The outcome of alien tree invasions in Puerto Rico

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Invasive alien tree species in Puerto Rico often form monospecific stands on deforested lands that were previously used for agriculture and then abandoned. Most native pioneer species are incapable of colonizing these sites, and thus introduced species have little competition from native trees. Alien trees may dominate sites for 30 to 40 years, but by that time native species begin to appear in the understory. By 60 to 80 years, unique communities comprising both alien and native species are found on these sites. This phenomenon is a response to a change in the disturbance regime of Puerto Rico's landscape, brought about by intensive agricultural land use and abandonment. The invasion of a site and the formation of an alien-dominated forest serve important ecological functions, such as repairing soil structure and fertility, and restoring forest cover and biodiversity at degraded sites.

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Worst-case scenarios for alien species invasions generally involve the formation of monocultures. This causes changes in the stocks, flows, and pathways of materials and energy, and may even trigger changes in the trophic structure and species composition of ecosystems (Vitousek and Walker 1989). But how permanent are these changes? Do affected ecosystems remain as they appear following invasion? Do they return to their initial condition – including the original species composition – or is the invasion an event that sets in motion irreversible changes and new ecosystems, as predicted by Tansley (1935)? The answers to these questions are critical because of the increased social attention being paid to invasive species and the high costs and difficulties associated with eradication. The effectiveness of our recommendations about what to do with species invasions will depend on our ability to anticipate the long-term outcome of these events along with a prediction of future conditions.

Here I review the results of research that highlights the invasion, establishment, and long-term species turnover of new forests dominated by alien species in Puerto Rico. These forests occur on sites that have undergone deforestation, extended agricultural use, and eventual abandonment (Lugo and Helmer 2004). The outcome of the species invasions that leads to these new forests is quite different from that expected based on the initial stages, as the new forests are dynamic and exhibit dramatic changes in species composition.

This review describes a case study, rather than a general phenomenon. It is important for others to analyze the long-term records of vegetation change following land-use change to see if the phenomenon seen in Puerto Rico repeats itself elsewhere.

In a nutshell:

- Alien tree species invasions are a response to the abandonment of lands degraded by agriculture
- Alien tree species occupy a wide variety of environmental conditions, but individual species have discrete environmental tolerances
- Invasive alien tree species facilitate the establishment of other alien species, as well as native and endemic species, on previously unavailable sites
- The development of a diverse plant community with a new mix of species that includes alien and native species is often the long-term outcome of alien tree species invasion
- These new plant communities function normally and provide ecological services, such as rehabilitation of soils and biodiversity; they are responding to novel disturbance regimes introduced into these landscapes by human activity

■ Land-cover change and species introductions

Puerto Rico has experienced a substantial turnover of flora species over its 30 to 40 million years of evolutionary history (Graham and Jarzen 1969). The island was nearly 100% forested before its discovery in 1493 by Europeans and the native tree flora consisted of about 547 species (Little *et al.* 1974). By the 1940s, however, only 6% of forest cover remained, while much of the rest of the island was farmed (Roberts 1942). Furthermore, only about 1% of the original forest area remained unmodified.

Much of the agricultural land in Puerto Rico was abandoned during the second half of the 20th century (Figure 1), leading Rudel *et al.* (2000) to identify the period of 1950 to 1990 as proportionally the largest event of forest recovery anywhere in the world. Simultaneously, human popu-

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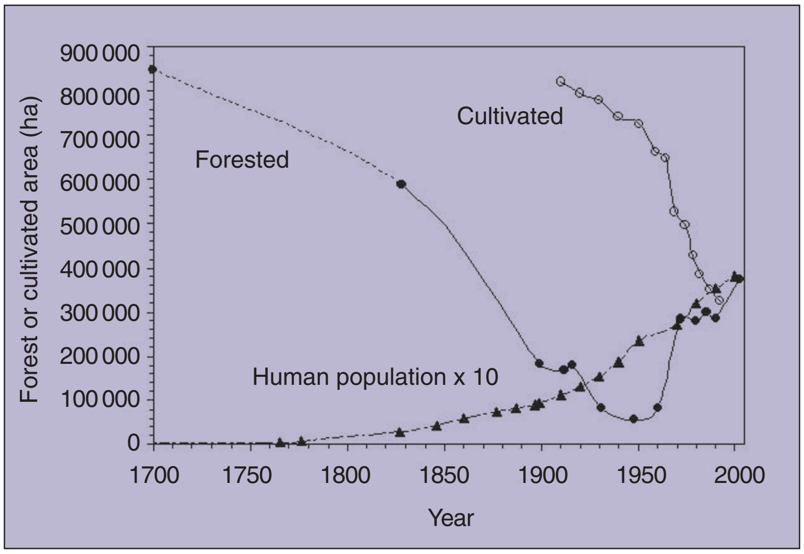

Figure 1. *Change in the area of forest cover and active agriculture in Puerto Rico. Forest area data are from USDA Forest Service inventories and agricultural land-use data are from the USDA Natural Resources Conservation Service.*

lation density increased to about 450 people per km^2, and urban land cover to 14% (López *et al.* 2001). Continuous agriculture in Puerto Rico led to high levels of soil erosion, soil compaction, and the choking of river channels with sediment; in one extreme case, because of anthropogenic disturbance such large quantities of sediments were exported to streams that the result was a downstream decrease in channel size (Clark and Wilcock 2000). It will take about 130 years for rivers to export the sediment accumulated in the river channels away (Larsen and Santiago Román 2001). The land use or type of crop planted influences the level of soil erosion. For example, scientists have ranked the erosive potential of different land uses as follows, from highest to lowest level of erosion caused: exposed soil, tobacco, sugar cane, pastures, shade coffee, logging (Smith and Abruña 1955). The landscape as a whole has experienced cycles of land fragmentation and consolidation of forested and urban fragments in response to economic activity (Lugo 2002).

The alien tree species that invaded the degraded abandoned fields in Puerto Rico were present on the island prior to the abandonment of the land. Species introductions increased the tree flora to 750 species (Little *et al.* 1974), as many of the introduced alien species naturalized; that is, they established and sustained wild populations without the benefit of human intervention. Of the approximately 118 naturalized tree species in Puerto Rico, about 45 were introduced by Europeans before the 20th century, 35 were imported during the 20th century as ornamentals, roughly the same number were introduced for agricultural and forestry purposes, and the balance were probably introduced by indigenous peoples prior to settlement by Europeans (Francis and Liogier 1991). These species originate from tropical and subtropical areas worldwide: 55 from the New World, 13 from Africa and adjacent Mediterranean shores, and 50 from Asia, mostly from India and Oceania. This influx of tree species, vectored by human activity, has had important ecological consequences for island forests.

The environmental preferences of these naturalized species are not homogeneous (Figure 2). Francis and Liogier (1991) identified 74 rainfall ranges within their island habitats, which I have combined into 14 to illustrate the variety of rainfall conditions that these species prefer. A large number of species grow in regions that feature a moist to wet climate (ie average annual rainfall of 1500 to 3800 mm), a soil pH range of 5.0 to 7.5, medium soil fertility, and well drained but moist soils.

The alien species naturalized in Puerto Rico also exhibit a wide range of reproductive and invasive capacities (Figure 3). Most exhibit a slow rate of spread and infrequent to abundant regeneration. Francis and Liogier (1991) identified 16 naturalized species as now common on the island and 16 species which would become common within the next century. In island-wide forest inventories, five alien tree species form part of the list of 13 most important species (Figure 4), although the majority of the naturalized species are rare and infrequent (Figure 3). However, the presence of these species on the island influences forest composition and function.

Three of the alien species illustrate some of the contrasting characteristics of successful exotic invaders. White siris (*Albizia procera*) is a nitrogen-fixing, light-demanding, evergreen legume that competes successfully with pasture grasses. This species is shade intolerant, prefers roadsides and disturbed sites, and is wind dispersed (Chinea 1992). The African tulip tree (*Spathodea campanulata*) is a nearly deciduous, light-demanding, shade-intolerant and wind-dispersed species (Francis and Lowe 2000) that grows best in open areas characterized by high temperature and low humidity. The rose apple (*Syzygium jambos*) is an evergreen, shade-tolerant species, dispersed by vertebrates or runoff (Francis and Lowe 2000), and is capable of invading closed-canopy forests.

■ Invasion rates

Analysis of forest inventory data revealed that land-use history and substrate were the most important determinants of tree-species composition in sites invaded after agricultural activity had ceased (Chinea and Helmer 2003). Small-scale studies throughout Puerto Rico showed the same results on abandoned pastures, shade coffee, tobacco, other crops, charcoal pits, and houses (Aide *et al.* 1995; Zimmerman *et al.* 1995; Aide *et al.* 1996; Molina Colón 1998; Aide *et al.* 2000; Álvarez Ruiz 2002; Chinea 2002; Marcano Vega *et al.* 2002). Invasive alien species such as the African tulip tree and guava (*Psidium guajava*) dominated recently abandoned lowland pastures, whereas

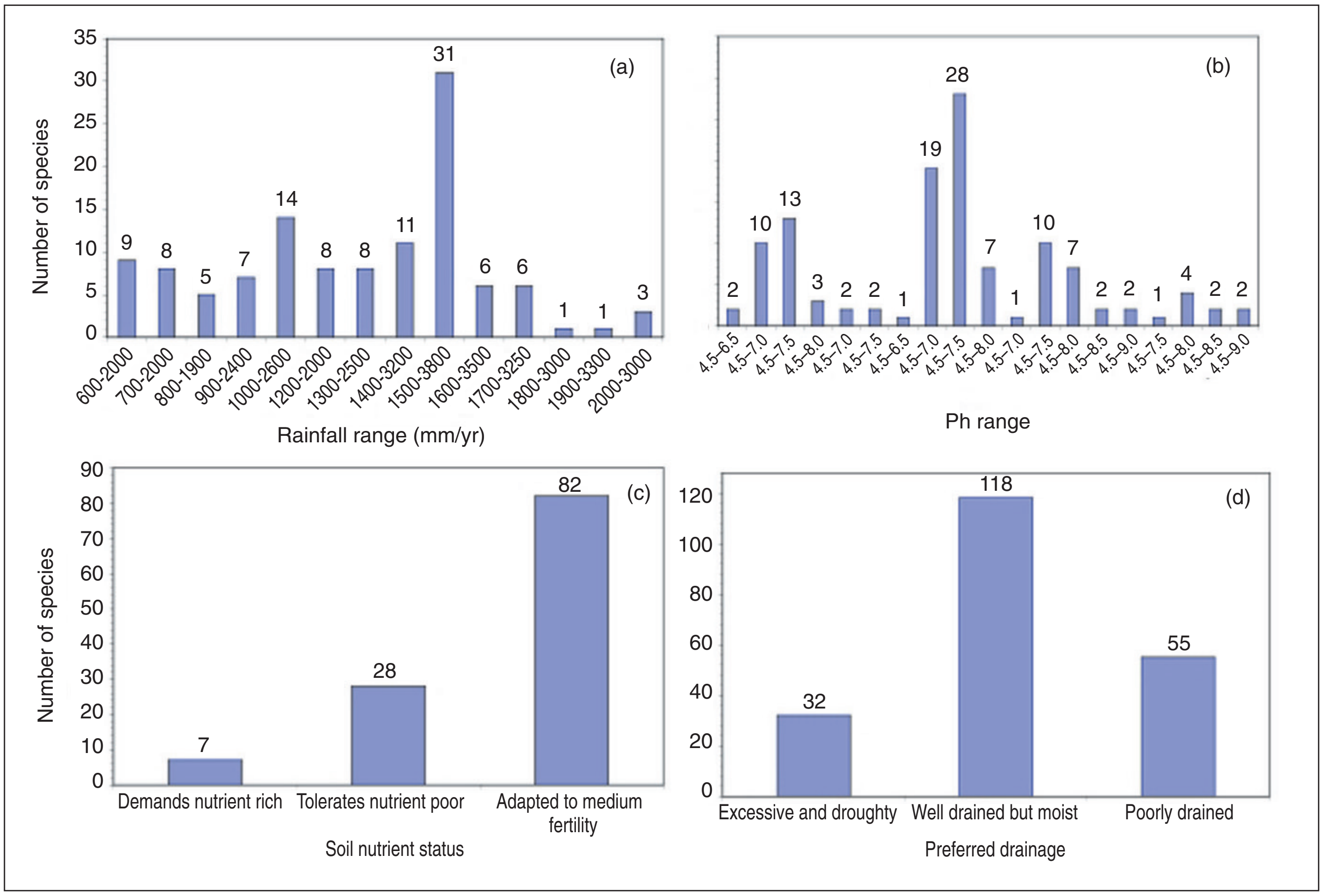

Figure 2. *Environmental preferences of naturalized alien tree species in Puerto Rico. Numbers at the top of the graph represent the number of species. The analysis was a species by species assessment based on literature and field observations (Francis and Liogier 1991).*

rose apple invaded shade coffee forests and native forests (Aide *et al.* 2000; Álvarez Ruiz 2002). Both African tulip tree and rose apple invade riparian areas (Heartsill Scalley and Aide 2003). White siris is the only species that invades bulldozed areas (Chinea 2002). These species can dominate individual stands and at times form monocultures. White siris can spread at a rate of up to seven ha per year (Chinea 1992), while the alien bamboo (*Bambusa vulgaris*) spreads at a comparatively leisurely 32 m^2 per year (O'Connor *et al.* 2000). The African tulip tree has more than tripled its importance value (IV, measured as the relative basal area plus relative tree density) island-wide in 22 years, from 2.6% in 1980 to 10% in 2002 (Figure 4). After 20 to 25 years, the success of the African tulip tree's invasion is evident in its high productivity and vigor on different soil types (Table 1).

■ After the invasion

Stands of African tulip trees allow light to penetrate to the forest floor during their deciduous period, a factor which contributes to a greater occurrence of native species in the understory as compared to closed-canopy shade coffee. For example, Helmer and Chinea (2003) found an average of seven native species (± 4.0 SD, n = 16) with an average IV of 59% in stands where African

Table 1. Structure of 20–25 year-old stands of African tulip tree (*Spathodea campanulata*) in Puerto Rico (Francis and Lowe 2000)

Soil order	Mean diameter* (cm)	Mean height* (m)	Tree density* (trees per ha)	Basal area† (m^2 per ha)
Inceptisol	33.7 + 5.8	19.2 + 0.7	1846	51
Ultisol	35.4 + 4.3	21.8 + 1.5	1432	41
Inceptisol	43.5 + 2.9	26.5 + 0.7	2769	74
Oxisol	45.8 + 2.7	21.3 + 0.3	350¶	53

Data were collected on 0.0314-ha plots; standard error is shown after the mean * Dominant and co-dominant trees † For all stems >0.5 cm diameter at breast height
¶Had been thinned

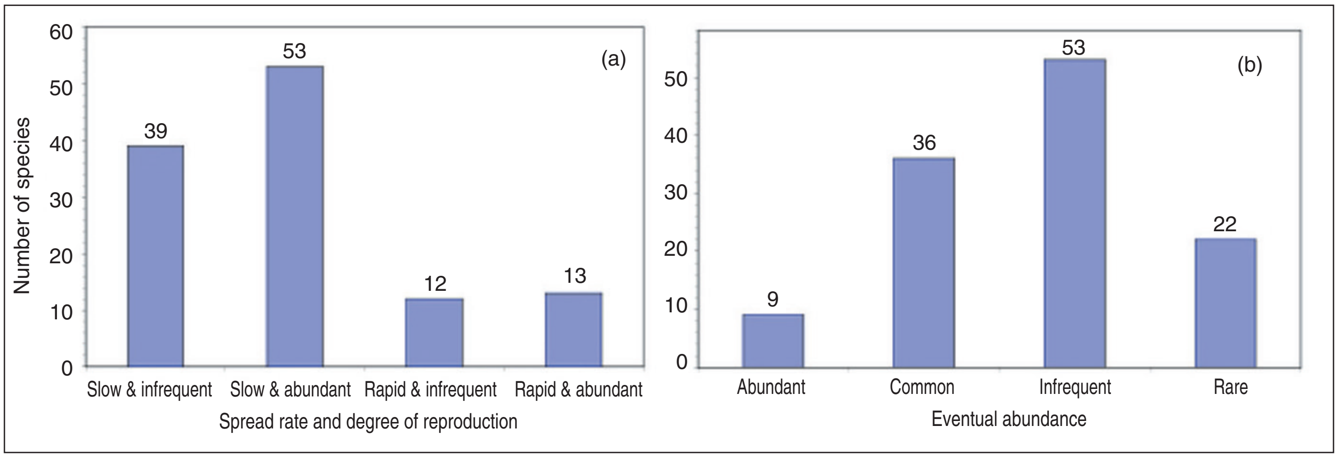

Figure 3. *Rate of spread (slow or rapid), degree of reproduction (infrequent or abundant), and eventual abundance of naturalized alien tree species in Puerto Rico. The number at the top of the graph represents the number of species. The analysis was a species by species assessment based on literature and field observations. The category "infrequent" for eventual abundance means an eventual habitat of less than 100 ha (Francis and Liogier 1991).*

tulip dominated the canopy (Figure 5). These results suggest that native species tolerate or even benefit from this common alien species. On the other hand, the changes in microclimate induced by the canopy of African tulip favors the establishment of native species while limiting its own regeneration, because African tulip is shade intolerant and a poor competitor with the native species regenerating in its shade. As a result, the dominance of African tulip trees lasts about 40 years after the invasion and then declines sharply over subsequent years as native species recolonize the stands (Figure 6; Aide *et al.* 2000). Other shade intolerant species such as guava behave in much the same way. An exception is rose apple, which invades closed-canopy forests. However, its abundance in these forests is associated with past human disturbance (Álvarez Ruiz 2002; KA Brown pers comm).

The process of native species establishment under the canopy of alien species occurs throughout Puerto Rico (Wadsworth and Birdsey 1985; Aide *et al.* 2000; Lugo and Helmer 2004). The resulting forest stands have tree-species densities that exceed those of native forests (Pascarella *et al.* 2000). For example, depending on previous land use, an hectare of alien-dominated forest supports between 59 to 74 tree species with a diameter at breast height (dbh) exceeding 11.5 cm. However, an hectare of mature native forest in Puerto Rico growing under similar climatic conditions supports about 50 to 52 tree species with a dbh of 4 to 5 cm (Lugo and Brandeis in press). Maturity here is used to indicate a forest older than 50 years with a low rate of change in biomass, wood volume, basal area, tree density, and species per unit area.

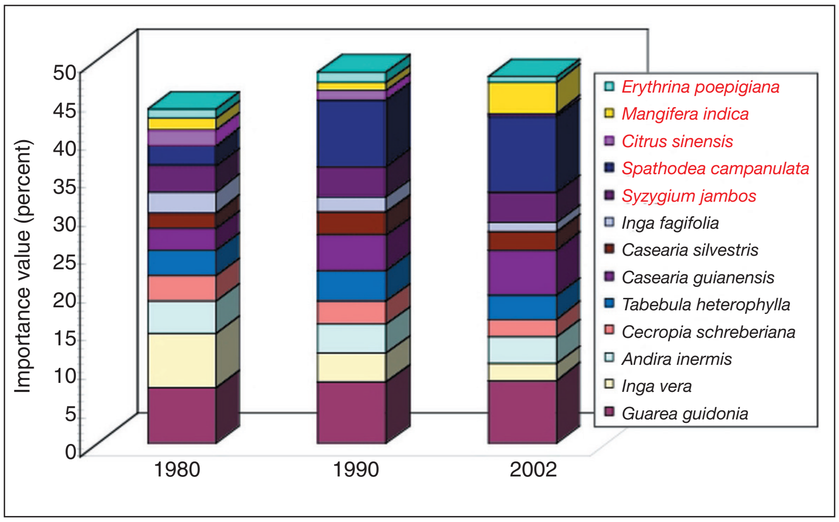

Figure 4. *The importance value of the most common tree species in three island-wide forest inventories in Puerto Rico (Lugo AE and Brandeis TJ in press). The importance value is the sum of the relative basal area and relative density of each species, expressed as a percentage. Alien species are in red.*

Marcano Vega *et al.* (2002) found that structural characteristics and species composition of forests originating from the abandonment of shade coffee and pastures converged after 30 to 40 years. Others found convergence of basal area and other structural features of forests on abandoned lands after 40 to 60 years of succession (Aide *et al.* 1995; Zimmerman *et al.* 1995; Aide *et al.* 1996; Rivera and Aide 1998; Aide *et al.* 2000; Pascarella *et al.* 2000). Chinea (2002) found similar results in a chronosequence of up to 73 years; these stands exhibit a species composition different to those of native forests of similar age. Even after 80 years of succession, species composition differs from that of native forests of the same age (Aide *et al.* 2000; Silver *et al.* in press).

In all instances, however, it was difficult to differentiate the structure and physiognomy of mature alien-dominated forests from that of native forests of similar age; furthermore, the species composition of mature alien-dominated forests differed from that of the species-poor forests at the time of invasion. In general, native and shade-tolerant species increased in importance with increasing age of the stand, while alien species decreased in importance, as did light-demanding species. Notably, endemic tree species are among the native species that develop under the canopy dominated by exotics (Table 2).

■ Functioning of alien forests

The rapid development of tree density, basal area, and tree height in stands of invading tree species (Table 1) reflects their high levels of primary productivity (Francis and Lowe 2000). The rate of basal area accumulation in these forests (2 to 3 m^2 per ha per year) is two to seven times faster than basal area accumulation in most successions of native species summarized by Brown and Lugo (1990). However, not all tree invasions involve high rates of biomass accumulation. Silver *et al.* (2000) found that biomass accumulates at slower rates in succession on cleared and abandoned land. Succession on abandoned agricultural land was faster than succession on cleared land, but slower than succession on abandoned pastures. In another study, the rate of biomass accumulation in abandoned pastures was found to be slower than succession of native species after hurricane disturbances (Aide *et al.* 1995). The legacy of human use influences both the rate of biomass accumulation during forest development and species composition.

Figure 5. *A 25-year-old forest dominated by African tulip trees (*Spathodea campanulata*). The understory is experiencing an invasion by native tree species under the canopy of the African tulip tree.*

The root systems of invading species, combined with the return of litter to the forest floor and the activity of non-native earthworms (Figure 7), also change soil structure and chemistry. For example, soil bulk density is high at the time of invasion of abandoned agricultural lands, but as forest succession advances, soil bulk density decreases significantly (Weaver *et al.* 1987). In addition, the forests accumulate nutrients, large quantities of which return to the forest floor, to add to the soil nutrient and organic mat-

Table 2. Percentage of endemic and alien tree species, contribution of alien species to importance value (IV), and number of species in various forest types in Puerto Rico. The listing of forest types is in decreasing level of anthropogenic disturbance

Forest type	**Percent of total number of species***		**Percent of IV**	**Total number of species**
	Endemic species	**Alien species**	**Alien species**	
Urban forest	0	24.2	65.6	33
Young karst forest	6.2	22.4	43.6	161
Young moist forest	5.0	20.0	49.1	140
Reverted moist forest	0.3	22.6	52.5	31
Reverted wet forest	5.6	22.2	54.0	18
Young inactive shade coffee	0	27.3	22.9	22
Old inactive shade coffee	6.2	21.0	38.3	81
Oldest inactive shade coffee	0	19.0	18.4	42
Young wet forest	6.9	16.7	25.6	72
Mature karst forest	6.0	8.4	12.5	83
Dry forest	5.7	13.6	7.8	88
Mature moist forest	10.0	6.3	41.4	80
Mature wet forest	4.1	13.5	25.6	74
Lower montane wet forest	26.7	0	0	30
Upper montane wet forest	15.5	5.2	2.6	58

Data are island-wide for the year 2002; data are from Lugo AE and Brandeis TJ (in press)
*The remaining percentage of species correspond to native species that are not endemic to Puerto Rico

*Figure 6. A 45-year-old forest dominated by African tulip trees (*Spathodea campanulata*). The understory is now almost a thicket.*

ter content (Lugo *et al.* 1990; Cuevas and Lugo 1998; Wang *et al.* 1991; Meenakshi Sundaravalli and Kailash Paliwal 2002). The nitrogen (N) and phosphorus (P) concentration (mg per g) of young and mature leaves of African tulip trees were 30.0 and 3.76, and 27.0 and 1.65, respectively. The concentrations in young leaves were higher than those reported by Martínez Sánchez (2003) for 11 species representing different functional groups in the neotropics (with one exception for N), and also higher than those reported for 141 species by Sánchez *et al.* (1997) in Puerto Rico (with four exceptions for N). Such high concentrations of nutrients in leaf tissue coupled with low re-translocation rates and high litter fall translates into increased nutrient enrichment of litter and soil.

As alien species invade riparian communities, the detritus from these species (eg leaves) enter streams (Heartsill Scalley and Aide 2003), and thus becomes a part of the grazing and detrital food chain (O'Connor *et al.* 2000). In feeding experiments, the native shrimp *Xiphocaris elongata* consumed leaves of the alien invasive bamboo, rose apple, and African tulip tree. However, their consumption of African tulip tree leaves was faster than that of any other species (T Crowl and T Heartsill Scalley pers comm). The consumption of leaves by grazers, decomposers, and herbivores demonstrates that the trophic structure of the new forests incorporates the products of primary productivity, irrespective of whether they are from native or invasive species.

Successful aliens in Puerto Rico must survive windstorms, as cyclonic events are part of the disturbance regime of the island. Rebecca Ostertag and W Silver (pers comm) found no difference in the effect that two hurricanes had on native versus alien tree species in the Luquillo Experimental Forest. The presence and persistence of alien species in mature forests established on abandoned lands suggests that these species continue to survive and grow there following hurricanes and canopy closure. The light-demanding alien trees present in the mature stages of succession may be adults of the cohort that invaded the site, or they may be trees that reproduced and regenerated in forest gaps.

In summary, invasive alien tree species are persistent in Puerto Rico's landscape. The changes they have introduced in the microclimate (light and air temperature) due to canopy closure, combined with changes in soil structure and chemistry, function to repair degraded lands and facilitate the re-establishment of native species under their canopies. Birds, bats, insects, and ants act as vectors for seeds from nearby forests (Wunderle 1997), which germinate and develop into seedlings and saplings in alien-dominated forests (Wadsworth and Birdsey 1985).

■ Animals

The changes in plant species composition on abandoned agricultural land also occur for animals. As a result of the presence of alien species, the number of birds (Brash 1984), earthworms (Borges 1996), aquatic invertebrates (Williams *et al.* 2001), and ants (Torres and Snelling 1997) increases. In the case of earthworms, alien species dominate in active pastures, but decrease in density and biomass with succession, whereas native species tend to increase (Sánchez de León *et al.* 2003). However, in mature forests that originated on abandoned land, alien earthworms are still dominant in terms of biomass and density (Figure 7), although the diversity of native earthworms is greater than that of alien species (five species to one). No alien earthworm species are present in undisturbed native forests. It appears that the legacy of human activity influences both floral and faunal species composition and abundance.

■ Conclusions

The species composition of Puerto Rican forests evolved over millions of years in response to changes in climate, geological formations, and topography (Graham and Jarzen 1969). Human arrivals to the island found a suite of native species that could cope with a disturbance regime dominated by particular frequencies and intensities of climatic events such as drought, hurricanes, floods, and landslides. This disturbance regime triggered successions dominated by native tree species (Lugo and Helmer 2004).

However, the increasing intensity of human activity on the island substantially altered the disturbance regime during the second half of the past century by creating large areas of open, abandoned lands. A human-induced disturbance regime is chaotic and ecologically unpredictable because it involves human activity that is responding to social and economic factors. High temperatures, low humidity, compacted soil, and low fertility prevented native pioneer species such as *Cecropia schreberiana* from colonizing abandoned open fields (Silander 1979; Zimmerman *et al.* 1995). In fact, few native tree or shrub species dominate succession in abandoned and degraded fields (Aide *et al.* 1996; Chinea 2002; Chinea and Helmer 2003). A notable exception is the native shrub white camasey (*Miconia prasina*) (Aide *et al.* 2000).

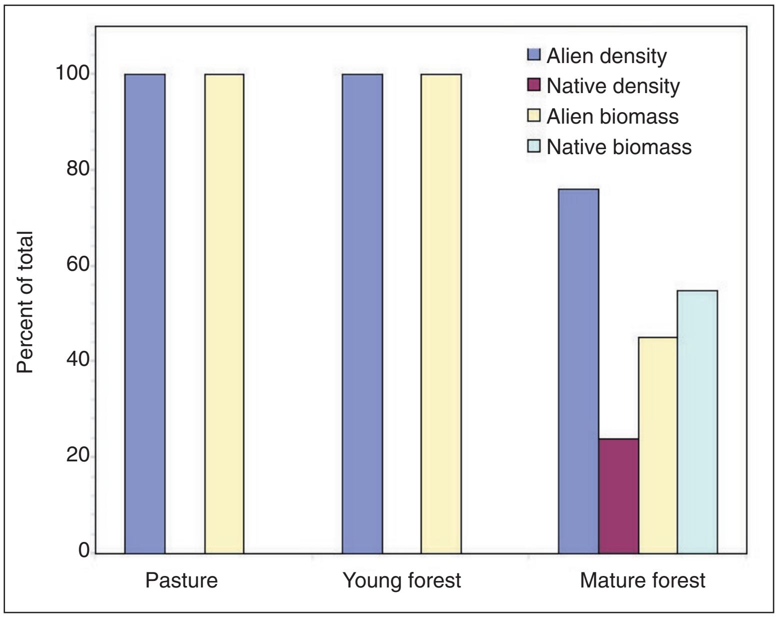

Figure 7. *Change in density and biomass of alien and native earthworms along a successional chronosequence in Puerto Rico. Each point is the mean of three sites. Pastures were active, young forests were 25–40 years old, and mature forest were greater than 77 years of age. Based on data in Sánchez de León* et al. *(2003).*

In the absence of invasion by alien tree species, the outcome of many abandoned agricultural lands is the establishment of pastures. These pastures are in various states of arrested succession and cover large land areas in Puerto Rico. Planting experiments with alien tree species have shown that after 8.5 years, unplanted controls remain pastures, while the planted aliens restore tree cover and diverse understories of native species, most of them (90%) dispersed by birds and bats (Parrotta 1995, 1999).

The legacy of site degradation coupled with intense human activity on the island has resulted in new conditions that give alien species a competitive advantage. The mixture of alien and native tree species that eventually invaded these sites sorted themselves through a process of self-organization according to their capabilities and the diversity of conditions imposed by the different levels of disturbance or legacies of past human activity. The alien trees dispersed, regenerated, and functioned without human intervention, just as native species do. The new disturbance regime triggered new trajectories of succession that lead to new ecosystem states featuring novel combinations of species and different rates of flows and stocks of materials and energy.

In the future, it is probable that the Puerto Rican forests will continue to function as they do today, but with different species compositions and rates of ecological processes, in response to continuing human effects on the landscape, and to climate change. The network of public lands with relatively undisturbed vegetation is critical for the future species composition of forests, as they provide a steady supply of seeds from native species.

Other countries have experienced dramatic changes in the species composition of their forests over large areas as a result of human activity. Foster *et al.* (2002) reviewed the changes in New England after large-scale abandonment of agricultural fields. As Davis (2003) points out, about 4000 plant species introduced into North America (excluding Mexico) during the past 400 years have become naturalized; thus, a substantial fraction of the alien flora has become part of the plant communities of North America without an apparent or proportional negative effect on community structure or function. Dupouey *et al.* (2002) reviewed events in Europe, where agricultural use left a legacy of environmental change that has lasted for millennia. There too, alien species invasions vectored by human activity accounted for dramatic changes in the flora (Rich and Woodruff 1996).

In the tropics, Turner *et al.* (1995) found a substitution of native species by alien species over a 100-year period in an isolated fragment of lowland tropical rainforest in Singapore. At a larger scale, the Maya modified and enriched the tropical forests of Central America to suit their needs. The magnitude of the change baffled biogeographers, who were faced with unexpected tree distributions and the realization that humans had in fact changed and managed forests previously considered pristine (Rico Gray *et al.* 1985; Gómez-Pompa and Brainbridge 1995).

These examples do not imply value to alien species invasions. They simply demonstrate that ecological phenomena underpin these invasions and that further study of these occurrences is needed, in order to gain an understanding of the causes and consequences of such events.

In spite of the generalized naturalization of alien invaders in Puerto Rico, native species enrichment through succession is not a characteristic of all monocultures of alien species. A notable example in Puerto Rico is the monoculture of the cayeput tree (*Melaleuca quinquenervia*). Even after several decades of growth, this species maintains monocultures, much as it does in South Florida (Serbesoff King 2003). A key difference between cayeput monocultures and the generalized behavior of alien trees in Puerto Rico is the presence of fire and flooding in regions dominated by cayeput and the absence of such events in upland areas. Cayeput invades abandoned agricultural lands that flood and burn, and generally out-competes and overgrows grasses under these conditions. While native tree monocultures do exist in parts of Puerto Rico where there is chronic soil saturation or flooding (Lugo *et al.* 1995), there are no native tree species capable of withstanding both flooding and fire. Fire, salinity, and chronic flooding are extreme environmental factors that are difficult to cope with, even for most alien species, and such factors will often arrest tree succession. As a result, the presence of these factors often leads to the establishment of monocultures, particularly in the absence of a native species pool capable of regenerating in the conditions created by human activity.

The long-term outcome of alien species invasions in Puerto Rico underscore the need for ecological research to address the processes responsible for the establishment and function of ecosystems dominated by alien species. Only through such research will we be able to demonstrate the emergence of new combinations of species and the legacy of human activity embedded in the biota.

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