) were measured at both sites over two years. In MC, the mean annual precipitation was c. 3400 mm, with the highest rainfall occurring from November till March. The mean annual air temperature recorded at a height of one metre under a closed canopy was 23°C (daily range in hottest season: 22.5-26°C; seasonal range of mean maximal daily temperature: 23-26°C), and the mean annual air humidity 98% (daily range: 95-100%). At CR, the annual rainfall was c. 3450 mm, mean annual air temperature 22°C, and air humidity was almost constant and close to 100%.

The field studies were conducted in stands dominated by one of three species - *Cinnamomum verum* (CIN)*, Northea hornei* (NOR)*,* and *Falcataria moluccana* (FAL). A stand was defined as an area of at least 10*10 m^2 where the canopy was dominated by one species: FAL stands consisted of one big tree, NOR stands were clumps of 4-6 trees at MC and 10-15 trees at CR, and CIN stands were within extensive areas dominated by *C. verum*. Stands of all three species were available at MC but *F. moluccana* was absent at CR. With three replicates (at least 100 m apart) of each type and site, this yielded a total of 15 stands.

The invasive tree *Cinnamomum verum* Presl (syn. *C. zeylanicum*; true Cinnamon) is the most abundant woody species on most granitic islands of the Seychelles. It grows in all habitats from sea level to the highest inselbergs (exposed rocky outcrops), and has been the dominant canopy species in many upland forests since the early 19th century. The species is a native of lowland, evergreen climax forests of the Western Ghats of India and Sri Lanka where it occurs up to an altitude of 1800 m asl. It forms a small tree 10-15 m tall. The leaves and bark are rich in volatile secondary compounds, especially eugenol and cinnamic aldehyde.

The invasive *Falcataria moluccana* (Miquel) Barneby and Grimes (syn. *Albizia falcataria* (L.)

Fosberg and *Paraserianthes falcataria* (L.) Nielsen) is common in the Seychelles from sea level to mid-altitude forests, especially on deeper soils in valleys. However, it can also grow in poor and degraded soils both in the Seychelles and in other areas. It is native to the Moluccas, New Guinea, New Britain, and the Solomon Islands, but has become a problematic invader in the Seychelles and on many Pacific islands including those of Micronesia, French Polynesia and Hawai'i. It is a fast growing (up to 6 m per year), nitrogen-fixing tree and can attain a height of more than 30 m.

The endemic *Northea hornei* grows from sea level to the highest mountain tops. It is the most common native tree in upland forests, especially in montane cloud forests. It is usually 10-12 m high but can reach 20 m.

Plant species

Six native and six invasive woody species (including the three species already described) were used in the decomposition studies (Table 1). These species are amongst the commonest in the Seychelles, and together account for > 95% of mature trees in most mid-altitude and montane forests (C. Kueffer, unpublished data). The remaining canopy species are mostly various native palms and pandans that were not included in this study. Both the native and invasive groups include a range of ecological types: early successional species that do not regenerate under an undisturbed canopy; widespread species with a broad ecological amplitude and common in both closed canopy forests and in extreme habitats such as inselbergs; and late successional species that occur as the dominant or co-dominant canopy species in closed canopy forests. While the invasive species were mainly present as medium to large trees, the native species were mostly small to medium trees. This bias reflects the vegetation history of the Seychelles: native trees are mainly small because large sized species were heavily exploited in the past, while many invasive woody species were introduced for timber production and therefore large trees (Kueffer and Vos 2004).

Litter quality

To collect freshly fallen leaf litter, nets were set out one metre above the ground at three to five sampling sites per species at MC. The nets were emptied each week from mid-February to mid-March 2004. Six to 15 air-dried subsamples of litter per species (from different sites and sampling dates) were oven-dried at 55°C for 96 h to determine the dry matter content. These samples were ground and analyzed in the laboratory of the Geobotanical Institute, Zurich. Total C and N concentrations were determined using a CNS-2000 analyzer (LECO, St Joseph, MI, USA). Kjeldahl N and P concentrations were determined colorimetrically (after 1 h digestion at 420°C with 98% H_2SO_4 and Merck Kjeltabs) on a flow injection analyzer (FIA, TECATOR, Höganäs, Sweden).

Because extremely low concentrations were recorded in some litter samples, we sent some of the material for analysis in a different laboratory. Litter of four species (3 samples: *N. hornei, C. verum*, 2 samples: *M. eleagni, F. moluccana*) was analysed at the laboratory of the Institute of Landscape Ecology, University of Utrecht, using a different Kjeldahl method (1 h digestion at 200°C and 2 h at 340°C with 98% H_2SO_4 and a $CuSO_4$-$NaSO_4$-Se-catalyst). Potassium (K) content was also measured in these samples. P measurements were in both series partly below detection level in the case of *N. hornei*. These values were set to the lowest measured value for the analyses.

Table 1 Description of the twelve species included in this study. Nomenclature: Friedmann (1994) except *Falcataria moluccana* (*Paraserianthes falcataria* in Friedmann (1994)). The species were grouped into three ecological groups: early successional (ES), ubiquitous (U), and late successional (LS). A small tree has a height of < 10 m, a large tree of > 15 m. Data for leaf size is taken from Friedmann (1994). Date of introduction is adapted from Kueffer and Vos (2004).

Species name	Family	Growth form	Group	Leaf size (mm)	Status	Date of introduction
Alstonia macrophylla	Apocynaceae	Tree	ES	200 x 65	Invasive	c. 1950s
*Cinnamomum verum**	Lauraceae	Tree	U	115 x 60	Invasive	1772
*Falcataria moluccana**	Leguminosae	Large tree	ES	11 x 5 leaflets	Invasive	c. 1910
Pentadesma butyracea	Guttiferae	Tree	LS	170	Invasive	c. 1910
Psidium cattleianum	Myrtaceae	Small tree	U	50 x 28	Invasive	c. 1850
Syzygium jambos	Myrtaceae	Tree	LS	160 x 38	Invasive	1787
Aphloia theiformis$^+$	Flacourtiaceae	Small tree	ES	55 x 23	Native	
Canthium bibracteatum	Rubiaceae	Small tree	ES	60 x 28	Native	
Dillenia ferruginea	Dilleniaceae	Tree	LS	200 x 100	Endemic	
Memecylon eleagni	Melastomataceae	Small tree	U	38 x 17	Endemic	
*Northea hornei**	Sapotaceae	Tree	LS	185 x 70	Endemic	
Timonius sechellensis	Rubiaceae	Small tree	ES	73 x 38	Endemic	

* Species used for the stand comparison; + subsp. *madagascariensis* var. *seychellensis*

Total phenolics were extracted by shaking 50 mg subsamples for 1 h with EtOH 50%. After centrifugation at 8'000 rpm, the concentration of soluble phenolics in the supernatant was determined with the Folin Ciocalteu method, using tannic acid as a standard. Photometric analysis (absorbance at 760 nm) was performed on an Uvi Light XT2 spectrophotometer (Secoman, Ales, France).

The biochemical activity of tannins in the same litter extracts was determined through assays based on the inhibition of the enzyme α-amylase by tannic acids (adapted from Wint, 1983). We mixed 200 μl leaf extract or standard solution (tannic acid, Bender and Hobein, Zurich, Switzerland, in 50% ethanol) with 200 μl enzyme solution (50 mg l^{-1} α-amylase from *Bacillus subtilis*, FLUKA 10069, in H_2O) and waited 10 min (tannin-enzyme reaction) before adding 8 ml of starch solution (1.7 g l^{-1} soluble starch and 2.2 g l^{-1} NaCl in phosphate buffer with pH 6). After a further 20 min (hydrolysis of starch by the amylase) 1 ml of the mixture was added to 4 ml iodine indicator (16 mg I_2 and 0.4 g KI in 400 ml H_2O). The absorbance at 580 nm was proportional to the concentration of starch remaining after hydrolysis, i.e. to the inhibition of a-amylase activity, and therefore proportional to the concentration of tannins in leaf extracts or standard solutions.

Litter from the same collection period was used to determine the specific leaf litter area (SLA_{litter}) by image analysis. Entire leaves were air-dried, placed under a glass plate with graph paper as a background, and photographed using a digital camera (Nikon Coolpix 995, 3.34 Megapixels). Dry weight was determined by oven-drying (55°C, 96 h) and then weighing. The images were analyzed for leaf area using Adobe Photoshop™ 7.0.

Litter decomposition: field experiment

This litter decomposition experiment was performed at both the Mare aux Cochons and Congo Rouge sites using litter collected at Mare aux Cochons. Equal amounts of air-dried litter from the different collecting nets were mixed to yield one pooled sample per species. The material was cut into pieces of roughly 200-300 mg and subsamples of 1-1.5 g were packed into 9*9 cm^2 bags made of polyamide net with a 0.4*0.6 mm mesh. Additional incubations using litter-bags with a coarser mesh size of 2*2.5 mm showed that the exclusion of the soil fauna did not affect interspecific or inter-site comparisons. In April 2004, the litter-bags were placed horizontally on the soil under the natural litter layer in the three replicate stands per stand type. There were four replicate litter-bags per species and stand, of which two were collected after 3 months (95 days) and two after 10 months (320 days); means of these two replicates per incubation time were used in data analysis. During the first three months, cellulose (cotton) was also incubated as reference material. The decaying litter was carefully removed from the bags, cleaned of all extraneous material, oven-dried (55°C for 96 h) and then weighed. At the second collection, ten samples were excluded because the litter could not be cleaned satisfactorily.

For three species - *C. verum*, *N. hornei* and *F. moluccana* - N and P contents of litter were determined after 3 and 10 months on the forest floor (three samples per stand type) using the methods already described.

Litter decomposition: microcosm experiment

To test whether litter decomposition was nutrient-limited at our stands, a microcosm experiment was carried out in which the decomposition of cellulose and litter of *C. verum* and *N. hornei* was investigated in soil samples with different nutrient additions. Soil from the top 10 cm was collected from various random points at each of the 15 stands (for MC CIN, organic and mineral soils were mixed at a 1:1 ratio). The bulked soil from each stand was mixed thoroughly, passed through a 4 mm sieve, and used to fill 1-l pots. There were four nutrient treatments: a control with no added nutrients, + nitrogen, + phosphorus, and + complete fertilizer (+All). The fertilizer treatments were achieved by adding the following amounts of nutrients per pot: + N - 313 mg N as NH_4NO_3; + P - 125 mg P as NaH_2PO_4; + All - 3.1 ml of an all-in-one garden fertilizer (Wuxal, Maag Agro, Dielsdorf, Switzerland) supplying 313 mg N, 136 mg P, 165 mg K, and trace amounts of B, Cu, Fe, Mn, Mo, Zn and Vitamin B1. Each treatment was replicated three times for each stand type.

Both litter collected at MC in August 2004 and cotton cloth (cellulose) were used in this experiment. The material was sown into litter bags and each bag was inserted into a small vertical slit in the soil to ensure that there was close contact between the bag and the soil. To estimate nutrient availability, two ion exchange resin bags (see below) were placed in the centre of the pots with the control and +All treatments.

The microcosm experiment was installed in a greenhouse at 250 m asl.; it was started on 16.8.2004 and harvested 80 days later on 5.11.2004. The litter or cellulose was carefully removed from the decomposition bags, cleaned of all extraneous materials, dried at 55°C for 96 h, and weighed to determine mass loss.

Litterfall and soil properties

To measure litterfall, one litter trap (area 1*1 m^2; height 1.5 m) was set up in each of the 15 stands; they were located at random except that they were at least 1.5 m away from the trunk of the nearest adult tree. They were emptied every two weeks for 88 days at MC and 67 days at CR. The standing crop of leaf litter on the forest floor was measured at two random points per stand, using a 0.5*0.5 m^2 wooden frame. The air-dried litter was sorted into four types (*F. moluccana*, *C. verum*, *N. hornei* and others), oven-dried at 70°C for 24 h, and weighed.

Four of the five stand types had relatively uniform soil conditions, with either a continuous O horizon (CR CIN, CR NOR and MC NOR) or no accumulated organic material (MC FAL). However, the soil under MC CIN was variable, and so we sampled separately areas with and without an organic O-horizon. Thus two sub-stand types were recognised: MC CIN-min ("min" for mineral, i.e. A-horizon exposed to the surface by erosion) und MC CIN-org ("org" for organic, i.e. well developed O-horizon).

Two soil cores (depth 10 cm, diameter 7 cm) were taken at random from each stand. A subsample was mixed with two parts rainwater and the pH determined using a portable pH meter (Hanna Instruments HI 98127, pHep). The remaining soil was passed through a 4 mm sieve and oven-dried at 80°C for 48 h. It was stored in paper bags until total C, N and P concentrations could be determined using the methods already described for the litter samples.

Estimates of the availabilities of mineral N and P were obtained using ion exchange resin bags made from polyamide fabric (4*3 cm^2; mesh 60 µm; Sefar, Hausen, Switzerland) filled with 1.7 ± 0.1 g of a mixture of Dowex-1 (nitrate and phosphate exchanger) and Dowex-50 (ammonium exchanger) at a ratio of 1:0.7 (adapted from Güsewell *et al.* 2005). Two bags per stand were placed in vertical slits in the soil at a depth of 5-10 cm. They were removed after 71 days at MC and after 67 days at CR and stored at air temperature in airtight bags for transfer to Switzerland. They were later washed for 10 seconds with deionised water and then extracted during 90 min under constant shaking in 50 ml 0.5N HCl. Subsamples were neutralized with 2N KOH and used to determine NH_4-N and NO_3-N concentrations in a flow injection analyzer (FIA, Tecator, Höganäs, SE), and PO_4-P concentrations as described by Watanabe & Olsen (1965) using a Uvi Light XT2 spectrophotometer. From these nutrient concentrations we calculated the amounts of NO_3-N, NH_4-N, and PO_4-P captured per resin bag, providing a relative measure of soil nutrient availability.

Bioassay

To determine whether the soils of the five stand types differed in fertility and nutrient limitation, a bioassay was carried out using *C. verum* as a phytometer. Seedlings of *C. verum* two months old were planted into pots filled with soil from the five stand types (one pooled sample per stand type, collected as for the microcosm decomposition experiment). Five treatments were applied to each soil with six replicates for the control, +N and +P treatments, and four replicates for the +NP and +All treatments, yielding 26 pots per stand type and 130 pots in total. The pots were placed in a greenhouse (65% of ambient light) at 250 m asl. The position of the pots was randomized weekly during the experiment.

Pots were fertilized weekly with increasing amounts of nutrients according to plant biomass gain (final additions were five times initial additions). Based on the biomass of 6 months old *C. verum* seedlings (3.25 g dry mass, E. Schumacher, unpublished data) and on conversion factors of 40 mg g^{-1} for N and 8 mg g^{-1} for P, a total 140 mg N (as NH_4NO_3) and/or 30 mg P (as NaH_2PO_4) were applied. The +All treatment consisted of 1.4 ml Wuxal containing 140 mg N and 61 mg P per plant (cf. microcosm decomposition experiment).

Plants were watered regularly. After six months (June to November 2004) the height and number of leaves per plant were measured. Plants were then harvested and both the fresh and dry weights recorded (drying at 55°C for 96 h).

Statistical analyses

Litter characteristics were analyzed using an ANOVA with status (invasive, native) as a fixed factor. Species was nested as a fixed factor within status. We defined species as a fixed factor because the twelve species made up more than 95% of the total abundance of woody species in the studied habitats, and were specifically selected according to three ecological groups.

The field decomposition experiment in MC was analysed with status and stand type (MC CIN, MC NOR, MC FAL) as fixed factors. Species was nested as a fixed factor within status. The decomposition experiment in CR was analysed with species (*N. hornei*, *C. verum,* cellulose) and stand type (CR CIN, CR NOR) as fixed factor. Decomposition data after 3 and 10 months were analysed separately. The microcosm decomposition experiment was analysed with species (*N. hornei, C. verum,* cellulose) and stand type (MC CIN, MC NOR, MC FAL, CR CIN, CR NOR) as fixed factors.

The stand comparisons (litterfall, soil chemistry, bioassay) were tested with stand type (MC CIN-min, MC CIN-org, MC NOR, MC FAL, CR CIN, CR NOR) and (for the bioassay) treatment as fixed factors. The two replicate measurements per stand for the soil chemistry analysis were averaged before statistical analysis.

Unless stated otherwise, differences between treatments or stand types were tested with a Tukey test. Data were transformed as necessary to meet the assumptions of ANOVA. Statistical analyses were performed with JMP V5.1 (SAS Institute Inc.).

Results

Litter quality

We found differences between native and invasive species in all of the litter properties measured (Table 2). On average, invasive species had higher concentrations of N and P concentrations, a larger specific leaf litter area, lower C:N and C:P ratios, and lower total phenolics and tannin contents than native species. However, these differences in average values were mainly due to the strong contrast between two early successional invasive species - *A. macrophylla* and *F. moluccana* - and the late successional endemic *N. hornei*. Of the species dominating in the three stand types, *N. hornei* had particularly low N and P concentrations, a low SLA_{litter} and a high tannin content, *C. verum* had a particularly high P concentration and low tannin content, and *F. moluccana* had high concentrations of both N and tannins.

Litter decomposition experiment

In the field experiment, the litter of invasive species decomposed faster than that of native species (Table 3), the mean difference being 32% over the first 3 months, and 18% over 10 months. Litter mass loss after 3 months correlated positively with SLA_{litter} ($r = 0.57$, $P = 0.05$) and negatively with tannin content ($r = -0.73$, $P = 0.007$). Mass loss was best predicted by a multiple regression that included SLA_{litter}, tannin content and C:N ratio (r^2 adj = 0.75, $P = 0.003$) or SLA_{litter}, tannin content and P concentration (r^2 adj = 0.74, $P = 0.003$).

At MC, litter mass loss after 3 months was significantly greater in CIN stands than in the other stands (% mass loss: CIN: 28.4%, FAL: 23.8%, NOR: 24.7%), and the difference between CIN and FAL stands was also significant after 10 months. At CR, *C. verum* litter mass loss after 3 months was faster in CIN than in NOR stands (25.5% and 20.1%, respectively; $P = 0.02$) but the decomposition of *N. hornei* litter was unaffected by stand type.

During decomposition, litter of *N. hornei* immobilized more P and retained more N than litter of *F. moluccana* and *C. verum* (Fig. 1). These results were similar at MC and CR and did not differ among stand types, except for a higher immobilization of P after 10 months in FAL compared with NOR and CIN stands (124% v. 96% and 99%, respectively; $P = 0.001$).

Table 2 Mean concentrations of nitrogen, phosphorus, total phenolics and tannins (as tannic acid equivalents), and mean specific leaf litter areas (SLA) for leaf litter of six native and six invasive woody plant species (with standard errors; N = 6-16, except for polyphenols for which N = 3-6). Results of one-way ANOVA‘s (native vs. invasive species) are also shown: ***, $P < 0.001$; **, $P < 0.01$.

Species	N (mg g^{-1})	P (mg g^{-1})	N:P	C:N	C:P	phenolics (mg g^{-1})	tannins (mg g^{-1})	SLA (cm^2 g^{-1})
Invasive								
Alstonia macrophylla	14.1	0.37	38	35	1324	17	2	155
	(0.9)	(0.01)		(2)	(46)	(4)	(0)	(10)
Cinnamomum verum	9.2	0.46	20	56	1070	45	3	95
	(0.5)	(0.01)		(3)	(29)	(2)	(0)	(3)
Falcataria moluccana	15.1	0.39	39	32	1217	112	83	162
	(0.4)	(0.01)		(1)	(24)	(4)	(7)	(9)
Pentadesma butyracea	11.6	0.40	29	43	1249	26	14	68
	(0.7)	(0.01)		(3)	(44)	(4)	(4)	(3)
Psidium cattleianum	6.7	0.38	18	71	1228	39	12	51
	(0.3)	(0.01)		(4)	(35)	(6)	(10)	(2)
Syzygium jambos	6.7	0.37	18	74	1356	110	17	67
	(0.2)	(0.01)		(2)	(25)	(24)	(4)	(3)
Native								
Aphloia theiformis	7.7	0.36	21	64	1251	75	6	78
	(0.3)	(0.01)		(2)	(29)	(5)	(1)	(2)
Canthium bibracteatum	8.7	0.39	22	55	1236	36	33	65
	(0.3)	(0.01)		(2)	(45)	(13)	(17)	(3)
Dillenia ferruginea	6.4	0.34	19	78	1401	92	99	46
	(0.5)	(0.02)		(6)	(86)	(11)	(2)	(2)
Memecylon eleagni	6.3	0.35	18	70	1369	46	35	70
	(0.1)	(0.02)		(2)	(45)	(5)	(6)	(7)
Northea hornei	5.0	0.22	23	105	2756	129	109	27
	(0.1)	(0.03)		(2)	(267)	(15)	(11)	(1)
Timonius sechellensis	6.8	0.33	20	75	1524	50	37	75
	(0.5)	(0.01)		(6)	(55)	(10)	(14)	(4)
Invasive (mean)	10.6	0.40	27	52	1241	58	22	100
Native (mean)	6.8	0.33	21	74	1590	71	53	60
ANOVA (F, p)	147***	43***	29***	147***	30***	12**	45***	229***

Table 3 Litter decomposition rates from the field decomposition experiment. Data are means from the three stand types in MC. The table shows the k-value from a fitted exponential decay function (Olson 1963), and % litter mass loss after 3 and 10 months. The mean and standard error are given (N = 9), and the F ratio and significance level (***, P < 0.001; **, P < 0.01) from a one-way ANOVA (native vs. invasive species) are indicated in the final two rows.

Species	k (yr^{-1})	3 months (%)	10 months (%)
Invasive			
Alstonia macrophylla	1.63	44.3 (1.5)	67.3 (2.6)
Cinnamomum verum	0.88	25.1 (6.7)	51.4 (2.9)
Falcataria moluccana	1.10	31.4 (1.7)	56.1 (3.0)
Pentadesma butyracea	0.90	24.0 (1.7)	53.2 (4.1)
Psidium cattleianum	0.73	19.7 (1.4)	46.1 (2.9)
Syzygium jambos	0.93	30.4 (1.4)	51.1 (2.1)
Native			
Aphloia theiformis	1.26	34.4 (2.2)	62.5 (2.8)
Canthium bibracteatum	0.69	21.0 (1.2)	43.2 (3.6)
Dillenia ferruginea	0.61	14.9 (1.4)	41.4 (3.7)
Memecylon eleagni	0.63	21.8 (0.6)	39.4 (2.0)
Northea hornei	0.36	10.2 (0.7)	26.8 (1.8)
Timonius sechellensis	1.27	30.3 (2.1)	65.7 (4.1)
Cellulose		17.1 (6.7)	
Invasive (mean)	1.03	29.2	54.7
Native (mean)	0.80	22.1	46.5
Status		106.4***	25.2***
Stand type		13.4***	6.3**

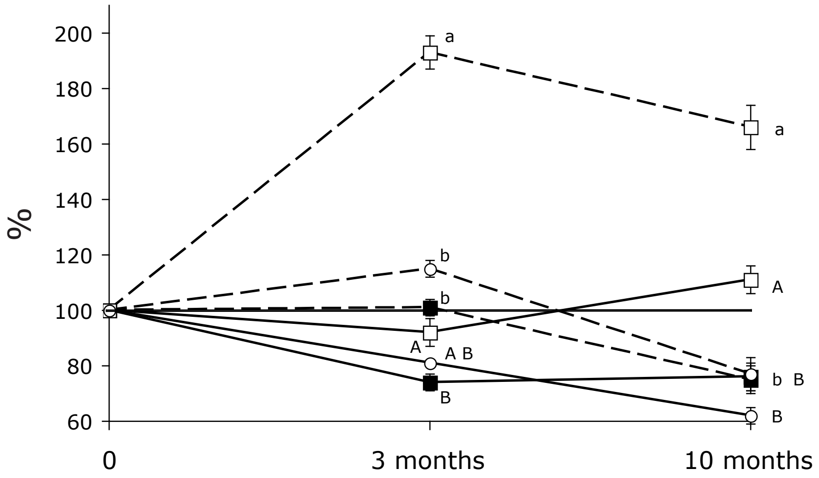

Fig. 1 N and P immobilization during litter decomposition after 3 and 10 months. Immobilization was calculated as the remaining total nutrient amount in the decomposed litter as a percentage of the total nutrient amount in the initial litter mass. Average values for all stands in Mare aux Cochons are given. Solid line for N, dashed line for P. Open quadrats for *Northea hornei*, filled quadrats for *Cinnamomum verum*, and open circles for *Falcataria moluccana* litter. Differences of N (capital letters) and P (lower cases) immobilization between species after 3 and 10 months, respectively, were tested with a Tukey test.

In the microcosm experiment, *C. verum* litter (27.8%) decomposed significantly faster than either *N. hornei* litter (16.2%) or cellulose (17.4%). Cellulose decomposition was accelerated by the +All treatment compared to the control (Fig. 2a), and it was also faster in soil from FAL than in soils from CIN or NOR stands (Fig. 2b). There were no comparable treatment and stand type effects for *N. hornei* and *C. verum* litter.

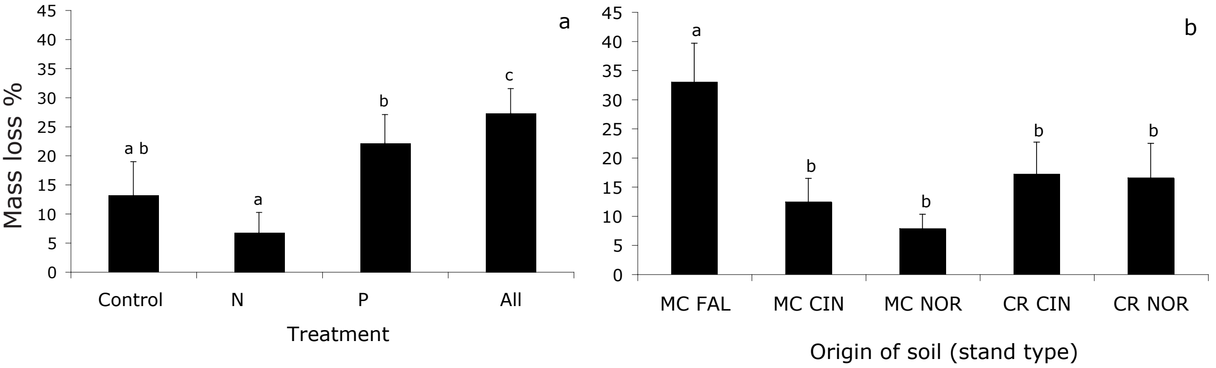

Fig. 2 Decomposition of cellulose in the microcosm experiment: **a)** mean (+ se) mass loss (%) per treatment over all stands in Mare aux Cochons (N = 15) and **b)** means (+ se) per stand type over all treatments (N = 12). Stand type refers to the stand type where the soil was collected, i.e. *Falcataria moluccana* (FAL), *Cinnamomum verum* (CIN) or *Northea hornei* (NOR) in either Mare aux Cochons (MC) or Congo Rouge (CR). Differences were tested with Tukey test (after one-way ANOVA).

Stand comparison

The average litterfall at NOR stands (both sites, and extrapolated to 12 months) was 5.11 t ha^{-1} yr^{-1}, compared to 5.08 t ha^{-1} yr^{-1} at FAL stands and only 2.17 t ha^{-1} yr^{-1} at CIN stands (Table 4). Differences in litterfall between the MC and CR sites (for CIN and NOR stands only) were small and not significant. On average, 20% of the litter collected came from species other than those of the stand.

The litter layer in the various stands appeared very different: in NOR stands it was thick and well developed, while in FAL stands it was very thin and patchy. And these visual impressions are reflected in the data for litter standing crop, which was highest in NOR (mean for both sites 5.32 t ha^{-1}), intermediate in CIN (2.57 t ha^{-1}), and low in FAL (1.64 t ha^{-1}). In FAL two thirds of the litter was from outside the stand, while in the other stands about 20% was allochthonous (Table 4). Litter standing crop in CIN and NOR stands did not significantly between the two study areas. Turnover rates of autochthonous litter (i.e. litterfall/standing crop) were much higher in FAL stands than in CIN and NOR (6.8, 0.9 and 1.0 yr^{-1}, respectively).

Table 4 Litterfall and litter standing crop in three stand types (Cinnamomum verum CIN, Northea hornei NOR, Falcataria moluccana FAL) on two altitudes (mid-altitude Mare Cochons MC, montane Congo Rouge, CR). Data for total mass and % of exogenous litter of total mass is given (mean and se, N = 3). Differences between stand types were tested with Tukey-test.

Site	*Stand type*	*Litterfall*		*Litter standing crop*	
		tha^{-1}yr^{-1}	% exogenous litter	tha^{-1}	% exogenous litter
MC	CIN	2.20 (0.48) a	19.5 *	2.55 (0.39) ab	20.8 +
MC	NOR	5.23 (0.01) b	25.8 †	5.06 (1.16) bc	25.7 †
MC	FAL	5.08 (0.41) b	26.8 †	1.64 (0.28) a	66.5 †
CR	CIN	2.15 (0.28) a	16.3 +	2.58 (0.22) ab	4.6 +
CR	NOR	4.99 (0.94) b	17.2 *	5.58 (0.29) c	13.1 †

* mixture of species; † > 75% *C. verum*; + > 75% *N. hornei*

Using the mean nutrient concentrations of litter collected at MC, we estimated quantities of N and P in the annual litterfall. These estimates indicate that the return of N and P in NOR stands was roughly 50% higher than in CIN stands (N: 31.7 v. 19.5 kg ha^{-1} yr^{-1}; P: 1.5 v. 1.0 kg ha^{-1} yr^{-1}). The equivalent values for FAL are less reliable because leaf petioles, for which nutrient concentrations were not determined, made up an important fraction of litterfall. However, estimates based on N and P contents of 'leaf' litter (i.e. leaflets only) yield values of N that are over twice as high as those for NOR (68.6 kg ha^{-1} yr^{-1}) and values of P that are a higher by a factor of 1.4 (2.1 kg ha^{-1} yr^{-1}). Calculated in the same way, the mean quantities of tannins reaching the forest floor in litter were 417, 17, and 312 TAE kg ha^{-1} yr^{-1} in the NOR, CIN and FAL stands, respectively.

Soil chemistry differed significantly among the six stand types (Table 5). Soil pH and C:N ratio in FAL stands were significantly lower than in the mineral soil of CIN stands, while NO$_3$-N availability (ion exchange resin) was higher. Availability of PO$_4$-P in FAL was below the limit of detection by ion-exchange resins. NOR stands had lower P availability and higher C:N and C:P ratios than CIN stands (across both altitudes).

Table 5 Chemical properties of soils from three stand types (Cinnamomum verum CIN; Northea hornei NOR, Falcataria moluccana FAL) at two altitudes (mid-altitude Mare Cochons MC, montane Congo Rouge CR). For MC CIN organic O-horizon (-org) and surface exposed mineral A-horizon (-min) were separately analyzed. Mean and standard error are given (N=3) (b.d.l.: below detection level). Ion exchange resin (IER) data is given as mg l-1 of extraction solution. The F ratio and significance level from a one-way ANOVA and a priori contrasts (between mineral and organic soils) are indicated in the final three columns.

	MC FAL	MC CIN-min	MC CIN-org	MC NOR	CR CIN	CR NOR	Stand type	FAL–CIN	CIN–NOR
C (mg/g)	64 (7)	47 (13)	399 (44)	472 (23)	435 (79)	492 (30)	26***	0	0
N (mg/g)	3.8 (0.5)	2.1 (0.5)	15 (1.0)	14.6 (1.1)	18.1 (3.1)	16.4 (1.2)	21***	1	1
P (mg/g)	0.28 (0.01)	0.29 (0.04)	0.41 (0.04)	0.38 (0.01)	0.52 (0.05)	0.39 (0.05)	6**	0	5*
C:N	17 (0)	22 (2)	26 (2)	33 (4)	24 (1)	30 (1)	10***	5*	12**
C:P	224 (27)	155 (22)	978 (86)	1261 (103)	827 (83)	1305 (161)	29***	0	17***
pH	4.4 (0.1)	4.7 (0.1)	4.2 (0.1)	4.3 (0.1)	4.3 (0.1)	4.4 (0.1)	5*	5*	2
IER-NO$_3$-N	4.7 (0.9)	1.6 (0.4)	1.5 (0.3)	1.7 (0.2)	1.1 (0.1)	1.1 (0.1)	10***	25***	0
IER-NH$_4$-N	1.6 (1.1)	4.6 (3.4)	1.7 (0.5)	2.3 (1.3)	3.2 (1.5)	1.5 (1.0)	1	1	0
IER-N total	6.3 (1.9)	6.2 (3.1)	3.2 (0.7)	3.9 (1.5)	4.3 (1.6)	2.5 (1.0)	1	0	0
IER-PO$_4$-P	b.d.l.	3.9 (3.6)	0.6 (0.3)	0.5 (0.5)	1.1 (0.4)	b.d.l.			

In the bioassay of soils from different stand types, the relative growth rate of the *C. verum* seedlings was significantly affected by fertilizer treatment ($P < 0.001$), stand type ($P < 0.001$) and treatment x stand type ($P = 0.007$). Overall, the following significant treatment effects were found: complete fertilizer > P and NP > control, Addition of P had a more pronounced positive effect in FAL than in CIN soils; and addition of N had a negative effect in the CIN and FAL soils, but a positive effect in the NOR soils (Fig. 3). Complete fertilizer always increased growth, but the effect was larger in MC than in CR soils.

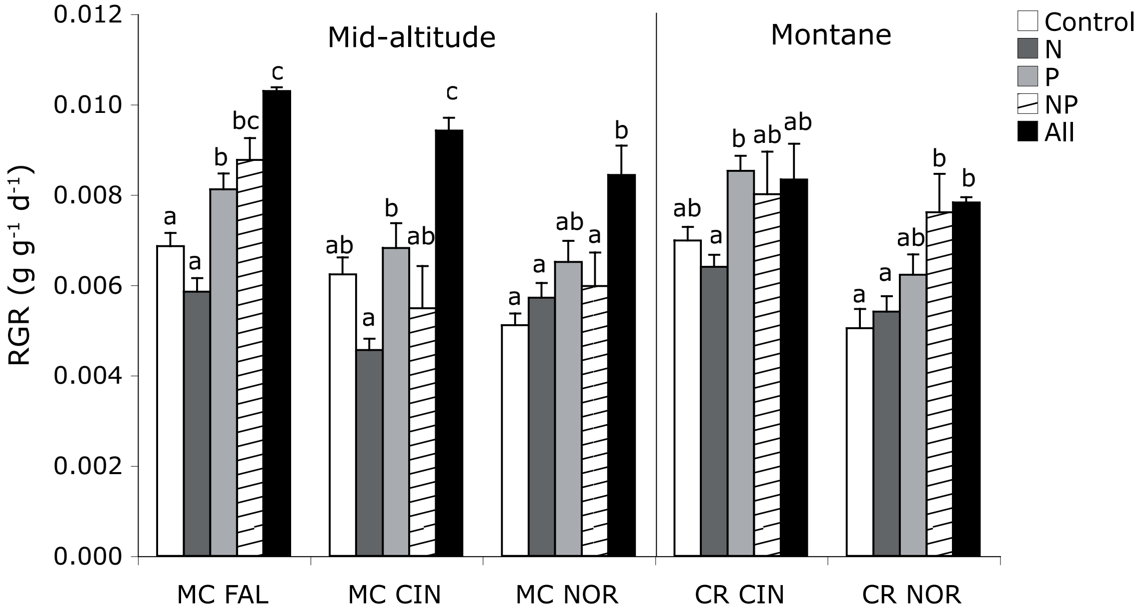

Fig. 3 Bioassay experiment with *Cinnamomum verum* seedlings and soils from five stand types (abbreviations as in Table 5). Mean (+ se) of relative growth rates based on the increase in above ground biomass. Differences among treatments were tested for each stand type with a Tukey test.

Discussion

Do invasive plant species produce litter of greater quality?

The differences in average leaf litter properties between native and invasive woody plant species in the Seychelles are similar to those reported from Hawai'i (Vitousek and Walker 1989, Baruch and Goldstein 1999, Allison and Vitousek 2004, Rothstein et al. 2004, Hughes and Denslow 2005). In both regions, litter of invasive species contained more nutrients and less polyphenols, had a higher specific leaf area (SLA), and decomposed faster than that of native species. For some parameters the contrast between invasive and native species is even stronger in the Seychelles than in Hawai'i: for example, Dietz et al. (2004) found that the average SLA of green leaves was twice as high in invasive species, whereas similar data from Hawai'i show a difference of only 22.5% (Baruch and Goldstein 1999). Since high SLA and leaf nutrient concentrations are correlated with rapid resource acquisition and growth under high light availability (e.g. Cornelissen et al. 1997, Pattison et al. 1998), we predicted that the invasive species are much faster growing than most native species in the Seychelles. Experimental studies with seedlings and saplings of native and invasive species confirm this to be the case, especially under high light conditions (E. Schumacher & C. Kueffer, unpublished data).

Table 6 Nutrient concentrations of green leaves (Kjeldahl N and P determined in 1-3 pooled samples per species), and relative difference in nutrient concentrations between green and senesced leaves as an estimate of nutrient resorption efficiency (N %, P %) for the 12 studied species.

Species	N (mg g^{-1})	P (mg g^{-1})	N:P	N (%)	P (%)
Invasive					
Alstonia macrophylla	27.27	1.00	27.3	48	63
Cinnamomum verum	12.17	0.78	15.6	25	41
Falcataria moluccana	41.63	1.52	27.4	64	74
Pentademsa butyracea	14.22	0.69	20.6	18	42
Psidium cattleianum	10.52	0.68	15.5	36	44
Syzygium jambos	12.44	0.75	16.6	46	51
Native					
Aphloia theiformis	13.90	0.81	17.2	44	56
Canthium bibracteatum	12.88	0.68	18.9	32	43
Dillenia ferruginea	11.56	0.70	16.5	45	51
Memecylon eleagni	10.91	0.65	16.8	42	46
Northea hornei	9.26	0.62	14.9	46	65
Timonius sechellensis	13.70	0.71	19.3	51	54

The green leaves of the species we studied varied very widely in their N and P contents. By far the highest concentrations of both nutrients were in the invasive species *Falcataria moluccana*, but leaves of the early successional invasive *Alstonia macrophylla* were also much richer in these elements than other trees (Table 6). At the other extreme, the native *N. hornei* had the lowest levels of N and P. However, N and P concentrations in litter vary not only because species differ in the concentrations of these nutrients in their leaves, but also because they resorb these nutrients to different degrees before the leaves are shed. Nutrient resorption also varied widely among species (18-64% for N; 41-74% for P), and was always greater for P than for N; but there were no consistent differences in resorption between native and invasive species. In absolute terms, litter N and P concentrations were often below the levels defined by Killingbeck (1996) as indicative of complete resorption (7 mg g^{-1} for N and 0.4 mg g^{-1} for P), suggesting that in many species the physiological limits for resorption had been reached.

The legume *Falcataria moluccana* was a notable exception to an otherwise clear trend for lower tannin contents in invasive than in native species. In fact, high polyphenol contents appear to be common among tropical legumes (Palm and Sanchez 1991, Mafongoya et al. 2000); and without this species, the average tannin content of the native litter was 550% that of the invasive litter. In Hawai'i, Rothstein et al. (2004) found a similar contrast in tannin contents between one native and one invasive woody species. Differences of this magnitude are likely to influence significantly both litter decomposition and soil nutrient availability (Palm and Sanchez 1991, Kraus et al. 2003).

Although the litter of the late successional native species *N. hornei* contrasted strongly with that of two early successional invasive species (*Alstonia macrophylla*, *F. moluccana*), differences among other species, both native and introduced, were rather small. This demonstrates that no simple generalizations can be made about the litter of native *versus* invasive plants, and that the ecological behaviour of individual species is also important in explaining variation in leaf traits. The litter of *N. hornei,* for example, also differs from that of many native species. However, because of its abundance it may have a particularly strong influence on ecosystem processes in the upland forests; the species accounted for 50-65% of the native trees in our study area, but before human disturbance it was probably even more abundant, together with other late successional endemic species with similar ecological traits. Among the invasive species, the pantropical, shade-tolerant trees *P. cattleianum* and *S. jambos* had low values for both N concentration and SLA, as has also been reported from other regions (Baruch and Goldstein 1999, Lal et al. 2001). Indeed, variation in leaf characteristics among invasive species was larger than among native species, clearly demonstrating that co-occurring invasive species do not exhibit the same ecological strategies.

Does the litter of invasive plant species decompose faster?

In the field experiments, the litter of invasive species tended to decompose faster than that of native species. These differences can be attributed mainly to the thinner leaves (i.e. higher SLA) and lower tannin contents of invasive species. At very infertile sites, initial rates of decomposition are determined more by the carbon quality and polyphenol content of litter than by its nutrient concentrations (Hobbie 2000, Bridgham and Richardson 2003); however, as much of the polyphenol content leaches out within a few months (Hättenschwiler et al. 2003, Kraus et al. 2003), these compounds probably play only a minor role in long-term litter decomposition.

Decomposition rates of invasive species on Hawai'i were also faster on average than those of natives (Vitousek and Walker 1989, Scowcroft 1997, Allison and Vitousek 2004, Rothstein et al. 2004). However, as in the Hawai'an study, we also found a considerable overlap in decomposition rates (k) between the groups of native and invasive species, and the values we measured for invasive species (ranging between 0.7 and 1.6 yr^{-1}) are typical of native species from other tropical montane forests (cf. Scowcroft 1997). The litter of the native *N. hornei* proved to be the most intractable; not only did it decompose slowly but it also immobilised considerable amounts of exogenous P during the first year of decomposition. In contrast, the litters of F. *moluccana* and *C. verum* released nutrients during the same period despite the fact that they both had high C:N and C:P ratios compared to the values cited as the critical ratios for immobilization (20-30 for C:N and 200-300 for C:P; cf. Bridgham and Richardson 2003). This strongly suggests that low C quality was the major factor limiting decomposition, whereas N and P dynamics were mainly determined by a source-sink dynamics between litter and site nutrient availability (Bridgham and Richardson 2003). Studies from Hawai'i have also shown a trend for stronger nutrient immobilization in native litter than in that of invasive species (Vitousek and Walker 1989, Allison and Vitousek 2004, Rothstein et al. 2004).

Litter decomposition rates and nutrient dynamics differed little among the five stand types investigated, probably because they were primarily determined by recalcitrant forms of carbon in the litter (Hobbie 2000, Aerts et al. 2003). However, the fact that in the microcosm experiment cellulose decomposition was stimulated in the complete fertilizer treatment suggests that there may have been co-limitation of decomposers by P and N (and possibly also by particular micronutrients present in the fertilizer). Our results contrast with those obtained in Hawaii, where litter mass loss and N and P dynamics differed between stands of native and invasive species (Vitousek and Walker 1989, Rothstein et al. 2004).

Are stands of invasive plant species more fertile?

An important assumption of our study is that any differences in site conditions among the various stands were due to the presence of different tree species. Although we cannot exclude that the various stands became established because of pre-existing site differences, we think this possibility is unlikely; all trees are found under a wide variety of environmental conditions (Kueffer and Vos 2004), and the stands selected were small, i.e. only a few trees, and located in apparently uniform areas. Furthermore, although the two areas (MC and CR) had very different management histories, the differences observed between CIN and NOR stands were similar in both areas. Only the fact that FAL stands occurred exclusively on mineral soil may have biased the stands comparison, and to account for this we compared these with the mineral soils of CIN stands.

Our study revealed four main differences among the stand types in factors related to nutrient availability. First, there was a 25-times higher input of tannin in NOR compared to CIN stands, and the input of total phenolics was an order of magnitude higher in NOR. The implications of these differences for nutrient availability need further investigation as polyphenols can either reduce or increase nutrient availability to plants (Kraus et al. 2003, Hättenschwiler and Vitousek 2004). Second, P concentrations (total and ion-resin extractable) were higher in CIN than in NOR stands while C:N and C:P ratios were lower. Third, N was mainly mineralised as nitrate in FAL soils but as ammonium in CIN; this difference was also evident in the microcosm experiment after fertilisation with organic N. While nitrification increases the availability of N for some plants it can also lead to higher leaching losses (Bardgett 2005). Fourth, P availability was lower, and P was more limiting for plant growth (at least of *C. verum* seedlings) and litter decomposition in FAL than in CIN stands. The lower soil pH of the FAL stands might have contributed to these differences by enhancing P fixation to Fe and Al hydroxides (Bardgett 2005). Alternatively, efficient P uptake may have reduced P availability, as was suggested for *F. moluccana* in plantations (Binkley and Ryan 1998). The invasive N-fixing shrub *Ulex europaeus* also lowered pH in Hawaii, which was paralleled by increased levels of Al and decreased levels of Ca, Mg and K in the soil (Leary et al. 2006).

Despite these significant effects, we were surprised by the general weakness of the impacts of *C. verum* and *F. moluccana* on nutrient availability. In particular, the enhancement of soil N availability by the F. *moluccana* was negligible compared to the 17- to 121-fold increases in N availability under F. *moluccana* on young volcanic flows in Hawai'i (Hughes and Denslow 2005). Although we did not measure N-fixation, we observed nodules containing the characteristic pink colour of leghaemoglobin on the roots of both trees and saplings of F. *moluccana* (C. Kueffer and H. Olde Venterink, pers. obs.). Similarly, the increase in P availability in CIN stands was much smaller than might have been expected from the data on litter properties.

We can think of three reasons why nutrient conditions in the three stand types were not more different. First, the stands we studied were small, so that 'edge effects' may have played a role. For example, the litter of *F. moluccana* probably also contributes significantly to nutrient input through litterfall in the other stands. We did not measure this contribution, but observed that, because of the tall, broad tree canopies formed by this species, the small leaflets are widely scattered.

Second, the soils in the granitic Seychelles are very infertile, and concentrations of N, P, K, Ca and Mg are very low (Varley 1971, Dobrovol'skiy 1986). The N and P contents of litter and fresh leaves of the native *N. hornei* were similar to those of *Metrosideros polymorpha* at the oldest, P-limited sites in Hawai'i (Vitousek 2004), and the litter K content of *N. hornei* (0.26 mg g^{-1}) was only about 50% of the lowest values found for *M. polymorpha* in Hawai'i (0.51 mg g^{-1}) (Hobbie and Vitousek 2000). The litter decomposition experiments and the bioassay indicate that biotic processes were limited by P together with other nutrients (probably K, given that the fertiliser used in the complete fertilizer treatment contained no Ca or Mg). So, the impact of invasive species on the availability of other nutrients such as K may also be relevant. Indeed, litter K content was much higher in the invasive species we studied (*C. verum*: 2.20 mg g^{-1}; *F. moluccana*: 1.68 mg g^{-1}) than in the native species (*N. hornei*: 0.26 mg g^{-1}, *M. eleagni*: 0.68 mg g^{-1}).

The generally low levels of nutrients in upland soils may also explain why several N-fixing species, some of them invasive in the lowlands (e.g. *Leucaena leucocephala*) and others used in reforestation schemes in the uplands (e.g. *Albizia lebbeck* or *Gliricidia sepium*), have been unable to invade established forest stands (Kueffer and Vos 2004). It is significant that most of the trees that do invade upland habitats, such as *F. moluccana* or *Acacia mangium,* have mechanisms to promote nutrient uptake, such a mycorrhizal symbioses or the exudation of organic acids (reviewed in Chapter 1). The most successful of the invasive species, *C. verum,* forms a very dense root mat in the topsoil, making it an aggressive competitor for belowground resources (see Chapter 3). From these observations we conclude that more effective nutrient uptake by invasive species probably counterbalances any effects they may have on nutrient availability due to faster litter decomposition or N-fixation.

Third, there may indeed be effects of invasive species on nutrient cycling that only become evident in the longer term. In the short-term, faster decomposition appears to increase the uptake and turnover of nutrients without affecting nutrient pools in the soil. However, when the trees die, the larger nutrient pools contained in their biomass will be released in a large pulse; and because such a pulse will coincide with high light availability, it is likely to favour fast-growing, alien species (Adler et al. 1998, Ostertag and Verville 2002). Thus even in very nutrient-poor forests, non-native species could facilitate further invasion by altering the nutrient cycle, as has been suggested in other cases (Simberloff and Von Holle 1999, Vitousek 2004).

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Chapter 3

Strong belowground root competition shapes tree regeneration in invasive *Cinnamomum verum* forests

Abstract

Plant species invading nutrient-poor ecosystems are likely to have their greatest impact on the native plant community by competing for resources belowground. We investigated how root competition by an invasive tree, *Cinnamomum verum,* affects regeneration in nutrient-poor tropical secondary forests in the Seychelles.

We performed three trenching experiments to investigate the effects of severing the root systems of mature trees on the growth of juveniles. These experiments had the following objectives: (i) to compare the responses of native and invasive saplings to release from root competition, (ii) to compare how seedlings (< 50 cm tall) and saplings (> 50 cm tall) of *C. verum* respond to trenching, and (iii) to compare the response of *C. verum* seedlings to trenching in forest stands with and without *C. verum* as the dominant species.

The results indicate that the dense topsoil root mat produced by mature *C. verum* trees suppresses the growth of young trees. Growth responses to trenching were stronger for seedlings than saplings, and stronger for juveniles of invasive than of native species. We conclude that stands of *C. verum* exert a strong belowground filtering effect on seedling regeneration. This effect is likely to influence secondary forest succession by selectively reducing the establishment of invasive and small-seeded species.

Because of the bias in invasion biology towards relatively nutrient-rich, productive ecosystems, few studies have investigated the role of belowground resource competition in plant invasions. Our results for a very infertile, phosphorus-poor ecosystem show that root competition by an alien species can exert a strong influence on forest regeneration. We suggest that this mechanism may be of general importance in nutrient-poor tropical forests invaded by alien tree species.

Introduction

While many studies have focused on the introduction, establishment and spread of invasive alien plants (Mack et al. 2000, Dietz and Edwards 2006), few have investigated whether these species persist and have an influence on their habitat in the longer term (Blossey 1999, Lugo 2004, Hobbs et al. 2006). Thus, more emphasis has been given to studying the invasibility of habitats (i.e. the vulnerability of native plant communities to invasion) (e.g. Levine, Adler and Yelenik 2004) than to how an invasive plant affects regeneration of native species (Levine et al. 2003). However, to predict how vegetation will develop in heavily invaded plant communities such knowledge is important (e.g. Lugo 2004).

Changing the balance of resource competition in a community is one of the most obvious ways through which a dominant invasive plant can affect both growth and persistence of established individuals and population regeneration or colonization by seedlings (Tilman 1993, Levine et al. 2003, Stevens et al. 2004, Yurkonis and Meiners 2004). Judging from the literature, it may appear that plant invasions usually increase aboveground competition for light rather than belowground competition for nutrients (Levine et al. 2003, Fagan and Peart 2004 *and references therein*). However, existing studies may be biased towards invasive species of habitats with high productivity. In habitats with low productivity, belowground competition for nutrients is likely to be more important than aboveground competition (e.g. Coomes and Grubb 2000, Dietz and Edwards 2006).

Most invasive species of tropical forests are light-demanding, and it has been hypothesised that the main cause of enhanced habitat invasibility is disturbance that leads to increased light availability (Fine 2002). However, invasive trees such as *Spathodea campanulata* or *Psidium guajava* that dominate early secondary successions after major anthropogenic disturbances are not able to sustain their dominance because they cannot regenerate in shade (Aide et al. 2000, Lugo 2004). In contrast, shade-tolerant invasive trees such as *Syzygium jambos* and *Psidium cattleianum* sometimes form extensive, mono-specific stands (Huenneke and Vitousek 1990, MacDonald et al. 1991, Aide et al. 2000, Kingston and Waldren 2003, Lugo 2004) that may be able to persist. This is because these species produce a dense canopy that shades out the seedlings of most other tree species, but they can themselves regenerate thanks to their large seeds (in the case of *S. jambos*), shade-tolerant juveniles and vegetative shoots (Huenneke and Vitousek 1990, Aide et al. 2000, Weber 2003). Hence, in many tropical forests the long-term dominance of the canopy by invasive trees may depend on how well regenerating trees of the same species can cope with the shortage of the light resource imposed by the adult trees.

Even under an undisturbed canopy, however, light availability may not always be the most important factor influencing forest regeneration; the effects of belowground competition have been less studied but may also be important, especially in nutrient-poor forests such as those dominated by the invasive tree *Cinnamomum verum* Presl (true Cinnamon) on the granitic islands of the Seychelles (Fleischmann 1997, Kueffer and Vos 2004). In the mid-altitude forests of Mahé, the largest island of the Seychelles, *C. verum* makes up more than 80% of the canopy while in disturbed montane forests it accounts for 30-40% of the canopy. These forests, which occur on soils with very low soil nutrient availability, especially of phosphorus (see Chapter 2), are of low stature and do not cast a very dense shade. Because of their relatively uniform structure and the dominance of one species, *C. verum,* they provide a convenient system for investigating the long-term consequences of an invasive tree species on a forest community. In particular, they are suitable for studying the importance for forest development of root competition between invasive and native species.

The aim of this study was to investigate the ecological impact of *C. verum* dominance on forest regeneration in the Seychelles. The two main hypotheses were: (i) that *C. verum* severely restricts tree regeneration through strong belowground competition for resources; and (ii) that *C. verum* influences the course of forest succession by differentially affecting regeneration of native and invasive tree species.

We performed root trenching experiments to investigate the effects of belowground competition on the growth of juveniles of several native and invasive woody species. These experiments were carried out in three forest sites - two dominated by *C. verum* and one an abandoned plantation with little *C. verum*. Our study highlights the relevance of belowground competition for understanding the impacts of invasive trees in nutrient-poor tropical forests. Although the *C. verum*-dominated forests are young and almost monospecific, the mature trees exert strong belowground competition on juvenile trees, particularly affecting seedlings by means of a dense topsoil root mat.

Methods

Species

Cinnamomum verum Presl (syn. *C. zeylanicum*; the true Cinnamon) is a native of lowland evergreen climax forests in the Western Ghats of India and Sri Lanka where it occurs up to an altitude of 1800 m asl. The tree grows 10-15 m tall and forms a very dense mat of fine roots in the topsoil (2-4 kg dry fine root mass per m^2 in the uppermost 20 cm of the soil in Seychelles

Table 1 Characterisation of the 9 target species of the trenching experiment. Nomenclature follows Friedmann (1994). The species were grouped into two ecological groups: light demanding (LD) and shade tolerant (ST) species. The number of replicate individuals per treatment (C: control, T: trenching treatment) and species is also given. The approximate relative abundance of each species in the sapling layer in Mare aux Cochons (MC) was estimated based on 118 circular plots (r ≥ 3 m) along 7 transects.

Species	Family	Ecological group	Status	C	T	Abundance in MC (%)
Alstonia macrophylla	Apocynaceae	LD	Invasive	12	12	1
Cinnamomum verum	Lauraceae	ST	Invasive	11	12	45
Psidium cattleianum	Myrtaceae	ST	Invasive	14	13	10
Syzygium jambos	Myrtaceae	ST	Invasive	13	14	10
Aphloia theiformis *	Flacourtiaceae	LD	Native	14	10	5
Canthium bibracteatum	Rubiaceae	LD	Native	15	12	1
Memecylon eleagni	Melastomataceae	ST	Native†	15	11	3
Northea hornei	Sapotaceae	ST	Native†	11	11	8
Timonius sechellensis	Rubiaceae	LD	Native†	11	8	2

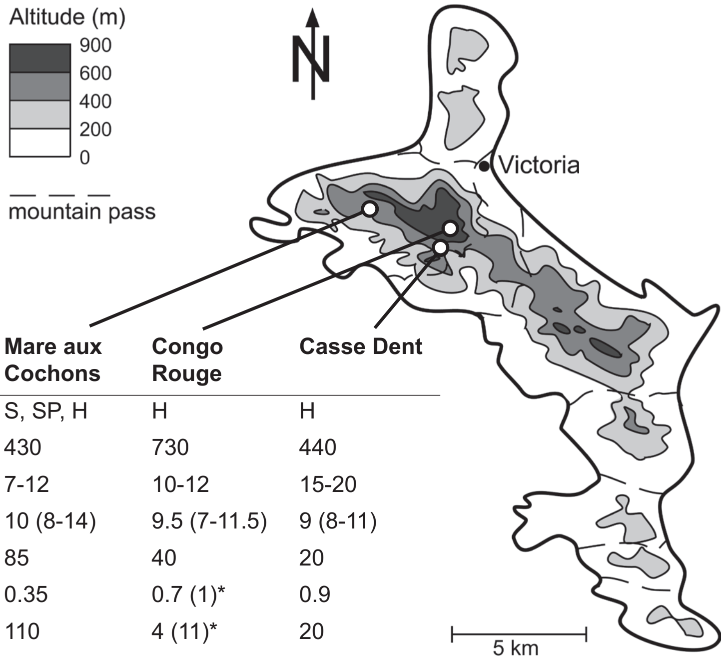
*subsp. *madagascariensis* var. *seychellensis*
†Endemic species

[C. Kueffer, unpublished data]). It was introduced to the granitic Seychelles in the 1770s and rapidly invaded the forests as these were exploited for timber (Stoddart 1984, Kueffer and Vos 2004). Thanks to its highly nutritious, fleshy fruits, *C. verum* is efficiently dispersed by native frugivorous birds, and by the mid-19th century it had become the dominant canopy species in most upland forests. From the beginning of the 20th century until the 1970s, feral *C. verum* was intensively used to provide oil of cinnamon. Today, the species is the most abundant tree in the Seychelles and grows in all habitats from sea level to the highest montane forests at 900 m asl.

In the forests studied, it was convenient to distinguish between a 'seedling' layer composed of juvenile trees < 0.5 m tall (80% of all seedlings were between 10 and 20 cm tall) and a 'sapling' layer with juveniles > 0.5 m tall (cf. Coomes and Grubb 1998). Five native and four invasive tree species that were common in the sapling layer were used as target species for the trenching experiment (Table 1). Both groups include light demanding and shade tolerant species (cf. E. Schumacher, unpublished data). In addition, saplings of *C. verum* were used as 'phytometers' to allow comparisons among different forest types.

Study sites

The study was carried out in two mid-altitude forest sites (Mare aux Cochons (MC) and Casse



	Mare aux Cochons	Congo Rouge	Casse Dent
Experiments	S, SP, H	H	H
Altitude (m asl.)	430	730	440
Canopy height (m)	7-12	10-12	15-20
% Light transmittance	10 (8-14)	9.5 (7-11.5)	9 (8-11)
% C. verum in canopy	85	40	20
Sapling density (m^{-2})	0.35	0.7 (1)*	0.9
Seedling density (m^{-2})	110	4 (11)*	20

* including vegetative sprouts of *Psidium cattleianum*

Fig. 1 Location and characteristics of the three study sites on Mahé island. S, Sapling experiment; SP, seedling patch experiment; and H, habitat comparision. For light transmittance (given as % direct and diffuse light above the canopy transmitted to the sapling leaf layer) the median ± the quartiles are indicated. Canopy tree (*Cinnamomum verum*) and sapling density were estimated in several plots per site (total areas for adult/sapling and seedling data, respectively: 5000 m^2 and 65 m^2 (MC), 300 m^2 and 30 m^2 (CD) and 1500 m^2 and 60 m^2 (CR)).

Dent (CD)) and a montane forest (Congo Rouge (CR), see Fig. 1) within the Morne Seychellois National Park on the island of Mahé (4° S, 55° E, 154 km^2, Republic of Seychelles). Soils at the three sites are ferrasols (pH c. 4.5) with very low N and P availability. Plant growth appears to be limited mainly by the availability of phosphorus and possibly by other nutrients including potassium (see Chapter 2). In contrast to the other two sites, CR has a thick litter layer and a strongly developed organic topsoil horizon. During the study period the annual rainfall was c. 3400 mm in all three forests. However, CR has a much more persistent cloud cover and generally higher humidity than the other sites.

Mare aux Cochons is in a forested upland valley that was completely deforested at the beginning of the 20th century, and where *C. verum* was cropped until the 1970s. In this area *C.verum* trees account for c. 85% of the canopy trees. The canopy also includes few patches of *Syzygium jambos* and *Northea hornei*. The *C. verum* forest had a very dense layer of tree seedlings (>100 mainly *C. verum* individuals per m^2) but saplings were scarce.

Casse Dent is a plantation forest dominated by the alien tree *Sandoricum koetjape*, and with c. 20% *C. verum*. It is situated in the same upland valley as MC. The forest floor had fewer seedlings than at MC but many more saplings.

Congo Rouge, situated on a small plateau above MC and CD, is a heavily invaded montane cloud forest that was probably exploited at the end of the 19th century. *C. verum* dominates the canopy and accounts for 40% of all trees, but there are also patches of the endemic tree *Northea hornei*. The understory has many suckering plants of *P. cattleianum* but seedlings of all tree species are rare.

We performed three experiments. The first was designed to compare how saplings of native and invasive species respond to trenching, and was performed at the Mare aux Cochons site. The second, also at MC, investigated how strongly seedlings of *C. verum* are affected by trenching compared to saplings of the species. The third experiment compared the effects of trenching on the growth of *C. verum* 'phytometers' in forests with and without *C. verum* as the dominant species. This experiment used all three sites.

Experiment 1: Effects of trenching on saplings

The experiment was started in December 2002 and terminated in January 2005. Within an area of 100 x 1000 m^2 in MC (Fig. 1), 30 saplings (0.5-1.5 m tall) of each of the nine species were tagged and their positions recorded on a map. The plants were chosen to cover the range of light conditions in the forest, and were at least 5 m apart and more than 2 m from the nearest tree trunk. Half of the plants were randomly assigned to the trenching treatment and the remainder were left untrenched (controls). For the trenching, a 75 cm square was marked out with the sapling at the centre and four 40 cm slits were cut in the soil with a machete. As the fine roots were concentrated in the upper 40 cm of the soil (C. Kueffer, unpublished data), we assumed that this treatment eliminated almost all root competition from neighbouring trees. The same saplings were re-trenched every six months. All plants other than the target sapling were removed from the 75 x 75 cm quadrat centred on both untrenched and trenched saplings. Seedlings were carefully uprooted to minimize soil disturbance and saplings were cut at ground level.

For each sapling the height to the uppermost leaf, the stem diameter at forest floor level (measured using calipers) and the total number of leaves were recorded every six months. Light availability was assessed with hemispherical canopy photographs (Nikon Coolpix 995 digital camera equipped with FC-E8 fisheye converter) and analysed with Gap Light Analyzer 2.0 software (cf. Frazer et al. 2001). Camera settings were as in Frazer et al. (2001) and the camera was positioned 1.3 m above the ground and pointing upwards. For each sapling, two pictures were taken on an overcast day in 2004 with manual exposure compensation set to –0.7 or –1.0 eV, respectively. Both pictures were analysed and mean values were used to characterise light availability of each sapling.

By the end of the experiment, some saplings had been lost or damaged, so that data were available for between 8 and 15 replicates per species and treatment (Table 1). At the final harvest, one fully expanded leaf was collected from the top of each sapling to determine nutrient concentrations (no data for *Timonius sechellensis*). Four pooled samples per species and treatment, each from two to four different, randomly assigned saplings, were used to determine Kjeldahl P and N colorimetrically (after 1 h digestion at 420°C with 98% H_2SO_4 and Merck Kjeltabs) on a flow injection analyzer (FIA, TECATOR, Höganäs, Sweden).

Experiment 2: Effect of trenching on **C. verum** *seedlings*

This experiment was started in November 2003 and was terminated in December 2004. Eight pairs of 0.5 x 0.5 m^2 plots (trenched, control) were placed in monospecific seedling patches of *C. verum* distributed over the whole study area at MC. The two plots of a pair were spaced by c. 5 m. On average, there were 65 seedlings per plot (range: 19-153). Light availability was measured in the same way as in the sapling experiment; just above the seedling layer median light availability was 8.3% (range: 6.5%-19%). Each seedling within the plot was tagged with a nylon string, and its height and the number of fully expanded leaves were recorded. For each plot pair the trenching treatment was randomly assigned to one of the two plots. The trenching was applied 5 cm outside of the plot margins to reduce boundary effects, and was repeated six months after the beginning of the experiment.

At the end of the experiment all seedlings were cut at ground level and dry biomass of stems and leaves was determined after oven-drying for 2 days at 80°C. Relative growth rates of the seedlings were calculated per plot based on mean height and number of leaves at the start and end of the experiment.

Experiment 3: Effects of trenching on **C. verum** *saplings in different forest habitats*

This experiment used saplings of *C. verum* as phytometers to compare the effects of trenching in different forest types. It was performed at all three sites, using 9-12 saplings per site and treatment, and ran from November 2003 until January 2005. The plants at MC were the same as those used in experiment 1. In CD the saplings chosen were regularly distributed over an area of c. 400 x 50 m of homogeneous forest. In CR, the saplings were selected in two areas of

c. 250 x 30 m separated by c. 100 m distance and 20 m altitude, and they were selected only under a homogeneous *C. verum* canopy so that the effective study area could be interpreted as a forest dominated by *C. verum* similar to MC. Experimental treatments and measurements were the same as in experiment 1. We also sampled the topsoil below each *C. verum* sapling in MC and CD to check whether the trenching had had a direct effect on soil nutrient content. For this purpose, five samples of two or three randomly pooled saplings were used. Kjeldahl N and P concentrations were measured as described above. In MC, there were no effects of the trenching treatment on total soil N or P ($P \geq 0.5$), while there was a non-significant trend towards increased nutrient concentrations in the trenched plots in CD (N: 2.9 v. 1.9 mg g^{-1}, P: 0.43 v. 0.38 mg g^{-1} ; $P \geq 0.07$).

Data analysis

For experiment 1, we tested the effect of the trenching treatment on (i) the relative growth rate (RGR) of the saplings (using stem height and diameter and number of leaves), and (ii) growth allocation (number of leaves per unit stem length). For each parameter we used an ANOVA model with treatment (trenching, control), species status (native, invasive) and light transmittance as fixed factors. Species identity was nested in species status as a random factor. Three-way interactions were not significant ($P > 0.4$) and were not included in the model. Type III sums of squares were used to correspond to the unbalanced design (four native and five invasive species). Light transmittance values were standardized within species to make the data comparable among species. Sapling height at the start of the experiment was included in the model as a covariable.

The trenching effect on relative growth rates was slightly stronger in the first measurement period (from December 2002 to May 2003) than in the other periods (repeated measures MANOVA). We excluded this first measurement period from the analyses to reduce the risk of a treatment artifact, e.g. initial nutrient pulses due to decomposition of cut roots. All analyses were therefore performed using the data from May 2003 to January 2005. Leaf:height ratio was log-transformed and RGR stem height and diameter square root-transformed to remove heteroscedasticity.

For experiment 2, the trenching effect was analysed using a two-tailed paired student’s t-test.

For the phytometer experiment, we used a full factorial ANOVA model with trenching treatment (trenching, control) and site (Mare aux Cochons, Casse Dent, Congo Rouge) as fixed factors. Sapling height at the start of the experiment and light transmittance were included in the model as covariables.

All statistical analyses were performed with JMP V 6.0 (SAS Institute Inc. 2005).

Results

Effects of trenching on sapling growth

All plants survived the course of the experiment except for four saplings of *Timonius sechellensis*. However, almost 10% of the saplings lost a major proportion of their leaves or stem height (>20% in 6 months in at least one measurement period). This phenomenon was rather evenly distributed among species and treatments except for two heavily affected native species - *T. sechellensis* (8 individuals) and *Aphloia theiformis* (6 individuals).

In the invasive species, RGR for leaf number and stem height increased significantly with light transmittance; the linear regressions show that both measures of RGR approximately doubled over the observed range from 6% to 16% light transmittance (RGR leaf number: r^2 adj = 0.05, P = 0.01; RGR stem height: r^2 adj = 0.1, P < 0.001). In the native species there was no such relationship (r^2 adj ≤ 0.01, P > 0.1; significant interaction between light transmittance and species status, see Table 2).

Untrenched saplings growing beneath a canopy dominated by *C. verum* canopy grew very slowly. Relative growth rates (RGR) based on leaf number ranged from -0.33 to 0.19 yr^{-1}, while equivalent values based on stem height and diameter were 0.04 to 0.14 yr^{-1} and 0.05 to

Table 2 Statistical parameters (ANOVA) of the sapling trenching experiment. Indicated are the F-ratios and significance levels (***: P < 0.001, **: P < 0.01, *: P < 0.05, significant ones in bold) of main or interaction effects on relative growth rates (RGR, yr^{-1}) and allocation (number of leaves per unit stem length, cm^{-1}).

Source of variation	RGR			Allocation
	number of leaves	stem height	stem diameter	Leaf:height
Species status† (S)	2.61	2.58	2.57	0.13
Trenching (T)	**18.44*** **	**9.59** **	**9.06** **	**6.66** **
Light transmittance (L)	0.74	1.42	2.10	3.06
S x T	0.06	3.69	3.11	0.30
S x L	**8.10** **	**12.08*** **	1.92	0.66
T x L	1.39	0.11	0.30	0.52
Initial sapling height	0.37	**4.89***	0.29	0.50

† invasive vs. native

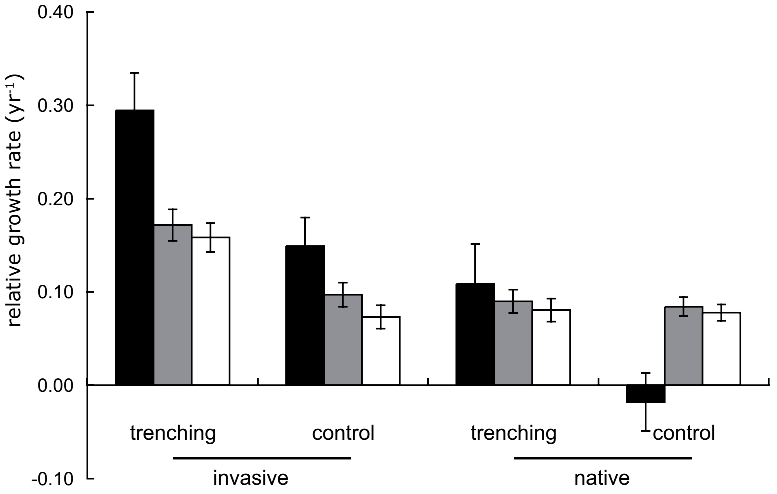


Fig. 2 Annual relative growth rates of leaf number (black bars), stem height (grey bars) and stem diameter (open bars) of trenched and control saplings compared between invasive and native species (means ± SE). See text and Table 1 for further information.

0.12 yr^{-1}, respectively. Apart from a higher rate of leaf development in the invasives ($P < 0.001$) there were no differences in the relative growth rates between untrenched native and invasive saplings ($P > 0.2$; Fig. 2).

All measures of RGR tended to be significantly higher in the trenched than in the untrenched control saplings (Fig. 2, Table 2). However, there was large variation among species within and between the two groups. Whereas the invasive species profited generally from trenching ($P \leq 0.08$) the native species only showed an increase in the rate of leaf development (Fig. 2). The non-endemic natives *Aphloia theiformis* and *Canthium bibracteatum*, both light demanding species, were the only saplings that lost leaves under control conditions. When these two species were excluded from the analysis, the RGR of leaf number in the native species was only slightly (20%) higher under trenched conditions than in the controls (RGR of 0.13 yr^{-1} and 0.11 yr^{-1}, respectively).

Effect of trenching on C. verum *seedlings*

Untrenched *C. verum* seedlings grew very slowly and increased in height and number of leaves by only c. 10% in 13 months. In contrast, trenched seedlings increased the number of leaves by c. 60% and grew 30% taller in the same period. As a result, RGR of stem height was almost three times and RGR of leaf number almost five times higher in trenched compared to untrenched *C. verum* seedlings (Fig. 3, $P < 0.004$). Over 13 months, seedlings in trenched plots developed 50%

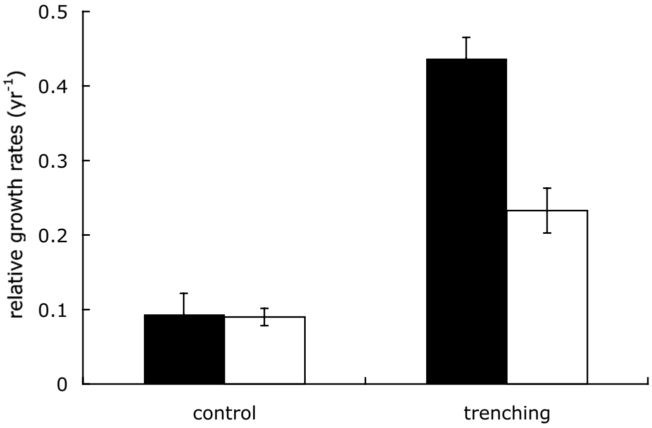


Fig. 3 Annual relative growth rates of leaf number (black bars) and stem height (open bars) of trenched and untrenched *C. verum* seedlings (N = 8 paired plots; means ± SE).

more dry aboveground biomass than control seedlings, this difference being equivalent to 40 g m^{-2} in a plot with an average seedling density. The ratio of dry leaf biomass to total aboveground biomass was also higher in trenched than in control plots (0.52 vs. 0.45, P = 0.02).

Effects of trenching on C. verum *saplings in different forest habitats*

There were no consistent effects of treatment and site on the relative growth rates of the saplings at the three sites (P ≥ 0.4), though stem growth of saplings was higher at Casse Dent (P = 0.003). The interaction between site and habitat was, however, significant for both RGR leaf number

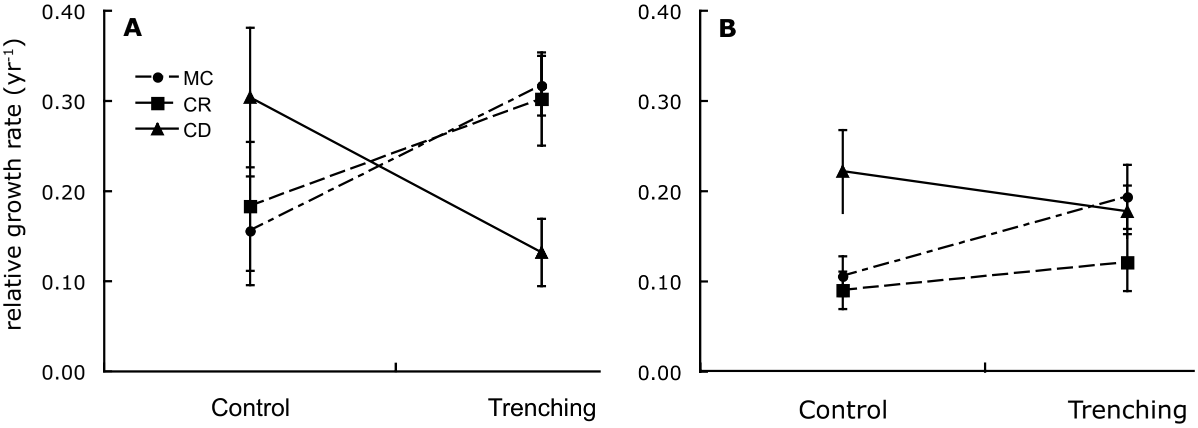


Fig. 4 Relative growth rates of leaf number (A) and stem height (B) of trenched and untrenched saplings of the phytometer *C.verum* in three different sites (habitats; Mare Cochons MC, Congo Rouge CR, Casse Dent CD) (N = 9-14 saplings per site and treatment, mean ± SE).

(P = 0.007) and RGR stem height (P = 0.02; Fig. 4): in contrast to the two sites where *C. verum* was dominant (Mare aux Cochons and Congo Rouge), root trenching at Casse Dent reduced rather than increased the relative growth rates of leaf number and stem height of *C. verum* saplings compared to control saplings. For the relative growth rate of stem diameter the trend was the same but was not significant (P = 0.2).

Discussion

The impact of belowground resource competition on seedling and sapling growth in Cinnamomum verum *forests*

The results presented here support our first hypothesis - that belowground competition strongly limits the growth of young trees in forests dominated by *C. verum*. While light penetration to the forest floor in the *C. verum* forests was relatively high (an average of c. 10% light transmittance), the availability of soil nutrients, particularly phosphorus, was very low. This was the case even in comparison to an infertile Amazonian caatinga forest (Coomes and Grubb 1998), where saplings tended to have slightly higher foliar nutrient concentrations (14.1 mg g^{-1} N and 0.84 mg g^{-1} P) than those at Mare aux Cochons (11.7 mg g^{-1} N and 0.72 mg g^{-1} P). Thus, it is not surprising that reduced competition for nutrients by trenching had a pronounced effect on juvenile growth (see also Coomes and Grubb 2000, Barberis & Tanner 2005 *and references therein*). Further evidence that trenching altered the relative importance of nutrients and light as limiting factors is provided by the increased allocation of aboveground biomass to leaf production in the trenched seedlings and saplings (compare Tilman 1988, Coomes and Grubb 1998, Lewis and Tanner 2000), with both invasive and native saplings producing significantly more leaves per unit stem length than in control plots (0.64 v. 0.52 cm^{-1}). There was also a trend for the leaves of trenched saplings to have higher N and P concentrations (P = 0.08), which combined with the higher leaf production is an indication of higher nutrient uptake.

Although these results suggest that saplings benefited from trenching because it reduced belowground competition for nutrients, it is important to consider other possible explanations. One possibility is that the result was caused by a pulse of nutrients resulting from the death of severed roots. However, this explanation seems unlikely because the enhanced growth was sustained over two years, while soil N and P concentrations beneath trenched plants were no higher at the end of the experiment than beneath control plants. In view of the high rainfall in the study area, it is also unlikely that competition for water caused the enhanced growth of trenched seedlings. Furthermore, plant growth varied little among measurement periods, despite the fact that mean monthly rainfall per period varied from 250 mm to 400 mm. Finally there is the possibility that secondary metabolites produced by *C. verum* played a role. However, although the leaves, bark and roots of this species are rich in secondary metabolites, particularly eugenol and cinnamic aldehyde (Purseglove 1991), that have been shown to be phytotoxic (e.g. Tworkoski 2002), it is hard to see how allelopathy could have affected our results. As all *C. verum* derived plant material remained in place in the trenched plots it seems very improbable that the response of seedlings to the treatment was due to lower concentrations of allelochemicals. In addition, seedlings grown in pots with soil from *C. verum* stands tended to grow better than those grown in pots with soil obtained from beneath native trees (soils with fertilizer added; data not shown) which is the opposite of what would be expected if toxic compounds had accumulated in *C. verum* soil.

The differing responses to trenching of seedlings and saplings are probably the result of *C. verum* trees producing a mat of fine roots in the uppermost 10-20 cm of the soil. Whereas the roots of seedlings are restricted to this zone of high competition from mature trees, the roots of saplings reach further down, partly escaping intense competition. As a result, seedling growth might become almost arrested, resulting in a dense layer of stunted seedlings (< 600 individuals per m^2) that rarely grow taller than 20 cm. Based on mean seedling density and data on annual seedling emergence we estimate a turnover rate of > 10 years for the seedlings in this layer, indicating a very low seedling mortality compared to that reported in other tropical forests (Turner 2001). Such ‘persistent seedling banks’ have been found in other forests, both temperate and tropical, but mainly in response to deep shade (Horvitz et al. 1998, Grime 2001).

Coomes and Grubb (1998), working in highly infertile caatinga forests in the Amazon, found similar growth responses of seedlings to trenching, and even more pronounced responses of saplings. This shows that juvenile trees in other nutrient-poor tropical forests respond similarly to increased availability of belowground resources. However, the study of Coomes and Grubb (1998) and other related studies (e.g. Lewis and Tanner 2000) were performed in natural, multi-species forests, and it is generally assumed that colonizing and establishing individuals experience less competition in younger, species-poor plant communities (e.g. Naeem et al. 2000, Levine, Adler and Yelenik 2004). Our study demonstrates that belowground competition can have a major impact on juvenile tree growth even in a young secondary tropical forest with one dominant alien species. The main difference between our results and those of Coomes and Grubb (1998) is that seedlings in the *C. verum* forest responded much more strongly to trenching than saplings, presumably as a result of the dense root mat of *C. verum*. In species-rich forests there is usually spatial partitioning of the rooting depth between different canopy species (see Casper and Jackson 1997), which may lead to a more homogeneous distribution of root competition among different stages of juvenile trees.

Differences between saplings of native and invasive species in their response to trenching

In support of our second hypothesis we found a much stronger growth response to trenching in invasive than in native saplings while under control conditions relative growth rates were similar in the two groups (although two native species had very low rates of leaf development). Our findings have important implications for the invasibility of nutrient-poor tropical forests. First, it appears that improved nutrient availability may generally favour the growth of alien tree saplings over those of native trees, thereby increasing forest invasibility (Davis, Grime and Thompson 2000, Daehler 2003). This may reflect the generally higher plasticity in response to increased resources of fast versus slow growing species that has been found for juveniles of other tropical forest trees (Veenendaal et al. 1996, Lewis and Tanner 2000, Lawrence 2003). Second, there was much variation among species in the response to trenching, indicating that colonization success under elevated nutrient availability is rather species-specific. The problematic, shade-tolerant invasive tree *Psidium cattleianum*, for example, responded particularly strongly, a result consistent with its strong response to added fertilizer in other experiments (E. Schumacher & C. Kueffer, unpublished data). Hence, this species may benefit more strongly than other alien trees to increased nutrient availability. Third, it is important to consider not only sapling growth but also the earlier stages of establishment. The strong belowground competition resulting from the root mat of mature *C. verum* trees may act as a ‘regeneration filter’. It seems likely that two regeneration strategies are particularly vulnerable to such filtering: small-seeded species that do not have sufficient resources in their seeds to extend the seedling roots below the root mat (compare Coomes and Grubb 2003), and nutrient-demanding invasive species that cope with infertile soils through efficient mechanisms of nutrient uptake (e.g. lateral root systems) (reviewed in Chapter 1). In contrast, many native species appear able to cope with the root mat, thanks partly to lower nutrient demands and partly to a more strongly developed taproot in seedlings.

In fact, the relative abundance of native species in Mare aux Cochons was higher in the saplings (28%) than in the seedlings (12%; excluding *C. verum* seedlings), suggesting that survivorship of native seedlings was higher than that of invasive species (see Annex 2). Survival from the seedling to the sapling stage was apparently particularly poor for *C. verum* as well as for the early-successional invasive *Alstonia macrophylla*. In contrast, it was high in large-seeded species such as the native *Northea hornei* (seed diameter: c. 6 cm) and the invasive species

Chrysobalanus icaco (seed diameter: c. 2.5 cm). Support for the idea that species with large seeds are better able to regenerate in *C. verum* forests comes also from the observation that such species, both native (e.g. *Northea hornei, Pandanus hornei*) and alien (e.g. *Pentadesma butyracea, Syzygium jambos*), often occur as monospecific patches in *C. verum* forests.

Between-forest variation in competitive effects on tree saplings

While the response of *C. verum* saplings to trenching was strongly positive at CR and MC, there was no significant treatment effect in the third forest (CD). Neither light nor nutrient availability varied significantly among the three sites, and the results suggest that the difference was due to the dominance of *C. verum* at CR and MC, and its scarcity at CD. Thus the intensity of belowground competition was probably species-specific and attributable to the root mat of *C. verum*, rather than being a general characteristic of mid-altitude forests on nutrient-poor soils in the Seychelles.

The reduced growth of trenched *C. verum* saplings at CD was unexpected, and was probably due to the roots being damaged by the treatment. In fact, the mean RGRs of initially small trenched saplings (0.5-0.75 cm stem height) were similar to those of the control saplings (indicating no growth response to trenching) while the larger trenched saplings had considerably lower RGRs probably due to their root systems being more damaged (there were no such differences between control saplings of different size). Possibly, the lateral development of the root system in *C. verum* saplings is more constrained in *C. verum* dominated forests, reducing the risk of damage due to trenching. If correct, this would further underscore the distinctness of belowground conditions in *C. verum*-dominated forests.

Implications for forest succession

As invasive juvenile trees, particularly those of *C. verum* itself, appear to be more negatively affected by the *C. verum* root mat filter than native species, two different successional trajectories can be proposed for these forests. If some form of disturbance were to reduce belowground competition or otherwise increase nutrient availability, invasive species would probably regenerate most strongly. However, if the vegetation were left undisturbed, then saplings of native species would tend to prevail and would gradually replace *C. verum* in the canopy. It has recently been argued that less shady, early successional tropical forests that are dominated by light-demanding, alien woody species facilitate the regeneration of often bird-dispersed native pioneer species (Lugo 2004, Neilan et al. 2006). However, these forests are also vulnerable to the establishment of other alien species (compare Tecco et al. 2006). In contrast, undisturbed *C.*

verum forests may provide rather high resistance against colonization by nutrient demanding invasive species. This would present an example of the effects of an invasive species on ‘fellow invaders’ being negative, i.e. the opposite of an ‘invasional meltdown’ (Simberloff and Von Holle 1999). Hence, *C. verum* dominated forests may represent nurse habitats for the regeneration of native vegetation (compare e.g. D’Antonio and Meyerson 2002, Neilan et al. 2006, Tecco et al. 2006) as long as the propagule pressure of native species is sufficient.

Conclusions

The results of our study characterize the dominant invasive canopy tree *Cinnamomum verum* as a transformer species (Richardson et al. 2000) in the very nutrient poor forests of the Seychelles. Although being young and almost monospecific, the adult plants in *C. verum* forests appear to exert strong belowground competition on juvenile trees, particularly affecting seedlings by means of a dense root mat that is confined to an upper soil layer. As a consequence, forest regeneration is not only delayed, despite relatively high light availability, but the dense root mat also acts as a selective filter that suppresses the growth of small-seeded species and those with a high nutrient demand.

The mechanisms for strong belowground competition in *C. verum* dominated forests and their possible consequences for forest regeneration might also apply to several other invasive tree species that show indications of causing strong belowground competition, e.g. *Pentadesma butyracea* (Guttiferae; C. Kueffer, unpublished data). Indeed, the importance of belowground impacts of invasive trees in infertile forests may be much higher than previously thought.

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Chapter 4

The role of invasive woody plants in plant-frugivore interactions in the Seychelles

Abstract

Although close to 50% of woody invasive species are bird-dispersed, there have been few studies on the interactions between birds and invasive plants. We studied plant-frugivore interactions on an oceanic island of the granitic Seychelles, with special emphasis on the implications of frugivory for the spread of invasive species. The Seychelles has a small frugivorous fauna, and most native and invasive woody species are dispersed by the same three bird species, a bulbul (*Hypsipetes crassirostris*), a fruit pigeon (*Alectroenas pulcherrima*) and an invasive Mynah (*Acridotheres tristis*), while some larger fruits are also dispersed by a fruit bat (*Pteropus seychellensis*).

Nutritional analyses showed that invasive species produce fruits of higher quality in terms of energy than the native species of the Seychelles; this was mainly due to a lower water content, resulting in a higher relative yield, a higher energy content, and a tendency for higher sugar and fat contents. The most abundant invasive tree, *Cinnamomum verum,* accounting for > 80% of the canopy trees in most inland habitats, produces fruits of particularly high fat and protein content. In a selection experiment in which individuals of the endemic bulbul (*Hypsipetes crassirostris*) were presented with a choice of fruits, the fruits of *Cinnamomum verum* were preferred over those of all native trees except one.

It is argued that the presence of high quality fruits of invasive species can have both negative and positive impacts on native plant populations. If the native plants are in competition with invasive species for seed dispersers, then they could suffer increased dispersal limitation. On the other hand, by permitting higher densities of frugivore species, alien species may also promote dispersal of native plants.

Introduction

Invasions of alien plant species pose major threats to biodiversity and ecosystem functioning (Millennium Ecosystem Assessment 2005), especially on oceanic islands (Denslow 2003). However, neither the factors that make a species invasive (‘invasiveness’) (Kolar and Lodge 2001) nor the role invasive plants play in an ecosystem are well understood (Zavaleta et al. 2001, D’Antonio and Meyerson 2002, Levine et al. 2003).

Close to 50% of the global woody invasive flora is bird-dispersed (Binggeli 1996) and bird dispersal is regarded as an important criterion in weed risk assessment systems (Pheloung et al. 1999). Nevertheless, studies on the interaction between birds and invasive plants have been rather few (cf. Gosper et al. 2005). A better understanding of this relationship (Richardson et al. 2000) is needed for predicting the invasiveness of particular invasive plants and their role in ecosystem functioning.

Fruit traits can contribute to making a plant invasive. This can occur if birds prefer the fruits of invasive species over those of native species, so that the invasive species is dispersed more effectively (Vila and D’Antonio 1998); this effect is likely to be most important in the early phase of invasion when the species is still rare. There is evidence that small fruits (less than about 15 mm in diameter) that are dispersed by a wide range of different birds (‘generalized dispersal syndrome’) predominate among invasive plants (Richardson et al. 2000, Renne et al. 2002, Gosper et al. 2005). In contrast, the few studies that have compared the nutritional quality of native and alien plants have shown no consistent trend (Nelson et al. 2000, Gosper 2004, Corlett 2005).

The impact that fruits of invasive species may have on the ecosystem as a whole can be positive or negative. Where invasive species compete with native plants for seed dispersers, the impact is likely to be negative (cf. Gosper et al. 2005). Oceanic island ecosystems tend to be vulnerable to disruption of seed dispersal because they have a naturally species poor frugivore fauna, and populations of these animals are often reduced by human activities; indeed, loss of dispersers is seen as one of the major threats to rare plants on islands (e.g. McConkey and Drake 2006). Many oceanic islands were heavily deforested in the past and are now in a process of secondary succession. The relative abundance of propagules of native and invasive plants, and the relative effectiveness with which these propagules are dispersed can have an important influence on the course of the succession (compare e.g. Lugo 2004). Alternatively, invasive plants may provide native frugivore species with an important food resource (see e.g. D’Antonio and Meyerson 2002, Gosper et al. 2005, Neilan et al. 2006); and thereby contribute to the survival of rare frugivorous species or the maintenance of high frugivore densities that may lead to an increased dispersal of native species.

We investigated the impact of bird-dispersed invasive woody species upon plant-frugivore interactions on an Indian Ocean island in the Seychelles group. The inland habitats of the granitic Seychelles provide an ideal study system because the number of woody plant species is small (c. 75 native and 25 invasive woody species) and most of them have fleshy fruits. The original frugivore fauna consisted mainly of various lizards (*Mabuya* spp.), a giant tortoise (now extinct), an endemic fruit bat (*Pteropus seychellensis seychellensis*), and six bird species. The latter included two mainly insectivorous white-eyes (*Zosterops modestus*, only c. 300 individuals left on one small island; *Z. semiflava*, extinct), two fruit predatory parrots (*Coracopsis nigra barklyi*, c. 300 individuals left on one island*; Psittacula eupatria wardi*, extinct), a bulbul (*Hypsipetes crassirostris*), and a fruit pigeon (*Alectroenas pulcherrima*, a genus related to the *Ptilinopus-Ducula* fruit pigeons). Today, four frugivore species - the bulbul, the fruit pigeon, the fruit bat and an invasive Mynah (*Acridotheres tristis*) - are probably responsible for most of the seed dispersal.

The study poses three main questions:

(1) What is the relative importance of the three main native frugivores (a bulbul, a fruit pigeon, and a fruit bat) in dispersing the fruits of native and invasive woody species? And, do native and invasive plants share a common generalized dispersal syndrome (i.e. are their fruits dispersed by the same group of dispersers)?

(2) Do native and invasive plants produce fruits of similar nutritional quality for frugivorous birds? And, are fruit preferences of the commonest endemic frugivorous bird in the Seychelles, the bulbul *Hypsipetes crassirostris,* explained by difference in fruit quality?

(3) What is the impact of woody invasive plants on frugivore-plant interactions in the granitic Seychelles?

To address these questions we compared various measures of fruit quality of 22 common native and invasive woody species. We were particularly interested in the fruit quality of *Cinnamomum verum*, since this is by far the most abundant invasive species, accounting for > 80% of the canopy trees in most inland habitats. If this species provides fruits of particularly high quality, then it could have important consequences for plant-frugivore interactions on the islands of the Seychelles. To investigate fruit preferences of *Hypsipetes*, we performed choice experiments using captive birds.

Methods

Classification of dispersal syndromes

All published information concerning the fruit characteristics of native and invasive woody plants of the Seychelles was compiled (Robertson 1989, Friedmann 1994, Skerrett et al. 2001) and experts (12 biologists with extensive field work experience in Seychelles) were interviewed about fruit preferences of the various native frugivore species. The list of native plant species was taken from Beaver (2000), and the list of endemic species from Wise (1998). Strictly beach fringe and mangrove species were excluded. Non-woody species were not included because only a few of them (e.g. the native creeper *Cassytha filiformis* Lauraceae) produce fruits that are eaten by frugivores.

Based on the compiled data we classified plant species into five dispersal classes: wind, *Hypsipetes*, *Alectroenas*, *Pteropus* and others. We assumed that fruits could be broadly classified into different frugivore dispersal syndromes according to fruit size (e.g. Corlett 1998, Turner 2001). The classification was determined based on the maximal fruit size that is known to be swallowed by *Hypsipetes* viz. *Alectroenas*; this was 10 mm (relatively hard fruits with one to a few seeds) or 13-15 mm (soft fruits with many seeds) for *Hypsipetes* and 20 mm for *Alectroenas*. The classification was validated based on known frugivory interactions and typical characteristics for the respective dispersal syndromes (i.e. fruit color and odour, tree height), and adapted in a few cases (especially two cauliflorous species and two *Pandanus* species where classified as *Pteropus* dispersed). A species classified as *Hypsipetes* dispersed may also be disperse by *Alectroenas* or *Pteropus*; a species classified as *Alectroenas* dispersed may also be dispersed by *Pteropus*.

Plant material

The plant species used in the study included 14 native and 9 invasive woody species (Table 1); the species range from shrubs to large trees and include members of 13 plant families. The native plants include 11 species that are endemic to the Seychelles, and three (*Aphloia theiformis*, *Canthium bibracteatum* and *Dracaena reflexa*) that also occur on other Indian Ocean islands. Most of the invasive species are common in semi-natural to natural mid-altitude habitats in the Seychelles, though *Lantana camara* and *Litsea glutinosa* are mainly restricted to lowland areas.

The fruits were collected in secondary forests and inselberg (rocky outcrop) vegetation on

Table 1 Details of the native and invasive plant species investigated, with information on plant growth form, fruit characteristics and the fruit parameters measured (including fruit preference experiment with *Hypsipetes crassirostris)*. For asymmetric fruits the minimum diameter is given. A small tree is defined as one with a maximum height of < 10 m. The number of fruits collected for the morphological and chemical analyses (N) is indicated in four categories (a: 10-25, b: 25-50, c: 50-75, d: > 100).

Species	Family	Fruit diameter (mm)	Height	Fruit color	Fibre	Protein	Sugar	Fat	Relative yield	N	*Hypsipetes* experiment
Native species											
*Aphloia theiformis**	Flacourtiaceae	10	small tree	white	X	X	X		X	b	
Canthium bibracteatum	Rubiaceae	5.5	small tree	orange	X	X	X	X	X	d	X
Dillenia ferruginea	Dilleniaceae	9.5	tree	orange	X	X	X	X	X	d	X
Dracaena reflexa	Liliaceae	11.5	shrub	red					X	b	
Erythroxylum sechellarum	Erythroxylaceae	6	small tree	red	X	X	X	X	X	d	X
Gastonia crassa	Araliaceae	10	small tree	black	X	X	X		X	a	
Memecylon eleagni	Melastomataceae	8.5	small tree	black	X	X	X	X	X	d	X
Nephrosperma vanhoutteana	Palmae	12.5	tree	red	X	X	X	X	X	b	X
Paragenipa wrightii	Rubiaceae	9.5	small tree	red	X	X	X	X	X	d	X
Phoenicophorium borsigianum	Palmae	8	tree	red	X	X	X	X	X	b	
Psychotria pervillei	Rubiaceae	6	shrub	black					X	b	
Roscheria melanochaetes	Palmae	6.5	small tree	red					X	b	
Syzygium wrightii	Myrtaceae	18	tree	black	X	X	X	X	X	a	
Timonius sechellensis	Rubiaceae	9.5	small tree	black	X	X	X	X	X	b	
Invasive species											
Ardisia crenata	Myrsinaceae	9	shrub	red	X	X	X		X	b	
Chrysobalanus icaco	Chrysobalanaceae	32.5	small tree	red	X	X	X	X	X	d	
Cinnamomum verum	Lauraceae	9	tree	black	X	X	X	X	X	d	X
Clidemia hirta	Melastomataceae	7.5	shrub	black	X	X	X	X	X	d	
Lantana camara	Verbenaceae	5.5	shrub	black						c	X
Litsea glutinosa	Lauraceae	10	Small tree	black	X	X	X	X	X	d	X
Memecylon caeruleum	Melastomataceae	9	shrub	black	X	X	X	X	X	a	
Psidium cattleianum	Myrtaceae	35	small tree	red	X	X	X	X	X	b	
Syzygium jambos	Myrtaceae	24.5	tree	white	X	X	X	X	X	c	

*subspec. *madagascariensis* var. *seychellensis*

300 to 600 m asl., plus one coastal inselberg (c. 100 m asl.), on the island of Mahé (4° S, 55° E, 154 km^2, Republic of Seychelles). These mid-altitude secondary forests were almost completely deforested in the early 19th century and have since been invaded by the invasive tree *Cinnamomum verum* that now typically makes up more than 80% of the canopy (Kueffer and Vos 2004). In *Cinnamomum* forests native woody species are rare in the canopy (c. 5-10% of the individuals) but more abundant in the sapling layer (c. 15-30%) (C. Kueffer, unpublished data). In contrast, inselbergs, that are scattered within the secondary forests on the scale of one to a few km^2, harbour c. 80% native species (Fleischmann et al. 1996).

Between 10 and several 100 ripe fruits per species (Table 1) were collected from February to September 2004 from at least two and usually 3-4 sites for the chemical analyses, and occasionally from only one site for those species where only the morphology and water content were determined. The fruits were collected in the wild, except for the two lowland species (*Lantana camara, Litsea glutinosa*; from gardens), and *Phoenicophorium borsigianum* (botanical garden in Victoria).

Fruit quality

The seeds were separated form the pulp and counted; and the length and width of the fruits and seeds were measured using a caliper accurate to 0.05 millimetres. Fruits and seeds were weighed (accuracy of 1 mg) before and after drying at 40-50 °C for 4 days to determine water content and dry mass per fruit. The samples were then stored in plastic bags with silica gel for transport to the laboratory in Switzerland.

All chemical analyses were performed at the Swiss Federal Research Institution for Farm Animals and Dairy Farming (ALP) in Posieux, Switzerland. For the chemical analyses, the dried pulp was ground in a laboratory mill with a one millimetre sieve and 750 rpm. The following minimal dry fruit masses were used for the chemical analyses: 5 g (fat), 1 g (sugar, fibre) and 0.5 g (protein). A constant dry matter content was determined with a thermographic system (at 105°C for 2 h 40); the water content (of the already dried and transported material, see above) was very constant between the different species (5%-10%), indicating that the water content measurements determined at 50°C, and used for the analyses, were reliable.

Crude fibre as determined by the Weende method (von Lengerken 2004) represents the content of organic structural material such as cellulose or lignin that is not dissolved in a weak acid or base (similar to the conditions in animal digestion). The plant material was dissolved in an acid (1.25% H_2SO_4 solution, 1 h at 95°C) and a base (1.25% KOH solution, 1 h at 95°C). The insoluble residue was then washed with water and acetone, dried (1 h at 130°C), weighed and ignited at 530°C for 1 h. The loss in weight on ignition was identified as crude fibre.

For the determination of the total sugar content, the sample was extracted with 80% ethyl alcohol (EtOH) (shaken at 80°C for 1 h). After filtration, total sugar content was quantified colorimetrically based on a reaction with 1 g 3,5-Dihydroxyltoluol (Orcin) in 1 l 70% sulphuric acid (H_2SO_4) (calibrated with sucrose).

Crude protein was determined using the DUMAS method (von Lengerken 2004). Crude protein content was calculated from the total nitrogen content by multiplication with 6.25. Nitrogen content was determined with an FP-2000 nitrogen analyzer (LECO, St. Joseph, MI, USA) after complete oxidation of the plant material at c. 1100°C.

Crude total fat was determined with a Soxhlet system (Soxtec Avanti 2050; Foss, Denmark). The plant material was hydrolised in boiling 10% HCl solution for 1 h (Berntrop method), and then extracted with petrol ether at 40 – 60°C in the Soxhlet system.

Fruit preference experiment with **Hypsipetes crassirostris**

Hypsipetes crassirostris (Seychelles Bulbul, Pycnonotidae, Passeriformes) belongs to a tropical Asian genus with 4 endemic species and 2 endemic subspecies in the Western Indian Ocean. *Hypsipetes* is a relatively large (25 cm), territorial woodland species with a broad diet including insects, lizards, leaves, flowers and fruits. It is very common on the granitic islands of the Seychelles, occurring from the coast to tops of the highest mountains, and with an estimated density of > 1000 birds per square kilometre (Skerrett et al. 2001).

With the aid of a tape recorder playing bulbul calls, birds were caught in mist nets placed in the same locations where fruits were collected (see above). Each of the eight birds caught was weighed, measured and a blood sample was taken for sex determination (analysed at the School of Biological Sciences, University of East Anglia, Norwich, England). We caught six males, one female and one bird of unknown sex, of which two birds were juveniles. For two to three days before being used in the experiments, the birds were fed with garden fruits such as bananas, papayas, golden apples and mangos and with animal material including spiders, insects and gecko tails. Such supplementary feeding was continued throughout the experimental period.

The fruit preference experiment was performed from March to August 2004 in an aviary (length: 6.3 m, depth: 2.9 m. height: 3.2 m; Sans Souci forestry station, 250 m asl.). The preference trials lasted for 3 to 6 days and took place in the morning, from 7.00 a.m. to c. 11.00 a.m. and/or in the afternoon from 3.30 p.m. to c. 5.30 p.m. Between 3 to 11 trials were performed at any one period. The experiments were always performed by the same person. One trial consisted of presenting fruits of two different species separated by c. 15 cm on a flat board. For this, the fruits were placed randomly in one of two Petri dishes. We controlled for fruit mass rather than number when confronting the birds with a choice between a species with small fruits and a species with large fruits, i.e. several small fruits of the first species were presented to match the total mass of one large fruit of the second species. We noted which fruit was chosen first by the bird, whether it was swallowed or only pecked, and whether the second fruit was also pecked or swallowed. Between two trials there was a break of five to ten minutes. The fruits were collected at the same locations as for the chemical analyses, and used either freshly collected (30% of the fruits) or after storage in a freezer. For all species, both frozen and unfrozen fruits were used, and no apparent difference in the selection for frozen or unfrozen fruits was observed.

We were interested in the fruit preference for native species in comparison with the most abundant invasive species *Cinnamomum verum*. We therefore performed trials with 6 native and 2 invasive species against *Cinnamomum*. These trials were alternated with trials where two species other than *Cinnamomum* were offered. This reduced the risk that an oversupply of *Cinnamomum* fruits would bias the experiment, and allowed us to compare the preference against *Cinnamomum* with the preference against other fruits for the tested species. With this experimental design, c. 50% of the total fruits offered were from *Cinnamomum*, and two thirds of the experiment involved *Cinnamomum*. The sequence of fruit species in the trials was randomized and differed between experimental periods and birds.

To estimate gut passage time, the first fruit fed in the morning was of a single species. The bird was then observed until the seeds of this species were dropped. At that time the bird had eaten no fruits of the tested species for at least 20 hours so that we were sure that the dropped seed was not from a fruit eaten previously.

Calculations and statistical analyses

The energy content of the pulp was calculated based on the following conversion factors: 5.2 kcal g^{-1} (protein), 9.3 kcal g^{-1} (fat), and 4.0 kcal g^{-1} (sugar) (Watt and Muriel 1963).

For the correlation analyses between the fruit preference of *Hypsipetes* (fruit preference experiment) and fruit characteristics, water content and relative yield for *Lantana camara* were derived from data in the literature (Corlett 2005).

The differences in fruit characteristics between native and invasive species were tested with a one-way ANOVA (native v. invasive). *Litsea glutinosa* was excluded, because extreme values of two Lauraceae species (together with *Cinnamomum verum*) would have biased the results. The data for fat content and overall profitability of the energy content were log-transformed to meet the assumptions of ANOVA.

All statistical analyses were performed with JMP V 6.0 (SAS Institute Inc. 2005).

Results

Dispersal syndromes among the native and invasive woody plants

The literature review and expert questionnaires revealed that 80% to 90% of the endemic woody species in Seychelles are dispersed by frugivores while six species are wind-dispersed (Fig. 1). A further eight species were classified as ‚others', including six species for which the dispersal is not known (possibly frugivores), one species with a possible endozoochorous dispersal (*Pisonia sechellarum*), and the coco de mer *Lodoicea maldivica* which has no dispersal agent (except gravity). In contrast, only about two thirds of the invasive woody species are dispersed by frugivores, the others being either wind (4) or gravity (4) dispersed.

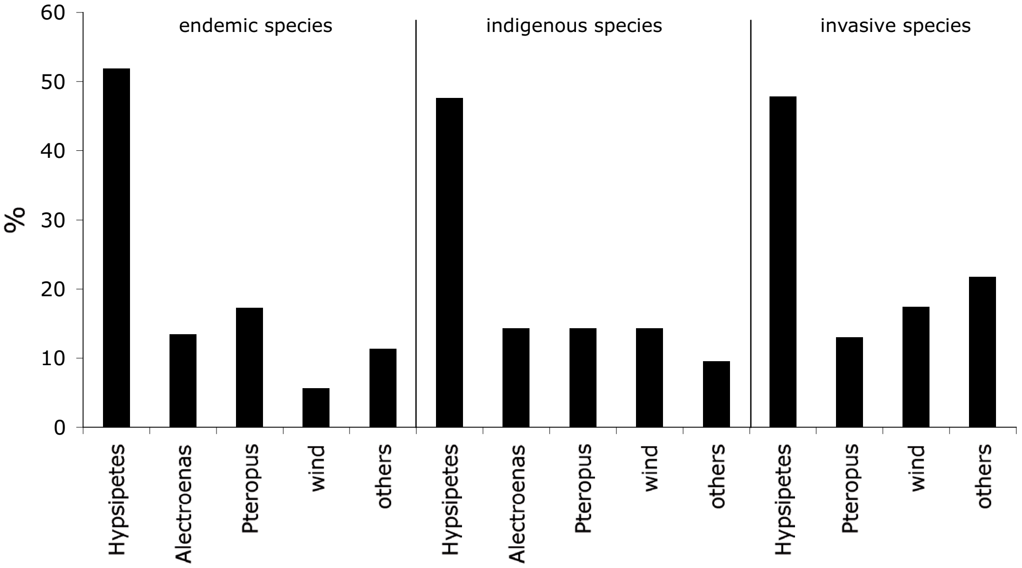

Fig. 1 Inferred dispersal mode of the woody endemic (52 species), indigenous (native but not endemic, 21 species) and invasive (23 species) flora of the granitic Seychelles expressed as a percentage of each of the respective category.

Half of the woody species of the endemic, indigenous and invasive floras have *Hypsipetes* fruits, i.e. relatively small fruits (< 10 (-15) mm diameter) that may be chosen by several frugivorous species, especially *Hypsipetes* but also *Alectroenas, Pteropus*, *Zosterops* or *Coracopsis* (and the invasive *Acridotheres*).

Among the endemic species there are three species with dehiscent fruits containing small seeds that may be dispersed by *Hypsipetes* or *Zosterops*; one was classified as *Hypsipetes* dispersed (*Pittosporum senecia*), the other two (*Excoecaria benthamiana*, *Glionnetia sericea*) were included in ‚others'. About 10 native species have fruits that may be small enough (smaller than 5-6 mm in diameter) to be dispersed by *Zosterops* or lizards.

Three species of invasive trees have large, soft fruits containing many small seeds (2 *Psidium* spp., *Carica papaya*); although these fruits cannot be swallowed whole by *Hypsipetes* or *Acridotheres,* they were included in the category of the *Hypsipetes* dispersed species because the small seeds are dispersed after ingestion of fruit parts. One invasive species with mimetic fruits (*Adenanthera pavonina*) may occasionally also be swallowed and dispersed by *Hypsipetes* or *Alectroenas* (included in ‚others').

Ten native (indigenous and endemic) but no invasive species were classified in the category ‚*Alectroenas*', i.e. neither *Hypsipetes* nor *Pteropus* fruit size, and 12 native species were classified as *Pteropus* dispersed, including one cauliflorous species (*Colea seychellarum*), two Sapotaceae (*Northea hornei, Mimusops sechellarum*) and two pandans (*P. balfourii, P. sechellarum*). A pandan (*P. hornei*) and a palm (*Verschaffeltia splendida*) classified as ‚others', may also be *Pteropus* dispersed.

The fruit sizes of the woody native species are evenly distributed within the size ranges of the three frugivores syndromes (median: *Hypsipetes* 7.5 mm, *Alectroenas* 13.5 mm, *Pteropus* 35 mm). Half of the *Hypsipetes* fruits are red or orange, and c. 40% are black (plus three white and one yellow); c. 80% of the plants bearing them are shrubs or small trees (< 10 m height). Apart from one black and one yellow fruit, the *Alectroenas* fruits are all red or orange, and the plants bearing them are both small and large trees (plus one shrub, *Dracaena reflexa*). 75% of the *Pteropus* fruits are green or brown (plus a yellow, red and orange one), and c. 60% are large trees (no shrubs). In total, there are c. 20% shrubs, 50% small trees, and 30% large native trees. Among the invasive species, there are 47% red and 40% black fruits (plus 2 yellow ones), and 87% are shrubs or small trees.

Differences in fruit quality between native and invasive woody plants

The fruits of invasive species had a lower average water content than those of native species, resulting in a c. 50% higher relative yield, i.e. ratio of dry pulp to total wet fruit weight including seeds (Table 2). The seed burden, i.e. the seed to total fruit weight ratio, did not differ between the two groups.

Table 2 Mean wet fruit weight, water content of the pulp, seed burden (% wet seed: total fruit weight) and relative yield (% dry pulp weight: total wet fruit weight) of 14 native and 8 invasive woody species in the Seychelles. The group means (excluded *Litsea glutinosa*), and the F-ratio and P-value from a one-way ANOVA (native, invasive) are also shown: ***, P < 0.001; **, P < 0.01.

Species	fruit weight (mg)	water content %	seed burden %	relative yield %
Native species				
Aphloia theiformis	431	86.67	7.89	12.36
Canthium bibracteatum	167	79.63	35.33	15.05
Dillenia ferruginea	932	85.92	4.72	13.44
Dracaena reflexa	1857	86.00	43.46	11.05
Erythroxylum sechellarum	290	88.27	38.28	8.48
Gastonia crassa	954	85.81	8.39	13.09
Memecylon eleagni	424	83.84	35.85	15.35
Nephrosperma vanhoutteana	2303	89.51	48.24	7.07
Paragenipa wrightii	867	86.58	9.00	12.31
Phoenicophorium borsigianum	324	87.60	60.49	7.73
Psychotria pervillei	104	90.36	19.23	7.21
Roscheria melanochaetes	187	83.49	42.25	9.78
Syzygium wrightii	5124	87.26	43.17	8.90
Timonius sechellensis	891	82.42	34.12	13.11
Invasive species				
Ardisia crenata	220	82.76	60.45	10.75
Chrysobalanus icaco	16137	89.32	24.82	8.56
Cinnamomum verum	723	65.89	52.56	22.36
Clidemia hirta	230	76.00	4.50	21.80
Litsea glutinosa	621	74.17	51.37	17.06
Memecylon caeruleum	625	77.68	44.8	15.41
Psidium cattleianum	21380	74.45	24.72	20.49
Syzygium jambos	6884	77.44	53.57	14.69
native (mean)		86.0	30.7	11.1
invasive (mean)		77.6	37.9	16.3
ANOVA (F,P)		**14.59*** **	0.70	**8.50** **

Although the fibre, protein, fat and sugar contents of dry pulp did not differ significantly between native and invasive fruits (Table 3), in each case the highest values were found in fruits of invasive species. These high values ranged from approximately double the median value for the native species for fibre, protein and sugar to 30 times as high for fat. The average energy value of fruits (calculated from the protein, sugar and fat contents) was 45% higher, while the overall profitability (OP, i.e. energy content per total wet fruit weight) was about twice as high for invasive than for native species.

When the fat-rich fruits (invasive: *Cinnamomum,* native: *Erythroxylum*), that are typically low in sugar content (Jordano 1995, Corlett 1996), were excluded from the analysis, the sugar content

Table 3 Nutritional composition of 11 native and 8 invasive woody species in mg or kcal (energy content) per g dry pulp. The overall profitability (OP) of the energy content is calculated, based on the relative yield, as the energy content per g of total wet fruit weight. The group means (excluded *Litsea glutinosa*), and the F-ratio and P-value from a one-way ANOVA (native, invasive) are also shown: *, $P < 0.05$.

Species	fibre	protein	fat	sugar	energy	OP energy
Native species						
Aphloia theiformis	80	57		162		
Canthium bibracteatum	112	40	7	351	1.667	0.252
Dillenia ferruginea	59	57	10	276	1.493	0.201
Erythroxylum sechellarum	55	46	128	351	2.834	0.240
Gastonia crassa	75	41		270		
Memecylon eleagni	133	28	7.5	400	1.815	0.279
Nephrosperma vanhoutteana	231	57	13	131	0.941	0.067
Paragenipa wrightii	217	43	21	208	1.251	0.154
Phoenicophorium borsigianum	112	93	14	46	0.798	0.062
Syzygium wrightii	171	45	11	244	1.312	0.117
Timonius sechellensis	247	39	8	188	1.029	0.135
Invasive species						
Ardisia crenata	180	51		232		
Chrysobalanus icaco	81	28	7	421	1.895	0.162
Cinnamomum verum	264	62	252	39	2.822	0.631
Clidemia hirta	210	73	51	380	2.374	0.518
Litsea glutinosa	46	113	350	36	3.987	0.680
Memecylon caeruleum	94	36	48	451	2.438	0.376
Psidium cattleianum	240	24	7	264	1.832	0.255
Syzygium jambos	176	52	10	255	1.383	0.203
native (mean)	135.6	49.6	24.4	238.8	1.461	0.17
invasive (mean)	177.9	46.6	62.5	291.7	2.124	0.36
ANOVA (F,P)	1.56	0.13	1.00	0.83	**4.72***	**6.99***

of the invasive fruits was on average c. 50% higher (333.8 v. 227.6 mg g^{-1}, P = 0.06), and in both intra-generic comparisons in the dataset (*Memecylon elagni* v. *M. caeruleum*, *Syzygium wrightii* v. *S. jambos*) the invasive species had a 5-10% higher sugar content. Among the sugar-rich species (*Cinnamomum* and *Erythroxylum* excluded to account for the different relative frequency of fat-rich fruits in the native and invasive fruit sample), the mean fat-content of the invasive species was twice that of the native ones, and in one intra-generic comparison (*Memecylon*), the fat content was 6.5-times higher in the invasive species. The differences between the sugar-rich native and invasive species in sugar and fat contents were stronger when the overall profitability (OP) was calculated based on the relative yield, i.e. invasive species had on average a 3.5-times higher OP of fat (P = 0.08) and a 1.7-times higher OP of sugar (P = 0.05).

Among the native species, the sugar and protein contents of pulp were negatively correlated (r = -0.8, P = 0.005), and the palm *Phoenicophorium borsigianum* had particularly high protein and low sugar contents.

Fruit preference by **Hypsipetes crassirostris**

In the pairwise selection tests using fruits of *Cinnamomum verum* as the control, preference values ranged from 5% to 64% for different fruits (Fig. 2). For all species except *Dillenia ferruginea* and *Litsea glutinosa*, *Cinnamomum* was chosen in more than 50% of the trials. However, there were considerable differences between individual birds in their preference for *Cinnamomum* (41%-75%), and one individual never selected *Cinnamomum* or any other black fruit.

The only fruit characteristic that was correlated with fruit preference was the relative yield (r = 0.7, P = 0.06). The preference for the fat-rich fruits of the endemic *Erythroxylum sechellarum* was very low in trials with *Cinnamomum* (5%) but relatively high in the trials with other species (52%).

Gut passage time of *Hypsipetes* in captivity was c. 15 minutes (median: 14 min, quartiles: 11-20 min, max: 35 min, N = 77 trials with 5 different fruit species).

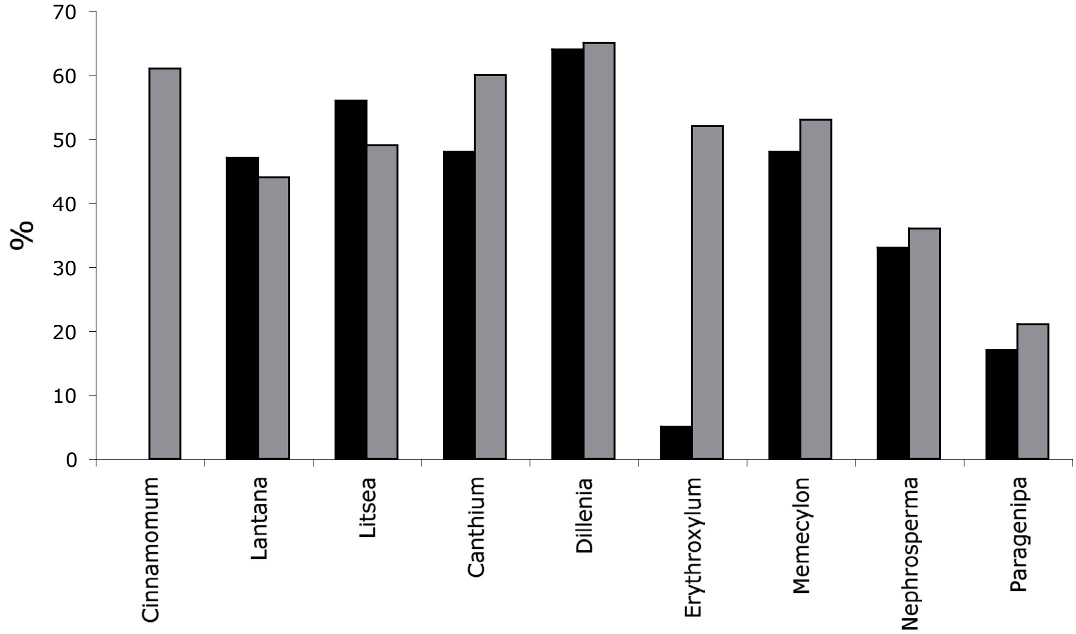

Fig. 2 Results of the selection experiment using captive individuals of *Hypsipetes crassirostris* (Seychelles Bulbul) and the fruits of 6 native and 2 invasive woody species. The black bars show the percentage selection of each species when *Cinnamomum verum* fruits were offered as the alternative (N = 15-33 trials per species); the grey bars show the percentage selection when one of the other species was offered as the alternative. For *Cinnamomum* the mean of the preferences against the 8 other species is given.

Discussion

Dispersal modes of native and invasive woody species

With 80% to 90% of plants being animal dispersed, the importance of zoochory among the endemic woody species in Seychelles is similar to that for woody floras of other tropical rainforests (Herrera 2002). Among invasive species, inefficient dispersal by gravity is surprisingly common (c. 25%), suggesting that these species have profited from human activities (e.g. planting for timber production or erosion control). Thanks to their large seeds, where these species have established they commonly form more or less pure stands which regenerate vigorously.

On the basis of size, the fruits of the native flora could be readily assigned to one of the three main native frugivores, with about 63% to *Hypsipetes* (red or black, from shrubs or small trees, 3-12 cm diameter), 17% to *Alectroenas* (red, small trees, 12-20 cm), and 20% to *Pteropus* (green or brown, large trees, > 20 cm) dispersed species. However, the overlap of frugivory niches is clearly large. Only some five to ten of the *Hypsipetes* species (e.g. *Canthium sechellense,* *Psychotria silhouettae, Schefflera procumbens*) have fruits too large to be dispersed by *Zosterops* or lizards, and because these species are understorey shrubs they may also not be chosen by *Alectroenas*. Similarly, of the *Alectroenas* species only two indigenous and one endemic species (*Carissa edulis, Dracaena reflexa, Nephrosperma vanhouetteana*) are probably not dispersed by *Pteropus,* or by *Hypsipetes* (e.g. dispersal of the small seeds of *Paragenipa wrightii*); and about half of the *Pteropus* fruits may also be water or tortoise dispersed. In summary, at least half of the species may be interpreted as forming part of a ‚generalized dispersal syndrome' (cf. Renne et al. 2002, Gosper et al. 2005), meaning that they are dispersed by both *Hypsipetes* and *Alectroenas* (and most probably also by at least one more native guild, i.e. *Zosterops*, or *Pteropus*). Additionally, the invasive *Acridotheres tristis* is today also an important disperser of these fruits. The animal dispersed invasive species include some of the most abundant invasive species (*Cinnamomum verum, Lantana camara, Psidium cattleianum*), as well as rapidly spreading recent introductions (*Dillenia suffruticosa, Clidemia hirta*). However, only some of them exploit the opportunity of a generalized dispersal syndrome; while others are exclusively *Hypsipetes* (and possibly *Acridotheres*) dispersed.

The paucity of fleshy fruits specifically adapted to dispersal by *Alectroenas* can be related to apparent gaps in the systematic composition of the Seychelles flora. With the exception of the palms, families with species producing relatively large fat or protein rich fruits (e.g. *Burseraceae, Lauraceae, Meliaceae, Myristicaceae, Rutaceae, Solanaceae*, see Jordano 1995, Corlett 1996, Corlett 1998) are lacking in the endemic flora of the Seychelles, while for example in neighbouring Magadascar these types of fruit are important components of the diet of specialist frugivorous birds (Snow 1981, Corlett 1998, Nelson et al. 2000, Meehan et al. 2002, Oliveira et al. 2002). In the Seychelles, some of the small and sugar rich fruits that are also dispersed by *Hypsipetes*, e.g. palms, *Erythroxylum*, *Trema orientalis* (Snow 1981), *Moraceae* and possibly *Campnosperma seychellarum* (Anacardiaceae) or *Araliaceae* species, seem to provide the relatively high contents of fat or protein required by *Alectroenas*.

Why should this guild of large-fruited trees be largely absent from the Seychelles? Possibly the islands are too small or too isolated to allow for a tight mutualism between large-fruited, bird dispersed plants and *Alectroenas* (blue pigeons typically have flight ranges of several 100 km, Shanahan et al. 2001). On many larger or less isolated oceanic islands, e.g. in the Pacific (Nelson et al. 2000, Meehan et al. 2002), in the Mascarenes (Bosser et al. 1976-), or in Macronesia (Oliveira et al. 2002) several of the typical plant families eaten by specialist frugivores are present and make up an important portion of the diet of, sometimes very large, fruit pigeons. In Tonga (Western Polynesia), for instance, nine different species of fruit pigeons have evolved (Meehan et al. 2002). An interesting contrast, and a possible parallel with the Seychelles, is provided by the tiny and remote Pitcairn Islands; the endemic fruit pigeon species of these islands is small and the flora, and consequently the diet of the fruit pigeon, consists entirely of small-fruited families such as the *Urticaceae* or *Rubiaceae* (Brooke and Jones 1995, Kingston et al. 2004).

Alternatively, it has been written that *Alectroenas* has a gizzard stomach that destroys digested seeds (Skerrett et al. 2001). This would be a strong selective force for a reduced attractiveness of fruits to *Alectroenas*. However, the closely related fruit pigeon genera *Ptilinopus* and *Ducula* do not have a gizzard stomach (cf. Corlett 1998), and we successfully germinated *Ficus* seeds after digestion by *Alectroenas*. More probable is that fruit predation by parrots may have played a role. The two native parrot species probably fed on *Alectroenas* fruits (for *Coracopsis* see Goodman and Benstead 2004), and on the Seychelles, where only a fruit pigeon species has dispersed these fruits, the fruit predation by two parrot species may have made up a more important proportion of the frugivory interactions.

There are important differences in the feeding ecology of *Hypsipetes* and *Alectroenas* that may be significant for their role as dispersal agents. *Alectroenas* is capable of consuming large amounts of fruits, and often feeds for a long time in a single tree before moving to a nearby tree to digest its food. Fruit pigeons fly long distances and have prolonged digestion passage times of 20 to 530 min (cf. Shanahan et al. 2001). In contrast, we recorded gut passage times of 5 to 20 min for *Hypsipetes,* and similar values have been reported for other bulbul species (5-47 min cf. Shanahan et al. 2001). Thus, dispersal by *Alectroenas* may lead to infrequent long-distance dispersal events, but mainly to highly clumped seed deposits (in the Seychelles seedlings of different palm species often occur in clumps, C. Kueffer, pers. obs.), while *Hypsipetes* dispersal leads to a scattered distribution on a small scale (a conclusion also supported by seedling regeneration data from the Seychelles, L. Kronauer & C. Kueffer, unpublished data).

Differences in fruit quality between native and invasive woody plants

Our results showed that invasive species produce fruits of higher quality in terms of energy than the native species of the Seychelles; this was due to a lower water content, resulting in a higher relative yield, a higher energy content, and a tendency for higher sugar and fat contents. In contrast, there was no difference between the two groups in protein content, though this is often thought to be the most limiting resource of specialist frugivores (e.g. Corlett 1998, Jordano 2000, Pryor et al. 2001).

The mean water content of the invasive fruits (77.6%) was similar to values reported for bird-dispersed fleshy fruits in the global angiosperm flora (71.8%, Jordano 1995), fleshy fruits of the native flora of Hong Kong (78%, Corlett 1996), and alien plants in Hong Kong, Australia and New Zealand (76-78%, N = 12-15 species per region, Williams and Karl 1996, Corlett 2005, Gosper et al. 2006), while the native species had a considerably higher water content (86%). A possible explanation for the differing pulp water content of the native fruits may be that watery fruits are typically sugar-rich while fat-rich fruits have a low water content (Corlett 1996). In fact, there was only one fat-rich native fruit in our sample (*Erythroxylum sechellarum*). But when only the fat-poor, bird-dispersed fleshy fruits of the alien or native species from Hong Kong were analysed, they still had a lower water content (median: 80% derived from Corlett 1996, Corlett 2005). The nearly significant correlation between relative yield and fruit preference in the captivity experiment with *Hypsipetes* indicates that the difference in water content and relative yield may be relevant for fruit choice and consequently for dispersal efficiency by *Hypsipetes*.

In contrast to our study, published data show no trends for any morphological or nutritional differences between native and alien or invasive fruits (Nelson et al. 2000, Corlett 2005, Drummond 2005, Gosper et al. 2005). However, in most studies only a few invasive and/or native species were included, and some studies compare native with alien species while others specifically address invasive species. The only comprehensive study, comparing the alien and native flora of Hong Kong, found no differences except trends for larger fruits and a lower seed load in the invasive species (Corlett 2005).

The observed differences in fruit quality in this study may stem from particularities of fleshy fruits of a small oceanic island flora rather than of invasive species. There are several possible explanations why plants on oceanic islands may profit less from the production of fruits of high quality. First, it has been assumed that efficient dispersability is of reduced importance for the fitness of island plants (Carlquist 1965, Whittaker 1998). Second, the very low plant diversity on islands may lead to a flatter dominance-diversity curve than in species-richer ecosystems (e.g. Hubbell 2001), i.e. most species are common. Because of frequency- or density-dependent effects, common species may need to invest less in fruit quality than rare species to attract birds (compare Stephens and Krebs 1986). Third, generalist frugivorous species with a broad dietary niche, typical for oceanic islands, may show a relative low selectivity for species with a higher fruit quality, which was also indicated by the generally high plasticity of preference patterns between individuals in the *Hypsipetes* captivity experiment. In addition, phenology, i.e. the daily availability of ripe fruits, may determine fruit choice, especially of specialist frugivores, more than fruit quality.

The role of invasive woody plants in frugivore-plant interactions

Differences in fruit quality between invasive and native species may contribute to the invasiveness of certain species. This could explain the very effective dispersal of *Cinnamomum verum* fruits; these have higher fat and protein contents than most native species and in the selection experiments with *Hypsipetes* were the most preferred fruits apart from those of the native *Dillenia ferruginea*. Interestingly, the native species richest in fat, *Erythroxylum*, showed a very low attractiveness against *Cinnamomum*, but a high one against other fruits, which may indicate that fat content played an important role for the selection of these particularly fat-rich fruits. In the field, where searching and picking fruits costs time and energy, it may be particularly relevant, that the fruits of *Cinnamomum* have a fruit size very close to the maximal size that can be swallowed by *Hypsipetes*, and that therefore the protein and fat intake per fruit (single fruit profitability) is particularly high, i.e. 3.5 and 55 times higher than the median of the native species, respectively.

It can be expected that the preference of *Alectroenas* for *Cinnamomum* is even more pronounced than of *Hypsipetes*. In contrast to sugar digestion, effective fat digestion needs long gut passage times (Witmer and Van Soest 1998, Levey and Martinez del Rio 2001), typical for large, specialist frugivores such as *Alectroenas* but not for small, omnivorous species such as *Hypsipetes*. Nevertheless, *Hypsipetes* also showed a high preference for fat rich fruits, which may have to do with the presence in the Seychelles flora of small, fat rich fruits (see above).

The preferential selection of *Cinnamomum*, that makes up more than 80% of the canopy in many inland forests, may have serious negative impacts on the native plant diversity. *Cinnamomum* fruits prolifically during the main fruiting season of many native plants (February to May) and may reduce the dispersal of native species which are competing for the same seed dispersers. Most inland habitats in Seychelles are secondary forests dominated by alien species that are in a process of colonization by native species from surrounding remnants patches of native vegetation (e.g. inselbergs); i.e. most native species are rare or absent in the adult layer but more frequent in the juvenile layer (C. Kueffer, unpublished data). A secondary succession towards a forest with a higher frequency of native species (compare Lugo 2004) therefore depends critically on efficient dispersal by frugivores.

The presence of *Cinnamomum* may also have had very important positive impacts on the native frugivorous fauna, particularly *Alectroenas*. Prior to human colonization of the Seychelles, *Alectroenas* probably depended largely on a few *Ficus* and palm species that produce large fruit crops, fruit non-synchronously among individual trees, and produce fruits that are relatively rich in protein and minerals (Jordano 2000, Nelson et al. 2000, Ruby et al. 2000). In order that there were daily fruiting trees available, these species must have been very abundant on the landscape scale. By the early 19th century, most area of the granitic Seychelles was deforested. Probably the fruit production of the invading *Cinnamomum* and possibly other alien trees in gardens acted as alternative food sources and assured the survival of the species. Today, palms are relatively frequent, but the total number on the landscape scale is probably small compared with the undisturbed state prior to human settlements, and *Ficus* species are relatively rare, especially in inland habitats. So, *Alectroenas* probably depends heavily on alien fruit sources, e.g. *Cinnamomum* or *Cananga odorata* in gardens. Similarly, *Pteropus* today probably almost exclusively lives on alien fruits plus several fig species and some pantropical coastal native trees. Large seeded endemic trees are probably dispersed only rarely, which may contribute to their declining populations.

Overall, the capacity of frugivores to switch to alien food sources has been important for their survival. It has been recognised that the rare *Coracopsis* (Evans 1979) and the critically endangered *Zosterops* (G. Rocamora, pers. comm.) have both benefited from the large availability of alien fruits. And while all except one insectivorous bird and bat species of the granitic Seychelles are threatened, two of the frugivorous bird species, *Alectroenas* and *Hypsipetes*, and the fruit bat species remain abundant.

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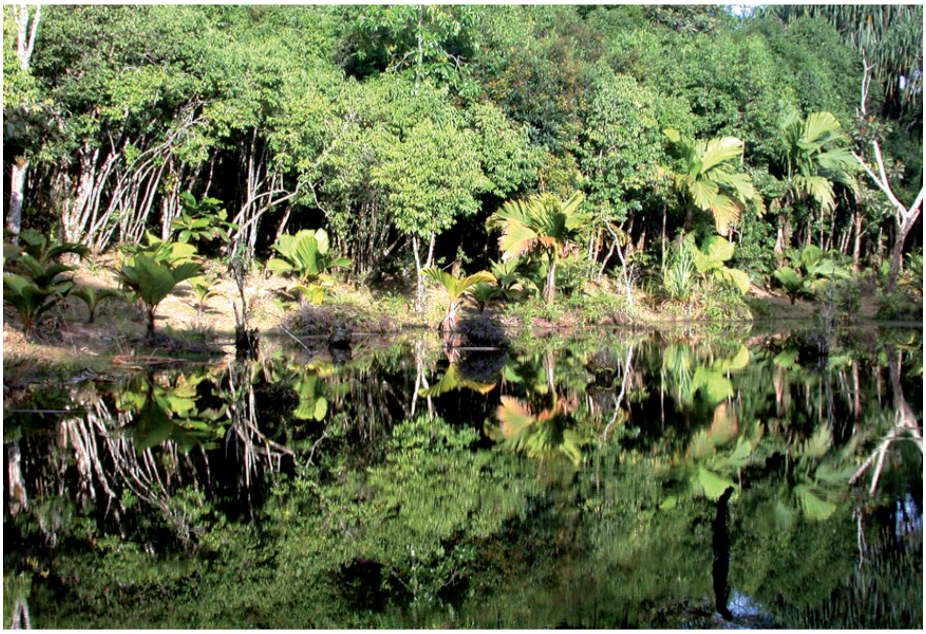
Chapter 5

Integrative ecological research: Case-specific validation of ecological knowledge for environmental problem solving



Abstract

Taking ecology as an example, I discuss the contribution of a disciplinary natural science to environmental problem solving. I argue that both disciplinary and transdisciplinary research are required to solve complex environmental problems, and that their roles are complementary. To tackle such problems, there must be a reciprocal exchange of knowledge between science and application, a process that has been called ‘mutual learning’. This exchange is most effective in application contexts where the scientific and social complexities are relatively bounded. I call these contexts ‘trading zones’. Transdisciplinary research can help to build such trading zones.

The concept of the trading zone is illustrated taking the example of ecology and adaptive management. I argue that an ecological research strategy that may be termed ‘integrative ecological research’ is particular relevant in the context of this trading zone. Integrative ecological research seeks to explain the complexity of specific field or real-world situations, and should be viewed as complementary to other types of ecological research.

My analysis is illustrated with a bottom-up research collaboration combining plant-ecological research and ecosystem management in the Seychelles (Indian Ocean).

Introduction

Taking ecology as an example of a disciplinary natural science that plays an important role in solving environmental problems, I discuss the potential and limitations of ecological research for environmental problem solving. I first clarify the relevance of disciplinary knowledge in solving environmental problems and then discuss how problem solving can itself influence the nature of ecological research. This second part relates to the question of how environmental research can better deal with the complexity of real-world environmental systems as opposed to laboratory settings. I illustrate my analysis with a concrete ecological research project in the Seychelles (Indian Ocean) (see textbox).

Linear models of knowledge diffusion from science to application are not valid in the environmental sciences; in other words, we cannot assume that relevant knowledge is first produced by the sciences and subsequently taken up by management. I argue that reciprocal knowledge exchange between science and application is necessary when dealing with environmental phenomena characterised by high uncertainty; this relationship may be called ‘mutual learning’. However, for this to happen an appropriate context (‘trading zone’) must be framed for the interaction between science and application. Framing such an application context involves determining the roles of different types of knowledge (e.g. from the natural and social sciences or from traditional knowledge), understanding their inter-relationships, and agreeing upon their relative importance to the particular case.

In the second part of this article I discuss one type of application context, namely the adaptive management of species and ecosystems. The adaptive management of ecosystems is regarded as one of the greatest of all environmental challenges (Millennium Ecosystem Assessment 2005). The example of adaptive management shows how mutual learning between science and application can develop in a particular context. In order to allow mutual learning, both science and management have to “accommodate” each other’s inputs. I am in this article particularly interested in how this may work in the case of the involved science, i.e. how ecological knowledge production within this application context may fit into the disciplinary framework of ecology. This perspective from within a scientific discipline on scientific knowledge for environmental problem solving is relevant for two reasons. First, the provision of scientific expertise for management cannot be discussed without considering the potentials and constraints of scientific knowledge production. Second, the quest to generalize and systematize knowledge is central to scientific research. It has often been argued that this objective should not be given up in applied research (e.g. Shrader-Frechette and McCoy 1993, Scholz and Tietje 2001, Hirsch Hadorn 2003). One strategy is to validate and generalize results of applied research through *existing disciplines* (compare e.g. Tress et al. 2005). An alternative strategy would be to develop new theoretical frameworks beyond classical disciplines through *transdisciplinary research* (e.g. Hirsch Hadorn 2003).

The relevance of disciplinary research for environmental problem solving

Framing of environmental problems based on human agency

According to Hirsch (1995) an environmental problem can be defined as a negative impact on nature including its anthropogenic causes and the remediation of these causes. It follows that the design of problem-solving strategies has to be based on the societal dimensions of human choices regarding practices influencing natural systems (Hirsch 1993). The role and relevance of disciplinary sciences therefore depend on which solutions are considered acceptable by the stakeholders and decision-makers. For instance, in response to climate change, alternative strategies such as reducing the level of atmospheric CO_2 (e.g. dumping of CO_2 in the deep sea, planting of forest CO_2 sinks), reducing anthropogenic CO_2 output (e.g. research on hydrogen cars, investing in public transport systems, lifestyle changes) or adapting to a changing climate (e.g. dams, acceptance of palm-dominated wild forests in southern Switzerland) may be envisaged. These alternative responses call for different types of scientific knowledge.

Post-normal situations

Funtowicz and Ravetz (1993) have pointed out that environmental problem solving is a process that is often constrained both by high scientific uncertainty and by high decision stakes or more generally high social complexity. Sources of social complexity include the number and diversity of stakeholders, the potential for conflicts of interest or of values, and weak institutional frameworks. Societal problems that are characterised by high uncertainties and high social complexity have been called *post-normal* (Funtowicz and Ravetz 1993). In post-normal situations, disciplinary research has limited relevance. Several legitimate interpretations of the tentative scientific evidence may be used in different ways by the various stakeholders (Funtowicz and Ravetz 1993).

Complementarity of disciplinary and transdisciplinary research

Against this background, some authors have concluded that disciplinary research is only relevant where environmental problem solving is conceptualized in a way that fits to disciplinary research questions and where social complexity is low (e.g. Funtowicz and Ravetz 1993, Scheringer et al. 2005). It has also been suggested that a new type of transdisciplinary research can assist in problem solving in cases where environmental problems need to be conceptualized beyond classical disciplines and/or where social complexity is high (e.g. Hirsch Hadorn 2003, Scheringer et al. 2005). In a general sense, it can be said that there is a trade-off between efficient and reliable knowledge production in closed settings (e.g. in disciplinary science) and inclusion of a variety of diverging opinions and expertise (e.g. in the public arena or in transdisciplinary research). Disciplinary and transdisciplinary research thus complement each other for environmental problem solving (Fig. 1). Transdisciplinary research can help build a consensus on how an environmental problem should be framed; this process will involve determining which practices need to be considered, which stakeholders should be involved, and what expert knowledge is needed (negotiation zone, Fig. 1). Where the conceptual and

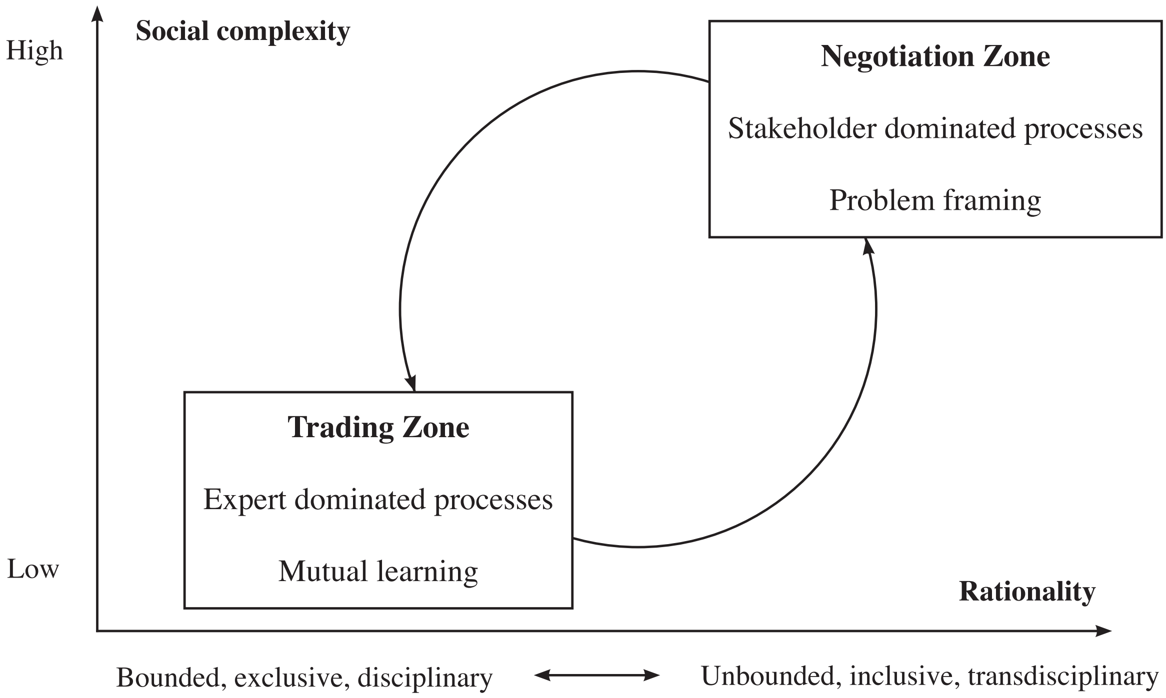


Fig. 1 Funtowicz and Ravetz (1993) categorized societal problem solving according to two axes: scientific uncertainties and decision stakes. They argue that applied research is suited for situations of low uncertainties and stakes and a new type of science is needed for post-normal situations of high uncertainties and stakes. I propose a more dynamic metaphor whereby stakeholder processes where a consensus on the problem framing is formed alternate with mutual learning between experts where specified problems are addressed.

social complexity are reduced through such a consensus, specific questions can be tackled by disciplinary research, which may subsequently improve transdisciplinary research. In summary, it is important to recognise that disciplinary research is relevant to environmental problem solving only under particular boundary conditions. Nevertheless, the knowledge produced by the disciplinary sciences deserves a special status even in situations of high scientific uncertainty and social complexity (Collins and Evans 2002).

Trading zones between users and producers of disciplinary knowledge

Application contexts where the scope of both the scientific and social issues are clearly bounded may be called ‘trading zones’ (compare Galison 1999). In these circumstances, the responsible decision-makers, the relevant expert knowledge, and the potential solutions can be relatively well defined. Thus, the closed setting of a trading zone permits intensive and reciprocal interactions among well-defined groups of experts, stakeholders and decision-makers (so called ‘mutual learning’). Nevertheless, the expert knowledge is tentative, incomplete and uncertain. Through an interactive process, rather than a transfer of ‘frozen facts’, both the users and the producers of the knowledge gain a better understanding of the relevant uncertainties and unknowns in a particular context. Mutual learning enables the producers and users of knowledge to built up interactional expertise (Collins and Evans 2002), i.e. a common language and the ability to understand the respective contexts of knowledge production and use.

Trading zones in ecology

Throughout its history, ecology has developed in close interaction with particular applications contexts (Bocking 1997) (Fig. 2). As a consequence, the users of ecological knowledge have guided and shaped ecological research (Bocking 1997). For instance, early British plant ecology was closely linked to the formation of The Nature Conservancy, a nature conservation body. One of the most important funding bodies of postwar American ecology was the Atomic Energy Commission, with its mission to assess the risks of nuclear bombs and reactors. Similarly, many ecological research programmes were developed in the context of practical problems in agriculture, forestry or fisheries. Over the past twenty years two divergent trading zones between ecology and application have emerged: the adaptive management of species and ecosystems, and the science and policy of global environmental change. In strategic documents for ecological research, a shift can be observed from a focus on particular ecosystems and species (e.g. Orians et al. 1986) to a focus on global issues (e.g. Palmer et al. 2004). Kwa (2005) reconstructed the emergence of the trading zone between ecology and global change science.

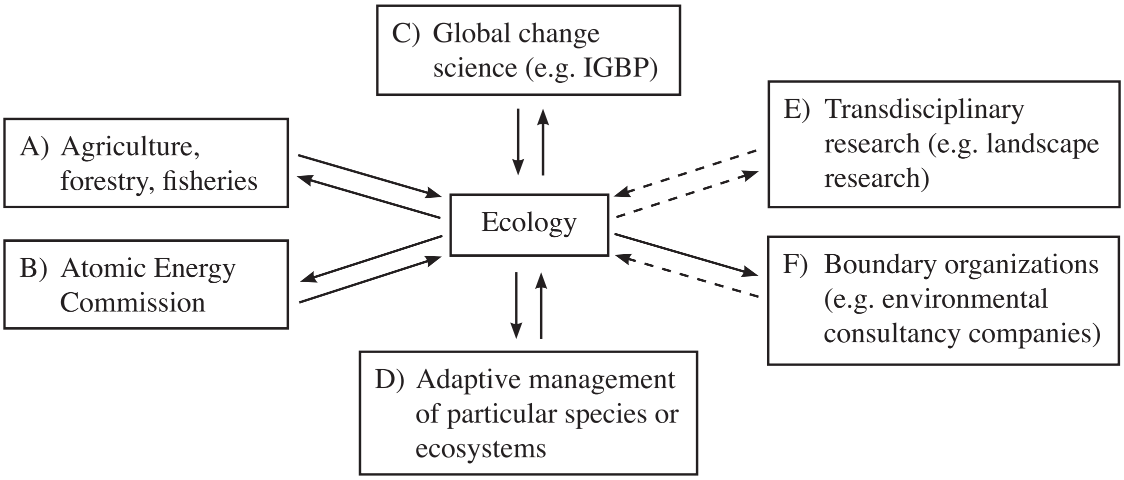


Fig. 2 Ecological research developed in the past and should develop in the future in close interaction with application contexts (trading zones) that enable a reciprocal knowledge transfer (mutual learning). The figure shows example of past (A, B), current (C, D), and possible future (E, F) trading zones. Full lines indicate existing and dashed line potential knowledge transfer.

I focus in the following on the trading zone between ecology and the adaptive management of particular species and ecosystems. With time new trading zones may emerge involving ecology. For instance, bridges between disciplinary and transdisciplinary research are increasingly built in the field of landscape ecology (e.g. Tress et al. 2005). And boundary organizations (Guston 2001) such as environmental consultancy companies play an increasing role as intermediates in the dialogue between ecology and application.

I have emphasized the importance of trading zones between ecology and application for the co-production of knowledge under uncertainty. However, to come back to the previous discussion, this does not mean that such trading zones may not be disturbed and may not break up. In the case of ecosystem management, problem solving may either remain the domain of ecosystem managers and scientists, or social processes may legitimately interfere more or less strongly. Typical examples of such interference include the debate about the role of protected natural areas for development in developing countries (Naughton-Treves et al. 2005), and stakeholder conflicts related to ecological restoration of landscapes (e.g. Gross and Hoffmann-Riem 2005).

The trading zone between ecology and adaptive management

Adaptive management

Today it is commonly accepted that the management of real-world problems such as the protection of a species or an ecosystem calls for a learning approach (e.g. Walters and Holling 1990, Gross et al. 2005). Relevant knowledge is uncertain and incomplete and management interventions often have unanticipated outcomes. Adaptive management means ‘learning by doing’; management practices are continuously adapted according to experience and in response to interventions by stakeholders.

There has been considerable discussion about the role of adaptive management in societal problem solving (Gross and Hoffmann-Riem 2005, Gross et al. 2005), and the prerequisites for the process to function effectively; the latter include access to ecological research (e.g. Walters and Holling 1990) and appropriate institutional settings (Lee 1993, Folke et al. 2005). Much less well understood is the way that the results of adaptive management may feed back upon ecological research (but see e.g. Slobodkin 1988, Shrader-Frechette and McCoy 1993). Adaptive management needs a transparent synthesis of the available ecological knowledge on the particular case under consideration. I argue in the following that such case-specific or integrative ecological research plays also an important role in ecological research complementary to other research strategies. Then I illustrate how a consistent research methodology - what may be termed ‘case-study research in ecology’ - is developing to support learning between integrative ecological research and adaptive management.

Integrative ecological research

I propose a categorization of three clusters of research strategies in ecology, which may be characterised as hypothetico-deductive, inductive, and integrative (compare e.g. Weiner 1995).

1. The *hypothetico-deductive* approach that characterises much work in laboratory sciences such as physics (Murray 1992). According to this approach, experiments are designed under simplified conditions in order to test hypotheses derived from theory. Classical examples of the use of this approach in ecology come from population ecology (e.g. Turchin 2001).
2. The *inductive* approach is data-driven. Inductive generalizations are gained through statistical modelling of large datasets, and meta-analysis of published studies (e.g. Brown 1995). For instance, consistent empirical relations between leaf characteristics of plants such as longevity, nutrient concentrations or thickness were found (Wright et al. 2004).

3. The *integrative* approach seeks to explain the complexity of specific field or real-world situations (Orians et al. 1986, Slobodkin 1988, Walters and Holling 1990, Peet 1991, Walters 1991, Shrader-Frechette and McCoy 1993, Haila and Taylor 2001, Carpenter 2002, Roe 2004, Ives and Agrawal 2005). Field research and experiments and simulation modelling are common methods. Long-term ecological research on a particular ecosystem is often the basis for such integrative research (e.g. Vitousek 2004). Epithets that have been used to characterise such integrative ecological research are 'case-by-case analyses', 'just-in-time ecology for management' (Roe 2004); 'heuristic', 'multiple working hypotheses', 'multiple types of evidence', 'wholistic' (Shrader-Frechette and McCoy 1993); or 'multicausal, integrative explanations' (Carpenter 2002).

The three approaches use different strategies for dealing with the tensions between scientific generalization and real-world complexity. The hypothetico-deductive approach uses the classical strategy of the laboratory sciences in which artificial, enclosed systems are built to test theories. The problem inevitably arises of how the research results relate to the open systems of the real-world. The inductive approach describes patterns that are sufficiently dominant so that other aspects of real-world complexity can be dismissed as contributing random noise. However, this approach is not particularly useful when the patterns described are either too trivial or too general to explain real-world phenomena. The integrative approach attempts to study real-world complexity directly, but it is often not clear whether knowledge gained from one study can be applied to other cases; and therefore validation across cases is needed.

It is an unresolved question to what extent ecological research can be designed in analogy to laboratory sciences such as physics. By stating this, I touch on a debate that has accompanied ecology since its birth at the beginning of the 20th century (e.g. Orians et al. 1986, Slobodkin 1988, Peet 1991, Haila and Taylor 2001, Kohler 2002). In my opinion, the integrative research strategy that seeks to understand the complexity of concrete real-world cases is a necessary complement to the hypothetico-deductive and inductive research strategies. Scientific generalizations in ecology have to be sensitive to the contingencies of particular cases such as an ecosystem or a species (compare e.g. Peet 1991). The relative importance of knowledge about local aspects versus generalizations depends on the particular research question or management problem (e.g. Walters 1991).

Case study research in ecology: methodological innovations for integrative ecological research

Specific methodologies and an evolution of the epistemological thinking are needed for integrative ecological research (compare Haila and Taylor 2001). For instance, the epistemological status of simulation modelling for understanding real-world systems is currently under discussion (e.g. Beven 2002, Prisley and Mortimer 2004). In field research, new methods are continually being developed, e.g. for quantifying the strengths of species interactions (Wootton and Emmerson 2005), or for reconstructing the history of ecosystems (e.g. Egan and Howell 2005). In the following I shortly present some conceptual and methodological developments from applied ecological research at the interface between ecology and adaptive management.

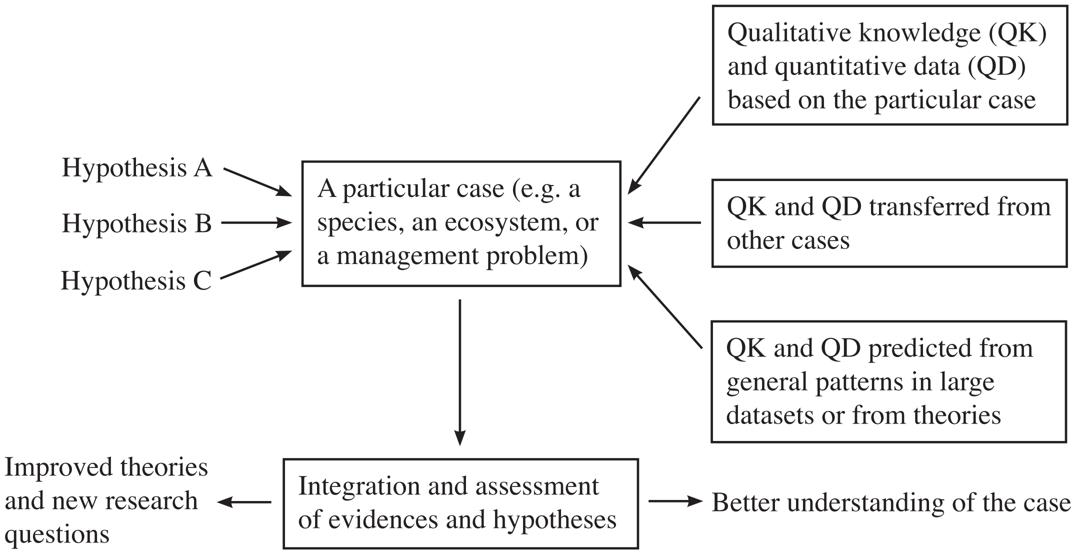


Fig. 3 In case study ecological research multiple hypotheses are tested and integrated based on multiple evidences and for a particular case. Such research combines qualitative knowledge (e.g. experience-based knowledge of practitioners or theoretical reasoning) and quantitative data that are based on the particular case, transferred from other cases, or predicted from general patterns in large datasets or from theories.

Shrader-Frechette and McCoy (1993, 1994) have discussed the epistemological and methodological implications of ecological research that is focused on particular real-world management problems in reference to the concept of case study research (Yin 2003). Case study research has developed in many research fields including environmental research (Scholz and Tietje 2001). According to Shrader-Frechette and McCoy (1993, 1994), the objective of case study research in ecology is the compilation and assessment of different forms of knowledge on a particular case in a structured and transparent way (Fig. 3). Very often, case studies draw upon local knowledge from traditional knowledge or practitioners (e.g. Fry 2001, Sheil and Lawrence 2004). The approach can be characterized as one of comparing multiple working hypotheses. According to Shrader-Frechette and McCoy (1993, 1994) an important issue is to balance the goal to reduce the risk of stating something as true that is in fact wrong (i.e. reducing type I statistical errors) with the goal to reduce the risk of neglecting something as not proven that is in fact true (i.e. reducing type II statistical errors).

There are two main phases in a case study: the building of plausible hypotheses, and the gathering and assessment of evidence to support or refute the different hypotheses. The essential process in the first phase is to represent all relevant hypotheses. Possible methods are expert workshop, Delphi survey (Hess and King 2002), the re-analysis of existing datasets through exploratory statistics and retrospective analysis (Sit and Taylor 1998), and collaborative simulation model building (Costanza and Ruth 1998). The nub of the second phase is to present the relevant evidence in a transparent way, and to assess the relative uncertainties and risks (of management options) that are attached to the different hypotheses. Typical methods include: qualitative weight of evidence methods (Marmorek and Peters 2001), extended peer-review systems (Marmorek and Peters 2001), decision analysis (Sit and Taylor 1998), simulation modelling including sensitivity analysis, scenario building, or model evaluation (Prisley and Mortimer 2004).

Conclusions

I have presented a strategy for ecological research that I call ‘integrative ecological research’. Integrative ecological research seeks to explain the complexity of specific field or real-world situations, and benefits from the co-production of knowledge by experts from science and management (‘mutual learning’, see textbox). Such case-specific research is valuable to both ecological research and environmental management – for instance the adaptive management of ecosystems.

General ecological theory has so far been of limited use for environmental management (e.g. Shrader-Frechette and McCoy 1993). Then again, applied research and management that are not well grounded in ecological science risk to neglect important processes. Integrative ecological research has the potential to build a bridge between ecological science and concrete management problems and thereby facilitates the production of case-specific and validated ecological knowledge that is particularly suited to assist environmental decision making.

The need in ecology for integrative research on particular real-world cases has been recognized throughout the history of the discipline (e.g. Peet 1991, Kohler 2002, Ives and Agrawal 2005). However, often integrative ecological research and other research strategies have been perceived as competing or even mutually exclusive alternatives; or case-specific research (often termed ‘natural history’) has been judged as an inferior research practice. I have argued that the various ecological research strategies are complementary, and that the special contributions of integrative research, both methodologically and theoretically, deserve to be better appreciated. Acknowledging the value of pluralistic research in ecology will facilitate the integration of conceptual and methodological innovations from applied ecological research and from other environmental natural sciences (as exemplified by the paragraph ‘case study research in ecology’). Interestingly, the complementarity of “empirical-inductive, hypothesis-deductive, and complex system modelling styles of conducting scientific research” was pivotal in the historical development of modern meteorology (Davies 2005).

Reliable knowledge about the relevant natural processes is a necessary but not a sufficient condition for sound environmental management. Environmental problems are first and foremost social, political and cultural issues (for ecology see e.g. Ludwig et al. 2001). There is therefore also a need for stakeholder processes where the particular interests and values involved are discussed and a consensus is formed on the framing of environmental problems. Very often, however, these interests and values become entangled with scientific interpretations (for ecology see e.g. Wallington and Moore 2005 *and references therein*), particularly when the scientific information is uncertain. Nevertheless, it is important to be clear whether in a particular process the main debate is about expertise or about negotiating conflicting interests and values (Collins and Evans 2002). I have called the first type of process ‘trading zone’ and the second type ‘negotiation zone’. Of course, values and interests still play a role in the background in trading zones and *vice versa* for facts in the negotiation zone, but transparency about the objectives and scope of particular processes will help in dealing with the complexity of environmental decision-making and will thus improve environmental problem solving. With a similar concept in mind, Gross and Hoffmann-Riem (2005) use the term ‘accommodation’ to describe the recursive and tight interaction between processes for the articulation of interests and processes for knowledge production in adaptive management.

I have focused here on processes in which mainly facts are debated (trading zones). In transdisciplinary research a rich methodology is developing for negotiating and framing issues where values and facts are entangled (e.g. Pohl and Hirsch Hadorn 2006), i.e. for negotiation zones. In this sense, disciplinary and transdisciplinary research complement each other for environmental problem solving.

Plant ecological research in Seychelles: a bottom-up research collaboration

In bottom-up research collaborations between scientists and practitioners new research questions and the recognition of new management problems evolve over time in response to each other, rather than following rigid scientific and management goals set at the beginning of the collaboration. A contrasting approach would be top-down oriented research programs (e.g. Troumbis et al. 2001).

The research collaboration in Seychelles

The research project of the Geobotanical Institute (ETH Zurich) in the Seychelles (Indian Ocean) exemplifies a long-term, bottom-up research collaboration between scientists and practitioners (Fig. 4). The research collaboration with the Ministry of Environment and Natural Resources and several NGOs encompasses both applied research on vegetation mapping, red data listing of rare plants, habitat restoration and sustainable use of forest products, and ecological research on the evolution and ecology of invasive (non-native) plants, island floras and tropical forests. Also, the Geobotanical Institute is a lead organization in the setting up of a national and regional network for invasive species management, the development of a National Strategy for Plant Conservation, capacity and public awareness building, and the publication of the plant conservation newsletter 'Kapisen'[1].

The collaboration is situated in the trading zone between ecology and adaptive management; in the context of nature conservation and protected areas. So, the collaboration is mainly confined to a well-defined group of nature conservation practitioners and decision-makers. However, in several instances we have transgressed these boundaries. The national strategies for invasive species management and plant conservation involve actors from agriculture, horticulture, customs, tourism, education, and the media. We also conducted a project on sustainable exploitation of the invasive Cinnamon together with the spice industry. Further, we initiated in collaboration with 'seed sustainability'[2] a research project on sustainable ecotourism that has so far involved scientists from marketing, economics, geography and environmental sciences.

Integrative ecological research

Our long-term research project integrates studies on vegetation composition and dynamics, impacts of native and invasive plants on nutrient cycling through mechanism such as litter decomposition or root competition, the physiology of native and invasive juvenile trees, seed dispersal by birds, and herbivory. The comprehensive approach allows comparing the data with extensive case studies in Hawaii or Puerto Rico (Lugo 2004, Vitousek 2004). For management, for instance, an integrative picture of the widespread seed dispersal by birds on different spatial scales, strong root competition by the invasive tree Cinnamon (*Cinnamomum verum*), differences in the demand for nutrients and light between native and invasive species, and regeneration patterns of native and invasive juveniles in forests dominated by Cinnamon may lead to a re-assessment of the role of Cinnamon for nature conservation and to new practices in ecological restoration (Kueffer 2003). Cinnamon is generally considered to be very problematic because it is the most abundant invasive plant species in Seychelles. However, these new results may indicate that Cinnamon is an effective barrier against the invasion of other invasive species and may facilitate the regeneration of native species. Therefore in a pilot project small patches of native vegetation have been replanted scattered in Cinnamon forests (Fig. 4). The hope is that birds will disperse the native species from these patches and that the Cinnamon forests will serve as nursery habitat for the regeneration of the native species.

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[1] Kapisen provides more information and references related to the discussed applied projects (http://www.geobot.ethz.ch/publications/books/kapisen).

[2] *seed sustainability* is a project platform for transdisciplinary research (http://www.seed-sustainability.ch)

Implications for management

The close interaction between scientists and practitioners facilitated the immediate interpretation of tentative scientific results for management and the setting up of pilot projects to validate research results for management. In return, local knowledge of the practitioners improved research, e.g. when formulating hypotheses, choosing appropriate sites and species for experiments, identifying species in the juvenile stage, interpreting unexpected outcomes of field experiments, or growing juveniles for laboratory experiments. We made special efforts to increase the accessibility of local knowledge. Unpublished knowledge of practitioners was documented in a regional study on invasive species management and habitat restoration in the Western Indian Ocean (e.g. Kueffer et al. 2004). The plant conservation newsletter 'Kapisen' particularly encourages local and visiting biologists to publish personal field observations that may not fit well in a scientific paper.

Thanks to the long-term collaboration applied research questions were defined according to priority needs for management and the feasibility of research. Recent projects such as the red data listing project were initiated because they have been identified as a priority by the National Strategy for Plant Conservation. Research results of the collaborative projects as well as international scientific results flew directly into management planning and action, e.g. the zoning of a National Park or the management plan of an invasive species. Empirical surveys have shown that research results are rarely used in nature conservation management except through direct interactions with scientists (Pullin and Knight 2005). Ecological research, applied research and actual management projects developed in parallel, for instance for habitat restoration (see above & Fig. 4). Importantly, trust and a common language built up that allow a transparent discussion of the validity and limitations of the scientific results for management.

Fig. 4 Bottom-up research collaborations such as the one of the Geobotanical Institute in Seychelles allow the participatory framing of environmental problem solving. For instance, a workshop was held in Seychelles to develop a consensus among experts and stakeholders on priorities in plant conservation and applied ecological research (left photo: Eva Schumacher). Also, mutual learning is facilitated. For instance, in a combined research project on the plant physiology of light use and habitat restoration techniques scientists and practitioners worked together in artificially created forest gaps (right photo: Christoph Kueffer).

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General Conclusions and Management Implications

Woody plant invasions in nutrient poor tropical forests: Synthesis and perspectives

Plants invasions in ecosystems characterised by high environmental stress

The classical conceptual model of plant invasions predicts that stressed ecosystems, for instance those with low nutrient or water availability, are more resistant to plant invasions than more productive habitats (Alpert et al. 2000). The typical invasive plant is characterised as a fast-growing species that can exploit pulses of increased resource availability in productive habitats (Dukes and Mooney 1999, Davis et al. 2000, Lake and Leishman 2004, Blumenthal 2005). Consequently, the focus of much research on impacts of invasive plants has been on productive habitats where invasive species are expected to increase soil nutrient availability through high rates of biomass and nutrient turnover or N-fixation (Ehrenfeld 2003).

More recently, evidence has been accumulating that some species are also able to invade stressed ecosystems such as very nutrient poor ecosystems; examples have been reported from South Africa, Australia and on oceanic islands (e.g. Witkowski 1991, Musil 1993, Stock et al. 1995, Dunbar and Facelli 1999, Kendle and Rose 2001), inselbergs (Burke 2003), and alpine ecosystems (Dietz 2005). It may well be that these ecosystems were less invaded in the past mainly because they experienced less anthropogenic disturbances, e.g. because they are situated in remote areas or were of less interest to agriculture. In the future increased anthropogenic disturbance or increased propagule pressure from alien species may increase the frequency of invasions into such stressed ecosystems (Burke 2003, Dietz 2005, Millennium Ecosystem Assessment 2005). In particular, in the tropics invasions of infertile secondary habitats after deforestation and soil degradation may become common in the future (see General Introduction). In line with the precautionary principle, a better understanding of the impacts of invasive plants in stressed ecosystem is therefore urgently needed.

This study has provided information on the impacts of invasive woody species in nutrient poor tropical secondary forests. Based on these results, it seems that two contrasting types of invasive species, stress-tolerators and competitors, may invade nutrient poor tropical secondary forests, and that these two groups have very different impacts on nutrient cycling. Anthropogenic disturbances leading to increased light availability may be the relevant factor triggering a switch between the two alternative invasion scenarios. Further, propagule pressure (the mass of propagules arriving at a site) may be a particularly relevant factor explaining successions in nutrient poor ecosystems, because it appears that habitat dominance is more difficult to maintain through belowground than aboveground competition.

Ecological strategies of invasive plants in nutrient poor ecosystems

In low nutrient sites, invasive species may be either adapted to tolerate a low intake of nutrients or to scavenge and compete effectively for low levels of nutrients. These two ecological strategies may be called ‘stress-tolerators’ (*sensu* Grime 2001) and ‘competitors’, (*sensu* Tilman 1982), respectively.

Examples of the stress-tolerator strategy are provided by two of the study species, *Syzygium jambos* and *Psidium cattleianum* (table 2 in Chapter 1, Chapter 2). Both are shade-tolerant and, by producing large seeds or through vegetative growth, are able to regenerate under a closed canopy; and the low nutrient content and specific leaf area of their leaf litter are typical for many native species and for stress-tolerators (compare Grime 2001).

Competitors in nutrient-deficient soils, e.g. *Falcataria moluccana* (table 2 in Chapter 1, Chapter 2, Wiederkehr and Anderegg 2001 and C. Kueffer, pers observation), commonly possess special mechanisms for an efficient uptake of nutrients, such as mycorrhiza, exudation of organic acids, or cluster roots. Through an effective uptake of nutrients they may be able to sustain N-fixation, fast growth rates and high nutrient contents in their leaves. Competitors often have a sparse canopy with a high light transmittance, and they regenerate only in gaps or under a disturbed canopy. Indeed, light may necessarily be a limiting resource for competitors because their nutrient uptake mechanisms, e.g. mycorrhiza or N-fixation (van der Heijden and Sanders 2002, Vitousek et al. 2002), are carbon-demanding. Nevertheless, they may sustain a long-term dominance of a habitat through belowground competition (compare Chapter 3).

Cinnamomum verum is a particularly interesting species because it combines typical characteristics of both ecological strategies. Thanks to its dense topsoil root mat (Chapter 3) it is a strong belowground competitor, but it is relatively shade-tolerant (Fleischmann 1999) and has leaf properties intermediate between stress-tolerators and competitors (except for a high phosphorus content that may have to do with an efficient uptake mechanism) (Chapter 2). This 'opportunistic' combination of traits may explain the high abundance of *C. verum* in the Seychelles (Chapter 1), having enabled it not only to colonise deforested land but also to maintain long-term dominance of closed canopy forest. Invasions of *Cinnamomum camphora* in tropical Australia represent a very similar case of an invasion of deforested land und subsequent habitat dominance by a species with an 'opportunistic' combination of traits (see Scanlon and Camphor Laurel Taskforce 2000, Panetta 2001, Peng et al. 2003, Weber 2003, Neilan et al. 2006).

Impacts on nutrient cycling in nutrient poor tropical forests

Impacts on nutrient cycling by stress-tolerators versus competitors

Because their litter has similar properties to that of the native species, stress tolerators probably do not have a direct impact upon nutrient cycling (compare Chapter 2), either in the short-term or in the long-term after possible replacement of the species by other native or invasive species (Fig. 1). However, invasive stress-tolerators may differ from native species in properties such as growth rates, primary productivity or leaf longevity and thereby alter nutrient cycling. A better understanding of the relative ability of stress-tolerant invasive and native species to increase growth rates in response to resource pulses will be important to predict the impact of stress-tolerant invaders (see PhD E. Schumacher, in prep.).

In contrast, the competitors have a strong potential to influence nutrient cycling (Chapter 2). Their impact on nutrient cycling will, however, depend on whether they only redistribute nutrients between pools and fluxes within a stand or affect nutrient imports and exports.

In the first case ('nutrient redistributors'), fluxes will usually increase and nutrient pools will be increased in the living biomass and decreased in the dead biomass. The increase of nutrient pools in the living biomass may lead to larger nutrient pulses after dieback, while increased fluxes increase plant nutrient availability immediately. This may increase the invasibility of forest stands in the short-term, but only if the established plants are not effectively competing for the nutrients (compare Chapter 3). Otherwise, they will be successively replaced by colonizing species, and their long-term impact on nutrient cycling may then be minor (Fig. 1). *C. verum* may be an example of a nutrient redistributor (compare Chapter 2). It seems to effectively compete for nutrients released from litter and organic matter decomposition in the topsoil (Chapter 3), but does not seem to forage in deep soil or to attain soil bound nutrients through mechanisms such as the exudation of organic acids (Chapter 1).

In the second case (‘nutrient importers/exporters’), invasive species may import nutrients through N-fixation, rooting in soil depths not penetrated by native species (Jobbagy and Jackson 2004, Vanderhoeven et al. 2005), or freeing nutrients bound to the soil matrix and not attainable to native species. Alternatively, they may increase nutrient exports, for instance through increased leaching by lowering the soil pH. Changes in nutrient import and export may lead to lasting impacts on the nutrient budget of a site that remain even after dieback or removal of the invasive species (compare e.g. Adler et al. 1998) (Fig. 1). According to our data, *Falcataria moluccana* has the potential to act as a nutrient importer/exporter, both through N-fixation and an enhancement of nitrification (which may increase leaching) (Chapter 2). In addition, *F. moluccana* may alter the nutrient budget by exudation of organic acids for freeing nutrients bound to the soil matrix (see Table 2 in Chapter 1).

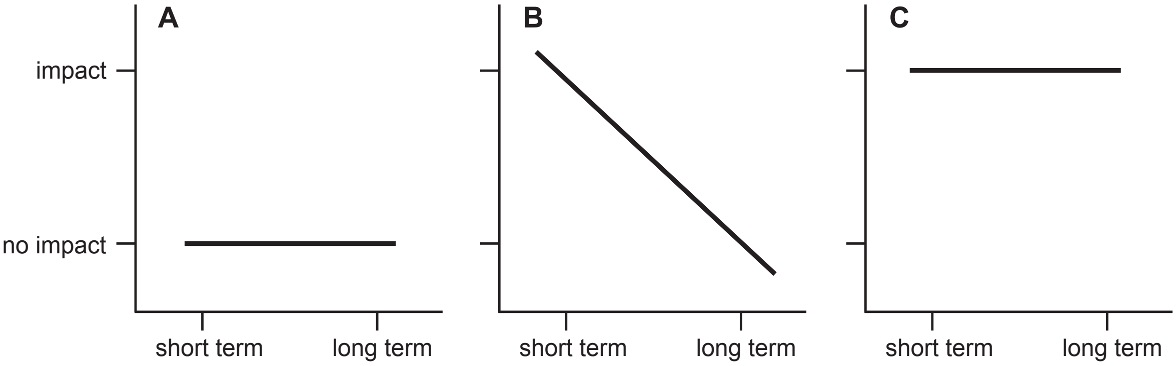


Fig. 1 A conceptual model to predict the impact of invasive alien species on nutrient cycling in infertile ecosystems. (**A**) Stress-tolerators are predicted not to change nutrient cycling compared to most native species, neither in the short-term nor in the long-term after possible replacement by other native or invasive species. (**B**) Competitors that are ‚nutrient redistributors’ may lead to an alteration of nutrient cycling in the short-term that will disappear in the long-term after replacement. (**C**) Competitors that are ‚nutrient importers / exporters’ will alter the nutrient budget both in the short-term and after replacement in the long-term.

The vulnerability of nutrient poor ecosystems to impacts by invasive species

It can be concluded that invasive plants do have the potential to alter nutrient cycling in nutrient poor ecosystems. In these systems, invasive stress-tolerators represent a distinct ecological strategy that is less important in productive habitats. However, competitors are more likely to alter ecosystem processes in stressed ecosystem because they typically are nutrient importers/ exporters.

Invasions by stress-tolerators versus competitors are thus two strongly contrasting possible scenarios in stressed ecosystem. Which of the two prevails, and therefore the long-tem impact of invasion on ecosystem processes, is likely to be determined by the disturbance regime. If undisturbed, only stress-tolerators may be able to invade and there may be little potential for ecosystem impacts. However, with a high level of disturbance, nutrient importers/exporters may bring about a shift from a nutrient-poor to a nutrient-rich ecosystem state, facilitating the entry of further plant species typical of productive habitats.

Future studies in the granitic Seychelles

A better understanding of the impacts of different types of native and invasive trees on plant available nutrients in very low nutrient habitats and their short- and long-term consequences for ecosystem functioning are recommended as a main objectives of future research. Studies in the granitic Seychelles may, in several regards, contribute to future research in this direction.

First, research in Hawaii (Vitousek et al. 1995, Chadwick et al. 1999) illustrates that oceanic islands are valuable models to study long-term soil development. It has been shown that with increasing soil age, rock-derived nutrients such as phosphorus become limiting compared to nitrogen that is of atmospheric origin. Preliminary data from the very old soils in the Seychelles confirm this pattern but suggest that potassium and magnesium may also become severely deficient, and nitrogen levels remain very low (Chapter 2). Based on a detailed empirical dataset on soil nutrient contents in Seychelles, the role of several particularities of the Seychelles may be investigated to contribute to a refined model of soil development: i. the Seychelles consist of granitic, not volcanic, parent material that has experienced a far longer history of continuous weathering than any other oceanic island group (Chapter 1), ii. with the possible exception of a very rare endemic woody liana (resembling *Acacia pennata*) there are no native N-fixing species in inland habitats in Seychelles, iii. there are no active volcanoes in the Seychelles contributing to atmospheric nutrient deposits, iv. nutrient inputs through continental dust may be up to an order of magnitude higher in Seychelles than Hawaii (Duce et al. 1991, Rea 1994), v. sea-salt derived inputs may be more important on the tiny islands of the Seychelles, vi. the steep topography of the Seychelles may increase erosion frequency (compare Porder et al. 2006), and vii. inselbergs (rocky granite outcrops) may be a source of freshly weathered parental material for the surrounding forest.

Second, to evaluate possible differences between the impact of stress-tolerant invasive and native species on nutrient cycling a better understanding of the ecological traits of the native flora is needed. Interestingly, the variance in leaf litter properties between different shade-tolerant native species (e.g. *Memecylon eleagni* and *Northea hornei*) is larger than the variance between shade-tolerant invasive and most native species (e.g. *Syzygium jambos* and *Memecylon eleagni*) (Chapter 2). Extremely low litter quality of dominant species in nutrient poor ecosystems (such as *Northea hornei* in the Seychelles) has also been reported from arctic ecosystems and from other old, highly weathered soils (e.g. Aerts and Chapin III 2000, Wardle 2002, Vitousek 2004, Wardle et al. 2004). These extreme characteristics may either reduce the risk of ecosystem nutrient loss by leaching or be a competitive strategy of the dominant species by reducing nutrient availability for other species. If the first proposition is of relevance, the replacement of dominant native species such as *Northea hornei* (or pandans, palm and tree ferns that may have similarly recalcitrant litter) by other shade-tolerant native or invasive species may have important consequences for nutrient cycling, e.g. by increasing leaching. Even within stress-tolerant species there may thus be important differences in traits relevant for nutrient cycling, either between native oceanic islands species (compare Kitayama and Itow 1999) and invasive species, or between different groups of native species.

Third, the study of nutrient importers/exporters such as *Falcataria moluccana* or *Acacia mangium* may be particularly interesting in Seychelles because of the wide range of environmental conditions – e.g. the contrast between highly leached soils in upland habitats and phosphorus-rich soils on nearby bird-nesting islands, or the rainfall gradient from 1600 to 3500 mm yr^{-1} (Chapter 1), that may allow one to study how the impacts of these species vary according to environmental conditions. Also, the small but widely scattered stands of *F. moluccana* (Chapter 2) allow one to study the influence of isolated invasive trees upon the surrounding forest, e.g. by root foraging, litter dispersal (compare Chapter 2), microclimate effects (e.g. through a sparse canopy or a high water demand), influencing forest dynamics (e.g. by falling easily and opening large gaps), or altering the micro-organism communities. Such processes could explain how invasive species may accelerate their spread from ‘nascent foci’ (Moody and Mack 1988) in an early phase of an invasion through an impact on soil properties of the area ‘to be invaded’.

Fourth, the possible co-limitation of biotic processes by several very scarce nutrients, such as nitrogen, phosphorus, potassium or magnesium (see Chapter 2), may allow one to compare the ability of native and invasive species to cope with the scarcity of different nutrients that show very different behaviours in the soil (e.g. Jordan 1985, Casper and Jackson 1997, Wardle 2002, Vitousek 2004, Bardgett 2005). If a nutrient type could be identified that is particularly limiting to invasive species, it may allow to develop soil management strategies that increase the habitat resistance against these species (compare e.g. Wassen et al. 2005).

The role of a neglected factor: propagule pressure

It has long been recognized that colonization or invasion processes are driven by two factors that interact with the traits of the involved species: habitat invasibility and propagule pressure (e.g. Johnstone 1986, Williamson 1996, Lonsdale 1999, Tilman 2004). Accordingly, the number of establishing individuals of a colonizing species (invasion success) is a function of the number of propagules that arrive at a site (propagule pressure) and the probability of successful establishment from an arriving propagule (invasibility) (Kueffer et al. 2003). This conceptual model has its roots in current theoretical ecology and has the potential to reconcile neutral and niche-based theories of community assembly (Tilman 2004). Empirical data confirm that propagule pressure is a major driver of alien plant invasions both on a regional (e.g. Williamson 1996, Lonsdale 1999, Lockwood et al. 2005) and a local scale (e.g. Parker 2001). Similarly, secondary successions in tropical forest are driven by the size and composition of the local propagule pool (Chazdon 2003).

Despite the high relevance of propagule pressure in non-equilibrium population dynamics such as invasions or secondary successions, the processes behind the building up of propagule pressure at a site have rarely been studied (cf. With 2002, Gosper et al. 2005). However, insights from both landscape ecology (With 2002) and studies on frugivore-plant interactions (Gosper et al. 2005) indicate that the vulnerability of a habitat to invasion on a landscape scale depends on how propagule pressure is shaped by habitat characteristics such as fragmentation or the composition of the local frugivores community.

Patterns of propagule pressure in the Seychelles

Preliminary data (estimated over 2 years using seed traps and seedling removal quadrats in three sites; C. Kueffer, data not shown) indicate that propagule pressure decreases from lowland and mid-altitude forests (5-8 new seedlings per m^2 and year) to montane forests (0.8-1.2 new seedlings per m^2 and year), while the proportion of native species increases from 5-10% (lowland to mid-altitude forests) to 50-65% (montane forests). In all three sites only two to three native species account for c. 75% of the native propagule pressure. However, a relatively high diversity of native species was present in small numbers (Annex 2). Interestingly, three of the common native species in the propagule pressure were palms (*Phoenicophorium borsigianum, Roscheria melanochaetes*, *Nephrosperma vanhoutteana*), while the most common species besides the palms in mid-altitude and montane forests was *Dillenia ferruginea* (the most preferred fruit in the captivity experiments with Seychelles bulbul, see Chapter 4), and two of the species colonizing lowland forests are probably dispersed exclusively by fruit pigeons (*Dracaena reflexa* and *N. vanhoutteana*, see Chapter 4), further illustrating the important role of bird-mediated dispersal

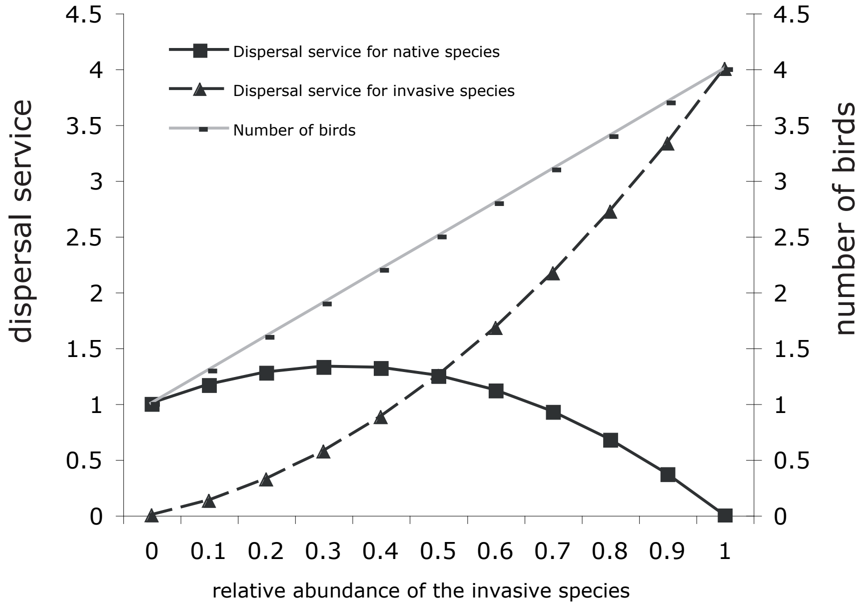
(Chapter 4). Similarly, the propagule pressure of the invasives is almost exclusively due to four or five (lowland to mid-altitude forest) or two (montane forest) invasive species.

Relationship between the proportion of invasive high-quality fruit trees in the forest and frugivore dispersal service

A good understanding of the role of propagule pressure for woody species invasion in Seychelles requires knowledge on frugivore-mediated seed dispersal (Chapter 4). It seems likely that positive feedbacks between fruit-bearing invasive tree species (that provide the food base for frugivores) and frugivores (that spread these plant species) may be an important mechanism that increases the vulnerability of habitats to invasions on the landscape scale.

A simple conceptual model illustrates possible processes (Fig. 2, see legend for detailed explanations). It is assumed that there is one invasive species and one native species that occupy a fixed number of vegetation patches. Because of the markedly higher fruit quality of the invasive compared to the native species (Chapter 4), and the assumed food limitation of bird density, the number of birds at the site is a function of the relative abundance of the invasive species. On the basis of the parameters used the model predicts that there is an optimum relative density of the invasive species, where the dispersal service for the native species (in absolute numbers) is highest (Fig. 2). For the invasive species, the dispersal service increases continuously with increasing relative abundance of the invasive plant. So, invasive plants may, through a feedback on bird densities, accelerate spreading rates, and either increase or decrease re-colonization rates of native species depending on relative abundances. Such a positive feedback between invasive plants and birds may be accentuated when the birds preferentially feed on invasive fruits (compare Chapter 4), and because higher densities of frugivores seem to increase dispersal efficiency through more frequent social interactions that force the frugivores to move around more (McConkey and Drake 2006). Positive feedbacks between fruit-bearing invasive trees and frugivore birds (possibly involving the invasive Indian Mynah (*Acridotheres tristis*), may have been particularly important in an early phase of rapid spread of *C. verum* in the early 19th century (Chapter 1). The model predicts also that the spread of *C. verum* may have initially increased re-colonization by native species but this facilitation may rapidly have declined due to competition for dispersers by *C. verum* (see Fig. 2).

Fig. 2 A conceptual model to predict the feedback of the relative abundance of an invasive species on the dispersal service provided by the frugivorous bird community. Model assumptions are: (i) the sum of the relative abundance of the native (RA_{native}) and the invasive species ($RA_{invasive}$) is always one, (ii) an invasive plant supports 4-times more birds than a native plant (for instance, the energy content per *Cinnamomum verum* fruit is about 4-times higher than the median of the native species (see Chapter 4) and it can be assumed that the annual fruit production per *C. verum* tree is also higher), i.e. the bird density equals $RA_{native}*1 + RA_{invasive}*4$, (iii) the birds select fruits randomly, i.e. the selectivity is proportional to the relative abundance of the plant species but does not depend on the fruit type. The total dispersal service per plant species (i.e. the total number of dispersal events, e.g. in units of dispersal events per individual bird and day) is then calculated as the bird density times the relative abundance of the plant species.



Additive effects of competition and propagule pressure on habitat dominance

The example of *Cinnamomum verum* illustrates the importance of integrating studies on competitive interactions at a local scale and on propagule pressure processes at a landscape scale. The very high proportion of *C. verum* in the propagule pressure seems to be a necessary factor for the habitat dominance by *C. verum*, because the strong belowground competition does not facilitate its regeneration relative to other colonizing species (Chapter 3); thus it is thanks only to a high propagule pressure and seedling recruitment (Annex 2) that *C. verum* remains the most prominent species in the sapling layer. Consequently, the local habitat dominance by *C. verum* depends on the very high abundance of *C. verum* on the landscape (Chapter 1). It can be predicted that there is a threshold abundance of *C. verum* relative to other native or invasive species at the landscape scale below which *C. verum* will not be able to maintain local habitat dominance. From the moment when *C. verum* is being partly replaced by other species, the colonization of *C. verum* forests by other species may accelerate, because with a lower relative abundance of *C. verum* the habitat resistance to colonization through belowground competition may be reduced (see Fig. 3).

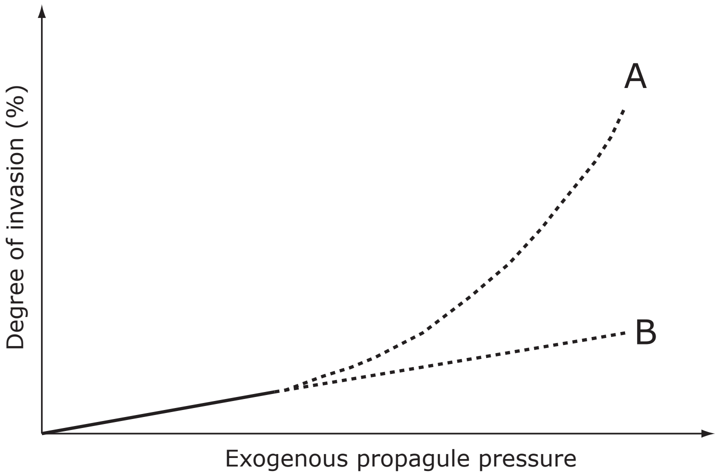


Fig. 3 The steady-state degree of invasion in *Cinnamomum verum* forests (DI, % abundance of species other than *C. verum*) as a hypothesised function of exogenous propagule pressure (PP, i.e. from species other than *C. verum*). At low levels of PP the DI increases linearly with increasing PP, while at higher levels of PP the habitat invasibility (i.e. the slope of the function) may change because of the replacement of the strong belowground competition exerted by *C. verum*. Thereby the DI at a given PP may be increased (when invasibility is increased; this may be the case when native species colonize the forest, **scenario A**), or remain constant (when belowground competition remains strong; this may be the case when invasive competitors colonize the forest, **scenario B**).

This interpretation of the case of *C. verum* is in accordance with the current understanding of dominance mechanisms of species-poor, native tropical forests, and with results from invasion biology on habitat invasibility (e.g. Levine et al. 2004, Davis et al. 2005). Tropical forests dominated by a single or a few native tree species occur naturally (Richards 1952, Connell and Lowman 1989). It appears that in these forests habitat dominance depends also on the ability of adult trees to compete efficiently for either aboveground (Hart 1990) or belowground resources (e.g. Newbery et al. 1997, Henkel 2003), and on adaptations that facilitate effective local recruitment. Competition for belowground nutrients involves mechanisms such as ectomycorrhiza, the formation of root moulds and dense surface root layers, or closed circuit cycling of nutrients through root foraging in decomposing litter, that may be tannin-rich and slowly decomposing or accumulating in ‘litter traps’ (e.g. Newbery et al. 1997, Henkel 2003). The maintenance of intraspecific regeneration is assured through mast fruiting, large seeds, shade-tolerant juveniles, or the formation of coppice shoots from the basal stem of adult trees (e.g. Connell and Lowman 1989, Newbery et al. 1997, Henkel 2003, Henkel et al. 2005), and possibly through carbon or nutrient transfer from adults to juveniles through ectomycorrhizal networks (Newbery et al. 2000).

It may be that propagule pressure is more important to maintain habitat dominance in nutrient poor sites than in productive sites; for example it has been predicted that on nutrient poor soils there are more opportunities for colonizing species to escape resource competition by a dominant species (Newman 1973, Casper and Jackson 1997, Cahill 2003). This may be the case because belowground competition appears to be size-symmetric in contrast to aboveground competition (Casper and Jackson 1997, Cahill 2003), or because in low-productivity habitats spatial distribution of soil resources is fine-grained and patchy (Crawley et al. 1999).

Implications for the management of invasive woody plant species in the Seychelles

Habitat management of mid-altitude and montane forests

The early introduction of *Cinnamomum verum* (Cinnamon) to the Seychelles may have been a lucky chance for Seychelles. If, for instance, *Psidium cattleianum* or *Falcataria moluccana* were introduced already in the 18th century, the landscape of the Seychelles may look different today. These species would mostly probably have successfully competed with Cinnamon and occupied at least part of the deforested land (compare Chapter 1). In the case of *Psidium cattleianum* this could have meant that dense thickets like in Mauritius would have formed (Lorence and Sussman 1986). *Falcataria moluccana* might have increased soil fertility to a degree that other invasive species such as *Leucaena leucocephala* or *Lantana camara* could have successfully invaded in inland habitats (compare Chapters 1 and 2). In contrast, Cinnamon may have promoted rehabilitation of ecosystems services in Seychelles following the devastating, large-scale deforestation of the islands, because the species seems to be effective in restoring degraded, laterite soil (table 2 in Chapter 1), an important food source for native birds (Chapter 4), possibly relative good habitat for native invertebrates (Kueffer and Vos 2004), and was of high value for the economy of Seychelles (Chapter 1). In particular, Cinnamon forests seem to provide a relatively good nursery habitat for the regeneration of many native species (Chapter 3), and the development of secondary forests richer in these species may be expected in the future. However, for this to happen a high propagule pressure of native plants has to be assured, and factors adverse to native regeneration have to be identified and managed.

Enhancement of native propagule pressure

Native propagule pressure is very low (see above and Annex 2) and an enhancement of native seed rain through weeding of remnants of native vegetation from alien species, and replanting of patches of native vegetation should be a priority for the rehabilitation of native vegetation (see above and Kueffer 2003, Kueffer and Schumacher 2005). Particularly, fruit bat and fruit pigeon dispersed species (see Chapter 4 and Annex 1) may only rarely be dispersed from small, isolated individual trees (e.g. in retreat habitats such as inselbergs), because fruit bats and fruit pigeons forage in groups on large trees with large fruit crops (compare Chapter 4).

A better understanding of the influence of spatial vegetation patterns on seed dispersal by frugivores may support the spatial planning of habitat restoration efforts. Restoration strategies at the landscape scale that take into account frugivore-plant interactions have been discussed for other regions (e.g. Holl 1998, Holl et al. 2000, Cardoso da Silva and Vickery 2002, Gosper et al. 2005), and need to be tested and adapted for the context of the Seychelles (Kueffer 2003, Kueffer and Schumacher 2005).

For instance, it can be assumed that large, specialist frugivores such as fruit pigeons (see Chapter 4) search for food across the whole island of Mahé (see Chapter 1). The spatial arrangement on the landscape scale may therefore be of reduced importance. The optimal strategy may be to create food patches that are large enough to attract fruit pigeons, but small enough that they will not supply enough food to meet the daily need of a fruit pigeon (so that the birds are forced to move between different food patches whereby they may disperse seeds over long distances).

Fruit pigeons often use isolated, large trees to digest (see Chapter 4). Consequently below these trees a high seed rain can be expected. Small gaps with single isolated trees may therefore be installed next to food sources, so that a native seed rain is dispersed directly to these prepared regeneration niches (compare e.g. Holl 1998).

Smaller woodland birds such as bulbuls (see Chapter 4), in contrast, have territories of a diameter of c. 200 m (Skerrett et al. 2001). In the Seychelles this typically means that they live in habitats completely dominated by Cinnamon. The challenge may be to plant native plants in a way that they successfully attract bulbul despite the competition of Cinnamon, and thus ensure that native species with a relative low fruit quality are dispersed. Food searching decisions of birds are hierarchical, i.e. they first search for patches of fruiting trees and then select single trees or fruits within a patch (e.g. Saracco 2001). If native species with high quality fruits are planted in patches together with native fruits with lower quality fruits, these patches as a whole might attract bulbuls, and successfully compete with Cinnamon (fruit neighborhoods, see Saracco 2001). For instance, fat-rich fruits such as those of *Erythroxylum sechellarum*, sugar-rich fruits such as *Memecylon eleagni*, fruits of palms, or mineral-rich fruits such as from figs may be used to design attractive native food sources. Within these patches, species with a relatively low fruit quality could be intermixed at a high relative abundance to assure their dispersal. It may additionally be interesting to assure on the scale of the territory that the different native food sources are characterised by species with differing fruit quality, e.g. sugar-rich versus fat-rich patches, to force the birds to move regularly between the different patches.

Habitat rehabilitation of mid-altitude *Cinnamomum verum* secondary forests

As long as Cinnamon mid-altitude forests are not disturbed, native species may successfully regenerate and compete with invasive species (compare Chapter 3 and e.g. Brown and Gurevitch 2004). However, we observed several factors that may hinder successful regeneration of native species and that need to be better studied.

- Seed predation by rats may reduce regeneration, especially of larger seeded species. In a seed sowing experiment with Cinnamon in the montane forest in Congo Rouge, in 4 out 6 positions 100% of several 100 seeds where removed or showed signs of rat predation within a week.
- Patches of invading *Syzygium jambos* in Cinnamon forests seem to hinder native plant regeneration. In the mid-altitude forest in Mare aux Cochons, we compared the number of native seedlings in seedling patches dominated by Cinnamon and *Syzygium jambos* (L. Kronauer & C. Kueffer, unpublished data). While we found no negative relationship between Cinnamon and native seedling abundances, at least up to a density of 80 Cinnamon seedlings per 0.25 m^2, native seedling regeneration was reduced with increasing *S. jambos* seedling density and completely suppressed at densities of more than 20 *S. jambos* seedlings per 0.25 m^2.
- Some species may need a particular regeneration niche that is no longer present in Cinnamon forests. For instance, we observed a very low sapling to seedling ratio for *Dillenia ferruginea* (Annex 2), indicating high seedling mortality. *D. ferruginea* was probably a co-dominant species of late-successional stages of natural mid-altitude forests (Vesey-Fitzgerald 1940) but has small seeds (c. 2 mm), untypical for regeneration in late-successional forest stages characterised by a thick litter layer and a closed canopy. A possible explanation may be that *D. ferruginea* regenerates preferentially on fallen logs and decaying tree trunks that were probably common in natural forests in Seychelles as results of slowly decomposing dead, old trees (Kueffer et al. 2003).

- The two native species *Aphloia theiformis* and *Timonius sechellensis* (and to a lesser degree the other native species) showed in the trenching experiment strong signs of an infection by a disease (see Chapter 3); maybe as a results of an infection by the alien fungus *Phytophthora cinnamoni* (to be investigated, compare Purseglove 1991, Schroth et al. 2000, Wilson et al. 2003). A high sapling mortality was also observed in the case of the rare *Craterispermum microdon* (see Annex 2). Further, an alien Homoptera (spiralling white fly, *Aleurodicus dispersus*) is fast spreading in mid-altitude forests and heavily attacks some native species such as *Aphloia theiformis* (C. Kueffer, pers. obs.).

Habitat management of montane forests

In contrast to mid-altitude Cinnamon forests, montane forests are apparently acutely threatened by the spreading of *Psidium cattleianum* through clonal suckers; we observed an average of seven sprouts of the size of a seedling per m^2 compared to a density of four seedlings per m^2 for the total of the other species (see Fig. 1, Chapter 3).

Additionally, in montane forests invasive trees seem, in contrast to native trees, to fall easily, whereby they form gaps that are subsequently invaded by invasive species (C. Kueffer, pers. observation) (compare Gerlach 2004); for instance by the recently introduced invasive shrub *Clidemia hirta* (Kueffer and Zemp 2004).

Montane forests seem thus to be more vulnerable than mid-altitude forests to the impacts of invasive species, and it appears that there is a high risk of an 'invasional meltdown' (Simberloff and Von Holle 1999), i.e. that invading alien species strongly facilitate further invasions. The preservation of the tiny remnants patches of undisturbed montane forests from any kind of disturbances seems therefore to be a high priority.

Assessing the impact of invasive plants in heavily invaded ecosystems

Classical models of the impact of invasive plants assume that the impact increases monotonically with the abundance of an invader (Fig. 4a). For instance, Parker et al. (1999) proposed a linear relationship, and defined the overall impact (I) of an invader as the product of the range size (R) of the species, its average abundance per unit area across that range (A), and the effect per individual or per biomass unit (E). Simberloff et al. (1999) hypothesised that impacts may even increase in a non-linear manner with the degree of invasion through synergistic interactions among invaders that may lead to accelerated impacts (invasional meltdown process). In Seychelles, invasions of montane forests may represent an example of an invasional meltdown process (see above).

In contrast, the assessment of the impacts of Cinnamon in mid-altitude forests in Seychelles appears to be more complex (see above). Cinnamon seems to play both positive and negative roles in secondary forests in Seychelles. In such 'novel ecosystems' (Hobbs et al. 2006) where new combinations of native and alien species have persisted over longer time periods, impacts of invasive species may not vary monotonically with abundance (Fig. 4b). Native species may have adapted to new species compositions and alien species may provide important ecosystem functions previously provided by native species. A partial reduction of the abundance of an invader may therefore reduce rather than increase habitat quality. It is questionable if a habitat stage of zero-invasion is ever reachable again, because this would probably require that the propagule pressure of invasive species on the landscape scale would be drastically reduced and a native vegetation cover would be restored to a degree that it could provide all necessary ecosystem functions again. Rather, it is probably more realistic to develop management strategies that understand alien species as integral parts of such novel ecosystems.

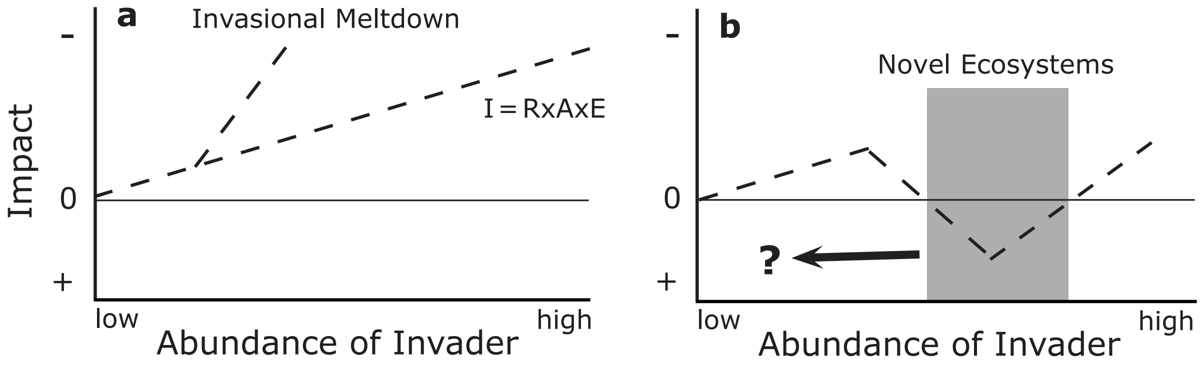


Fig. 4 Contrasting conceptual models of the impact of invasive plants. Classical models assume that the impact of an invader increases monotonically with the abundance of an invader (**a**). It is questionable if this model is appropriate in 'novel ecosystems', such as in the Seychelles, where new combinations of native and alien species have persisted over some time (**b**). See text for further information.

Screening of potentially new woody invasive species

The results of this study indicate that mainly invasive woody species with adaptations to infertile soils are problematic invaders in inland habitats in Seychelles, while other introduced alien species are invasive only in the lowland or not at all (even though many are listed as problematic invasive species in other countries, see e.g. ISSG Global Invasive Species Database) (Chapter 1). This observation may help to identify those alien species most likely to become invasive in Seychelles; i.e. these are species that are native and/or invasive in moist to wet subtropical to tropical climate and on very infertile soils (e.g. Australia, Australasia, Fynbos of South Africa, oceanic islands). In Table 1 some invasive species with these characteristics are listed (derived from Cronk and Fuller 1995, Weber 2003). Many of these species have traits typical for 'nutrient importers/exporters' (see above), i.e. there is a high risk that they have a long-term impact on nutrient cycling. The introduction of these species to the Seychelles should therefore be controlled at customs (compare Kueffer and Vos 2004), and species screening systems should be developed for the tropics in general with a strong emphasis on adaptations to nutrient poor soils (compare Rejmanek et al. 2005).

Table 1 Some potentially new woody invasive species in Seychelles predicted based on their native origin and/or invasiveness in moist subtropical to tropical regions with infertile soils.

Acacia dealbata	*Acacia saligna*	*Hakea drupacea*	*Pittosporum undulatum*
Acacia longifolia	*Casuarina glauca*	*Hakea salicifolia*	*Psoralea pinnata*
Acacia mearnsii	*Dipogon lignosus*	*Hakea sericea*	*Schefflera actinophylla*
Acacia melanoxylon	*Eucalyptus globulus*	*Paraserianthes lophanta*	*Toona ciliata*

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Annex 1

Plant-frugivore interactions reported from the Seychelles

compiled by Christoph Küffer and Lilian Kronauer

A1.1 Observations of frugivory on fruits of alien woody plant species. The information came from interviews with experts (O), reports in the literature (L), or published observations for the same genus of the frugivorous species on Aldabra (A). All tortoise observations are from Aldabra. Also shown are some records for the same plant species and same genus of the frugivorous species from Madagascar (Mad). The frugivorous species are: *Acridotheres tristis* (Common Mynah), *Alectroenas pulcherrima* (Seychelles Blue Pigeon), *Coracopsis nigra barklyi* (Seychelles Black Parrot), *Hypsipetes crassirostris* (Seychelles Bulbul), *Pteropus seychellensis seychellensis* (Seychelles Fruit Bat), and *Zosterops modestus* (Seychelles White-eye).

Plant species	***Hypsipetes***	***Alectroenas***	***Pteropus***	***Acridotheres***	**Others**
Adenanthera pavonina		O (?)			
Anacardium officinale			L	O	
Artocarpus heterophyllus	L (not dispersed)		L		
Artocarpus altilis			L		
Averrhoa bilimbi					*Coracopsis*
Cananga odorata	O (not dispersed)	O, L			
Camellia thea	L				
Carica papaya	O, L		L (in captivity)	O	*Coracopsis*
Ceiba pentandra	L				*Coracopsis*
Chrysobalanus icaco	O, L (not dispersed)			O	*Coracopsis*
Cinnamomum verum	O, L	O, L	no records	O	*Zosterops*
Ficus benghalensis		O	L		
Flacourtia jangomas	O (not dispersed ?)	O		O	
Lantana camara	O, A				*Zosterops*
Litsea glutinosa	O				
Melia azedarach					*Coracopsis* (Mad)
Mangifera indica	L (not dispersed)		O, L		*Coracopsis*
Musa spp.	O (in captivity)		L (in captivity)		
Ochna ciliata					tortoise
Passiflora suberosa	A				
Passiflora sp.	L				
Pentadesma butyracea	L (not dispersed)		O		
Pimenta officinalis		O			
Pithecellobium unguis-cati	L				
Psidium cattleianum	O, L (not swallowed)	O, L	L	O	*Coracopsis*
Psidium guajava	L (not swallowed)		L	O	*Coracopsis* (Mad)
Ptychosperma macarthurii		O			
Ricinus communis	A				
Sandoricum koetjape	L (not dispersed)		L		
Spondias cytherea	O, L (not dispersed)		L	O	*Coracopsis*
Syzygium aromaticum					*Pteropus* (Pempa Island, Tanzania)
Syzygium cumini					*Coracopsis*
Syzygium jambos	O (?) (not dispersed)		O, L (?)		*Coracopsis*
Syzygium malaccense			L	O	
Syzygium samarangense	L (not dispersed)		O, L		

A1.2 Observations of frugivory on fruits of native (indigenous or endemic) woody plant species. The information came from interviews with experts (O), reports in the literature (L), or published observations for the same genus of the frugivorous species on Aldabra (A). All tortoise observations are from Aldabra. Also shown are some records for the same plant species and the same genus of the frugivorous species from Madagascar (Mad) and Mauritius (Mau). The frugivorous species are: *Acridotheres tristis* (Common Mynah), *Alectroenas pulcherrima* (Seychelles Blue Pigeon), *Coracopsis nigra barklyi* (Seychelles Black Parrot), *Hypsipetes crassirostris* (Seychelles Bulbul), *Pteropus seychellensis seychellensis* (Seychelles Fruit Bat), and *Zosterops modestus* (Seychelles White-eye).

Plant species	***Hypsipetes***	***Alectroenas***	***Pteropus***	***Acridotheres***	**Others**
Allophylus sechellensis		L (?)			*Zosterops*
Aphloia theiformis	O, L		L (?)		*Pteropus* (Mau)
Barringtonia racemosa					No records for *Pteropus* from Mad
Brexia madagascariensis					*Coracopsis*
Calophyllum inophyllum		L	L		
Canthium bibracteatum	O			O	*Zosterops*
Carissa edulis		O			
Colea seychellarum					*Coracopsis*
Craterispermum microdon					*Coracopsis*
Deckenia nobilis	O, L				*Coracopsis*
Dillenia ferruginea	O, L	L			*Coracopsis*
Diospyros spp.					*Pteropus* (Mau)
Diospyros seychellarum	O (not dispersed)				
Dracaena reflexa	O (not dispersed)	O			
Erythroxylum sechellarum	O				*Zosterops*
Euphorbia pyrifolia		O (?)			
Ficus bojeri		O		O	
Ficus lutea	O, L	O, L, A	L	O	
Ficus reflexa	O (?)	O	L	O	*Zosterops*, tortoise
Ficus rubra		O	O	O	*Coracopsis*
Guettarda speciosa					tortoise
Ludia mauritiana		O			
Memecylon eleagni	O				*Coracopsis*
Mimusops sechellarum			L		
Nephrosperma vanhoutteana	O (not dispersed)	O			*Coracopsis*
Northea hornei			O, L		
Ochrosia oppositifolia			O, L		
Pandanus balfouri			O		
Pandanus sechellarum			O		
Pandanus spp.					tortoise (A), *Pteropus* (Mau)
Paragenipa wrightii	O, L (not swallowed)	O (?)			
Phoenicophorium borsigianum	O, L				*Coracopsis*
Phyllanthus pervilleanus	A	O, A		O	
Pouteria obovata		L			
Premna serratifolia	O	O, A		O	*Zosterops*
Scaevola sericea	O, A (not dispersed)	O, L, A			tortoise
Syzygium wrightii	O, L (not dispersed)	L	L		
Tabemaemontana coffeoides					*Zosterops*
Terminalia catappa			L		
Thespesia populnea					tortoise
Trema orientalis					*Alectroenas* (Mad), *Coracopsis* (Mad), *Hypsipetes* (Mad)
Verschaffeltia splendida					*Coracopsis*

Experts

- Katy Beaver, Plant Conservation Action Group (PCA)
- Rachel Bristol, Nature Seychelles
- Lindsay Chong Seng, Seychelles Island Foundation (SIF)
- Damien Doudee, Ministry of Environment and Natural Resources (MENR)
- Rodney Fanchette, MENR
- Chris Feare
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- Justin Gerlach, Nature Protection Trust of Seychelles (NPTS)
- Mike Hill, Nature Seychelles
- Lilian Kronauer, Geobotanical Institute
- Christoph Küffer, Geobotanical Institute
- James Millett, Nature Seychelles
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- Adrian Skerrett, Island Conservation Society

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Annex 2

Seedling, sapling and adult layer species composition of a mid-altitude and montane forest in Seychelles

Data collected by Lilian Kronauer, James Mougal, Terence Valentin and Christoph Küffer

Mare aux Cochons (mid-altitude forest)

A2.1 Seedling (height: ≤ 50 cm), Mare aux Cochons (mid-altitude forest)

Data source:
1577 0.5*0.5 m quadrats along 10 transects of c. 100 meters, total area: 394 m^2

Alien	
Adenanthera pavonina	14
Alstonia macrophylla	498
Ardisia crenata	2
Chrysobalanus icaco	4
Cinnamomum verum	57385
Melastoma malabathricum	1
Murraya koenigii	104
Psidium cattleianum	99
Sandoricum koetjape	2
Syzygium aromaticum	2
Syzygium jambos	1900
Native	
Aphloia theiformis	76
Campnosperma seychellarum	1
Canthium bibracteatum	6
Canthium sechellense	2
Colea seychellarum	9
Craterispermum microdon	58
Deckenia nobilis	4
Dillenia ferruginea	48
Dracaena reflexa	12
Erythroxylum sechellarum	34
Gastonia crassa	2
Grisollea thomassetii	0
Ixora pudica	4
Memecylon eleagni	31
Nephrosperma vanhoutteana	30
Northea hornei	4
Pandanus hornei	5
Paragenipa wrightii	3
Phoenicophorium borsigianum	429
Pouteria obovata	22
Psychotria pervillei	15
Roscheria melanochaetes	52
Timonius sechellensis	34
Verschaffeltia splendida	13
Total	**60905**

A2.2 Sapling, Mare aux Cochons (mid-altitude forest)

Survey A (Sapling: height: 0.5 – 3 m)
Data source: 90 circular plots (r = 3 m) along 10 transects of c. 100 meters, total area: 2545 m^2

Survey B (c. 500 m from survey A. Sapling: height > 0.5 m, stem girth at breast height (gbh) < 10 cm)
Data source: 24 circular plots (r = 6 m) along 2 transects of c. 300 meters, total area: 2’714 m^2

A

Alien	
Alstonia macrophylla	22
Chrysobalanus icaco	8
Cinnamomum verum	843
Melastoma malabathricum	4
Murraya koenigii	14
Psidium cattleianum	162
Sandoricum koetjape	3
Syzygium aromaticum	1
Syzygium jambos	559
Native	
Aphloia theiformis	71
Campnosperma seychellarum	1
Canthium bibracteatum	16
Colea seychellarum	1
Craterispermum microdon	0
Deckenia nobilis	1
Dillenia ferruginea	2
Dracaena reflexa	4
Erythroxylum sechellarum	11
Ficus lutea	1
Gastonia crassa	1
Gastonia sechellarum	1
Grisollea thomassetii	5
Ixora pudica	6
Memecylon eleagni	32
Nephrosperma vanhoutteana	1
Northea hornei	41
Pandanus hornei	1
Pandanus sechellarum	2
Paragenipa wrightii	8
Phoenicophorium borsigianum	31
Pittosporum senacia	1
Pouteria obovata	57
Psychotria pervillei	16
Roscheria melanochaetes	19
Timonius sechellensis	24
Verschaffeltia splendida	8
Total	1978

B

Alien	
Adenanthera pavonina	1
Alstonia macrophylla	13
Chrysobalanus icaco	3
Cinnamomum verum	490
Dillenia suffruticosa	1
Psidium cattleianum	114
Syzygium aromaticum	18
Syzygium jambos	3
Native	
Colea seychellarum	1
Dillenia ferruginea	7
Erythroxylum sechellarum	5
Memecylon eleagni	38
Nephrosperma vanhoutteana	2
Northea hornei	107
Pandanus hornei	9
Paragenipa wrightii	2
Phoenicophorium borsigianum	25
Pittosporum senacia	2
Psychotria pervillei	15
Roscheria melanochaetes	2
Timonius sechellensis	21
Aphloia theiformis	72
Canthium bibracteatum	13
Dracaena reflexa	1
Ixora pudica	1
Pouteria obovata	6
Total	972

A2.3 Adult, Mare aux Cochons (mid-altitude forest)

Survey A (Adult: height > 3 m)
Data source: 90 circular plots (r = 3 m) along 10 transects of c. 100 meters, total area: 2545 m^2

Survey B (c. 500 m from survey A. Adult: gbh > 10 cm)
Data source: 24 circular plots (r = 6 m) along 2 transects of c. 300 meters, total area: 2’714 m^2

A

Alien	
Adenanthera pavonina	3
Alstonia macrophylla	9
Artocarpus heterophyllus	1
Cinnamomum verum	503
Murraya koenigii	2
Psidium cattleianum	10
Syzygium jambos	21
Melastoma malabathricum	1
Native	
Aphloia theiformis	3
Canthium bibracteatum	2
Craterispermum microdon	5
Dillenia ferruginea	7
Memecylon eleagni	5
Nephrosperma vanhoutteana	4
Northea hornei	22
Pandanus hornei	11
Pandanus sechellarum	2
Paragenipa wrightii	2
Pouteria obovata	7
Psychotria pervillei	2
Roscheria melanochaetes	7
Colea seychellarum	1
Deckenia nobilis	1
Timonius sechellensis	1
Verschaffeltia splendida	1
Total	633

B

Alien	
Adenanthera pavonina	2
Alstonia macrophylla	1
Chrysobalanus icaco	4
Cinnamomum verum	818
Psidium cattleianum	3
Syzygium jambos	1
Native	
Deckenia nobilis	1
Dillenia ferruginea	15
Erythroxylum sechellarum	2
Memecylon eleagni	6
Northea hornei	35
Pandanus hornei	21
Phoenicophorium borsigianum	1
Psychotria pervillei	1
Roscheria melanochaetes	3
Timonius sechellensis	8
Verschaffeltia splendida	3
Aphloia theiformis	1
Canthium bibracteatum	1
Total	927

Congo Rouge (montane forest)

A2.4 Sapling (height > 0.5 m, gbh < 10 cm), Congo Rouge (montane forest)

Data source: 14 circular plots (r = 6 m) along 2 transects of c. 200 meters, total area: 1’583 m^2

Alien	
Chrysobalanus icaco	1
Cinnamomum verum	488
Melastoma malabathricum	1
Psidium cattleianum	498
Syzygium jambos	4
Native	
Aphloia theiformis	17
Canthium bibracteatum	3
Canthium sechellense	25
Cyathea sechellarum	2
Dillenia ferruginea	7
Erythroxylum sechellarum	16
Ficus bojeri	1
Gastonia crassa	66
Glionnetia sericea	8
Ixora pudica	3
Northea hornei	18
Pandanus sechellarum	219
Paragenipa wrightii	10
Phoenicophorium borsigianum	45
Psychotria pervillei	40
Rapanea sechellarum	1
Roscheria melanochaetes	20
Syzygium wrightii	4
Timonius sechellensis	35
Total	1532

A2.5 Adult (gbh >10 cm), Congo Rouge (montane forest)

Data source: 14 circular plots (r = 6 m) along 2 transects of c. 200 meters, total area: 1’583 m^2

Alien	
Cinnamomum verum	244
Psidium cattleianum	106
Native	
Aphloia theiformis	16
Colea seychellarum	1
Cyathea sechellarum	4
Dillenia ferruginea	10
Erythroxylum sechellarum	2
Ficus bojeri	1
Gastonia crassa	9
Ixora pudica	2
Northea hornei	95
Pandanus sechellarum	18
Paragenipa wrightii	5
Phoenicophorium borsigianum	65
Psychotria pervillei	1
Roscheria melanochaetes	77
Syzygium wrightii	1
Verschaffeltia splendida	2
Total	659

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Curriculum vitae

Name: Christoph Küffer

Date of Birth: 13th of April 1974

Nationality: Citizen of Täuffelen BE, Switzerland

Education

2000 – 2001	Scholarship at Collegium Helveticum, ETH Zurich Project title: *Computermodellierung als Grundlage für die Problemstrukturierung in der transdisziplinären Umweltforschung*.
1994 – 2000	Study of Environmental Natural Sciences at ETH Zurich Degree: Dipl. Umwelt-natw. ETH Thesis title: *Modellierung der Habitatsnutzung des Rothirsches* Cervus elaphus L. *im Gebiet des schweizerischen Nationalparkes - Ein individuenbasierter Ansatz.*
1994	Matura (high school graduation), Gymnasium Biel

Work experience

2006 –	Lecturer, *Technik, Energie und Umwelt* (Department of Information Technology and Electrical Engineering, ETH Zurich)
August 2005 –	Assistant, Environmental Philosophy Group, ETH Zurich (20%)
August 2005 –	Research associate, transdisciplinarity-net (Swiss Academies of Sciences) (www.transdisciplinarity.ch)
July 2005 –	Coordinator, Mountain Invasion Research Network (MIREN) (www.miren.ethz.ch) (20%)

2003 –	A founder and editor, *Kapisen – Seychelles Plant Conservation Newsletter* (www.geobot.ethz.ch/publications/books/kapisen)
2003 –	Coordinator, research project on sustainable ecotourism development in Seychelles (Department for Tourism and Transport, Vize Presidents Office, Seychelles and seed sustainability, Switzerland)
2003 – 2004	Freelancer, ETH Life web journal, ETH Zurich
2002 – 2005	Consultant for invasive species management, Seychelles Ministry of Environment and Natural Resources
Jan. – March 2002	Pilot study for the research project *Invasions of woody plants into Seychelles tropical forests*, Geobotanical Institute, ETH Zurich (50%)
2001 –	A founder and executive committee member, seed sustainability – platform for transdisciplinary research for sustainability (www.seed-sustainability.ch)
July – Dec. 2001	Assistant, Environmental Philosophy Group (ETH Zurich) (50%)

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DIETZ, H. & C. KUEFFER 2005. *Working lunch on plant invasions into mountain ecosystems*. GLOCHAMORE Open Science Conference on Global Change in Mountain Regions, October 2-6, Perth, Scotland. (working lunch organizer and chair).

KUEFFER, C. 2005. *Networking case studies in plant invasion ecology*. Mountain Invasion Research Network (MIREN) Launching Workshop. July 15-17, Vienna, Austria. (invited talk).

KUEFFER, C. 2005. *Mutual learning between scientists and practitioners in ecology*. 11th Annual International Sustainable Development Research Conference, June 6-8, Helsinki, Finland. (invited talk).

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KUEFFER, C. & E. SCHUMACHER 2005. *Research collaborations for plant conservation: Concepts, tools and examples*. The Global Partnership for Plant Conservation - Plants 2010 Conference. October 23-25, Dublin, Irland. (poster).

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