

EXOTIC PLANT INVASIONS IN TROPICAL FORESTS: PATTERNS AND HYPOTHESES

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OVERVIEW

In the tropics, exotic plants have been widely introduced for industrial timber, for land reclamation and forage crops, and as ornamentals. In spite of the apparent opportunity for naturalization and spread, invasive exotic plants are scarce in many continental tropical forests. We examine several conditions under which exotic species do pose substantial threats to tropical ecosystems or to their management. These include island ecosystems, open-canopied forests, fragmented or disturbed ecosystems, and forests managed for timber or crops. We explore four hypotheses to account for the scarcity of exotic species in many tropical forests: (1) tropical forests are resistant to invasions by exotic species because they are rich in species and functional groups; (2) native rainforest species competitively exclude exotic species; (3) high pest loads and high pest diversity in the tropics deter establishment and spread of exotic species; and (4) low propagule availability contributes to the rarity of exotic species in many tropical forests. While current research suggests that high species diversity *per se* is not likely to be an impediment to exotic species, functional group diversity, high competitive exclusion rates, and high pest loads all may confer a certain biotic resistance to the establishment and spread of exotic species in tropical forests. Similarly, high functional diversity and high productivity may increase the resilience of tropical forests to the kinds of ecosystem changes effected by invasive species in other ecosystems. However, we are unable to fully evaluate these hypotheses and their interactions in the absence of a better assessment of the actual exposure of tropical forests to exotic propagules and results from seed addition experiments to test the relative importance of biotic resistance and dispersal limitation in limiting the spread of exotic species into tropical forests.

INTRODUCTION

Tropical forests face myriad threats from human activities, including land conversion and habitat fragmentation, altered fire cycles, and defaunation (Sala *et al.* 2000). With some exceptions, however, few continental tropical forests appear to be affected strongly by invasive exotic plants (e.g., Ramakrishnan 1991, Whitmore 1991, Rejmánek 1996, Fine 2002). Rejmánek (1996) found only 42 exotic plant species known to invade tropical rainforests; of those, about half were known to invade forests only on islands and eight

were reported only from treefall gaps. Similarly, exotic species constitute small percentages of the floras of two tropical field stations, La Selva Biological Station in Costa Rica (7.6%) and Barro Colorado Island in Panama (21%), where exotic species are confined to pastures, clearings, or other highly disturbed sites (Foster and Hubbell 1990, Hammel 1990). A global survey of threats to biodiversity suggests that biotic exchange is secondary to other factors such as land-use change for tropical forests as it is for most forest ecosystems (Sala *et al.* 2000). The apparently low impact of exotic species on tropical forest ecosystems

could reflect biotic resistance (Mack 1996) to exotic invaders and/or historically low exposure to propagules from exotic species (Fine 2002). Both biotic resistance (in the form of impact from competitors, predators, and pathogens) and propagule availability (via reproductive output, vegetative spread, and dispersal) are important components of plant community composition (e.g., Turnbull *et al.* 2000) and have figured in rates of biotic change throughout evolutionary time. Of interest here is their role in the spread and impacts of exotic invasive species in tropical forest ecosystems. In this chapter we examine patterns of exotic plant invasions in tropical and subtropical forests and explore four hypotheses proposed to account for these patterns.

Our perception of the vulnerability of an ecosystem to invasive species has at least two components (D'Antonio and Dudley 1995): (1) the ease with which exotic species are able to establish and spread, and (2) the tendency for exotic species to alter ecosystem and community processes. Here we will use the term "ecosystem resistance" to describe the degree to which competition, predation, and disease limit the ability of exotic species to establish reproducing populations. A community with low ecosystem resistance will be more highly invasible than a community with high resistance. "Ecosystem resilience" will be used to describe the tendency for ecosystem processes to remain unchanged following exotic invasion. Thus ecosystem processes such as disturbance frequency or resource supply rates will remain relatively unchanged following establishment of an exotic species in a resilient community. Propagule pressure – a key component of the invasion cycle (D'Antonio and Dudley 1995) – is a function of sizes of source populations, seed production, and propagule dispersal, all of which reflect the ecology and introduction history of the invader rather than attributes of the ecosystem.

Figure 24.1 illustrates some of the processes that affect the establishment and impacts of a potential exotic invader. The impact of an exotic plant species on an ecosystem will be a function both of its abundance (population size and density) and of its capacity, relative to established species, to alter ecosystem structure and

processes. Propagule pressure, resource availability, and pressure from natural enemies all influence the probability that an exotic species will establish a reproducing population and the rate of growth of that population. Habitat fragmentation increases exposure of forests to propagule pressure from exotic species in nearby disturbed or managed ecosystems. Available resources, such as light and space, also are increased by disturbance and habitat fragmentation and decreased when pre-empted by native species via competition. Rates of competitive exclusion are thought to be highest where primary productivity and growth rates are high (e.g., Rosenzweig and Abramsky 1993). Similarly, high species and functional group richness is thought to reduce resources available to newly establishing exotic species. The complexity of the invasion process and scarcity of appropriate data preclude evaluation of the relative importance of the many factors affecting the impact of exotic species on tropical forests. Many of the processes illustrated in Figure 24.1 are interdependent and most studies focus on situations in which invasive species present substantial threats to the biotic integrity of ecosystems.

Moreover, there is a strong historic component to current distributions of invasive exotic plants. For example, Wu *et al.* (2004) suggest that the low number of naturalized exotic plant species per log (area) in Taiwan versus Japan reflects Taiwan's shorter history of introductions. The apparent vulnerability of Hawai'i's forests to invasive species reflects, in part, a history of large-scale introductions. Between 1910 and 1960, some 1026 taxa, all exotic except for 78 native species, were out-planted into forest reserves statewide (Woodcock 2007). This enterprise, carried out to restore Hawai'i's watersheds, also provided opportunity for the establishment and spread of invasive species into native forests at an unprecedented scale, and certainly affects our perceptions today of the vulnerability of Hawai'i's forests to exotic species.

Our objective here is to consider the circumstances under which invasive exotic plants have had strong ecological impacts on tropical ecosystems and to use these examples to provide insight into the attributes of some tropical rainforests that

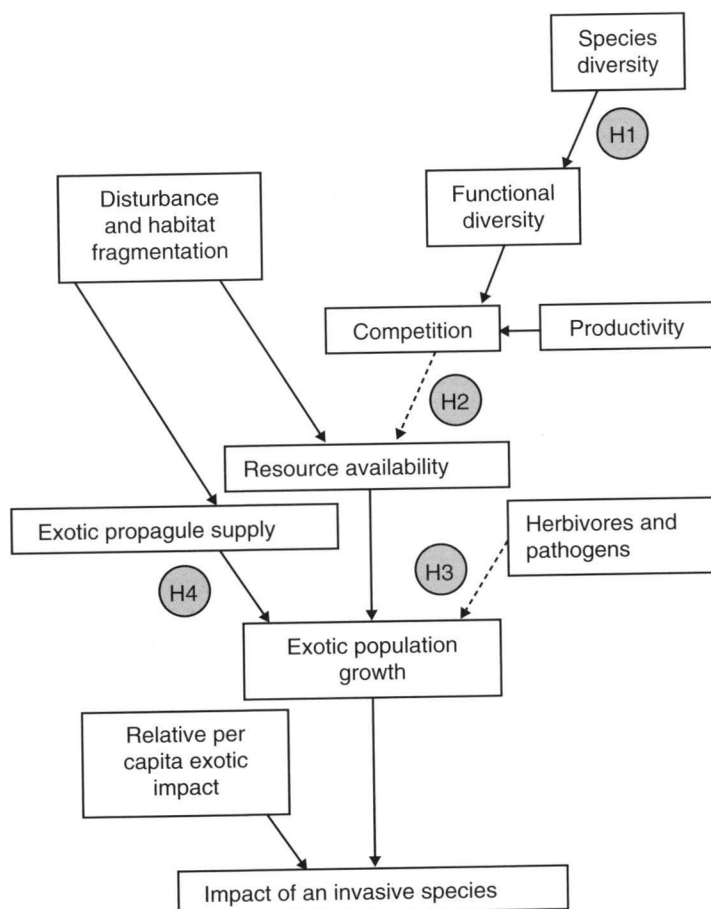


Figure 24.1 Conceptual diagram of factors affecting the impact of exotic plant invasions on a tropical forest ecosystem. Positive effects are shown with solid lines and negative effects with dashed lines. The diagram depicts a variety of interacting processes, some of which reflect attributes of the invaded community and contribute to its resistance to the establishment of new species. Others are attributes of the invading species that affect its ability to reach suitable establishment sites and to alter local ecosystem processes. H1 through H4 refer to hypotheses addressing these processes discussed in the text.

might account for the scarcity of exotic species in them. Our examples are drawn from the available literature, which necessarily addresses ecosystems that may be vulnerable to the establishment of exotics by virtue of location (islands, peninsulas) or exposure to frequent or historic disturbances. Cited examples are listed in Table 24.1 for ease of reference. We have found few examples of investigations in large tracts of intact continental forests,

so we will draw insights from examples on their fringes. For the same reason, we have defined tropical forests broadly to include forests in the tropics and subtropics under a wide range of climatic and edaphic conditions. We discuss several hypotheses that might account for scarcity of exotic plants in many tropical forest ecosystems, review the available information, and offer suggestions for future research.

Table 24.1 Exotic species cited in the text as invasive in tropical forests.

Exotic species	Growth form	Invasive range	Invaded ecosystems	Attributes of the invaded ecosystem	References
<i>Annona glabra</i>	Tree	Pacific Islands, Australia (Queensland), Vietnam	Fresh- or brackish-water wetlands; <i>Melaleuca</i> swamps (Queensland)	Open canopy, flooded soils	Humphries <i>et al.</i> (1991)
<i>Ardisia elliptica</i>	Shrub	Pacific Islands, Australia, USA (Florida)	Moist lowland forest and riparian areas	Forest understory	Horvitz <i>et al.</i> (1998)
<i>Broussonetia papyrifera</i>	Tree	Western Pacific, SE USA, Uganda	Tropical rainforest	Treefall clearings	Sheil <i>et al.</i> (2000)
<i>Cassia spectabilis</i>	Tree	Uganda	Tropical rainforest	Treefall clearings	Sheil <i>et al.</i> (2000)
<i>Chromolaena odorata</i>	Shrub	Pacific Islands, SE Asia, Australia	Tropical moist forest	Disturbances caused by ungulates, swidden agriculture	Chandrasekaran and Swamy (2000), Chandrasekara and Ramakrishnan (1994), Ghazoul (2004), MacDonald <i>et al.</i> (1988)
<i>Cinchona pubescens</i>	Tree	Pacific Islands, esp. Galápagos	Tropical moist upland forest	Island ecosystems, forest understory	MacDonald <i>et al.</i> (1988)
<i>Cinnamomum zeylanicum</i>	Tree	Pacific Islands, Seychelles	Tropical moist secondary forest	Island ecosystems, slopes, ravines	Fleischmann (1997)
<i>Clidemia hirta</i>	Shrub	Pacific Islands, Australia, Malaysia, Réunion	Tropical moist forest	Island ecosystems, forest understory	DeWalt <i>et al.</i> (2004), Wester and Wood (1977)
<i>Falcataria moluccana</i>	Tree	Pacific Islands, Singapore, Indonesia, Réunion, Seychelles	Tropical moist forest	Island ecosystems, open canopies, nitrogen-poor substrates	Hughes and Denslow (2005)
<i>Hedychium gardnerianum</i>	Herb	USA (Hawaii), New Zealand, Réunion	Tropical moist submontane forest	Island ecosystems, forest understory	Smith (1985)
<i>Lantana camara</i>	Shrub	Pacific Islands, Australia, India, SE Asia, Indian Ocean	Mesic and dry forests	Disturbances due to ungulates, swidden agriculture	Chandrasekaran and Swamy (2000), Chandrasekara and Ramakrishnan (1994), Ramakrishnan and Vitousek (1989)
<i>Melaleuca quinquenervia</i>	Tree	Pacific Islands, USA (Florida)	Subtropical forest/marsh ecotone	Flooded soils, open canopy	Ewel (1986)

<i>Melastoma candidum</i>	Shrub/tree	USA (Hawaii)	Tropical moist forest	Island ecosystems, disturbance, open canopy	Smith (1985)
<i>Miconia calvenscens</i>	Tree	USA (Hawaii), French Polynesia, Australia (Queensland)	Tropical wet and moist forests	Forest understory, disturbed areas	Meyer (1996), Conant <i>et al.</i> (1997)
<i>Mikania micrantha</i>	Vine	Pacific Islands, SE Asia, India, Australia	Tropical moist forest	Disturbed areas, open canopy	Chandrasekaran and Swamy (2000), Chandrasekara and Ramakrishnan (1994) Vitousek <i>et al.</i> (1987)
<i>Morella faya</i>	Tree	USA (Hawaii)	Tropical moist to wet forest	Island ecosystems, nitrogen-poor substrates, forest understory	
<i>Panicum maximum</i>	Grass	Pantropical	Tropical dry to moist forest	Disturbed areas including forest edges and clearings	Uhl and Kauffman (1990), D'Antonio and Vitousek (1992)
<i>Passiflora tarminiana</i>	Vine	USA (Hawaii)	Tropical moist forest	Island ecosystems, disturbed areas	Smith (1985)
<i>Piper aduncum</i>	Shrub/tree	Papua New Guinea, Fiji, Solomon Islands	Tropical moist forest	Forest edges, clearings, and secondary forest understory	Rogers and Hartemink (2000)
<i>Pittosporum undulatum</i>	Tree	Australian offshore islands, USA (Hawaii), Jamaica	Tropical moist montane forest	Island ecosystems, disturbed areas, forest understory	Bellingham <i>et al.</i> (2005)
<i>Psidium cattleianum</i>	Tree	Pacific Islands, Australia (Queensland, offshore islands), Indian Ocean	Tropical moist and wet forests	Island ecosystems, disturbances from ungulates and canopy opening, forest understory	Smith (1985), Huenneke and Vitousek (1990)
<i>Rubus alceifolius</i>	Shrub	Australia (Queensland, Christmas Island), Réunion	Tropical moist forest	Disturbances and forest clearings	Baret <i>et al.</i> (2003)
<i>Schinus terebinthifolius</i>	Tree	USA (Florida, Hawaii), Australia, Pacific Islands, Indian Ocean	Tropical seasonal and moist forests	Disturbed areas, clearings, open canopy	Smith (1985)
<i>Urochloa mutica</i>	Grass	Pacific Islands, Australia	Tropical swamps and riparian ecosystems	Flooded soils, disturbances, open canopy	Uhl and Kauffman (1990)

Notes: Information on ecology and invasive range from Space (2005). Literature references are examples only and not intended to be exhaustive. Space (2005) provides additional references.

INVASIBLE TROPICAL ECOSYSTEMS

While many tropical forests appear to be substantially weed-free, invasives can have strong impacts on mainland forest ecosystems where canopy structure is naturally open, where rainforests are fragmented or disturbed, or where forests are exploited for crops or timber, and on island ecosystems, where both disturbed and intact forest ecosystems are vulnerable.

Islands

Tropical islands are often seen as invasive-species hotspots because of both the abundance of exotic species and their impacts in those ecosystems (D'Antonio and Dudley 1995, Sax *et al.* 2002, Denslow 2003, Wu *et al.* 2004). The effects of these species are not confined to highly disturbed areas. For example, the flora of Hawai'i contains similar numbers of native (989) and naturalized exotic (1044) species (Wagner *et al.* 1999), among which are many that invade and alter native forests (Smith 1985). These include subcanopy trees, such as *Psidium cattleianum* Sabine (Myrtaceae), *Morella faya* (Ait.) Wilbur (Myricaceae), and *Schinus terebinthifolius* Raddi (Anacardiaceae); large herbs like *Hedy-chium gardnerianum* Ker Gawl (Zingiberaceae); shrubs such as *Clidemia hirta* (L.) D. Don and *Melastoma candidum* D. Don (Melastomataceae); and vines such as *Passiflora tarminiana* Cop-pens & Barney (Passifloraceae). Examples of forest invaders abound from other islands as well. *Pittosporum undulatum* Vent. (Pittosporaceae) invades montane rainforests of Jamaica (Belling-ham *et al.* 2005); *Cinchona pubescens* Vahl (Rubi-aceae) is a major forest conservation concern in the Galápagos highlands (MacDonald *et al.* 1988); *Rubus aceifolius* Poirlet (Rosaceae) invades the forests of Christmas Island and Réunion (Baret *et al.* 2003); *Cinnamomum zeylanicum* Blume (Lauraceae) invades forest in the Seychelles (Fleischmann 1997); and the neotropical under-story shrub *Piper aduncum* L. (Piperaceae) is spreading in lowland forest in Papua New Guinea (Rogers and Hartemink 2000). Sax *et al.* (2002)

note that, on average, islands have about twice as many exotic plant species as comparable mainland habitats.

However, not all tropical islands are character-ized by high densities of exotic species. In their summary of 20 island floras, Wu *et al.* (2004) show that tropical islands do not have notably more naturalized exotic species per unit log (area) than islands elsewhere nor do oceanic islands have a higher species density than continental islands (see also Rejmánek 1996, Sax *et al.* 2002). These patterns suggest that factors other than isola-tion or latitude likely affect invasibility of island ecosystems.

Open-canopied forests

Invasive exotic species strongly affect some main-land tropical forests as well, especially those with naturally open canopies, even when rela-tively undisturbed. *Melaleuca quinquenervia* (Cav.) S.T. Blake (Myrtaceae) invasion is altering the structure of the Florida Everglades where it invades scrub cypress habitats in the ecotone between upland pine forests and cypress swamps (Ewel 1986). *Annona glabra* L. (Annonaceae), a native of Florida and Central America, cre-ates dense thickets where it invades Queensland (Australia) *Melaleuca* swamp forests (Humphries *et al.* 1991). *Falcattaria moluccana* (Miq.) Barneby and J.W. Grimes (Leguminosae), a large nitrogen-fixing tree, invades undisturbed but open-canopied *Metrosideros* forests on recent lava flows in Hawai'i (Hughes and Denslow 2005). These examples also emphasize that high-stress habitats, such as frequently flooded or shallow soils, are also vulnerable to invasions if exposed to exotic species with appropriate physiological tolerances.

Disturbed forests

Chronic disturbances open forest canopies and provide opportunities for the spread of aggres-sive exotics. Such disturbances long have been recognized to predispose plant communities to exotic species establishment, in part because of the increase in resource availability they cause (Rejmánek 1989, Kitayama and Mueller-Dombois

1995, Mueller-Dombois 1995, Davis *et al.* 2000, Mack *et al.* 2002). On the continental island of Singapore, numbers of exotic species are positively correlated with canopy openness, but intact rainforest appeared to be resistant (Teo *et al.* 2003). In Florida (Horvitz *et al.* 1995) and Jamaica (Bellingham *et al.* 2005), canopy opening following hurricanes facilitated the growth of exotic species already present in the seed and seedling pool. The forests of the Western Ghats in India support large populations of native ungulates (Bagchi *et al.* 2004) and indigenous human populations practicing swidden agriculture. The understories of these forests are dominated by dense stands of *Lantana camara* L. (Verbenaceae), *Mikania micrantha* H.B.K. (Asteraceae), and *Chromolaena odorata* (L.) R.M. King and H. Robinson (Asteraceae), all of neotropical origins (Chandrashekar and Ramakrishnan 1994, Chandrasekaran and Swamy 2000).

Browsing and rooting by exotic ungulates frequently is associated with invasions of exotic plant species. In Hawai'i, pigs contribute to tree and shrub death, churn the soil, and disperse seeds of exotic species, facilitating the spread of *Psidium cattleianum* into moist forests (Aplet *et al.* 1991). Fensham *et al.* (1994) described high densities of *Lantana camara* in dry rainforest in northern Australia following impacts of pig digging and ground fire. In Pasoh Forest Reserve in Peninsular Malaysia, the native pig, *Sus scrofa*, strongly modifies the forest understory (Ickes *et al.* 2001) which may facilitate the spread of the neotropical understory shrub *Clidemia hirta*. Thus the disturbances associated with ungulate foraging are associated with the spread of exotic plant species both where ungulates are recent introductions and where ungulates are a historic component of the forest ecosystem.

Fragmented forests

Where rainforests are highly fragmented, they are subject to edge encroachment from grass fires, penetration of wind and light into the forest interior, high rates of canopy damage, and seed rain from adjacent clearings, all of which facilitate the establishment of disturbance-adapted species

(Laurance 1997, DiStefano *et al.* 1998). Naturally fragmented riparian forests in Seychelles are heavily invaded (Fleischmann 1997). In North Queensland, Australia, forest fragments are degraded further by a suite of exotic vines which smother canopy trees and understory (Humphries *et al.* 1991), a common pattern in fragmented tropical forests (Laurance 1997). Native vines and lianas have similar impacts on fragmented forests in Brazil (Tabáñez *et al.* 1997). In contrast, extensive intact Queensland rainforest appears resistant to invasions by exotic species, even when disturbed by occasional severe windstorms (Humphries and Stanton 1992). One consequence of forest fragmentation has been the alteration of successional trajectories by exotic species and the establishment on abandoned agricultural land of new forest types sometimes dominated initially by exotic species (Lugo and Helmer 2004).

Managed ecosystems

When coupled with exotic seed sources, disturbance and canopy opening due to logging and swidden agriculture also facilitate the spread of invasive species. *Chromolaena odorata* invades tropical dry forest in Thailand after extraction of *Shorea siamensis* Miq. (Dipterocarpaceae) for timber (Ghazoul 2004). In South and Central America, invasive African grasses, such as *Panicum maximum* Jacq. (Poaceae) and *Urochloa mutica* (Forssk.) T.Q. Nguyen (Poaceae), impede forest regeneration following logging or swidden agriculture and carry fire into the edges of intact forest (Uhl and Kauffman 1990, D'Antonio and Vitousek 1992). The high productivity, aggressive spread, and nutritious foliage of these exotic grasses have been important drivers of the conversion of Central and South American tropical forest to cattle pasture (Parsons 1972).

The considerable cost of controlling weeds in managed ecosystems in the tropics also is indicative of their potential to affect the course of secondary succession, forest restoration projects, and long-term forest management. For example, competition from exotic grasses and related increased fire frequencies are major impediments

to the restoration of tropical dry and mesic forest ecosystems (D'Antonio and Vitousek 1992, Cabin *et al.* 2000). Along with nutrient depletion, weed encroachment is a principal cause of field abandonment in swidden agriculture (Nye and Greenland 1960). Early fallow vegetation in tropical rainforest environments often is dominated by native pioneer species, but Ramakrishnan and Vitousek (1989) note that reducing the time between clearings in northeast India increased the dominance of invasive exotics such as *Lantana* and *Chromolaena* and other pantropical weeds. In tropical tree plantations, competition from both exotic weeds and native pioneer species is an important determinant of the success or failure of tree establishment (Wadsworth 1997). Tropical forest ecosystems may be especially vulnerable to the spread of exotic plants from swidden or logging operations. These activities not only provide disturbances that facilitate the establishment of exotic species, but are also the vehicle for the movement of novel species and varieties into lands adjacent to forest reserves (Denslow 2002).

This brief review suggests several generalizations: (1) exotic species are not perceived as a threat to most continental tropical forests; (2) nonetheless, invasive alien species do affect some tropical forest communities severely, notably those on islands, those with an open canopy structure, and those frequently disturbed or highly fragmented; and (3) invasive alien species present substantial problems in managed ecosystems in tropical environments where they alter successional trajectories, impede restoration, and may become propagule sources driving invasion into intact ecosystems.

IMPACTS OF EXOTIC PLANTS ON TROPICAL FORESTS

These examples stand in strong contrast to intact close-canopied forests where exotic plants are rare, even in treefall gaps. We discuss several hypotheses to account for the apparently high resistance of intact continental tropical forests to the establishment of invasive exotic plants. These hypotheses address different processes in exotic invasions as indicated on Figure 24.1.

Hypothesis 1. Tropical forests are resistant to invasions by exotic species because they are rich in species and functional groups

The idea that species-rich communities are less invadable than species-poor communities dates from the writings of Elton (1958), who suggested that more resources were likely to be pre-empted and more niches filled in species-rich than in species-poor communities. It has been offered as one of the central organizing tenets of invasion ecology (see reviews by Levine and D'Antonio 1999, Mack *et al.* 2002) and is an often-used example of the effects of diversity on ecosystem processes (Hooper *et al.* 2005). The relationship between native and exotic species diversity is negative when plot sizes are small (e.g., Fridley *et al.* 2004) and experimental manipulations of community structure have shown that species-rich communities resist establishment of new species more effectively than do less rich communities (Levine and D'Antonio 1999, Levine 2000, Tilman *et al.* 2001, Kennedy *et al.* 2002). In contrast, studies of grasslands (Stohlgren *et al.* 1999), riparian ecosystems (Levine 2000), islands (Lonsdale 1999, Sax *et al.* 2002), and continental ecosystems (Stark *et al.* 2006) show that at regional scales both native and exotic species richness are similarly correlated with environmental gradients – that is, native and exotic species richness are positively correlated and both increase along gradients of increasing resource supply. In the absence of direct evidence, however, these patterns are not sufficient to document competitive exclusion or resistance of diverse communities to exotic invaders. Two recent studies have shown that these patterns of negative and positive correlations do not differ from that predicted by a neutral model of no species interactions and that the relationship between exotic and native species richness depends on the area and/or number of individuals sampled (Fridley *et al.* 2004, Herben *et al.* 2004). At small plot sizes, native and exotic richness are negatively correlated because the number of individuals and species sampled is necessarily limited. At large plot sizes, the number of individuals and species sampled in a plot is more variable and

native and exotic species richness are positively correlated.

Thus there appears to be little support for the hypothesis that species richness makes communities more resistant to the establishment of exotic species. Diverse communities can be invaded where propagule pressure is high (Levine and D'Antonio 1999). At Semliki Forest Reserve, Uganda, high-diversity forests were no more resistant to exotic invasion than were the low-diversity plantations (Rejmánek 1996). The effectiveness with which the native community pre-empts available resources may be more important than diversity *per se* in impeding the establishment of exotic species (Davis *et al.* 1998, 2000, Shea and Chesson 2002, Denslow 2003 and see Hypothesis 2). Although key functional groups are more likely to be present in species-rich than in species-poor assemblages (Hooper *et al.* 2005), diverse ecosystems may be highly invulnerable when key functional groups are missing, as has been proposed for tropical islands (Kitayama 1996, Kitayama and Itow 1999, Lonsdale 1999, Fine 2002, Denslow 2003).

High diversity of functional groups may buffer continental tropical forests against the kinds of ecosystem and structural alteration caused by exotic species in other ecosystems. When invasive exotic species represent novel functional groups they are likely to alter community structure, disturbance regimes, or soil processes with ecosystem-wide consequences (Vitousek 1986). Tropical forests may be resilient to such ecosystem-altering consequences of exotic invasions when exotics do not add new functional groups to the plant community or have high per capita impacts relative to native species. Ecosystem processes such as nutrient and moisture supply rates are not easily altered in rainforest environments where moisture supply, nitrogen turnover rates, and net primary productivity are naturally high (Vitousek and Sanford 1987). The principal impact of exotic species on rainforest communities thus is likely to be through competition for space and resources rather than through alteration of ecosystem processes or disturbance regimes. Exotic vines and lianas may be an exception to these generalizations. While this is a well-represented functional group in mainland

tropical forests, a heavy infestation of lianas – exotic or native – can kill or damage canopy trees, prevent sapling growth, and contribute to the gradual degradation of rainforest structure (Humphries *et al.* 1991, Tabáñez *et al.* 1997, Horvitz *et al.* 1998).

Hypothesis 2. Native rainforest species competitively exclude exotic species

The ability of the native plant community to exclude potential invaders also will be a function, in part, of growth and dispersal rates of native species and of their ability to rapidly pre-empt resources. Two functional groups in particular may play important roles in reducing seedling establishment, thus contributing to invasion resistance in tropical forests (e.g., Rejmánek 1996, 1999, Fine 2002): (1) fast-growing pioneers of several growth forms that effectively occupy space and pre-empt resources in high-light environments, and (2) broad-leaved understory species that are able to persist in low-light environments.

High-light-demanding pioneers, including fast-growing trees, shrubs, large herbs, and lianas, are important components of forest regeneration processes because they quickly establish in large treefall openings or other disturbed areas, such as landslips or riparian corridors. These sites also provide establishment opportunities for exotic species in forest ecosystems (e.g., Rejmánek 1996, Knapp and Canham 2000, Webb *et al.* 2000, McDowell and Turner 2002). In Hawai'i several exotic *Rubus* species compete with the native *Rubus hawaiiensis* A. Gray for gap establishment sites (Gerrish *et al.* 1992) and, in the Budongo Forest, Uganda, spread of the exotics *Cassia spectabilis* DC. (Fabaceae) and *Broussonetia papyrifera* (L.) L'Hér. ex Vent. (Moraceae) is facilitated by gap openings (Sheil *et al.* 2000).

High rates of competitive exclusion in productive wet tropical forests have been suggested as a mechanism for the hump-shaped pattern of diversity across productivity gradients (e.g., Rosenzweig and Abramsky 1993) and high competitive exclusion rates likely reduce establishment success of exotic species as well as

native species. For example, new treefall openings are colonized by a combination of large-leaved herbs, vines, palms, and fast-growing, light-demanding trees, which rapidly reduce light levels near the ground (Walker *et al.* 1996, Denslow *et al.* 1998, Schnitzer *et al.* 2000). Genera such as *Cecropia*, *Trema*, *Balsa*, and *Macaranga* exhibit some of the highest growth rates observed among woody plants (Wadsworth 1997), with life-history characteristics similar to many invasive exotics. Where they are abundant, vines and lianas suppress seedling establishment and sapling growth in gaps (Putz 1991, Schnitzer *et al.* 2000). Where such pioneer species are rare, forests may be particularly vulnerable to the establishment of exotics. Horvitz *et al.* (1995) comment on the scarcity of pioneer species in the hardwood hammock flora of south Florida and speculate that exotic species (especially vines) in these hammocks usurped that role following the passage of Hurricane Andrew in 1992. On islands such as the Galápagos and Hawai'i, species with pioneer growth characteristics are sparse, possibly contributing to the invasibility of these ecosystems (Kitayama and Itow 1999, Denslow 2003). These species are able to convert high resource availability into rapid growth and high rates of production. Where invasive species increase productivity, such as through nitrogen addition to nitrogen-poor soils, competitive exclusion rates are expected to increase as well. For example, where the nitrogen-fixing tree *Falcataia mouluccana* invades Hawai'iian *Metrosideros* forest on nitrogen-poor soils, productivity increases but the native *Metrosideros* declines (Hughes and Denslow 2005).

At the other end of the shade-tolerance spectrum, understory palms, shrubs, ferns, and herbs produce dense shade at ground levels (Montgomery 2004). Where these species are common, seedling establishment is suppressed and seedling densities are low (Denslow *et al.* 1991, Farris-Lopez *et al.* 2004, Harms *et al.* 2004, Wang and Augspurger 2004). The inhibitory effect is strong on native species and likely would affect exotic species as well. The combined effect of fast-growing pioneers and shade-tolerant herbs and shrubs is to reduce site occupancy by seedlings and increase the importance of recruitment limitation in rainforest dynamics. While density

may be more critical than the number of species, redundancy within functional groups is likely to increase their distribution and impact.

Hypothesis 3. High pest loads and high pest diversity in the tropics deter establishment and spread of exotic species

In tropical forests, high diversity and abundance of natural enemies (herbivores and pathogens) occasionally may lead to high impacts of native pests on exotic species (e.g., Nair 2001, Novotny *et al.* 2003). Certainly, rates of leaf damage by herbivores and pathogens tend to be high, although variable among species, in tropical forests (Coley and Aide 1991, Coley and Barone 1996). Thus, native generalist herbivores, pathogens, and viruses may provide a biotic barrier to invasion (Mack 1996, Parker *et al.* 2006) if they are able to exploit exotic plants. High diversities of both pests and host plants, which reach their peak in the wet tropics for many taxa, may increase the probability that an exotic plant is suppressed by native herbivores, as shown by Prieur-Richard *et al.* (2002) in a Mediterranean plant community. In addition, generalist pest species may play important regulatory roles in population dynamics of tropical plants. For example, Augspurger (1984) describes the importance of damping-off fungi as a source of seedling mortality in the tropical forest understory. Oomycetes, a common group of damping-off fungi, can persist in the soil in the absence of hosts and exhibit low host specificity (Augspurger 1984, Hood *et al.* 2004). Among insect herbivores, most species are not monophagous but feed on multiple species within a genus or family (Coley and Barone 1996). Some common foliage-feeding herbivores, such as leaf-cutter (Attine) ants (Fowler *et al.* 1989, Farji-Brener 2001, Wirth *et al.* 2003) and orthoptera (Novotny *et al.* 2004), have broad diets. Leaf-cutter ants in particular are serious predators of a number of exotic crops, including citrus, eucalyptus, coffee, and cacao; Cherrett (1989) suggests that the susceptibility of so many crop species to this pest is due in part to their lack of defenses. A meta-analysis by Parker *et al.* (2006) showed that exotic invaders often are

repelled by native herbivores. We suggest that such generalist natural enemies may contribute to the apparent invasion resistance of tropical forests.

This biotic barriers hypothesis runs counter to one of the principal explanations of invasiveness—the enemy release hypothesis (ERH). This hypothesis proposes that the accidental or even intentional introduction of plants away from their native range is accomplished most often without concomitant introduction of the specialist herbivores, pathogens, and viruses that attack and limit their populations in their native range. If native species are limited by their own suite of natural enemies where exotics are introduced, then exotics may proliferate because of their relatively lower pest loads (Elton 1958, Maron and Vilà 2001, Keane and Crawley 2002). Indeed, there is evidence that, where introduced, some exotic tropical species have lower pest loads in their invasive than in their native range and lower pest loads than local native species in their invasive range. For example, invasive species on Mahé, the main island of the tropical Seychelles, suffered less leaf area loss to herbivores than native woody species (Dietz *et al.* 2004). Native pioneer species were especially susceptible to herbivores (C. Kueffer pers. comm.). In addition, a biogeographical comparison of the impact of natural enemies on the neotropical shrub *Clidemia hirta* in its native and introduced ranges found that plants were heavily attacked by insect herbivores and fungal pathogens in the native range, particularly in forest understory, but that they were relatively pest free in the introduced range (DeWalt *et al.* 2004). The consequences of pest-load reduction to *C. hirta* appear to include not only proliferation in the introduced range, but also invasion of forest understory, where it does not occur in its native range (DeWalt *et al.* 2004). The relative success of plantations of exotic species such as rubber (*Hevea brasiliensis* (Willd.) Muell.-Arg. [Euphorbiaceae]) and *Eucalyptus* (Myrtaceae) in the tropics is also attributable in part to their escape from heavy pest loads, particularly from specialists in their native ranges (Rosenthal *et al.* 1979, Gadgil and Bain 1999). Thus, some tropical plant populations may be regulated by natural enemies to the extent that release from these enemies leads to their proliferation in introduced ranges (DeWalt 2005).

Does a biotic barrier in the form of high pest loads contribute to the relative dearth of invasive exotic species in tropical forests? Does escape from natural predators give exotic species an advantage where they are introduced? Both of these hypotheses are compelling and supported by examples. Further evaluation awaits more information on the population-level effects of natural enemies on exotic species.

Hypothesis 4. Low propagule availability contributes to the rarity of exotic species in many tropical forests

The distribution and abundance of many forest plant species, in temperate as well as in tropical forests, are limited by failure to recruit seedlings to sites otherwise suitable to their establishment and growth (Clark *et al.* 1998, 1999a, Turnbull *et al.* 2000, Beckage and Clark 2003, Svenning and Wright 2005). Factors contributing to recruitment limitation include those affecting the size of the seed crop (fecundity and the density and distribution of adult trees), close and distant dispersal (Clark *et al.* 1999b), and post-dispersal factors such as pests and pathogens which affect germination and seedling establishment (Clark *et al.* 1998, Nathan and Muller-Landau 2000, Turnbull *et al.* 2000, Zimmerman *et al.* 2000). Dispersal and recruitment limitation increasingly are seen as major determinants of the relative abundances of species in forest ecosystems (Clark *et al.* 1999b, Harms *et al.* 2000, Nathan and Muller-Landau 2000, Hubbell 2001, Denslow *et al.* 2006).

Propagule supply also plays a major role in exotic species invasions (Von Holle and Simberloff 2005). For example, some of the strongest predictors of invasiveness are those that affect propagule distribution and abundance, including the duration, frequency, and area of exotic species introductions (Richardson 1999, Lockwood *et al.* 2005). Forests most likely to be free of exotic species are those with low exposure to propagules from urban or agricultural areas (Aragon and Morales 2004, Sullivan *et al.* 2005). Disturbed forests may be free of exotic species if propagule input is low. In Hawai'i Volcanoes National Park, montane rainforests heavily damaged by pig

browsing are little affected by exotic species where human traffic is low (T. Tunison personal communication). Forest fragmentation, road construction, and other sources of human disturbance are likely to expose adjacent forests to seed rain from exotic species. Fine (2002) has suggested that the scarcity of exotic species in tropical forests may reflect a more recent history of disturbance and fragmentation in tropical than in temperate forest. Although forest clearing and fragmentation is a more recent phenomenon in tropical than in temperate forests, human populations have lived in and exploited tropical forests for centuries. Further, natural disturbance regimes in wet tropical forests are high (Denslow 1987). It is unlikely that disturbance alone accounts for the distribution of exotic species.

Low exotic species abundances may reflect a historic lack of seed availability from species with appropriate physiological characteristics, such as shade tolerance, for establishment in tropical rainforest. Exotic plants, especially woody species, have been widely introduced in the tropics, often at grand scales. Extensive forestry, agricultural, and land-reclamation projects juxtapose large populations of exotic species with native forest. Many of these planted exotic species have life-history attributes similar to those of native pioneers and gap colonizers (Wadsworth 1997). For example, fast-growing species in the genera *Pinus*, *Tectona*, *Eucalyptus*, and *Gmelina* commonly have been planted for industrial timber (Wadsworth 1997), while many species and genotypes of *Leucaena*, *Albizia*, *Acacia*, and *Calliandra* have been introduced as utility species to rehabilitate degraded soils and provide fodder and firewood (Hughes and Styles 1989, Hughes 1994). Tropical forests may not be immune to the spread of such high-light-demanding exotic species, which may appear in natural forest clearings where they can impede regeneration of native species (Rejmánek 1996).

A more likely source of shade-tolerant species is ornamental plants which have been widely introduced into tropical habitats and are the source of many invasive species (Meyer and Lavergne 2004, Wu *et al.* 2004). Daehler (personal communication) estimates that 39% of the approximately 100 naturalized exotic species that

pose the greatest threat to Hawai'i's native ecosystems were introduced as ornamentals. Noteworthy examples of shade-tolerant ornamentals that have become invasive in tropical forests include *Miconia calvescens* DC. (Melastomataceae), a neotropical tree invasive in native forests of French Polynesia (Meyer 1996) and Hawai'i (Conant *et al.* 1997); *Ardisia elliptica* Thunb. (Myrsinaceae), which has become invasive in hammocks of south Florida (Horvitz *et al.* 1998); and numerous vines and lianas with shade-tolerant juvenile stages, such as *Merremia tuberosa* (L.) Rendle (Convolvulaceae) and *Jasminum dichotomum* Vahl (Oleaceae) (Horvitz *et al.* 1998), also invasive in south Florida.

In the absence of experimental additions of seeds (Turnbull *et al.* 2000), it is difficult to evaluate the role of propagule availability in limiting exotic species in tropical forests. Tropical forests, like their temperate counterparts, are not likely to be strongly affected by exotic plant invasions if the forests are buffered from exposure to propagule sources (e.g., Pyšek *et al.* 2002).

CONCLUSIONS

The scarcity of exotic plants recorded from intact continental tropical forests suggests that tropical forests may be resistant to invasions of exotic plants. High species and functional group diversity, high competitive exclusion rates, and high pest loads all may confer a certain biotic resistance to the establishment and spread of exotic species in tropical forests. Similarly, high diversity and high productivity may increase the resilience of tropical forests to the kinds of ecosystem changes effected by invasive species in other ecosystems. However, we are unable to evaluate these hypotheses fully because we cannot evaluate exposure levels of tropical forests to propagules of exotic species. There are exceptions to the general pattern of sparse exotic species in tropical forests. Prevention and control of invasive species on islands, in fragmented or disturbed ecosystems, and in managed ecosystems are all major conservation and management concerns in tropical forest environments. Lessons from islands and exploited ecosystems suggest that control of invasive exotic species

will assume increasing importance in the conservation of forest preserves as habitats become fragmented and exposed to increasing varieties of exotic species.

Our review highlights several areas in which further research would be productive. For example, what is the role of natural enemies (herbivorous pests and pathogens) in regulating native and exotic plant populations? We know little about the extent to which top-down factors control tropical plant populations, much less about their role in plant invasions. Basic research on the role of pests and pathogens in regulating species abundances may provide insight into the mechanisms of invasion as well as elucidating factors structuring plant communities. These issues also are related directly to the development of safe and effective biological control agents for wildland weeds (Denslow and Johnson 2006).

What are the roles of seemingly minor species such as understory shrubs and pioneer trees in regulating resource availability in tropical forest ecosystems? Our review suggests that competition from native pioneers may be critical in invasion resistance, yet these species are relatively sparse in intact rainforests. Recent research documents the importance of understory vegetation in reducing light levels near the ground (Montgomery 2004). Thus shrubs, ferns, and understory palms could play important roles in limiting exotic species establishment.

Experimental additions of seeds, propagules, or seedlings in tropical forest environments would provide important insights into processes limiting the establishment and spread of species (e.g., Turnbull *et al.* 2000) and how those processes vary within forests and across landscapes, regions, and species.

While forests in general, and tropical rainforests in particular, often appear more resistant to the establishment of exotic species than many other ecosystem types (Rejmánek 1989, Fine 2002), global change is likely to increase their vulnerability. Changing climate, altered disturbance regimes, and increased forest fragmentation and exploitation (Sala *et al.* 2000) may open forest canopies, and increased global movement of species, biotypes, pests, and diseases will provide

exposure to new species capable of taking advantage of local environmental opportunities.

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REFERENCES

- Aplet, G.H., Anderson, S.J., and Stone, C.P. (1991) Association between feral pig disturbance and the composition of some alien plant assemblages in Hawai'i Volcanoes National Park. *Vegetatio* 95, 55–62.
- Aragon, R. and Morales, J.M. (2004) Species composition and invasion in NW Argentinian secondary forests: effects of land-use history, environment and landscape. *Journal of Vegetation Science* 14, 195–204.
- Augspurger, C. (1984) Seedling survival of tropical tree species: interactions of dispersal distances, light gaps, and pathogens. *Ecology* 65, 1705–1712.
- Bagchi, S., Goyal, S.P., and Sankar, K. (2004) Herbivore density and biomass in a semi-arid tropical dry deciduous forest of western India. *Journal of Tropical Ecology* 20, 475–478.
- Baret, S., Nicolini, E., Le Bourgeois, T., and Strasberg, D. (2003) Developmental patterns of the invasive bramble (*Rubus alceifolius* Poirlet, Rosaceae) in Réunion island: an architectural and morphometric analysis. *Annals of Botany* 91, 39–48.
- Beckage, B. and Clark, J.S. (2003) Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84, 1849–1861.
- Bellingham, P.J., Tanner, E.V.J., and Healey, J.R. (2005) Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. *Journal of Vegetation Science* 16, 675–684.
- Cabin, R.J., Weller, S.G., Lorence, D.H. *et al.* (2000) Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration

- of a Hawaiian Tropical Dry Forest. *Conservation Biology* 14, 439–453.
- Chandrasekaran, S. and Swamy, P.S. (2000) Changes in herbaceous vegetation following disturbance due to biotic interference in natural and man-made ecosystems in Western Ghats. *Tropical Ecology* 36, 213–220.
- Chandrasekara, U.M. and Ramakrishnan, P.S. (1994) Successional patterns and gap phase dynamics of a humid tropical forest of the Western Ghats of Kerala, India: ground vegetation, biomass, productivity and nutrient cycling. *Forest Ecology and Management* 70, 23–40.
- Cherrett, J.M. (1989) Leaf-cutting ants. In H. Lieth and M.J.A. Weiger (eds), *Ecosystems of the World*. Elsevier, New York, pp. 473–489.
- Clark, J.S., Beckage, B., Camill, P. et al. (1999a) Interpreting recruitment limitation in forests. *American Journal of Botany* 86, 1–16.
- Clark, J.S., Macklin, E., and Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68, 213–235.
- Clark, J.S., Silman, M., Kern, R., Macklin, E., and HilleRisLambers, J. (1999b) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80, 1475–1494.
- Coley, P.D. and Aide, T.M. (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In P.W. Price, T.M. Lewinsohn, G.W. Fernandes, and W.W. Benson (eds), *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley & Sons, New York, pp. 25–49.
- Coley, P.D. and Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27, 305–335.
- Conant, P., Medeiros, A.C., and Loope, L.L. (1997) A multiagency containment program for miconia (*Miconia calvescens*), an invasive tree in Hawaiian rain forests. In J.O. Luken and J.W. Thieret (eds), *Assessment and Management of Plant Invasions*. Springer-Verlag, New York, pp. 249–254.
- D'Antonio, C.M. and Dudley, T.L. (1995) Biological invasions as agents of change on islands versus mainlands. In P.M. Vitousek, L.L. Loope, and H. Adersen (eds), *Islands: Biological Diversity and Ecosystem Function*. Springer-Verlag, Stanford, pp. 103–121.
- D'Antonio, C.M. and Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23, 63–87.
- Davis, M.A., Wragge, K.J., and Reich, P.B. (1998) Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* 86, 652–661.
- Davis, M.A., Grime, J.P., and Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88, 528–534.
- Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18, 431–451.
- Denslow, J.S. (2002) Invasive alien woody species in Pacific island forests. *Unasylva* 53, 62–63.
- Denslow, J.S. (2003) Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* 90, 119–127.
- Denslow, J.S., Ellison, A., and Sanford, R.E. Jr. (1998) Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology* 86, 597–609.
- Denslow, J.S. and Johnson, M.T. (2006) Biological control of tropical weeds: research opportunities in plant–herbivore interactions. *Biotropica* 38, 139–142.
- Denslow, J.S., Newell, E., and Ellison, A.M. (1991) The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23, 225–234.
- Denslow, J.S., Uowolo, A.L., and Hughes, R.F. (2006) Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia* 148, 118–128.
- DeWalt, S.J. (2005) Effects of natural enemies on tropical plant invasions. In D.E.R.P. Burslem, M. Pinard, and S.E. Hartley (eds), *Biotic Interactions in the Tropics*. Cambridge University Press, Cambridge, pp. 459–483.
- DeWalt, S.J., Denslow, J.S., and Ickes, K. (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85, 471–483.
- Dietz, H., Wirth, L.R., and Buschmann, H. (2004) Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. *Biological Invasions* 6, 511–521.
- Di Stefano, J.F., Fournier, L.A., Carranza, J., Marin, W., and Mora, A. (1998) Invasive potential of *Syzygium jambos* (Myrtaceae) in forest fragments: the case of Ciudad Colon, Costa Rica. *Revista de Biología Tropical* 46, 567–573.
- Elton, C.S. (1958) *The Ecology of Invasions of Animals and Plants*. Methuen, London.
- Ewel, J.J. (1986) Invasibility: lessons from South Florida. In H.A. Mooney and J.A. Drake (eds), *Ecology of Biological Invasions of North America and Hawai'i*. Springer-Verlag, New York, pp. 214–230.

- Ewel, J.J., O'Dowd, D.J., Bergelson, J. *et al.* (1999) Deliberate introductions of species: research needs. *BioScience* 49, 619–630.
- Farji-Brener, A.G. (2001) Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92, 169–177.
- Farris-Lopez, K., Denslow, J.S., Moser, B., and Passmore, H. (2004) Influence of a common palm, *Oenocarpus mapora*, on seedling establishment in a tropical moist forest in Panama. *Journal of Tropical Ecology* 20, 429–439.
- Fensham, R.J., Fairfax, R.J., and Cannell, R.J. (1994) The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, North Queensland. *Australian Journal of Ecology* 19, 297–305.
- Fine, P.V.A. (2002) The invasibility of tropical forests by exotic plants. *Journal of Tropical Ecology* 18, 687–705.
- Fleischmann, K. (1997) Invasion of alien woody plants on the islands of Mahé and Silhouette, Seychelles. *Journal of Vegetation Science* 8, 5–12.
- Foster, R.B. and Hubbell, S.P. (1990) The floristic composition of the Barro Colorado Island forest. In A.H. Gentry (ed.), *Four Neotropical Rain Forests*. Yale University Press, New Haven, pp. 85–98.
- Fowler, H.G., Pagani, M.I., Da Silva, D.A., Forti, L.C., da Silva, V.P., and Vasconcelos, H.L. (1989) A pest is a pest? The dilemma of Neotropical leaf cutting ants: keystone taxa of natural ecosystems. *Environmental Management* 13, 671–675.
- Fridley, J.D., Brown, R.L., and Bruno, J.F. (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology* 85, 3215–3222.
- Gadgil, P.D. and Bain, J. (1999) Vulnerability of planted forests to biotic and abiotic disturbances. *New Forests* 17, 227–238.
- Gerrish, G., Stemmermann, L., and Gardner, D.E. (1992) The distribution of *Rubus* species in the State of Hawai'i. Cooperative National Park Resources Studies Unit, Honolulu, Hawai'i. No. 85.
- Ghazoul, J. (2004) Alien abduction: disruption of native plant-pollinator interactions by invasive species. *Biotropica* 36, 156–164.
- Green, P.T., O'Dowd, D.J., and Lakes, P.S. (2004) Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. *Biological Invasions* 6, 1–9.
- Hammel, B. (1990) The distribution of diversity among families, genera and habitat types in the La Selva Flora. In A.H. Gentry (ed.), *Four Neotropical Rain Forests*. Yale University Press, New Haven, pp. 75–84.
- Harms, K.E., Powers, J.S., and Montgomery, R.A. (2004) Variation in small sapling density, understory cover, and resource availability in four Neotropical forests. *Biotropica* 36, 40–51.
- Harms, K.E., Wright, S.J., Calderon, O., Hernández, A., and Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404, 493–495.
- Herben, T., Mandák, B., Bímová, K., and Münzbergová, Z. (2004) Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology* 85, 3223–3233.
- Hood, L.A., Swaine, M.D., and Mason, P.A. (2004) The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest and soil. *Journal of Ecology* 92, 816–823.
- Hooper, D.U., Chapin III, F.S., Ewel, J.J. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. *Ecological Monographs* 75, 3–35.
- Horvitz, C.C., McMann, S., and Freedman, A. (1995) Exotics and hurricane damage in three hardwood hammocks in Dade County Parks, Florida. *Journal of Coastal Research* 21, 145–158.
- Horvitz, C.C., Pascarella, J.B., McMann, S., Freedman, A., and Hofstetter, R.H. (1998) Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications* 8, 947–974.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Huenneke, L.F. and Vitousek, P.M. (1990) Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: implications for management of native Hawaiian forests. *Biological Conservation* 53, 199–211.
- Hughes, C.E. (1994) Risks of species introductions in tropical forestry. *Commonwealth Forestry Review* 73, 243–252.
- Hughes, R.F. and Denslow, J.S. (2005) Invasion by an N-fixing tree, *Falcataria moluccana*, alters function and structure of wet lowland forests of Hawai'i. *Ecological Applications* 15, 1615–1628.
- Hughes, C.E. and Styles, B.T. (1989) The benefits and risks of woody legume introductions. In C.H. Stirton and J.L. Zarruchi (eds), *Advances in Legume Biology. Monographs in Systematic Botany*, Missouri Botanical Garden 29, pp. 505–531.
- Humphries, S.E., Groves, R.H., and Mitchell, D.S. (1991) Part I. Plant invasions of Australian ecosystems: a

- status review and management directions. *Kowari* 2, 1–134.
- Humphries, S.E. and Stanton, J.P. (1992) *Weed Assessment in the Wet Tropics World Heritage Area of North Queensland*. Report to The Wet Tropics Management Agency Report.
- Ickes, K., DeWalt, S.J., and Appanah, S. (2001) Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology* 17, 191–206.
- Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17, 164–170.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D., and Reich, P.B. (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417, 636–638.
- Kitayama, K. (1996) Patterns of species diversity on an oceanic versus a continental island mountain: a hypothesis on species diversification. *Journal Vegetation Science* 7, 879–888.
- Kitayama, K. and Itow, S. (1999) Above-ground biomass and soil nutrient pools of a *Scalesia pedunculata* montane forest on Santa Cruz, Galápagos. *Ecological Research* 14, 405–408.
- Kitayama, K. and Mueller-Dombois, D. (1995) Biological invasion on an oceanic island mountain – do alien plant species have wider ecological ranges than native species? *Journal of Vegetation Science* 6, 667–674.
- Knapp, L.B. and Canham, C.D. (2000) Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. *Journal of the Torrey Botanical Society* 127, 307–315.
- Laurance, W.F. (1997) Hyper-disturbed parks: edge effects and the ecology of isolated rain forest reserves in tropical Australia. In W.F. Laurance and R.O. Bierregaard, Jr. (eds), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, pp. 71–83.
- Levine, J.M. (2000) Species diversity and biological invasions: relating local process to community pattern. *Science* 288, 852–854.
- Levine, J.M. and D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87, 15–26.
- Lockwood, J.L., Cassey, P., and Blackburn, T.M. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20, 223–228.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.
- Lugo, A.E. and Helmer, E. (2004) Emerging forests on a abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190, 145–161.
- MacDonald, I.A.W., Ortiz, L., Lawesson, J.E., and Nowak, J.B. (1988) The invasion of highlands in Galápagos by the red quinine tree, *Cinchona succirubra*. *Environmental Conservation* 15, 215–220.
- Mack, R.N. (1996) Biotic barriers to plant naturalization. In V.C. Moran and J.H. Hoffmann (eds), *IX International Symposium on Biological Control*. University of Cape Town, Stellenbosch, South Africa, pp. 39–46.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., and Clout, M. (2002) Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* 10, 689–710.
- Maron, J.L. and Vilà, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95, 361–373.
- McDowell, C.L. and Turner, D.P. (2002) Reproductive effort in invasive and non-invasive *Rubus*. *Oecologia* 133, 102–111.
- Meyer, J.-Y. (1996) Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). *Pacific Science* 50, 66–76.
- Meyer, J.-Y. and Lavergne, C. (2004) *Beautes fatales*: Acanthaceae species as invasive alien plants on tropical Indo-Pacific Islands. *Diversity and Distributions* 10, 333–347.
- Montgomery, R.A. (2004) Effects of understory foliage on patterns of light attenuation near the forest floor. *Biotropica* 36, 33–40.
- Mueller-Dombois, D. (1995) Biological diversity and disturbance regimes in island ecosystems. In P.M. Vitousek, L.L. Loope, and H. Adersen (eds), *Islands: Biological Diversity and Ecosystem Function*. Springer, Berlin, pp. 163–175.
- Nair, K.S.S. (2001) *Pest Outbreaks in Tropical Forest Plantations: Is There a Greater Risk for Exotic Tree Species?* Center for International Forestry Research, Bogor, Indonesia.
- Nathan, R. and Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15, 278–285.
- Novotny, V., Basset, Y., Miller, S.E. et al. (2004) Local species richness of leaf-chewing insects feeding on woody plants from one hectare of a lowland rainforest. *Biological Conservation* 18, 227–237.
- Novotny, V., Miller, S.E., Cizek, L. et al. (2003) Colonising aliens: caterpillars (Lepidoptera) feeding on *Piper aduncum* and *P. umbellatum* in rainforests

- of Papua New Guinea. *Ecological Entomology* 28, 704–716.
- Nye, P.H. and Greenland, D.J. (1960) *The Soil Under Shifting Cultivation*. Technical Communication No. 51, Commonwealth Bureau of Soils, Harpenden.
- Parker, J.D., Burkepile, D.E., and Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science* 311, 1459–1461.
- Parsons, J.J. (1972) Spread of African pasture grasses in the American tropics. *Journal of Range Management* 25, 12–17.
- Prieur-Richard, A.K., Lavorel, S., Linhart, Y.B. and Dos Santos, A. (2002) Plant diversity, herbivory and resistance of a plant community to invasions, in Mediterranean annual communities. *Oecologia* 130, 96–104.
- Putz, F.E. (1991) Silvicultural effects of lianas. In F.E. Putz and H.A. Mooney (eds), *The Biology of Vines*. Cambridge University Press, Cambridge, pp. 493–501.
- Pyšek, P., Jarošek, V., and Kučera, T. (2002) Patterns of invasion in temperate nature reserves. *Biological Conservation* 104, 13–24.
- Ramakrishnan, P.S. (1991) *Ecology of Biological Invasion in the Tropics*. International Scientific Publications, New Delhi.
- Ramakrishnan, P.S. and Vitousek, P.M. (1989) Ecosystem-level processes and consequences of biological invasions. In J.A. Drake, H.A. Mooney, F. Di Castri *et al.* (eds), *Biological Invasions: A Global Perspective*. Wiley, New York, pp. 281–328.
- Rejmánek, M. (1989) Invasibility of plant communities. In J.A. Drake, H.A. Mooney, F. Di Castri *et al.* (eds) *Biological Invasions: A Global Perspective*. Wiley, New York, pp. 369–388.
- Rejmánek, M. (1996) Species richness and resistance to invasions. In G. Orians, R. Dirzo, and J.H. Cushman (eds), *Biodiversity and Ecosystem Processes in Tropical Forests*. Springer Verlag, New York, pp. 153–172.
- Rejmánek, M. (1999) Invasive plant species and invulnerable ecosystems. In O.T. Sandlund, P.J. Schei, and A. Viken (eds), *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, Boston, MA, pp. 79–102.
- Richardson, D.M. (1999) Commercial forestry and agroforestry as sources of invasive alien trees and shrubs. In O.T. Sandlund, P.J. Schei, and A. Viken (eds), *Invasive Species and Biodiversity Management*. Kluwer Academic Publishers, Boston, MA, pp. 237–257.
- Rogers, H.M. and Hartemink, A.E. (2000) Soil seed bank and growth rates of an invasive species, *Piper aduncum*, in the lowlands of Papua New Guinea. *Journal of Tropical Ecology* 16, 243–251.
- Rosenthal, G.A. and Janzen, D.H. (1979) *Herbivores, Their Interaction with Secondary Plant Metabolites*. Academic Press, New York.
- Rosenzweig, M.L. and Abramsky, Z. (1993) How are diversity and productivity related? In R.E. Ricklefs and D. Schluter (eds), *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, pp. 52–65.
- Sala, O.E., Chapin III, F.S., Armesto, J.J. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Sax, D.F., Gaines, S.D., and Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *American Naturalist* 160, 766–783.
- Schnitzer, S.A., Dalling, J.W., and Carson, W.P. (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88, 655–666.
- Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17, 170–176.
- Sheil, D. (1994) Naturalized and invasive species in the evergreen forests of the East Usambara Mountains, Tanzania. *African Journal of Ecology* 32, 66–71.
- Sheil, D., Jennings, S., and Savill, P. (2000) Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest. *Journal of Tropical Ecology* 16, 765–800.
- Smith, C.W. (1985) Impact of alien plants on Hawai'i's native biota. In C.P. Stone and J.M. Scott (eds), *Hawai'i's Terrestrial Ecosystems: Preservation and Management*. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu, HI, pp. 180–250.
- Space, J.C. (2005) *Pacific Island Ecosystems at Risk*. v 5.0. USDA Forest Service, Institute of Pacific Islands Forestry. (www.hear.org/pier).
- Stark, S.C., Bunker, D.E., and Carson, W.P. (2006) A null model of exotic plant diversity tested with exotic and native species-area relationships. *Ecology Letters* 9, 136–141.
- Stohlgren, T.J., Binkley, D., Chong, G.W. *et al.* (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69, 25–46.
- Sullivan, J.J., Timmins, S.M., and Williams, P.A. (2005) Movement of exotic plants into coastal native forests from gardens in northern New Zealand. *New Zealand Journal of Ecology* 29, 1–10.
- Svenning, J.C. and Wright, S.J. (2005) Seed limitation in a Panamanian forest. *Journal of Ecology* 93, 853–862.

- Tabáñez, A.A.J., Viana, V.M., and Dias, A.D.S. (1997) Consequências da fragmentação e do efeito de borda sobre a estrutura, diversidade e sustentabilidade de um fragmento de floresta de Planalto de Piracicaba, SP. *Revista Brasileira de Biologia* 57, 47–60.
- Teo, D.H.L., Tan, H.T.W., Corlett, R.T., Wong, C.M., and Lum, S.K.Y. (2003) Continental rain forest fragments in Singapore resist invasion by exotic plants. *Journal of Biogeography* 30, 305–310.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., and Lehman, C. (2001) Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845.
- Turnbull, L.A., Crawley, M.J., and Rees, M. (2000) Are plant populations seed-limited? A review of seed-sowing experiments. *Oikos* 88, 225–238.
- Uhl, C. and Kauffman, J.B. (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71, 437–449.
- Vitousek, P.M. (1986) Biological invasions and ecosystem properties: can species make a difference? In H.A. Mooney and J.A. Drake (eds), *Ecology of Biological Invasions of North American and Hawai'i*. Springer Verlag, New York, pp. 163–176.
- Vitousek, P.M. and Sanford, R.L. (1987) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17, 137–168.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., and Matson, P.A. (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238, 802–804.
- Von Holle, B. and Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86, 3212–3218.
- Wadsworth, F.H. (1997) *Forest Production for Tropical America*. Agriculture Handbook 710. USDA Forest Service, Washington, DC.
- Wagner, W.L., Herbst, D.R., and Sohmer, S.H. (1999) *Manual of the Flowering Plants of Hawaii*, 2nd Edition. University of Hawaii Press, Honolulu, HI.
- Walker, L.R., Zimmerman, J.K., Lodge, D.J., and Guzman-Grajales, S. (1996) An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. *Journal of Ecology* 84, 877–890.
- Wang, Y.-H. and Augspurger, C.K. (2004) Dwarf palms and cyclanths strongly reduce Neotropical seedling recruitment. *Oikos* 107, 619–633.
- Webb, S.L., Dwyer, M., Kaunzinger, C.K., and Wyckoff, P.H. (2000) The myth of the resilient forest: Case study of the invasive Norway maple (*Acer platanoides*). *Rhodora* 102, 332–354.
- Wester, L.L. and Wood, H.B. (1977) Koster's curse (*Clidemia hirta*), a weed pest in Hawaiian forests. *Environmental Conservation* 4, 35–41.
- Whitmore, T.C. (1991) Invasive woody plants in perhumid tropical climates. In P.S. Ramakrishnan (ed.), *Ecology of Biological Invasions in the Tropics*. International Scientific Publications, New Delhi, pp. 35–40.
- Wirth, R., Beyschlag, W., Ryel, R., Herz, H., and Holldobler, B. (2003) *Herbivory of Leaf-Cutting Ants: A Case Study on Atta columbica in the Tropical Rain Forest of Panama*. Springer-Verlag, New York.
- Woodcock, D. (2007) To restore the watersheds: early twentieth-century tree planting in Hawaii. *Annals of the Association of American Geographers* 93, 624–635.
- Wu, S.-H., Hsieh, C.-F., Chaw, S.-M., and Rejmanek, M. (2004) Plant invasions in Taiwan: insights from the flora of casual and naturalized alien species. *Diversity and Distributions* 10, 349–362.
- Zimmerman, J.K., Pascarella, J.B., and Aide, T.M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* 8, 350–360.