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RESEARCH PROJECT

Invasion of woody plants into the Seychelles tropical forests: habitat invasibility and propagule pressure

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Summary

1 Environmental change has often been put forward as a main reason for invasions by exotic plant species into natural habitats. Alternatively, or in addition, high propagule pressure has been hypothesized to be the single most important factor for biological invasions.

2 The objective of this study is to assess the relative importance of habitat invasibility and propagule pressure in an oceanic island ecosystem that has suffered from severe anthropogenic environmental change during the last 230 years and that is particularly prone to invasions by exotic woody plants. It is still an open question whether these invasions are mainly due to the high level of (prior) anthropogenic interference (number of introduced propagules, degree of habitat alteration) or whether they are an intrinsic characteristic of natural island ecosystems (low competitive ability of island species, low species diversity of island ecosystems).

3 To investigate habitat invasibility we analyze the role of three environmental factors, light, nutrients, and water stress, for the invasion process. We hypothesize that increased levels of light and nutrients facilitate invasion and that the native species are better adapted to water stress than the invasives.

4 To investigate propagule pressure we compare seed rain, seedling emergence, and tree demography in three forest habitats with differing environmental conditions, species composition and invasion history. We hypothesize that the forests are satiated with seeds of the few tree species that dominate the canopy but that for most others species, particularly the natives, recruitment limitation is a crucial factor.

5 We hope that the results of the study will help to understand why small oceanic islands are particularly prone to invasions. Our results will also be used to design efficient techniques of invasion control through habitat management and control of propagule pressure.

Keywords: nutrient limitation, recruitment limitation, root trenching, unused resources hypothesis, water stress

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Introduction

Small oceanic islands are particularly prone to invasion by exotics (e.g. Stone *et al.* 1992; Cronk & Fuller 1995; Lonsdale 1999). The long evolutionary isolation of many islands and species poverty have been suggested to facilitate the spread of introduced organisms (Cronk & Fuller 1995; D'Antonio & Dudley 1995; Lonsdale 1999). Islands may be also more affected by the consequences of environmental change, furthering invasions. In addition, due to the small size of island populations, they are vulnerable to demographic stochasticity and are easily overwhelmed by propagules from invasive plants (D'Antonio & Dudley 1995; Lonsdale 1999).

The Seychelles exemplify the situation of oceanic islands being susceptible to invasion (Gerlach 1996; Fleischmann 1997). They comprise a scattered group of about 100 granitic and coralline islands near the equator in the Western Indian Ocean. The largest island is Mahé (142 km^2), rising to 914 m. The native flora is small (some 200 species; 100 woody species), and has a high level of endemism (40%; c. 55% for woody species), compared to c. 1000 reported exotic species (c. 300 woody species). Of all oceanic islands, the Seychelles have had the longest time for the vegetation to develop by natural immigration and evolutionary processes. Today, the number of introduced species by far exceeds the number of native species, and a significant proportion of these are invading the remaining natural habitats.

For the understanding of successful invasions three components are particularly relevant: the characteristics of the species furthering invasions ("invasiveness"); the sus-

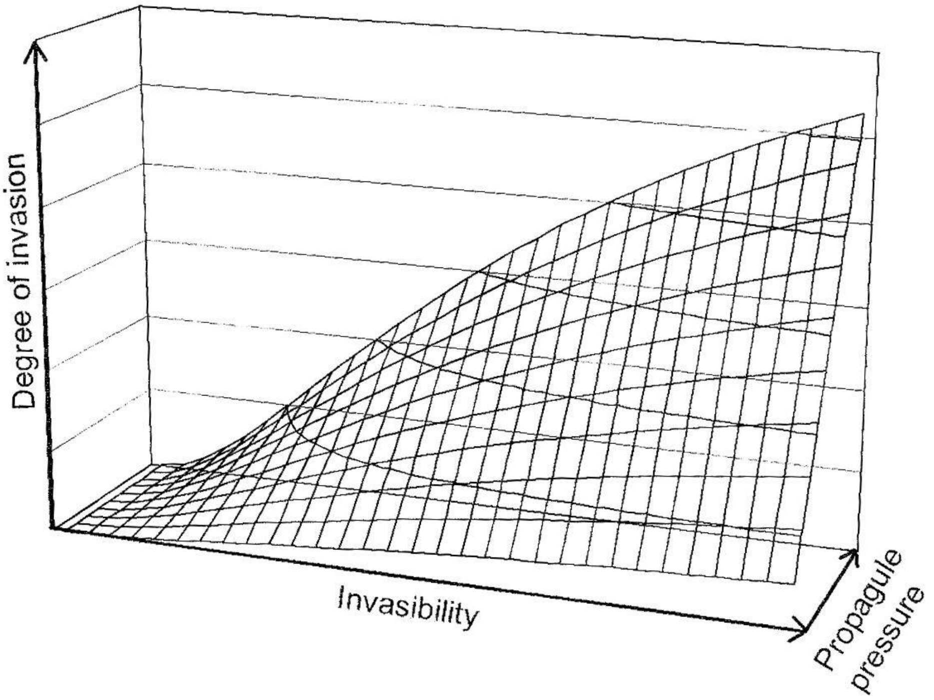

Fig. 1. Hypothesized relation between degree of invasion, invasibility and propagule pressure. The degree of invasion (individuals per area) is a function of both propagule pressure (number of seeds per area) and invasibility (percentage of successful individuals per arriving seeds). In this simple model, degree of invasion is assumed to be an S-shaped function of invasibility (i.e. environmental factors such as light, nutrient, water availability, cf. Fig. 2) and a linear function of propagule pressure. The degree of invasion is modeled as a function of both factors by multiplying their effects.

ceptibility of the habitat to invasions ("invasibility") and the number of propagules present or arriving at a site ("propagule pressure", see Williamson 1996; Lonsdale 1999). Here we focus on propagule pressure and invasibility, i.e. the contribution of environmental factors to invasion success. To distinguish between propagule pressure and invasibility, we draw a line between different life stages/processes: invasibility affects seed predation, seed germinability, and seedling and sapling growth and demography, insofar as they are determined by the target habitat conditions; propagule pressure includes adult fecundity, seed dispersal and propagule density at a given site (cf. Fig. 1).

The reasons why some communities are more invasible than others are still the subject of considerable debate. In undisturbed tropical forests, exotic species are rare, both on the mainland and on islands, while they often invade disturbed tropical forest (Fine 2002). We suggest two arguments that might explain why anthropogenic disturbances increase invasibility. From an evolutionary point of view, the invasibility of an ecosystem may increase when the conditions to which the indigenous flora is adapted change through anthropogenic impacts (Byers 2002). Alternatively, or in addition, anthropogenic disturbance may result in lower competition by native species, facilitating the establishment of new species due to higher levels of unused resources (Davis *et al.* 2000).

The role of propagule pressure in biological invasions on oceanic islands is poorly understood (Lonsdale 1999). Dispersal distances and population sizes of native species are often small, and frequent introductions of exotic species due to the position of many oceanic islands at the intersection of trading pathways can be expected (Cronk & Fuller 1995), which may increase propagule pressure of the exotics relative to that of the natives (Kolar & Lodge 2001).

The question whether adaptation to available niches or mass effects (propagule pressure) and chance effects structure species assemblages is one of the most pertinent questions in current community ecology (see for instance Hurtt & Pacala 1995; Hubbell *et al.* 1999; Turnbull *et al.* 2000; Hubbell 2001; Dalling *et al.* 2002). If seed dispersal is limiting ("recruitment limitation") less competitive species might grow in suitable microsites just because seeds of superior competitors failed to arrive at the site.

Our study investigates the relative importance of ecosystem invasibility and propagule pressure and their interactions to understand and predict invasions of alien woody plants into tropical forests on the main granitic islands of the Seychelles.

Research questions & hypotheses

We compare three different habitats that vary in the number of invasive species, relative abundance of the invasives, propagule pressure and disturbance history. We want to find out to what extent different degrees of invasion are due to variations in disturbance history („environmental change hypothesis") or variations in propagule pressure („propagule pressure hypothesis")

ENVIRONMENTAL CHANGE HYPOTHESIS

Light and nutrient availability

In general, light is the most limiting factor for plant growth in tropical forests. Therefore, increased light levels are among the most important consequences of disturbances, facilitating invasions of light-demanding alien plants in tropical forests (Duggin & Gentle 1998; Pattison *et al.* 1998; Fine 2002). In addition, studies of many natural systems have shown that fertilization can increase the dominance of non-native species (Dukes & Mooney 1999).

Before humans settled on the islands, the natural forests were probably rather closed. Wind-throw is a rare event on the Seychelles, since the islands are not hit by cyclones (Stoddart 1984). Natural gap dynamics on the Seychelles are probably mainly a function of the death of old trees, comparable to old stand dynamics in boreal forest. In more recent times, human activities such as felling of timber and the extensive planting of fast-growing species such as *Paraserianthes falcataria,* led to a more open and disturbed canopy.

For nutrients it is currently believed that either P or one of the basic cations are primarily limiting for growth in most lowland rain forests (Vitousek & Sanford 1986; Burslem *et al.* 1996; Tanner *et al.* 1998; Martinelli *et al.* 1999). Exceptions to this pattern are mountain tropical forests that are low in N (Vitousek & Sanford 1986; Tanner *et al.* 1998). In tropical forests infertile soils and conditions of moderate shade may result in nutrient limitation. Plants tend to be substantially more responsive to nutrient supply when grown in an irradiance typical of gaps and edges in natural forests than when grown under the rather shady conditions of the understory, but species differ markedly in the minimum irradiance at which they respond (Coomes & Grubb 1998). In the Seychelles tropical forests soil nutrient contents vary widely (total N, 0.05–3.4%; total P, 0.03-1.2 mg/100g; Wiederkehr & Anderegg 2001; Meuwly 2002; R. Mylonas & I. Sedivy, unpublished data), indicating that variations in nutrient availability may be an important factor for plant invasions.

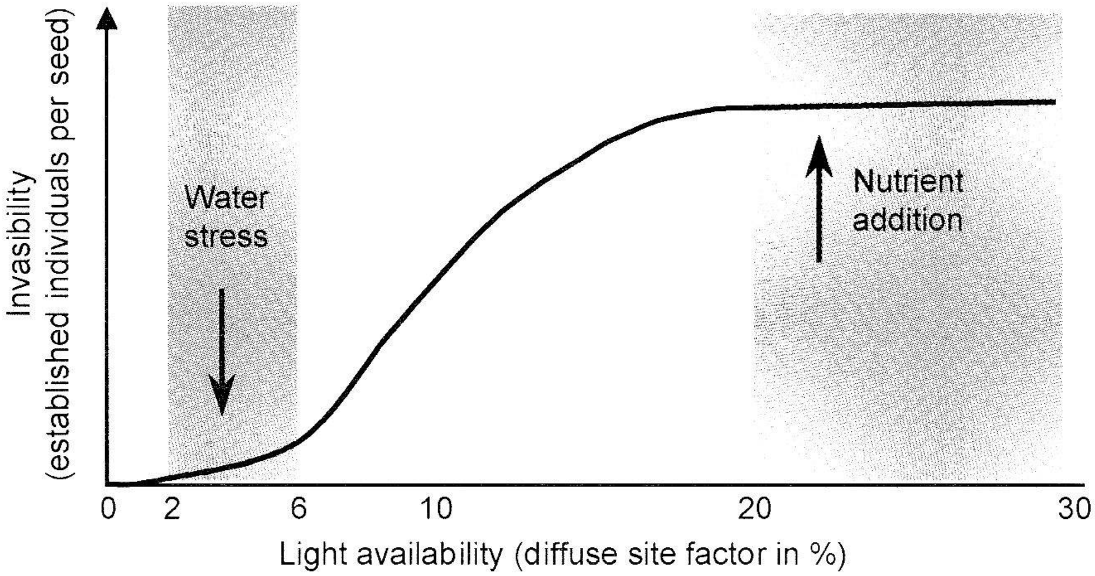

Fig. 2. *Hypothesized relation between invasibility and light, nutrient, and water availability. For invasive species we hypothesize that the success rate of emerging individuals per arriving seed (invasibility) is mainly a S-shaped function of light availability (quantified as diffuse site factor, dsf). At a dsf lower than 2%, all individuals die, and below 6% survival is low. Under ambient light availability (dsf above 6%) survival rate increases rapidly until it reaches a maximum (around a dsf of 20%). Water availability is mainly relevant at low light levels where survival is reduced by water stress. Nutrient availability is mainly relevant at high light levels, where maximal invasibility is increased by nutrient addition.*

We hypothesize that the growth of saplings of invasive species is more enhanced by increased levels of light and nutrients than the growth of saplings of natives. We suppose that the discriminating effect of elevated levels of light is stronger than that of nutrients and that the effect of elevated levels of soil nutrients is more pronounced under high light levels than in deep shade (Fig. 2).

Water stress

There is some evidence that water stress limits invasibility and that invasive species are less tolerant to water stress (Alpert *et al.* 2000). We know about no study that reports the effect of water stress on woody species invasions in tropical forests. The Seychelles experienced considerable climatic changes during their 65 millions years of separation both due to their shift of the latitudinal and longitudinal position and due to climatic changes in the region (see Willis & McElwain 2002). Thus, the native flora, but not the invasive flora, may be well adapted to water stress.

Increased seedling mortality during dry periods has been widely reported for tropical forests (Condit *et al.* 1995; Coomes & Grubb 2000; Gilbert *et al.* 2001). Shaded seedlings seem to suffer more from drought stress than seedlings growing in gaps, due to insufficient root growth (Fisher *et al.* 1991; Veenendaal *et al.* 1996; Poorter & Hayashida-Oliver 2000).

We therefore hypothesize that native species are better adapted to water stress than invasives and that the negative impact of water stress on growth and population development of seedlings and saplings is more pronounced in the shade (understorey) than in gaps (Fig. 2).

Competition

We hypothesize that interspecific belowground competition decreases with increasing anthropogenic disturbance, i.e. the older the forest habitat and the longer the time intervals between major disturbance events (e.g. timber felling) the higher the contribution of belowground competition to community composition and development.

PROPAGULE PRESSURE HYPOTHESIS

High propagule pressure generally contributes to the success of invasive species. However, the role of propagule pressure might be strongly modified by distinct spatio-temporal patterns so as to either benefit the native or invasive species in a disproportionate way. Recent experiments and models showed that there is a complex relationship between seed dispersal (propagule pressure) and population spread. Rare long-distance dispersal events (Clark *et al.* 1999; Nathan & Muller-Landau 2000) and widespread safe sites for recruitment (Bergelson *et al.* 1993) lead to increased population spread. Directed long-distance dispersal by frugivores might benefit invasive species (Directed Dispersal Hypothesis *sensu* Howe & Smallwood 1982). For instance, frugivorous birds disperse seed preferentially to gaps (see for instance Levey 1988; Wenny & Levey 1998). Invasive, light-demanding species, might profit more from directed dispersal to gaps than native species.

Mass effects

We hypothesize that in contrast to the natives the invasive species have a higher potential for colonization due to high production of propagules and/or their high abundance in the neighbourhood or within the habitat (mass effects). We suppose that recruitment in the investigated forests is at least partly dispersal-limited and that dispersal limitation is more pronounced for the native flora.

Table 1. *The plant species used for the trenching and water stress field experiments.*

Species	Family	Status	Max. height (m)
Alstonia macrophylla	Apocynaceae	invasive	15
Cinnamomum verum	Lauraceae	invasive	15
Pentadesma butyracea	Guttiferae	invasive	15
Psidium cattleianum	Myrtaceae	invasive	7
Syzygium jambos	Myrtaceae	invasive	10
Aphloia theiformis	Flacourtiaceae	native	12
Canthium bibracteatum	Rubiaceae	native	8
Memecylon eleagni	Melastomataceae	native	8
Northea hornei	Sapotaceae	native	20
Timonius sechellensis	Rubiaceae	native	8

Soil disturbance

There may be trade-offs between good dispersal abilities and traits conferring high competitive strength (e.g. Turnbull *et al.* 1999; Grime 2001). Larger seeds need less soil disturbance to produce successfully establishing seeds (Burke & Grime 1996). On the other hand, a high output of small, easily dispersed seeds increases propagule pressure.

We hypothesize that small-seeded wind- or bird-dispersed species profit from efficient seed dispersal that results in fast range expansion. As these species are more reliant on open ground for germination and establishment they will profit from increased soil disturbance.

Methods

SPECIES

The ten species (five native and five invasive) that are most prominent among the saplings in a wide range of fairly natural intermediate forests are used for field experiments. In both groups growth forms vary from small understorey trees to canopy trees (Table 1).

STUDY SITES

The study is conducted in three different forest habitats, all situated on Mahé. The habitats were chosen along an altitudinal gradient that parallels a gradient of human interference. The lowest site (Barbarons) is a disturbed lowland secondary forest (150 m asl), the intermediate site (Mare aux Cochons) is a secondary forest in the Morne Seychellois National Park (450 m asl), and the highest site (Congo Rouge) is a rather undisturbed mountain cloud forest (720 m asl).

Barbarons is situated along the west coast of Mahé. The area was used as a coconut plantation until the 1970ies and was replanted as for timber production afterwards. The height of the canopy is in the range of 18–25 m, with *Paraserianthes falcataria* building partly an emergent canopy.

Mare aux Cochons forms an upland valley on c. 450 m asl. The valley was completely deforested at the beginning of the 20th century. *Cinnamon* was cropped until the 1950ies in the area. The canopy is mainly composed of the exotic *Cinnamomum verum* and the endemic *Northea hornei*. The height of the canopy is 5–10 m.

Congo Rouge is situated above Mare aux Cochons on c. 720 m asl. It represents one of the best preserved mountain cloud forests in the Seychelles, and has a high concentration of endemic and indigenous plant species. The forest is invaded mainly by *Psidium cattleianum* and *Cinnamomum verum*. The height of the canopy is 10–12 m.

FIELD SURVEY

Forest structure is mapped in 50 circular plots per site (radius = 6 m). All tree species in the sampling plots are identified, and their stem diameter at breast height (dbh) is measured and re-measured after 1.5 years. The distance of every adult tree to the centre of the plot is measured. Within each plot all saplings (height > 0.5 m; dbh < 10 cm) are counted. At each site, seedlings are counted in 50 square 1-m^2 plots arranged regularly along two parallel 500 m transects.

At each site the diffuse light factor (dsf) is sampled with hemispheric photographs (Whitmore *et al.* 1993; Engelbrecht & Herz 2001; Ferment *et al.* 2001) using a digital camera (Englund *et al.* 2000; Frazer *et al.* 2001; Hale & Edwards 2002) and the computer software Gap Light Analyzer 2.0 (Frazer *et al.* 1999).

Air temperature and humidity is monitored in two different microsites, understorey and gap. In addition, in Mare aux Cochons and Congo Rouge, rainfall is monitored with a rain gauge. For Barbarons, rainfall data of the Seychelles Meteo Service will be used. At every site total soil N and P content, soil organic matter, soil porosity, the particle size distribution, and the characteristic soil desorption curve are determined.

Seed rain is monitored using 30 plastic bucket seed traps (Kollmann & Goetze 1998) per site, which are 25 m apart along two parallel 500-m transects. Seven duplicate seed traps per site are spaced by only 2 m to estimate small-scale spatial variability of seed rain.

EXPERIMENTS

Four experiments are carried out, of which two are aimed at testing the 'environmental change hypothesis', and the two others at testing the 'propagule pressure hypothesis'.

Nutrient addition and root trenching experiments

In Mare aux Cochons single saplings of ten species (five invasives and five natives) are used for a nutrient addition experiment combined with root trenching (Gerhardt 1996; Coomes & Grubb 1998; Ostertag 1998; Coomes & Grubb 2000; Lewis & Tanner 2000). Three treatments are installed: root trenching, root trenching and addition of an N-P-K fertilizer, and control. An area of 0.5 m x 0.5 m centred on a target sapling is trenched (all other seedlings and saplings are removed within the quadrat). The plots will be trenched every 6 months. We use 12 replicate plots per treatment, positioned along a gradient of light availability. Light availability at the sapling level is measured with hemispheric photographs (see above). Height, basal stem diameter (bsd), and number of leaves of the target saplings are measured once every six months. Degree of herbivory is estimated by counting affected leaves. The trenching and nutrient addition experiment is repeated in Barbarons and Congo Rouge with *Cinnamomum verum* as a phytometer species.

Water stress experiments

During the dry season (April-September) sapling growth and the growth of whole seedling communities is monitored in slope versus ridge position. The experiment includes two treatments: water addition and control.

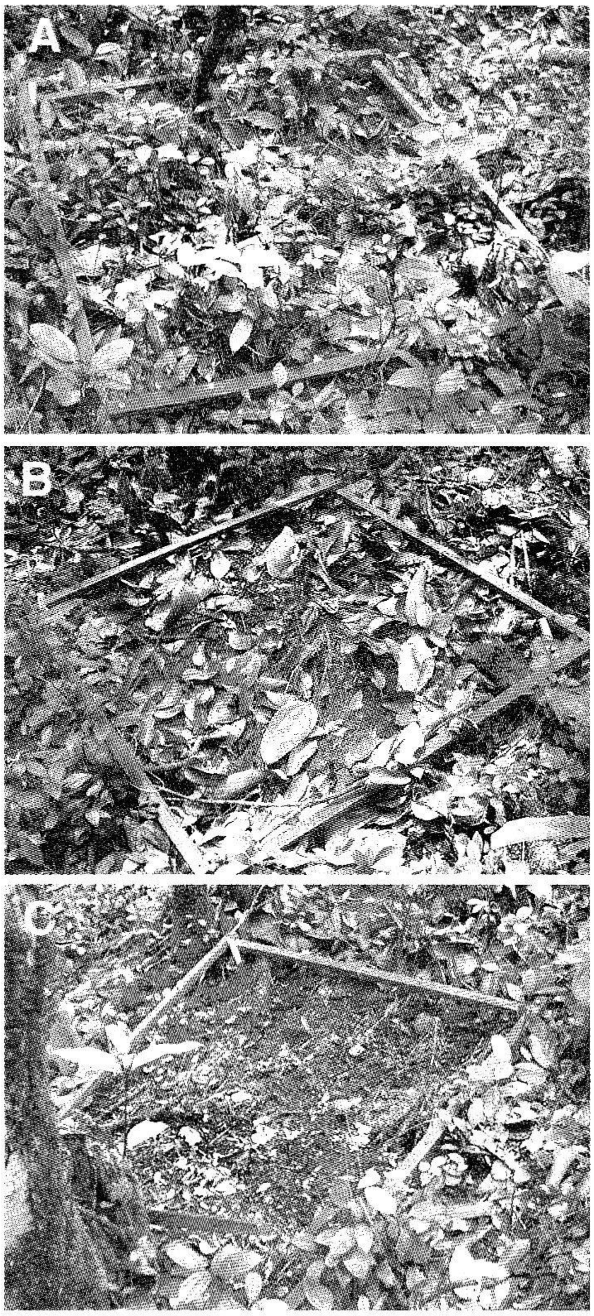

Fig. 3. Experimental plots of the removal experiment in an intermediate forest in Mare aux Cochons immediately after setting up the experiment. The three plots (each 1 m x 1 m) were randomly assigned to three treatments, i.e. (a) control, typical seedling community dominated by Cinnamomum verum, (b) seedling removal treatment, and (c) seedling and litter removal treatment.

Removal experiment

Propagule pressure is studied through removal experiments at the three sites (cf. Goldberg & Werner 1983; Beatty & Sholes 1988; Vazquez-Yanes *et al.* 1990; Molofsky & Augspurger 1992; Vazquez-Yanes & Orozco-Segovia 1992; Cintra 1997). Three differently treated plots (1 m^2) are established next to 20 seed traps per site with (a) control (untreated plot), (b) all seedlings and saplings removed, or (c) all seedlings und saplings as well as litter removed (Fig. 3). Germination and establishment of new seedlings is recorded in each plot every three months.

Sowing-out experiments

A sowing-out experiment is established in Mare aux Cochons (Turnbull *et al.* 1999, 2000; Moles & Westoby 2002). Seeds of five invasive and five native species are sown into ten pairs of two 1-m^2 plots, one without treatment, one with removal of all seedlings and litter. Germination and establishment of new seedlings is recorded every three months. In addition, the sowing-out experiment is repeated in Barbarons and Congo Rouge with seeds of *Cinnamomum verum* (as phytometer species).

Relevance of the research project

Our study will contribute to a better understanding of the peculiarities of woody plant invasions on small oceanic islands. It is still an open question if these processes are mainly due to the high level of (past) anthropogenic disturbance (number of introduced propagules, degree of habitat alteration) or intrinsic characteristics of natural island ecosystems (low competitive ability of island species, low species diversity of island ecosystems). We will provide an evaluation of the most important abiotic factors determining invasion success in tropical forests.

Our integrative analysis of the interaction between invasibility and propagule pressure will yield a more thorough understanding of the invasion processes and will improve the predictability of further invasions. Our approach is well founded in current community plant ecology and will contribute to the question whether recruitment limitation or adaptation to peculiar environmental conditions are the main determinants of woody species dynamics in the Seychelles tropical forests.

It is a further aim of the project to provide results that are directly applicable in conservation management in the Seychelles. The project is conducted in close co-operation with local partners, most notably the Forestry Section of the Seychelles Ministry of Environment. Our project should contribute to an improvement of habitat restoration techniques. A better understanding of the environmental factors that facilitate invasions help to define habitat management practices that contain further invasions and facilitate regeneration of native species.

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