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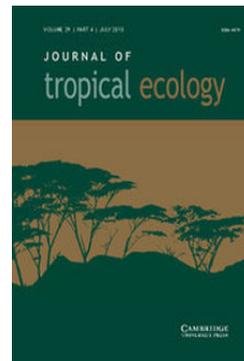
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## The invasibility of tropical forests by exotic plants

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**ABSTRACT.** Current research efforts to understand the relative invasibility of different plant communities have mostly ignored tropical forests. Only a few studies have treated invasive species in tropical forests, and recent worldwide analyses have not provided clear predictions concerning the relative invasibility of tropical forests. In this review, the extent to which exotic species have invaded tropical forests is summarized and four leading hypotheses to explain the apparently low frequency of invading plants in tropical forests are evaluated. In general, it is found that invasibility positively correlates with human disturbance, and that undisturbed tropical forests harbour few exotic species. To date, there is no evidence to attribute the low invasibility of undisturbed tropical forests to either their high species diversity or their high diversity of functional types. Instead, the low occurrence of exotic species in most tropical forests is most likely due to the fact that the great majority of exotic species that are transported to tropical countries lack specific life history traits, most importantly shade tolerance, necessary for successful invasion of undisturbed tropical forests. Unfortunately, this situation could change in the future with the expected increase in the plantation forestry of high-grade timber combined with common forestry practices that favour the cultivation of exotic species.

**KEY WORDS:** exotic species, functional diversity, propagule pressure, shade tolerance

### INTRODUCTION

Invasive plants are a major problem worldwide. Every year, exotic species become more prevalent, expanding their ranges into areas designated as nature reserves (Cox 1999). In a survey of 24 reserves worldwide, all were found to have exotic species, and some reserves harboured more exotic plant species than native species (Usher *et al.* 1988). Despite these facts, invasive

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species have rarely been implicated as a significant threat to the conservation of tropical forests.

Tropical forests have received attention both for their high biodiversity and the speed at which they are being destroyed. In many ways, the deforestation of tropical forests is a replay of the fate of temperate forests centuries earlier. Many of today's temperate-zone forests are fragmented remnants of their previous distribution, surrounded by a human-disturbed landscape. Even where temperate wildlands have been preserved as natural areas, managers find that native species are continually losing ground to exotic invaders. Will tropical forests also be overwhelmed by exotic species, or do tropical forests possess some resistance against invasive species?

While biological invasions have been the subject of intensive research in the last two decades, this research has generally ignored tropical forests (Drake *et al.* 1989, Groves & Burdon 1986, Williamson 1996). The biology of invasive species is well studied for only one tropical forest location: the Hawaiian Islands. But the combination of Hawaii's extreme isolation and heavy human disturbance makes it difficult to generalize the lessons that biologists have learned from Hawaii to other tropical forests. For mainland tropical forests, the common perception is that because of their high species diversity they are naturally resistant to invasion (Elton 1958, Holdgate 1986). At the same time, recent empirical studies have concluded that high exotic plant diversity correlates with high native plant diversity (Lonsdale 1999, Stohlgren *et al.* 1999). Needless to say, there is little current consensus about the invasibility of tropical forests.

In this paper, I first review the extent to which tropical forests are invulnerable. Next, I evaluate four competing hypotheses that could explain the patterns of tropical forest invasibility. Finally, I conclude with recommendations to minimize future damage to tropical forests by exotic species.

#### *Are tropical forests invulnerable?*

Almost all tropical areas contain at least one exotic species (Usher 1991). However, some tropical forests presumably suffer a greater impact due to exotic species than others do. How does one compare different forests in terms of their relative invasibility? Generally the approach has been to compare numbers of exotic species (Lonsdale 1999), or the proportion of exotic species to native species (Usher *et al.* 1988). When comparing different areas, researchers have controlled for area by measuring exotic species/log(area) (Rejmánek 1996). However, it is unclear whether measuring exotic species diversity really is the appropriate metric to compare relative invasibility. Indeed, many of the spectacular examples involving enormous impact by exotics on native systems have involved a single invading species (Vitousek 1990). To evaluate community invasibility, it would be more informative to know what portion of an area is covered by exotic plants (Rejmánek 1996), but these data are difficult to find

outside of small spatial scales. In addition, small-scale surveys of invasive species will be biased toward areas that contain exotic species. Determining how to accurately compare the relative impact of invasive species on different communities is a promising area of future research.

The term 'tropical forests' includes many forest types (cloud forest, dry forest, lowland rain forest, etc.) which may respond to plant invasions in different ways. However, while far from homogeneous, tropical forests do share two characteristics that immediately differentiate them from temperate forests. First, they are highly diverse. Even low-diversity tropical forests contain twice as many species as a diverse temperate forest (Gentry 1988). Second, although there are notable exceptions, there are few reports of them being heavily invaded by exotic species. Since there are so few studies that have even documented invasions in tropical forests of any type, the reader should be cautioned that most studies considered in this review pertain to plant invasions into lowland tropical moist to wet forest types. Future research may allow insight into invasibility differences among tropical forest types.

Since the existing data concerning exotic species are generally derived from plant species check-lists, or other informal surveys of exotic species, I cannot rigorously compare the invasibility of different tropical forests. However, there is sufficient anecdotal evidence to allow one to discern clear patterns in tropical forest invasibility.

Whether on islands or continents, undisturbed tropical forests very rarely harbour exotic species (Rejmánek 1996, Whitmore 1991). A review of exotic plants in the tropics reported 21 woody species invading undisturbed forest on islands, and 21 in mainland forests, and the list of exotic herbaceous plants was even shorter, only 14 species (Rejmánek 1996). For comparison, undisturbed temperate forests worldwide are reported to harbour approximately 100 exotic species (Rejmánek 1996); and, combining disturbed and undisturbed habitats, the continental United States of America contains more than 3000 exotic plant species (Kartesz & Meacham 1999).

While exotic species are rare in undisturbed tropical forests, exotic species readily invade disturbed tropical forests, often dominating and even irreparably changing the ecosystem. Tropical dry forest represents the most endangered forest in the world (Janzen 1988a). In Central America, less than 2% of tropical dry forest remains from an area that once covered 550 000 km<sup>2</sup> (Janzen 1988a). Similar amounts of tropical dry-forest destruction are reported from other parts of the world. Humans convert tropical dry forest to rangeland and agricultural land by introducing fire. Fire, an extremely infrequent ecosystem process in natural tropical dry forest, suppresses regeneration of native tree seedlings, and promotes the continued dominance of grasses, many of them exotic (D'Antonio & Vitousek 1992, Janzen 1988a, Parsons 1972). Invasive grasses produce highly flammable litter that encourages annual wildfires (D'Antonio & Vitousek 1992). Hence, exotic species can precipitate a secondary wave of habitat destruction by changing the ecosystem in such a way that facilitates their own dominance over native species.

In highly disturbed forests of the wet tropics, exotic species predominate. For example, the lowland areas of Hawaii have been completely overrun by exotic species, even within national parks (Vitousek 1990). Other disturbed tropical islands report a high incidence of exotic species, including Mauritius, Java, Guam, Tahiti, and Jamaica (Cronk & Fuller 1995, Meyer & Florence 1996, Rejmánek 1996). Highly disturbed tropical forests on the mainland or on very large islands also contain exotics. In Costa Rica, an exotic tree *Syzygium jambos* L. (Myrtaceae) is the most dominant tree species in a remnant patch of forest (Di Stéfano *et al.* 1998). The pioneer tree *Cecropia peltata* L. (Cecropiaceae) invades large clearings and heavily disturbed areas in Malaysia (Putz & Holbrook 1988). The shrub *Piper aduncum* L. (Piperaceae) forms monospecific stands in disturbed forest in Papua New Guinea (Rogers & Hartemink 2000). Exotic vines impact small reserves in Singapore (Turner *et al.* 1996, Whitmore 1991) and completely cover fragmented forest remnants in tropical Australia (Humphries *et al.* 1991), and exotic weeds invade coastal tropical Australia (Batianoff & Franks 1998). Highly disturbed areas in the Guyanas suffer a large impact from exotic weeds (Thomson 1988), as well as in the Ivory Coast (de Rouw 1991), and India (Saxena 1991). In addition, exotic species may subvert natural regeneration of tropical wet forests (de Rouw 1991, Saxena & Ramakrishnan 1984). Thus, all tropical areas are not necessarily resistant to exotic species. Whether fragmented or otherwise disturbed by humans, tropical forests worldwide suffer an impact from invasive species.

*Why do undisturbed tropical forests appear to harbour few exotic species?*

There are four leading hypotheses to explain why undisturbed tropical forests suffer low proportions of invading species:

- (1) Propagule pressure differences cause tropical forests to appear relatively unsusceptible to plant invasions.
- (2) Undisturbed forests in general are less prone to invasions, and tropical forests are no exception.
- (3) Tropical forests are highly diverse, and highly diverse communities resist invasions.
- (4) Tropical forests contain a high functional diversity, and high functional diversity resists invasions.

These four hypotheses are not mutually exclusive. In fact, different invasions may be explained by different combinations of these hypotheses. I will review these four hypotheses, and how they relate to the invasibility of tropical forests. In the conclusion, I will evaluate their relative importance in explaining tropical invasions.

#### PROPAGULE PRESSURE

Propagule pressure is the term used to describe the quantity of animals or plants (or seeds) that arrive in a target community. In general, the more propagules that arrive, the greater chance the species has of invading the community

(Newsome & Noble 1986, Simberloff 1989). Models have shown that even when an introduced species is an inferior competitor, it can invade if enough propagules are introduced, even into a community that experiences low levels of disturbance (Rejmánek 1989). Some of the more notorious invaders have required several introductions before they established. For example, the European starling *Sturnus vulgaris* was introduced several times to North America before the invasion succeeded (Williamson 1996). The successful invasion was a result of the introduction of 60–100 starlings, a greater number of propagules than previous introductions, suggesting that there was a critical number of starlings necessary to initiate the invasion. The relationship between number of birds introduced and the success of invasions has also been studied in New Zealand and Australia. In both cases, there was a positive linear relationship between invasion success and number of birds released (Fox & Fox 1986, Green 1997). For insects a similar pattern was detected for biological control introductions into Canada (Williamson 1989).

A similar study of invasive plants in Florida analysed a catalogue of seeds offered to the public between 1881–1937. For exotic species that were sold for only one year, there was a 1.9% chance of successful invasion. For plants sold for three decades, there was a 68.8% chance of success (Pemberton, in Enserink 1999).

Many exotic plants do not become invasive immediately after they are first introduced. For example, *Schinus terebinthifolia* Raddi (Anacardiaceae), a small ornamental tree, was introduced to Florida in the late 1800s, but did not become invasive for at least 60 y (Ewel 1986). Delayed invasions have been hypothesized to be due to genetic changes in the exotic species that increase their invasive potential (Blossey & Nötzold 1995). However, there is little evidence that most time-lag invaders have adapted to become more invasive (Crooks & Soulé 1999). A simpler explanation is that an exotic species improves its chances of becoming invasive at larger population sizes (Ewel 1986). Larger populations disperse greater numbers of propagules, one of the only factors to consistently be predictive of invasion success.

Life history traits of a plant also relate to its potential for high propagule pressure. For example, in undisturbed forests, trees in general have a very low probability of surviving from a seed to a reproductive adult, estimated from 1 in 10 000 to 1 in 1 000 000 (Rejmánek 1989). Most successful invasive trees are commonly planted ornamentals or escapees from forestry plantations, suggesting that only when trees are introduced in large numbers can they invade neighbouring forests. Mode of dispersal also influences the propagule pressure of an exotic plant. Plants that have generalized modes of dispersal are more likely to contribute high numbers of propagules to a community. For example, in Australia, rain-forest pigeons are generalist frugivores, and have contributed to the range expansion of exotic species that have bird-dispersed fruit such as *Cinnamomum camphora* (L.) J. Presl (Lauraceae) and *Lantana camara* L. (Verbenaceae) (Date *et al.* 1996).

Higher trophic levels may also mediate the effect of propagule pressure. The Janzen–Connell hypothesis predicts that herbivores and seed predators maintain diversity by reducing the numbers of surviving seeds (and seedlings) of more common species (Connell 1971, Janzen 1970). Exotic species, therefore, may gain an advantage when introduced into a new habitat if they escape their specialized predators. An experiment examining the escape from natural enemies hypothesis compared *Clidemia hirta* (L.) D. Don (Melastomataceae) in its native range in Costa Rica to an invasive population in Hawaii. Experimentally manipulating herbivory, DeWalt *et al.* (2001) found a significantly higher rate of mortality due to insects and pathogens in the native range, linking the invasion success of *C. hirta* in Hawaii to increased survivorship of enemy-free seedlings.

In one extraordinary example where two ecological analogues were introduced into the other's habitat, *Acacia longifolia* (Andr.) Willd. (Fabaceae), a native of mediterranean Australia was introduced to the mediterranean fynbos of South Africa, and *Chrysanthemoides monilifera* (DC.) Norl. (Asteraceae), a native of the fynbos, was introduced to mediterranean Australia. *Chrysanthemoides monilifera* increased its viable seeds in the soil from 50 m<sup>-2</sup> in its native fynbos habitat to 2000 m<sup>-2</sup> in Australia, and *A. longifolia* increased its viable seeds in the soil from 10 m<sup>-2</sup> in its native Australian habitat to 7400 m<sup>-2</sup> (Noble 1989). In this case, the mechanism for successful invasion appears to be each species' release from specialized seed predators, which increased by more than two orders of magnitude the numbers of propagules m<sup>-2</sup>.

Recent studies of heavily invaded riparian systems have indicated that propagule pressure is also a main factor in determining the number of exotic species found in a local area (Levine 2000, Planty-Tabacchi *et al.* 1996). Levine (2000) experimentally manipulated diversity and propagule pressure in natural tussock communities along a California river, and found that the number of exotic seeds added to a tussock predicted exotic species establishment better than how many species were already present in a tussock. A recent worldwide analysis of invasions (Lonsdale 1999) concluded that propagule pressure was potentially able to explain 56% of the variance among invaded sites. In addition, Lonsdale (1999) suggested that lack of substantial propagule pressure might explain the low incidence of tropical invasions, although he did not adequately survey tropical forests in his study.

*What evidence suggests that tropical forests have received low 'propagule pressure'?*

Rejmánek (1996) reviewed continental and insular invasions worldwide. He compared the proportion of exotic species in 115 tropical and temperate sites and found no differences between temperate and tropical islands in terms of their invasibility, while continental tropical areas were significantly less invaded (Rejmánek 1996). He wondered why, if propagule pressure was responsible for the temperate/tropical invasion pattern, tropical islands were as invaded as temperate islands. Moreover, there is no evidence that people

have brought fewer numbers of propagules to the continental tropics than they have to islands (Rejmánek 1996). In addition, disturbed areas of the tropics are often very highly invaded (see above), suggesting that propagule pressure, if strictly defined as the numbers of exotic propagules brought to a target community, is unlikely to explain why tropical forests are seemingly resistant to invasion. Thus, while the effect of propagule pressure is important, it does not appear sufficient on its own to explain why undisturbed tropical forests harbour few exotics.

Beyond the actual quantity of propagules, the traits of the individual species brought to a target community should determine invasion success. For example, invading species must be pre-adapted to the local conditions of the target community to survive, and invading species that have no functional analogue in the target community may be more successful. These factors will be addressed in the following sections.

#### UNDISTURBED FORESTS HAVE FEWER EXOTICS

Tropical forests may appear to be less invaded than temperate forests because undisturbed forests generally contain few exotics, and a much greater proportion of tropical forests remain undisturbed by humans, or have been disturbed only within the last few decades. Approximately  $6 \times 10^8$  ha of tropical forests are still undisturbed out of the original  $1.5 \times 10^9$  ha (40%), and most of the deforestation has occurred within the last 30 y (Braatz 1999, Lean & Hinrichsen 1992). In contrast, less than 5% of the forests in the United States and less than 2% of European forests are primary forest, and most temperate forests have been heavily disturbed for 100–1000 y (Lean & Hinrichsen 1992, McNeeley 1995). In addition, temperate forests are more fragmented than tropical forests, and fragmented forests are more likely to be susceptible to exotic species invasions (Janzen 1983). Therefore, if undisturbed forests are generally less invaded, and exotic species are associated with human disturbance, temperate forests should be more impacted by exotic species than tropical forests.

#### *Are undisturbed forests, in general, less invisable?*

As previously mentioned, there are many examples of exotic species found in disturbed tropical forests, and a dearth of such examples from undisturbed tropical forests. In general, disturbed areas are more likely to contain exotic species than undisturbed areas (Rejmánek 1989). Lonsdale (1999) compared sites within reserves with sites outside of reserves, and found that reserves harboured less than half as many exotic species. Moreover, many studies have found that disturbance of forests, either by humans or other animals results in higher numbers of exotic species (see review by D'Antonio *et al.* 1999). In the Olympic Peninsula of Washington, USA, per cent cover of exotics was lowest in mature forest (DeFerrari & Naiman 1994). Disturbance by feral pigs in

Hawaii, and water buffalo in Australia promotes exotic species (Cowie & Werner 1993, Cox 1999). In addition, forests, even when disturbed, may contain fewer exotic species than grasslands, riparian systems, and other open areas (Ehrenfeld 1997, Planty-Tabacchi *et al.* 1996). Thus, forests appear to be less invasible than many other communities, and undisturbed forests are less invaded than disturbed forests.

*Why does disturbance appear to promote invasions?*

One persistent idea in ecological theory is that disturbance promotes invasions by disrupting species interactions and thus diminishing the force of competition (Hobbs 1989). This hypothesis rests on the premise that strong species interactions resist invasion, a premise that will be treated in more detail in a later section. Disturbance may also encourage invasion by causing increases in the availability of a previously unused resource, thereby increasing the invader's chances of success (Davis *et al.* 2000).

An alternative hypothesis for why disturbance is associated with invasive species is that exotic species are introduced by humans, and humans are associated with high disturbance (Simberloff 1989). Most exotic plants that are intentionally introduced into new areas are for agricultural or ornamental uses (Binggeli 1996, di Castri 1989). Most unintentional exotics that are introduced worldwide are agricultural pests (Heywood 1989). All of these plants thrive in full sun, as humans invariably clear land to grow their food and build their homes. Consequently, most exotic species are not shade tolerant (Baker 1974, Mack 1996). To my knowledge, most studies that have found positive relationships between disturbance and number of exotic species have only considered exotic species that are pre-adapted for early successional environments (high-light conditions) (Gentle & Duggin 1997, Hobbs 1989, McIntyre & Lavelle 1994). Exotic species that are not tolerant of high-light conditions, therefore, may not respond favourably to disturbance.

When shade-tolerant plants are introduced to an area, they can invade forests without human disturbance. In Eastern North America, the Norway maple *Acer platanoides* L. (Sapindaceae) has invaded a 100-y-old forest in New Jersey (Webb & Kaunzinger 1993). *Acer platanoides* adults in 1996 accounted for 17% of the basal area of the forest; moreover, this species was by far the most common seedling and sapling beneath the canopy, indicating that it may dominate the future composition of the forest (Wyckoff & Webb 1996). In tropical Africa, the exotic *Maesopsis eminii* Engl. (Rhamnaceae) has escaped forestry plantations and is present in undisturbed pre-montane forest (Binggeli & Hamilton 1993, Viisteensaari *et al.* 2000). *Miconia calvescens* DC. (Melastomataceae) in Tahiti is rapidly replacing native forest vegetation in undisturbed forests (Meyer & Florence 1996). In Hawaii and Malaysia, *Clidemia hirta* (L.) D. Don (Melastomataceae) invades the understorey of undisturbed forest (Ickes & Williamson 2000, Wester & Wood 1977). In the Atlantic coastal rain forest of

Brazil, *Musa ornata* (Musaceae) forms dense carpets in the understorey (J. Den-slow, *pers. comm.*). Invasions by exotic plants, therefore, do occur without human disturbance.

If exotic plants respond positively to disturbance primarily because disturbance increases light levels, one would predict that disturbed areas with low light levels would have fewer exotic species than undisturbed areas with higher light levels. In fact, this is exactly the case in the Oregon Cascades. Here, the understorey of old-growth forests supports more exotic species than unthinned even-aged stands of regenerating secondary forest (Bailey *et al.* 1998). The unthinned even-aged stands allowed less light to reach the forest floor, suggesting that low light levels reduce opportunities for exotic species. In Hawaii, feral-pig disturbance causes more light to reach the understorey, which in turn promotes exotic species (Cox 1999). For several studies detailing successional series, the proportion of exotic species exponentially declined as the area grew into a closed forest (Rejmánek 1989). While this phenomenon may be due to higher propagule pressure at early successional stages, the same pattern was observed in a flooded system which received higher exotic propagules during late succession (Rejmánek 1989). Again, these data strongly suggest that light availability limits exotic species, and is presumably due to the high proportion of shade-intolerant species in the exotic species pool.

Tropical forests thus may be, in part, naturally resistant to invasion. Tropical understoreys receive significantly less light (1–2% of full sunlight) than temperate forests (3–4% full sunlight) (Canham *et al.* 1990). Therefore, since exotic species invading both temperate and tropical forests are rarely shade tolerant, a smaller percentage might successfully invade an undisturbed tropical forest because of the lower light availability. This fact could partly explain why the list of exotic species found in undisturbed temperate forests is more than twice as long as the list for undisturbed tropical forests (Rejmánek 1996).

Other life-history traits besides shade tolerance interact with habitat disturbance. For example, most tropical forests are dominated by vertebrate-dispersed plants, while the great majority of exotic herbaceous species are not vertebrate dispersed (Rejmánek 1996). Therefore, if vertebrate dispersal is favoured in undisturbed tropical forests, exotic herbaceous plants will have a reduced chance of successfully invading. Disturbed forests often contain fewer animal dispersers which results in the recruitment limitation of native vertebrate-dispersed species (Janzen 1988*b*), which could increase the odds for successful invasion by exotic species.

In addition, habitats that require tolerance to an abiotic stress such as xeric environments and mangroves are also rarely invaded (Loope *et al.* 1988, Lugo 1998, Rejmánek 1989) – even if disturbed. Human disturbance, therefore, is only a prerequisite for invasion when it creates a habitat for which the pool of potential exotics is pre-adapted. Humans do not often introduce plants that

are able to tolerate shade, salinity, and severe drought, and presumably this accounts for part of the explanation for why forests and 'stressful' habitats are rarely invaded.

#### DIVERSITY AND INVASIBILITY

There is a long-standing belief in ecological theory that a diverse community can better resist invasive species (Elton 1958). Tropical forests represent some of the most diverse communities on earth (Gentry 1988), and their relative freedom from invasions could stem from their high species diversity. However, recent empirical studies have increasingly challenged the hypothesis that community diversity resists invasions, with some studies finding that high species diversity actually is correlated with increasing numbers of exotic species (Levine & D'Antonio 1999, Lonsdale 1999, Stohlgren *et al.* 1999).

#### *Does diversity prevent invasibility?*

Elton (1958) noted that islands were more prone to invasion than mainland areas, and attributed this phenomenon to the lower numbers of species found in island communities. More species-rich communities are thought to utilize resources more completely, making it more difficult for an invading species to establish and successfully compete (MacArthur 1972). Islands, on the other hand, have fewer species on average than mainland, and should have more open niches, and therefore be less resistant to invading species (Elton 1958).

Theoretical models have confirmed Elton's ideas, and have concluded that increasing diversity decreases invasibility (Case 1990, Shigesada & Kawamoto 1997). In addition, experiments involving artificially constructed communities have also generally supported the idea that higher diversity decreases invasibility (McGrady-Steed *et al.* 1997, Stachowicz *et al.* 1999, Tilman *et al.* 1996).

However, the mechanism by which more diverse communities are able to resist invasive species in these experiments remains unclear. The increased resistance of more diverse communities may be due to the actions of key species, not the whole assemblage, and the lower invasibility of diverse communities could be attributed to the greater chance that key species were included (Huston 1997). Subsequent experiments have confirmed that functional group diversity (see below) was more highly correlated with lower invasibility than species diversity, although in some studies the effect of species diversity was still significant (Dukes 2001, Lavorel *et al.* 1999, Symstad 2000, Tilman *et al.* 1997).

Recent correlational analyses at large scales have not supported the hypothesis that species diversity confers resistance to invasion. Instead, many studies have observed a positive correlation between high native diversity and high introduced-species diversity (Lonsdale 1999, Stohlgren *et al.* 1999). Lonsdale (1999) reviewed 184 sites worldwide and found a significant correlation between native diversity and exotic diversity, although he did not control for

latitude. Stohlgren *et al.* (1999) found that, at the community scale, exotic species in grasslands were at their highest diversity where native species were most diverse, indicating that both sets of species were responding in the same way to environmental variation.

While many recent studies have linked high exotic richness with high native diversity, there is little evidence for a causal relationship between the two at large scales. In most cases, the result seems to stem from the fact that high diversity covaries with factors such as moisture and habitat heterogeneity, and these factors correlate with high exotic diversity (Levine & D'Antonio 1999, Lonsdale 1999). While diversity may resist invasions at the neighbourhood scale, this effect is swamped by environmental factors that covary with diversity as well as by high propagule pressure (Levine 2000).

*Does high diversity of tropical forests confer resistance to invasions?*

Rejmánek (1996) reviewed temperate and tropical sites and concluded that the data did not support the hypothesis that the high diversity of tropical sites was responsible for their low invasibility. First, African sites were less invaded than neotropical sites, even though the neotropics are more diverse. Second, islands with high numbers of species had higher numbers of alien species/log(area) than species-poor islands (Rejmánek 1996). While this analysis is problematic because the sites were not controlled for the effects of human disturbance, additional anecdotal evidence also supports the idea that the high diversity of tropical forests is unrelated to its invasion potential.

If high tree-species diversity resists invasions, one would expect monodominant forests to be more invulnerable. However, no difference in number of exotic species was found between species-rich and monodominant forests in Uganda (Rejmánek *et al.*, unpubl. data). An historical perspective also does not support the idea that diversity resists invasions. For example, the high species diversity of the South American mammal assemblage did not prevent its mass extinction when North America and South America became contiguous, and North American mammals invaded South America (Fryer 1991). In addition, some species of tree have pantropical ranges whose distributions are thought to be due to relatively recent dispersal events across oceans, indicating the potential for natural invasions in tropical forests during the last few million years (Rejmánek 1996).

#### FUNCTIONAL DIVERSITY AND INVASIBILITY

Functional diversity refers to the number of different functional groups present in a community. A plant functional group is a guild of morphologically similar species that have similar resource requirements and respond to environmental perturbations in similar ways (Chapin *et al.* 1996). The argument why functional diversity should decrease community invasibility is virtually identical to the argument provided for the effect of species diversity: that functionally

diverse communities will utilize resources more completely and thereby exclude invasive species (Symstad 2000). This leads to the prediction that if an invading species is of a functional group that is not represented in a target community, it will have an increased chance of a successful invasion (Mooney & Drake 1989). Since tropical forests contain a great diversity of functional groups (Box 1981), they may be therefore resistant to invasion by a novel functional group.

Experiments that have examined the effect of functional diversity on invasibility have found that greater functional diversity decreases invasibility (Lavorel *et al.* 1999, Symstad 2000, Tilman *et al.* 1997) by reducing the resource availability of the community (Dukes 2001). All of these experiments were conducted at small spatial scales. To date, no one has correlated functional diversity and invasibility at larger scales.

Communities with low functional diversity appear to be highly invasible. The fynbos of South Africa, while incredibly speciose, is functionally redundant (Cowling *et al.* 1994), and is invaded by many species of pines and acacias. One example is *Pinus radiata* D. Don (Pinaceae), a tree that escapes from nearby plantations. Trees are not part of native fynbos communities, perhaps because there are no native fire-resistant trees, and fire is a frequent occurrence in the fynbos (Cowling *et al.* 1994). *Pinus radiata* invades and forms monospecific stands, replacing the native shrub vegetation (Richardson *et al.* 1990). Similar examples of the invasion success of novel functional groups abound. In Hawaii, there are no native early successional trees that fix nitrogen, a limiting nutrient. An introduced tree *Myrica faya* Ait. (Myricaceae) fixes nitrogen and dominates early successional communities, preventing the natural succession by natives (Vitousek 1990). In the Florida Everglades, *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae) invades flooded grasslands. South Florida contains no native flood-tolerant, fire-resistant trees and *M. quinquenervia* is transforming the native grassland into a monodominant dwarf forest (Schmitz *et al.* 1997).

Isolated islands often have low functional diversity due to the reduced probability that all functional types from mainland pools will be able to arrive. Many isolated islands originally had no terrestrial mammals or reptiles. When humans brought these new functional types to isolated islands, the invaders were successful, often with disastrous consequences to native fauna (Elton 1958).

#### *Does functional diversity confer resistance in tropical forests?*

Tropical forests that are highly invaded are either isolated islands or highly disturbed by humans, or both. For isolated islands, there are examples of new functional types successfully invading. Rejmánek (1996) argues that one reason mainland tropical forests are not apparently invasible is because the early successional phase of tropical forests are dominated by fiercely competitive native species. On isolated islands, this functional group is probably less represented, making tropical island forests more easily invasible (Rejmánek 1996). However,

there is a continuum between functional diversity and species diversity, and it is therefore difficult to assign exotic species the category of 'novel functional type'. For example, *Miconia calvescens* successfully invades undisturbed forests in Tahiti, Hawaii and other Pacific islands (Meyer & Florence 1996). It has no obvious characteristic that separates it from native tree species, but instead has a combination of characters that allows it to invade successfully (i.e. shade tolerance, continuous reproduction, etc.). Similarly, in a study of Hawaiian bird invasions, Moulton & Pimm (1986) found that the best predictor of invasion success was the degree to which the invading bird's bill was morphologically different from its already-resident congener. Thus 'novel functional types' may be better invaders, but it may be difficult to identify them a priori. However, many tropical forests have without question a high functional diversity, which theoretically could reduce their invasibility.

#### CONCLUSION

Tropical forests, when undisturbed by humans, are at present rarely invaded. However, there is little evidence to support the idea that tropical forests are naturally resistant to invasions. Previous speculation that the high species diversity of tropical forests should decrease their potential invasibility remains unsupported by empirical studies (Rejmánek 1996). While experiments have shown that species diversity resists invasions at small scales, it appears that this effect is minor, and can be overwhelmed by propagule pressure (Levine 2000). The effect of functional diversity is also unknown, but it appears that functional diversity may be important only to explain the high invasibility of isolated islands. However, it is difficult to gauge the relative contribution of functional diversity to community invasibility without further experiments at larger scales. Since even highly functionally diverse rain forests can be invaded, it suggests that the effect of high functional diversity may also be overpowered by sufficient exotic propagule pressure.

While the diversity of a community is not predictive of its relative invasibility, both the extent to which a community has been disturbed by humans and the amount of propagule pressure imposed on a community consistently correlate with increasing impact by exotic species. When shade-tolerant exotic plants are able to disperse their seeds in large quantities (e.g. African plantations of *Maesopsis eminii* (Binggeli & Hamilton 1993)) they can invade even undisturbed tropical forest communities. Most exotic plants are not shade-tolerant, however, and depend on human disturbance to invade tropical forests successfully. Thus there appears to be an interaction between a life-history trait such as shade tolerance and anthropogenic disturbance that influences invasion success. Future research should consider the life-history traits of both potentially invasive species as well as the dominant species of the target community when trying to predict community invasibility, since exotic and native species in forests appear to respond to human disturbance in opposite ways.

*The future of tropical forests*

Tropical forests, when highly disturbed by humans, will continue to accumulate exotic species. Especially at risk are disturbed forests that are invaded by species that change ecosystem processes, such as fire frequencies. Tropical dry forest has all but vanished due to human impact, and it has been replaced for the most part by exotic grasslands. Tropical wet forest may also suffer the same fate, as exotics in highly disturbed wet tropical lowlands also predominate. However, there is some indication that even highly disturbed tropical forests can be restored. In Costa Rica, if fire is suppressed, tropical dry-forest tree seedlings can regenerate and native habitat can be recreated (Janzen 1988a). In Hawaii, managers have placed pig-proof fences around native forest remnants. These exclosures have resulted in both a reduction of exotic species and the successful regeneration of native species (Stone & Loope 1987).

To date, undisturbed tropical forests have been relatively free from invasion. This resistance, in my opinion, has largely been due to the fact that very few tropical shade-tolerant trees have been transported among tropical countries. Moreover, the great majority of tropical forestry is concentrated on low-quality wood for pulp or fuelwood, with less than 15% of tropical forestry devoted to timber production (Johns 1997). Low-quality wood species such as species in the genera *Pinus* (Pinaceae) and *Eucalyptus* (Myrtaceae), which account for more than 65% of all tropical plantation forestry (Evans 1992), are unlikely to invade undisturbed tropical forests for two reasons. First, they are not shade tolerant, so are unlikely to invade closed tropical forest (Evans 1992). Second, they are unlikely to invade high-light gaps since they cannot grow as fast as native pioneers such as *Cecropia* (Cecropiaceae), *Macaranga* (Euphorbiaceae) or *Ochroma* (Malvaceae), which are unsuitable for industrial wood production since they produce an extremely low density wood (Evans 1992).

The reason that shade-tolerant trees have rarely been transported between tropical countries is because high-quality hardwood (which generally comes from slow-growing shade-tolerant trees) has traditionally come from virgin forests (Johns 1997). However, if tropical deforestation rates continue unabated, the supply of virgin high-grade hardwood will soon become exhausted, and/or sequestered in reserves (Grainger 1988). At this point, it will become profitable to establish large plantations of shade-tolerant trees. As of yet, tropical plantations are almost wholly composed of fast-growing shade-intolerant low-quality timber species (Evans 1992, Grainger 1988). However, in the next quarter-century, plantations of high-grade timber (of which most species are shade tolerant) will sharply increase (Grainger 1988). While it would be ideal if future plantations could be planted with native species, foresters generally use whatever species is the most profitable irrespective of origin. In fact, foresters often prefer exotic species as they are less likely to be damaged by pests and pathogens (Evans 1992). As new species are currently being screened for tropical plantations, especially for timber production (Butterfield 1995), it seems

likely that more and more potentially invasive species will be transported between tropical areas. In the last 20 years, 45 species of woody legumes have been transported to 42 tropical countries, and many are already becoming invasive (Hughes & Styles 1989).

Once an exotic tropical tree that has generalized dispersers and pollinators is planted in large quantities, it should easily invade. In fact, there is reason to believe that an exotic shade-tolerant tree may be able to increase its proportional propagule pressure by escaping its seed predators or other specialized enemies. Therefore, I recommend that foresters first attempt to use native species for timber plantations, and second, that they choose species whose seed dispersal can be controlled.

Those who wish to predict the future of tropical forests need only to look at the history of temperate forests. In North America, humans removed 98% of the virgin forest in the East, and while much forest has regenerated, in many places different species are dominant (Cogbill 2000). The white pine *Pinus strobus* L. (Pinaceae) forests of the Great Lakes are all gone, replaced by other native species (Franklin 1988). Chestnuts (*Castanea dentata* (Marshall) Borkh. (Fagaceae)) and elms (*Ulmus americana* L. (Ulmaceae)), once dominant members of Eastern forests, are gone, victims of introduced diseases (Cox 1999). Finally, native species are being replaced by exotics such as Norway maple, an invasive that only recently has been noticed and may be exponentially increasing its population (Webb *et al.* 2000, Wykoff & Webb 1996). These changes occur slowly, and it is worth remembering that the bulk of tropical deforestation and disturbance has occurred only within the last few decades (Lean & Hinrichsen 1992), an insufficient amount of time to gauge the effect of such disturbance on future forest composition.

While habitat preservation must remain the top priority, biologists and conservationists should not neglect to consider the insidious threat of exotic species. While changes in tree species composition in temperate forests have not yet caused many extinctions, similar changes could be disastrous in the tropics due to the greater interdependence and complexity of tropical species interactions (Janzen 1983). There is still time to use our knowledge of forestry and the increasing understanding we have gained about the ecology of biological invasions to minimize the future impacts of exotic species on the world's tropical forests.

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