CHAPTER TWENTY

New mix of alien and native species coexists in Puerto Rico's landscapes

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'There is no controversy among scientists that nonindigenous species cause extinctions of native species.' . . . 'The increase in nonindigenous species-induced rates of extinction of native species on both local and global scales is a fact.'

D. M. Lodge and K. Shrader-Frechette 2003, p. 34 and 36

'The evidence so far points to the conclusion that invaders often cause extinction on oceanic islands and in lakes but rarely in the sea or in large land masses.'

G. J. Vermeij 1996, p. 6

Introduction

The advent of the Homogeocene (Putz 1997), Homogecene (McKinney & Lockwood 1999; Lockwood & McKinney 2001) or Homogocene (Lodge & Shrader-Frechette 2003) – the era of human domination of the world – is both a challenge and an opportunity to test the ingenuity of humans. Will we be able to establish a new and sustainable balance with the rest of the world's biota? To do so requires active management of biodiversity based on understanding the function and dynamics of ecosystems. Appropriately, the approach to the study of the biota is undergoing a shift from a taxonomic, distributional and evolutionary focus, to a paradigm that considers biodiversity and ecosystem function (Naeem 2002). This new approach is holistic and quantitative, and helpful in understanding the role of biodiversity in the Homogeocene (Lugo 1995, 2002a).

Much of the current literature on tropical biodiversity focuses on the negative effects of non-indigenous or alien species, particularly invasive ones. The general belief is that invasive alien species are a major cause of native-species extinction, as well as a large burden on the economy of many countries (Allendorf & Lundquist 2003). A special issue of *Biological Conservation* (Carey *et al.* 1996), a special section in *Conservation Biology* (Allendorf & Lundquist 2003), the Ecological Society of America's *Issues in Ecology* (Mack *et al.* 2000a) and a technical report in *Ecological Applications* (Mack *et al.* 2000b) all underscore the role of invading

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alien species in causing extinction of native species. However, the evidence to sustain the claims usually does not support sweeping generalizations such as the first one quoted above. Usually, such statements emerge from simulation models of global change (Walker & Steffen 1997; Sala *et al.* 2001), examples from particular locations (Hobbs & Mooney 1997) or unsubstantiated generalizations and extrapolations (Myers 1986, Alonso *et al.* 2001).

Dependence on global models to anticipate massive extinction of endemic species introduces confusion to the literature because references to these studies ignore their assumptions, the complex patterns of response of the models, and the dearth of empirical evidence to substantiate the predictions. As an example, Sala *et al.* (2001) modelled through the twenty-first century and, out of countless potential drivers of species extinctions, they ranked the potential effects of five of them: land use, climate, nitrogen deposition, biotic exchange and atmospheric CO_2. Biotic exchange, i.e. the effects of alien species on the native biota, ranked fourth overall as a driver of extinctions in the model simulations. For the tropics (Dirzo 2001) and other locations, the effect of biotic exchange on species extinction was negligible. Change in land use was the main driver of species extinctions. Many research studies support that conclusion and consistently show that the level of species extinctions is generally low except for particular locations such as lakes, rivers and some islands (below). In spite of the above, references to Sala's work, for example in Lodge and Shrader-Frechette (2003), ignore the context or limitations of the research.

Comprehensive large-scale analyses invariably fail to demonstrate that alien species are the root cause of massive native-species extinction. For example, Case (1996) studied the extinction and invasion of bird species in insular and mainland sites, including the Pacific Islands, and found direct correlation between rates of extinction of native species and rates of alien-species invasions. However, the two events responded to different causal forces. Anthropogenic disturbances including habitat conversion and degradation, and creation of new types of habitats, caused the extinction of native bird species well before the invasion of alien species. The aliens took advantage of empty niches in new or altered habitats (Grime 2002). Similarly, Davis (2003) points out that about 4000 plant species introduced into North America north of Mexico during the past 400 years naturalized. They now constitute nearly 20 per cent of the continent's vascular plant species without any evidence that a single native species has gone extinct from these introductions. Wohlgemuth *et al.* (2002) document the same trend for Europe, and Pitman *et al.* (2002) did so for the neotropical flora, concluding that habitat loss was the main cause for the extinctions they documented. Davis (2003) concluded that compared with intertrophic interactions and habitat loss, competition from alien species is not likely to be a common cause of extinctions of long-term resident species at global, metacommunity and even most community levels. However, alien species can affect native species through pathogens, change in disturbance regime or predation (Cowie & Robinson 2003; Davis 2003).

The debate on the extinction of species lacks information collected at the proper scales of time and space, leading invariably to confusion and a debate on values. For example, increasing evidence shows that species richness increases in most regions of the world owing to species introductions and the formation of new habitats by human activity (Case 1996; Rich & Woodruff 1996; Weber 1997; Grime 2002; Wohlgemuth *et al.* 2002; Davis 2003). The arrival of new species at these sites creates opportunities for the development of new ecological and evolutionary relationships (Abbott 1992; Vermeij 1996; Mooney & Cleland 2001; Davis 2003). However, many dismiss this information as unimportant because of the social value attributed to indigenous species, and the belief that alien species disproportionably affect them. For example, Lodge and Shrader-Frechette (2003) wrote:

> A focus on total species diversity at the local scale, including nonindigenous species, ignores the basis of the fear of the Homogocene that is shared by many in society, not just environmentalists: the high value placed on the uniqueness of regional biota. (p. 34)

Value-laden arguments, if unsupported by sound scientific evidence, lead to positions based on the 'nasty necessity of eradication' of species (Temple 1990) with a 'shoot first, ask questions later' approach (Allendorf & Lundquist 2003; Simberloff 2003). However, Zavaleta *et al.* (2001) discuss how such eradication approaches can also result in unexpected changes to other ecosystem components, including accidental adverse effects on native ecosystems. Moreover, some analyses suggest that homogenization of the biota is not synonymous with low diversity. Different regions of the world will be more similar to each other than they are now, but they will also be more diverse (Davis 2003).

Clearly, the issues associated with the spread of alien species are complex but we lack sufficient information to move the debate from a value-laden one to a scientifically based ecological discussion. Moreover, the focus of scientific attention is likely to influence how managers and policy makers design programs to address biodiversity issues. If the information they receive leads them to an eradication approach, such an approach will prevail. In Hawaii, agencies at all levels of government are funding an eradication program against *Eleutherodactylus portoricensis*, a frog introduced from Puerto Rico (Leone 2003). This expensive effort is an example of how a legitimate concern for conserving biodiversity might doom the effort. A poor scientific base for the control actions leads to actions that are expensive and ineffective, and the danger of causing a backlash in the political system that funds such activities (Lugo 1999).

The role that habitat conditions play in species establishment and turnover deserves increased scientific attention because it provides an alternative management approach for dealing with biodiversity issues. A relevant hypothesis to test is that which states that change in habitats, rather than the globalization of the world's biota, is a major cause of changes in global biodiversity. The management alternatives based on a habitat or ecosystem approach are dramatically different from those based on eradication. For example, one could address the growth of aquatic weeds on reservoirs through continuous removal of plants or by dealing with water quality and hydrology. The information demand and corrective measures for each approach are different.

Typically missing from information used to assess tropical biodiversity are assessments of the disturbance regime (natural and anthropogenic), data about current and past land use, and large-scale quantitative assessment of the distribution and long-term trends in the abundance of species. Without this kind of information, it is difficult to assess correctly the ecological role of biodiversity and avoid a generalized war on groups of species based on their time of arrival at particular geographic locations. Reliable field data are required for supporting informed decisions about the changes in biodiversity taking place in the tropics, and the role of alien species in particular. Repetitive forest inventories represent one mechanism for gathering objective and long-term, large-scale quantitative information about the relationship between biodiversity and anthropogenic and natural forces of change. Rich and Woodruff (1996) provide an example of this application of large-scale inventories for the temperate zone.

We report the preliminary results of an island-wide forest inventory in Puerto Rico currently in progress, focusing on species composition and their importance value in different forest types. We also analyse 22-year trends of species composition based on three island-wide forest inventories. For the most recent inventory (2002), we analyse the species composition by life zone (*sensu* Holdridge 1967), land-cover type, level of stand maturity and tree-species representation in three size classes. Our focus is on two measures of biodiversity at a large-scale level: the ranked importance value of species, and species composition in terms of their classification as alien or native, including endemic. Our objective is to shed light on the working hypothesis that alien tree species predominate in human-disturbed environments and that they are forming new forest types (*sensu* Lugo & Helmer 2004) by mixing with native species, including endemic species. We discuss our results in terms of their implications for current debates about the ecological roles of invasive alien species and the approaches needed for their management.

The significance of Puerto Rico

In many of the tropical areas, the increasing rate of deforestation and expanding human influences over the biota and landscape exacerbate the sense of urgency for the conservation of biodiversity. The focus is on anthropogenic disturbances (such as land-cover change), and introduction of new fire regimes and alien species to sites previously devoid of these influences. Because of the magnitude

Table 20.1 *List of peculiarities of Puerto Rico that allow it to be an excellent location to study the potential future states of continental tropical forests*

- An old biota with over 40 million years of evolutionary history (Graham 1996).
- Human habitation goes back for millennia.
- Located in the trade wind and hurricane region. It is anticipated that global climate-change phenomena will be detected early in this region in changing frequency and intensity of climatic events.
- A region with a diverse natural disturbance regime (hurricanes, volcanoes, earthquakes).
- A population density of >400 people/km^2.
- Territory was almost completely deforested (Birdsey and Weaver 1982) and has recovered to >40 per cent forest cover (Helmer *et al.* 2002).
- A location with one of the highest rates of land-use transformation in the twentieth century (Rudel *et al.* 2000).
- Landscape has evolved from highly fragmented to less so, and from almost 100 per cent forested to almost 100 percent agricultural, and then to about 15 per cent urban (Lugo 2002b).
- Excellent scientific knowledge of the biota (Figueroa Colón 1996a).
- Excellent documentation of environmental changes.
- Excellent infrastructure for accessing forests and for their scientific study.
- The economy is mostly dependent on outside subsidies for its food, energy and goods (Scatena *et al.* 2002). This means that human activity is so intense that the island cannot support its basic needs without significant outside help. For example, almost 100 per cent of the energy and food consumed in the island is imported.

of some of these anthropogenic effects, we often fail to consider the capacity of the biota to react to, and recover from, natural and anthropogenic disturbances (Lugo *et al.* 2002).

The significance of a country like Puerto Rico for studying these issues is that conditions in the island reflect a high intensity of human activity (Table 20.1) while the island is on the recovery phase of a full deforestation event. The deforestation event lasted from the time most of the island forests were converted for agricultural use during the nineteenth century, until large-scale abandonment of agricultural fields in the mid twentieth century. Since the 1960s, forest area in Puerto Rico has steadily increased to the current 45 per cent forest cover (Helmer *et al.* 2002).

Puerto Rico is an ideal location to study and anticipate the Homogeocene (Lugo 2004a). Having experienced the cycle of deforestation and reforestation following land-cover and land-use change allows scientists to evaluate ecological phenomena, such as the invasion of alien species, from a different perspective than that visualized in locations where the process of invasion is in its early stages. There are areas in Puerto Rico where the natural recovery of vegetation after the deforestation event is in its 80th year, long enough to see changes in

Table 20.2 *Number of plots, and forest area sampled (ha) by forest type*

Forest type	Number of plots	Area sampled
Dry forest	21	1.47
Young karst forest	54	3.78
Mature karst forest	7	0.49
Reverted moist forest	6	0.42
Young moist forest	36	2.52
Mature moist forest	7	0.49
Reverted wet forest	2	0.14
Young wet forest	13	0.91
Mature wet forest	7	0.49
Lower montane wet forest	3	0.21
Upper montane wet forest	5	0.35
Shade coffee forest	16	1.12
Urban forest	6	0.42
Total number of plots	**183**	**12.81**

All forest types are subtropical *sensu* Holdridge (1967). The methods describe the definition of each forest type.

species composition of whole forests. Moreover, the forests of the island have experienced low levels of species extinctions (Lugo 1988; Figueroa Colón 1996b).

Another advantage of Puerto Rico as a case study is the abundance of ecological studies at spatial scales that vary from traditional community-level studies to repetitive island-wide forest inventories. We review these data, and report results from long-term forest inventories. Because of the importance of these data to our discussion, we summarize in Appendix 20.1 the methodology used in the island-wide forest inventories and the indices we use to evaluate forest structure and composition. In addition, we summarize in Appendix 20.2 results from the latest inventory according to forest type (Table 20.2). We use these data to describe the pattern of species distributions in relation to human activity.

Dominance and species composition in space and time

Three island-wide forest inventories in Puerto Rico allowed us the opportunity of assessing spatial and temporal patterns of species dominance and composition on a large scale. Results (Appendix 20.2) reveal the following patterns among secondary forest stands throughout Puerto Rico:

- High importance values (>10 per cent) for the top-ranked tree species (Figs. 20.1 and 20.2, pp. 502 and 505).
- The highest importance value of the top-ranked tree species corresponded to young karst forest and urban forest, followed by shade-grown coffee, and

moist-forest stands, and finally by dry, wet and montane forests (Figs. 20.1 and 20.2).

- A gradient in the percentage of alien species from high percentages in urban, young karst and moist forests to low and/or almost no presence in dry, wet and montane forests (Table 20.3, p. 501).
- A gradient in the percentage of endemic species in the opposite direction to the gradient in alien species, i.e. high percentage in dry, wet and montane forests, and low percentage or absence in young karst, moist and urban forest (Table 20.3, p. 501).
- The species–area curves for the disturbed areas are steep and reach a higher number of species at the 1-ha sample than undisturbed and mature native forests (Fig. 20.3, p. 506).
- Over a period of 22 years, species composition and the importance values of top-ranked species changed in forest stands (Fig. 20.4, p. 508).
- The rapid spread of *Spathodea campanulata*, a species introduced to the island over a century ago, reflects the recent availability of abandoned lands for colonization. This species is shade-intolerant, cannot grow under close canopy and rapidly loses dominance when the canopy closes after about 40 years of growth (Aide *et al.* 2000).
- Although alien species continue to dominate several types of forests, the number of native species in seedling and sapling classes was higher than their presence in the tree size class (Table 20.3, p. 501).
- There is no indication that the dominant alien species will decline in importance in the near future because they are regenerating and maintaining their importance values (Table 20.5, p. 507) even in mature stands where we found fourteen alien tree species (Table 20.6, p. 508).
- Some native species grew only in mature stands. *Dendropanax arboreus* seems to prefer older abandoned coffee shade. *Manilkara bidentata*, a species that indicates fairly undisturbed forest stands, was rarely found: as a minor overstorey species in mature wet forest, and once as a seedling in mature karst forest.
- At least sixteen endemic tree species thrive in these new forest stands, and we found thirty-one endemic tree species in the 2002 inventory (Table 20.4, p. 503). The endemic *Cordia borinquensis* was present and regenerating in moist and wet mature stands only. The presence of endemic species in all size classes suggests that the high dominance of invasive alien species does not inhibit the establishment and growth of these endemic tree species.

These results confirm and expand the earlier analysis of Lugo and Helmer (2004) who concluded that the establishment of alien species and their mixing with native species resulted in the formation of new forest types. These forests are new because the species composition is different from that of the native forests described for the island.

Observations on individual species and forest types

- *Spathodea campanulata* continues to play a dominant role in the island's secondary forests, and will continue to do so well into the future because continuous change in land cover creates suitable habitat for the species.
- Dry forests, although degraded, do not have an alien species that fills the role of *S. campanulata* in moist and wet forests. Native species such as *Bursera simaruba*, *Andira inermis* and *Leucaena leucocephala* make up much of the dry forest. Apparently, the harsh natural conditions of dry forests prevent the dominance of alien species, but not their presence, as aliens contributed to 13.6 per cent of the dry forest tree species (Table 20.3). A similar situation occurred at the other extreme of the moisture gradient in the montane wet and rain forests. Montane forest, perhaps because of its unsuitability for other land uses and hence historical lack of disturbance, shows little colonization by alien species.
- In shade-grown coffee, the poor regeneration of the traditional shade coffee trees (*Inga* and *Erythrina* spp.) may allow *S. campanulata* and *Guarea guidonia* to dominate stands that were formerly managed as shade coffee once those stands are abandoned. *Spathodea campanulata* and *G. guidonia* dominate not only the tree size class of abandoned shade coffee, but also the sapling and seedling size classes. Therefore, these species will continue to be the major components in this forest type for a long time. However, abandoned shade coffee still holds an impressive number of native species in the sapling and seedling stages (Table 20.3), and we can expect that even if a small percentage of these trees reach the overstorey, forest diversity will increase over time.
- Alien species such as *S. campanulata* and *Albizia procera* dominated the urban forest. Chinea (2002) found that *A. procera* was more common on bulldozed abandoned agricultural land, and hypothesized that the species had a competitive advantage on these greatly disturbed sites. Under these conditions, *A. procera* showed high importance value, as did the dominant species in young karst. The gradient in importance values from high in young karst and urban, followed by intermediate values in shade coffee and moist forest, and low values in mature karst, dry, wet and montane forests (Table 20.3) suggests that the gradient of anthropogenic disturbance is a factor in the degree of dominance of the high-ranked species in these forests.
- Although alien species play prominent roles in karst, moist and wet forests, numerous native tree species, including endemic species, grow in the sapling and seedling classes, indicating that they have colonized secondary forests and are regenerating. The steep slope of the species–area curve and their higher species count than that of native undisturbed forest stands further support the notion that alien species enrich these emerging new forests and that native and endemic species are not inhibited or prevented by their presence in these forest stands.

Driving forces of change

The results of our large-scale analysis and those of Chinea and Helmer (2003) are similar to many small-scale studies in Puerto Rico (García Montiel & Scatena 1994; Zimmerman *et al.* 1995; Molina Colón 1998; Foster *et al.* 1999; Chinea 2002; Thompson *et al.* 2002). These studies establish that past land uses affect the species composition and alien-species invasion of sites. In addition, the type of land use and its intensity also have an effect. For example, different species occur and different levels of forest structure develop to the present if the past land use (at the time of the 1982 survey) was:

- Abandoned pastures (Aide *et al.* 1995; 1996; 2000).
- Active and abandoned coffee plantations (Birdsey & Weaver 1982; Franco *et al.* 1997; Rivera & Aide 1998; Rudel *et al.* 2000; Marcano Vega *et al.* 2002).
- Abandoned sugar cane, tobacco and other crop lands (Thomlinson *et al.* 1996; Rudel *et al.* 2000; Álvarez Ruiz 2002; Chinea 2002).
- Abandoned subsistence agriculture (Molina Colón 1998).
- Abandoned human habitation (Molina Colón 1998).
- Abandoned roads, even those with pavement (Heyne 1999).

Bulldozing also affects both the species richness and proportion of aliens in recovering forests (Chinea 2002). Roadside forests show gradients of species composition and alien species invasion in proportion to distance to pavement (Lugo & Gucinski 2000). In short, the preponderance of evidence from studies in Puerto Rico is that the land-use history of sites is a principal factor to consider when interpreting vegetation structure and composition.

Anthropogenic disturbances interact with natural disturbances and edaphic, climatic and geomorphologic gradients to create a new disturbance regime. The changes in species composition caused by these forces remain visible for decades and probably centuries (Thompson *et al.* 2002, Dupouey *et al.* 2002). The disturbance regime of most tropical forests continues to evolve because of increased human activity, global change, and their interaction with the natural disturbances that occur everywhere. For this reason, the structure and species composition of forests affected by these new disturbance regimes will also change. What might appear an out of control invasion by tree species, such as the monoculture forests of *Spathodea* in the lowlands of Puerto Rico, is in reality a response to an abandoned degraded agricultural site that within decades will be a diverse forest of a new mix of alien and native species (Lugo 2004b).

For the reasons given, management and conservation recommendations benefit from information based on whole ecosystem analysis. To better understand the biology of the biota it is best to consider the context of the conditions under which it exists. Future work on invasive species will require an understanding of the physical conditions at the site, including natural disturbances, and a historical perspective on past land covers and land uses. Such studies would be more effective in guiding policy and conservation actions.

Generality and implications of these results

The phenomena we describe are not exclusive to Puerto Rico. Foster *et al.* (2002) and Lugo and Helmer (2004), review similar phenomena in the eastern United States, and Dupouey *et al.* (2002) do so for Europe where agricultural use left a legacy of environmental change that has lasted for millennia. 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 rain forest in Singapore. The historical reality is that wherever humans dominate a landscape, plant and animal species that are useful to, or dependent on, people follow and thrive in the conditions created by humans (Crosby 1986). Many of these species naturalize, and form new species assemblages without harm to local species and without harm to ecological processes (Davis 2003). These invasions have important ecologic, economic and social benefits that require our attention. A dramatic tropical example of the close relationship between human economic activity and the composition and dynamics of the landscape is that of the Maya, who actively introduced species, changed the species composition of forests and managed the landscape to suit their economy and life styles (Gómez-Pompa & Brainbridge 1995). Forests so designed and managed by people created confusion among modern ecologists who thought that they were dealing with pristine natural ecosystems (Rico Gray *et al.* 1985).

Because it appears inevitable that the species composition of landscapes dominated by human activity will change, and given the likely invasion of those landscapes by alien species, it behoves us to learn about this phenomenon and develop policies and tools to cope with change. The following are some implications derived from the Puerto Rico case study:

- Given sufficient time, invasive alien species modify the conditions of degraded sites such that native species, including endemic species, can grow in sites previously unavailable to them.
- Diverse forests develop after abandonment of deforested and degraded sites. These forests contain new combinations of tree species that include alien, native and endemic species.
- Even if widespread invasive species such as *S. campanulata* dominate many types of forests and persist for decades, their presence and dominance is not incompatible with the development of a diverse forest community.
- Continuous forest inventory data is a useful tool for objective evaluation of forest communities over large geographic areas and over a long time.

New ecosystems emerging under intense anthropogenic disturbances offer an opportunity for conservation of biota in the Homogeocene. These systems are dynamic and subject to active management to achieve particular management objectives. The long-term and large-scale nature of this study allows a different perspective on the effects of invasive alien tree species. It appears that for trees in the Caribbean, a management strategy of eradication is not necessary if the goal is to sustain forest cover, high species richness and regeneration of endemic species.

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Appendix 20.1 Methodology used in island-wide forest inventories in Puerto Rico

We report data from a 2002 island-wide forest inventory of Puerto Rico. The previous tree inventories corresponded to 1980 (Birdsey & Weaver 1982) and 1990 (Franco *et al.* 1997), and were limited to moist and wet secondary forest and shade coffee. For the 2002 inventory (Brandeis 2003), we used a geographical information system (GIS) to place a standard grid of 2400-ha hexagons over the entire island and installed an inventory plot at the centre of each hexagon (367 sampling points) to sample all forest types. In areas of special interest, the sampling grid was 'intensified' by using the GIS to generate smaller, equal-sized hexagons within each of the base hexagons. The degree of intensification depended on the size of the inventoried area and the expected variation of its forests.

Using previous studies as a guide, we chose a sampling grid that was three times more intense than the standard forest-inventory base grid for inventorying the forests of the northern karst belt. We used a geology map and GIS to select an additional eighty-five sampling points, which fell on calcareous parent material. We used a similar approach to add sampling points within forest types of limited extent such as upper montane wet forest, and moist and wet forests growing on ultramaphic parent material. We intensified the base hexagonal twelve times, and used vegetation and geology maps in the GIS to extract additional sampling points. The inventory of urban forests in the San Juan Bay Estuary's watershed was also a 12 × base-grid intensification, which produced 108 systematic sampling points.

Field crews visited each sampling point and installed a forest inventory plot if the vegetation there met the USDA Forest Service's Forest Inventory and Analysis program's definition of forest: at least 10 per cent tree canopy coverage, and a minimum area of 0.4 ha, or at least 37 m wide if a strip. The reported number of plots by forest type and area sampled totalled 183 plots and 12.81 ha (Table 20.2).

Sampling plots were actually a cluster of four, 7.32-m radius subplots where total height and diameter at breast height (DBH) were measured on all trees with a DBH $\geq$ 12.5 cm. We also measured total height and DBH on all saplings (2.5 cm $\leq$ DBH $\leq$ 12.4 cm), and all seedlings (height $\leq$ 30 cm and DBH $\leq$ 2.4 cm). We identified and tallied all saplings and seedlings within 2.07-m radius micro-plots nested within each subplot. The total sampled area of each plot was 0.07 ha, but because there were 36.5 m between subplot centres, each plot is more representative of a larger area than is a single plot of the same area. Species designation as native, endemic or alien followed Molina and Alemañy (1997), and Little *et al.* (1974).

Forest-type categorization

We categorized inventoried forest stands using a combination of field-crew assessment of the forest type, land-use history and GIS coverage of life zone and geology. Karst forests were located on limestone geology in the moist-forest life zone. The other moist, wet and rain forests were located on volcanic geology with the exception of six stands growing on ultramaphic substrates. These were included with the moist- and wet-forest life zones. Dry-forest stands were located on limestone and alluvial substrates.

We used two methods to analyse temporal change in species composition. First, working only with stands surveyed in 2002, we subjectively derived stand ages (young, mature) from a combination of current and historic inventory data for moist, wet and rain forest. The mature versus young stand categories rely heavily on the field crew's assessment of the stand. Crews generally used the density of large overstorey trees, in addition to their experience in the local forests, as an indicator of stand maturity. When we classify a stand as mature, we do not imply that the stand is a primary forest, nor an undisturbed forest. Mature stands include late secondary forests and forest stands with little evidence of past disturbance. All forest stands suffered some kind of land-cover change in the past and thus they are secondary forests of different ages. The small number of stands categorized as mature is noteworthy (Table 20.2, p. 489). The lack of mature forest plots may reflect some bias in the methods used to assign that category to stands, but we believe it accurately reflects the scarcity of stands in this age class. We did not attempt to separate dry, lower montane wet or upper montane wet-forest stands inventoried in 2002 into young and mature subcategories, and stands that were shade-grown coffee were categorized slightly differently.

We categorized shade-coffee stands by estimating time since abandonment using past inventory data and the field crew's assessment of land-use history. The oldest category of abandoned shade-coffee stands were abandoned coffee stands in 1980 that had not lost forest cover to the present. Old abandoned shade-coffee stands were those abandoned after the 1990 inventory but recorded as actively managed in 1980. Stands abandoned after the 1990 inventory were designated young abandoned. If there was any doubt as to the history of the shade-coffee stand, the default chosen was the middle value: old abandoned. As a result of the changes in sampling design, we excluded in 2002 some stands of shade coffee included in the 1980 and 1990 inventories. In the 2002 forest inventory, there were only two recently abandoned shade-coffee stands and only three that we categorized as abandoned prior to 1980.

The second way we analysed temporal change was to group all stands of similar forest type and land-use history together, regardless of maturity, and compare these broader categories across inventory years. We grouped moist and wet forest into one broader category of secondary forest. We also examined shade-coffee stands as a single category, i.e. without estimating the time since abandonment. Using these broader categories, we examined changes in species composition in the data from 1980, 1990 and 2002 inventories. We excluded urban, dry and montane forest types from this analysis.

By urban forest, we mean forest stands within the San Juan Metropolitan Area, specifically in the watershed of Río Piedras, which discharges into the San Juan Bay estuary. These forests were in the moist-forest life zone, but we exclude them from summary data by life zone and do not examine temporal change in these stands because this was the first inventory of this forest type. However, they were not mature stands. Reverted forest stands are those that experienced a land-cover change between the 1990 and the 2002 inventories. These stands were returned to an earlier stage of succession during that time interval.

Importance values

Importance value, expressed as the average of relative density and relative basal area, is the metric used to gauge a tree species' presence and relative importance in each forest type. We calculated importance values for each species for trees and saplings. Seedling relative frequency was calculated, not a true importance value. Seedling relative frequency for the more commonly found species may be truncated. According to national inventory protocols, field crews count up to six individuals of a seedling species per micro-plot, and then stop. A value of six may actually represent more seedlings of that species, but there is no way to know exactly how many were in the micro-plot. We assume a species is regenerating at a site if it shows importance values in the tree and sapling size classes, as well as in a relative frequency for the seedlings.

For comparison of results from the previous forest inventories, we limited the analysis to those forest types inventoried each time and normalized the data to account for different sampling area. This limited the analysis to moist and wet secondary forests and shade coffee. The comparison involved the top-ranked forty-eight species in each inventory. We express all comparisons as percentage of the parameter (total importance value and/or number of species) in each inventory.

Species–area curves

We also constructed species–area curves using 2002 data for five of the forest types we studied and one for all forests combined. We limited the analysis to a one-hectare sample size because we have comparative information for undisturbed and mature native forests.

Appendix 20.2 Results of island-wide forest inventories by forest type

Dry, moist and wet forests

The importance value of the top-ranked tree species in moist secondary forests was higher, and the slope of the ranked importance-value curve was steeper, for the top four ranked species than for the top four of secondary forests in dry and wet life zones (Fig. 20.1). *Spathodea campanulata*, an alien species, had the highest importance value in moist forest. Alien tree species constituted 6.3 to

Table 20.3 *Percentage of endemic and alien tree species, contribution of aliens to importance value, and number of species by size class in various forest types in Puerto Rico*

	Percentage of total number of species		Percentage of IV	Number of species			
Forest type	Endemic species	Alien species	Alien species	Seedlings	Saplings	Trees	Total
Urban forest	0	24.2	65.6	NA[a]	20	19	33
Young karst forest	6.3	22.5	43.6	137	82	70	160
Young moist forest	5.0	20.0	49.1	106	61	67	140
Reverted moist forest	0.3	22.6	52.5	20	13	15	31
Reverted wet forest	5.6	22.2	54.0	14	3	6	18
Young inactive shade coffee	0	27.3	22.9	14	12	9	22
Old inactive shade coffee	6.2	21.0	38.3	55	30	34	81
Oldest inactive shade coffee	0	19.0	18.4	30	13	20	42
Young wet forest	6.9	16.7	25.6	54	26	38	72
Mature karst forest	6.1	8.5	12.5	58	34	36	82
Dry forest	5.7	13.6	7.8	65	56	30	88
Mature moist forest	10.0	6.3	41.4	58	28	38	80
Mature wet forest	4.1	13.5	25.6	54	24	43	74
Lower montane wet forest	26.7	0	0	22	16	17	30
Upper montane wet forest	15.5	5.2	2.6	44	22	27	58

[a] Data are not available.

The listing of forest types is in decreasing level of anthropogenic disturbance. Data are for the year 2002. Importance value is IV.

22.6 per cent of the species pool in moist secondary forests but accounted for 41.4 to 52.5 per cent of the importance value (Table 20.3). In wet forests, the share of the importance value of alien species is also higher than their representation in the species pool. The slope of the ranked importance value curves for the top four species in dry and wet forests was relatively flat (Fig. 20.1).

In dry forests, alien tree species made up 13.6 percent of the species pool but their share of the importance value was smaller (Table 20.3). *Bursera simaruba* and *Andira inermis*, both native, were the most important dry-forest species, and both species show signs of regeneration. *Leucaena leucocephala*, however, dominates the sapling and seedling classes. Of the eighty-eight species found in dry forest, seventy-five were native. We found dry-forest endemic species *Psidium insulanum, Thouinia striata, Rondeletia inermis*, and *Tabebuia haemantha*, along with indications that the last three species are regenerating (Table 20.4). *Prosopis pallida, Pithecellobium dulce, Albizia lebbeck, Tamarindus indica, S. campanulata, Melicoccus bijugatus, Acacia farnesiana, Persea americana, Sterculia apetala, Crossopetalum rhacoma, Parkinsonia aculeata* and *Swietenia macrophylla* were the alien species found

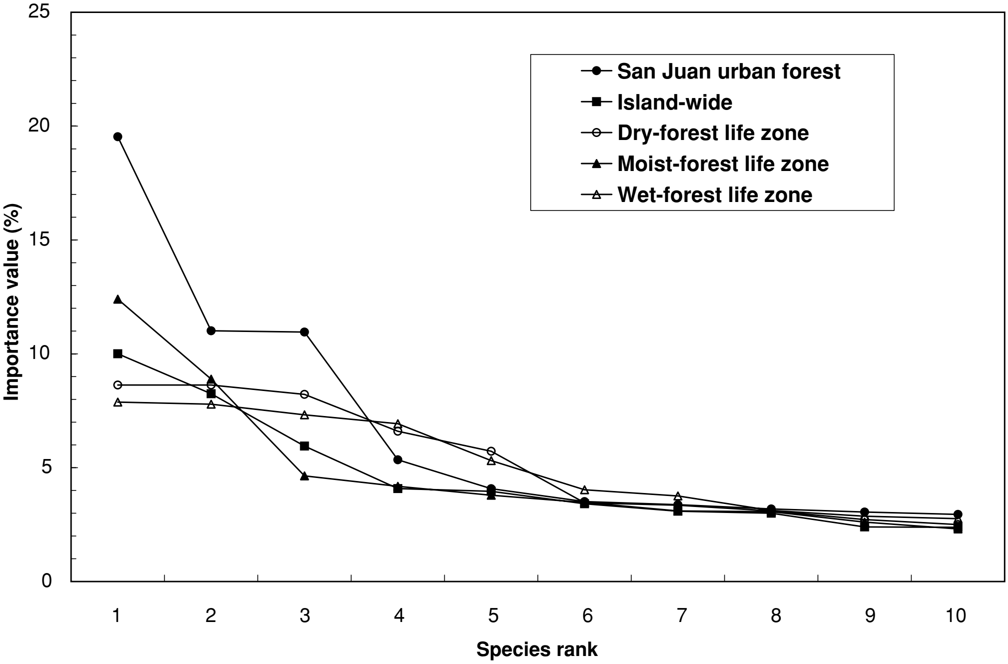

Figure 20.1 Ranked importance-value curves for secondary forests in three forest life zones, the urban forest, and an island-wide composite of secondary forests. All data are for 2002.

in dry forest, in their order of importance as an overstorey species. Most also showed sapling and seedling regeneration.

Lower and upper montane wet forests

What is most striking about the lower montane wet forests is the lack of alien species found (Table 20.3). In the upper montane wet forest, aliens make up a small proportion of the tree flora. *Syzygium jambos* and *S. campanulata* were minor components. We found *Spathodea jambos* regeneration, but not that of *S. campanulata*. Endemic tree species found in the montane forest include *Micropholis garciniifolia, Henriettea squamulosum, Cordia borinquensis, Croton poecilanthus, Hirtella rugosa, Byrsonima wadsworthii*, *Psychotria maleolens, Eugenia borinquensis, Ocotea moschata, Tetrazygia urbanii* and *Miconia pycnoneura*. These species made up 15.5 to 26.7 per cent of the tree flora, the highest values in the study (Table 20.3). Almost all of these endemic species also grew as seedlings (Table 20.4).

Karst forests

Spathodea campanulata dominates young secondary moist forest in the karst region. There were thirty-six alien species found in young karst stands (Table 20.3). The highest proportion of aliens occurred in the young karst forest.

Table 20.4 *Importance value of trees and saplings and relative density of seedlings of endemic species in various forest types throughout Puerto Rico*

Stand age/state	Species	Trees	Saplings	Seedlings
Shade-coffee forest				
	Thespesia grandiflora	1.37	0.51	
	Thouinia striata	1.38		1.38
	Wallenia pendula			1.38
	Antirhea obtusifolia	0.34		
	Cyathea portoricensis		0.51	
	Eupatorium portoricense			1.38
Dry forest				
	Psidium insulanum	3.99		
	Rondeletia inermis		0.21	0.56
	Tabebuia haemantha			0.19
	Thouinia striata		2.23	3.36
	Thouinia portoricensis		0.44	0.56
Moist forest				
Reversion	*Tabebuia haemantha*			4.82
Young	*Cordia borinquensis*	0.43	0.60	0.44
Young	*Gesneria pedunculosa*			0.30
Young	*Neea buxifolia*	0.22		
Young	*Tabebuia haemantha*	0.55	2.85	1.63
Young	*Thespesia grandiflora*	0.14		
Young	*Thouinia striata*		1.31	
Young	*Thouinia portoricensis*			0.07
Mature	*Byrsonima wadsworthii*	0.87		
Mature	*Cordia borinquensis*	0.70	2.20	0.68
Mature	*Miconia pachyphylla*		0.83	
Mature	*Sapium laurocerasus*	1.66		
Mature	*Tabebuia haemantha*			1.37
Mature	*Thespesia grandiflora*	0.89		
Mature	*Thouinia striata*	0.41		0.68
Mature	*Xylosma schwaneckeana*	0.86		
Karst forest				
Young	*Brunfelsia densifolia*	0.34		
Young	*Byrsonima wadsworthii*			0.05
Young	*Eupatorium portoricense*		0.11	
Young	*Gesneria pedunculosa*			2.22
Young	*Neea buxifolia*	0.27		
Young	*Psychotria maricaensis*		0.16	
Young	*Sapium laurocerasus*	0.41	0.40	0.05

(*cont.*)

Table 20.4 (*cont.*)

Stand age/state	Species	Trees	Saplings	Seedlings
Young	*Thespesia grandiflora*	0.13	0.12	
Young	*Thouinia striata*	2.34	3.00	2.26
Young	*Xylosma schwaneckeana*		0.10	
Mature	*Cordia borinquensis*	0.63	1.17	1.37
Mature	*Gesneria pedunculosa*			0.69
Mature	*Neea buxifolia*			3.44
Mature	*Rondeletia inermis*		0.84	0.69
Mature	*Thouinia striata*	1.58	1.73	0.34
Wet/rain forest				
Reversion	*Heterotrichum cymosum*			19.35
Young	*Henriettea squamulosum*		1.57	
Young	*Heterotrichum cymosum*			0.17
Young	*Hirtella rugosa*			0.34
Young	*Miconia foveolata*			0.34
Young	*Xylosma schwaneckeana*			0.17
Mature	*Cordia borinquensis*	2.38	1.24	0.56
Mature	*Cyathea portoricensis*			0.56
Mature	*Sapium laurocerasus*			0.56
Lower montane wet forest				
	Cordia borinquensis		5.07	1.69
	Croton poecilanthus	1.77	3.76	3.39
	Eugenia borinquensis	1.59		0.85
	Henriettea squamulosum	1.48	4.52	24.58
	Miconia pycnoneura		1.69	5.08
	Micropholis garciniifolia	5.29	12.13	7.63
	Psychotria maleolens			5.08
	Tetrazygia urbanii	0.71		
	Byrsonima wadsworthii		1.31	0.72
Upper montane wet forest				
	Cordia borinquensis	0.40	1.43	0.72
	Croton poecilanthus		3.43	1.08
	Eugenia borinquensis			0.72
	Henriettea squamulosum	1.24	1.49	1.80
	Hirtella rugosa		2.36	2.16
	Micropholis garciniifolia	1.87		
	Ocotea moschata			0.36
	Psychotria maleolens			7.19

Empty cells mean absence of the species.

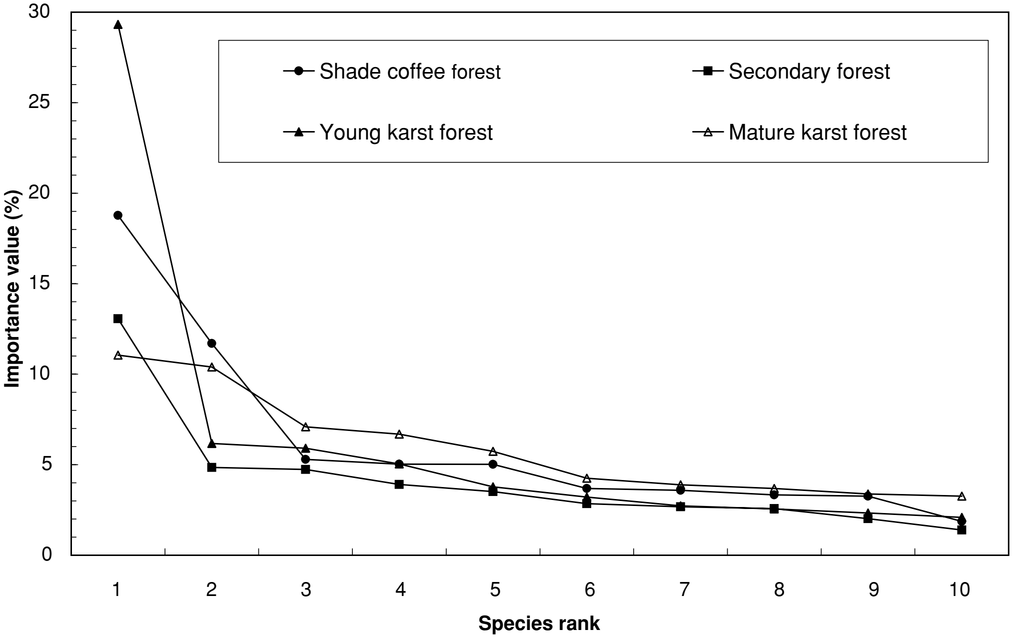

Figure 20.2 Ranked importance-value curves for shade coffee forest, secondary forest, young karst forest and mature karst forest. All data are for 2002.

Spathodea campanulata, Adenanthera pavonina, Senna siamea, A. procera and *Delonix regia* were relatively common alien canopy tree species also regenerating in young karst stands. However, there were 125 native species encountered, about half of which were found in the tree size class. Most of the native species also grew as saplings and almost all were found in the seedling class. The highest seedling, sapling and tree species counts in the study occurred in the young karst forest (Table 20.3). Compared to all forest types studied, this forest had the highest importance value for its top ranked species (Fig. 20.2). The second-ranked species had a low importance value compared with species ranked second in shade coffee and mature karst forest.

There were fewer plots measured in mature karst forest, which explains the fewer species found (82 total species in mature stands versus 161 species in young stands). However, there is still indication that alien species had a lower dominance in mature karst forest than they did in young karst forest (Table 20.3). *Spathodea campanulata* is much less important, less dominant, in mature stands. The native generalist species *G. guidonia* and *A. inermis* assume the dominant positions in the tree class, and the sapling class in the case of *G. guidonia*. Only seven alien species occurred in mature karst forest as compared with seventy-five native species found (Table 20.3). The slope of the ranked importance-value curve

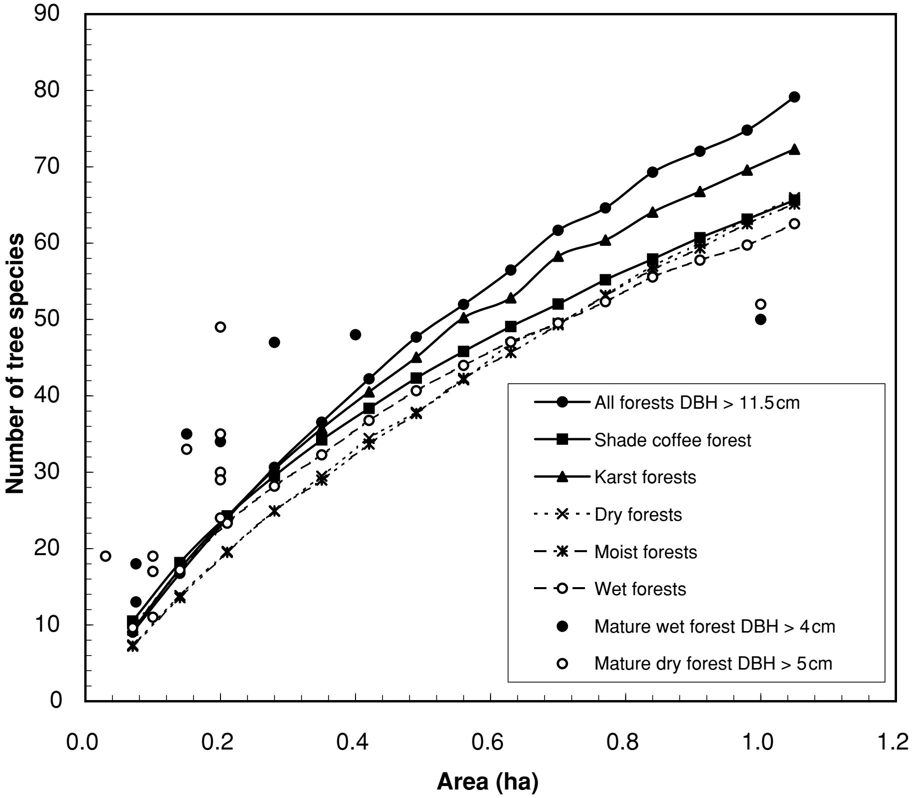

Figure 20.3 Species–area curves for five secondary forest types and for all forest inventory plots combined. Data are for 2002 and trees with diameters at breast height DBH > 11.5 cm. Individual points are for two types of undisturbed mature native forests in Puerto Rico (Lugo *et al.* 2002). Note the change in minimum diameter for these individual data points.

in mature karst was shallow indicating low dominance for the most important species (Fig. 20.2).

Shade-coffee forest

Guarea guidonia was the dominant species in shade coffee followed by *S. campanulata*. The importance value of these two species was responsible for the steep slope of the ranked importance-value curve for this forest type (Fig. 20.2). *Inga laurina* is a common sapling component that is only regenerating well in younger stands. *Inga vera* is also common, and minor, but more successful at regenerating in more mature stands. *Erythrina poeppigiana* is also widespread in shade-coffee and in some young moist and karst stands, but not as a sapling or seedlings. *Erythrina berteriana* is more successful at regenerating, but only in recently abandoned shade coffee.

Table 20.5 *Twenty-two-year trends in the number of species and the importance value of alien species in three forest types on Puerto Rico*

Parameter	1980	1990	2002
Shade-coffee forest			
Number of tree species	101	87	62
Alien species (% of total)	19.8	20.7	19.3
Importance value of alien species (%)	25.2	28.0	27.8
Secondary forest			
Number of tree species	207	215	223
Alien species (% of total)	13	13.5	19.7
Importance value of alien species (%)	20.3	19.3	28.1
Urban forest			
Number of tree species			33
Alien species (% of total)			21.0
Importance value of alien species (%)			53.5

Secondary forests include moist- and wet-forest life zones combined. Data for the urban forest in 2002 are for comparison. Empty cells mean absence of data.

Urban forest

The top-ranked three species of urban forests had higher importance values than the corresponding species in dry, moist, and wet forests (Fig. 20.1). Values are similar to those measured in the trees of shade coffee but lower value than those of young karst (Fig. 20.2). It appears that species richness is less in the urban forest than in other forested areas, but the sampling area has to increase before reaching such a conclusion. Alien species attain their highest importance and abundance in urban forests (Table 20.3). *Albizia procera*, an alien species, was the second-most important urban tree species that invades vacant barren and institutional lands with highly compacted soils.

Species–area curves

None of the five forest types in Fig. 20.3 saturated the species–area curve at the 1-ha level of sampling. Karst forests had the steepest curve and highest number of species at one hectare. Moist and dry forests had a slower rate of tree species accumulation in area sampled. Shade-coffee forest was initially intermediate between the extremes, but reached a similar number of tree species as moist and dry forests at the 1-ha sample. Wet forests started with a steep rate of species accumulation in area sampled but ended with the lowest number of species at the 1-ha sample.

Table 20.6 *Alien species found in mature stands of various forest types throughout Puerto Rico*

Species	Moist forest	Wet forest	Karst forest	Shade coffee forest	Trees	Saplings	Seedlings
Cananga odorata				1			1
Carapa guianensis	1				1		1
Ceratonia siliqua	1				1		1
Cordia oblique				1			1
Erythrina poeppigiana				1	1		
Eucalyptus robusta		1			1		
Ixora ferrea		1			1		
Mangifera indica		1	1		1		
Parkia biglandulosa		1					1
Pinus sp.				1			1
Spathodea campanulata	1	1	1	1	1	1	1
Syzygium jambos	1	1	1	1	1	1	1
Syzygium malaccense		1					1

1 means the species was found, empty cells mean it was not.

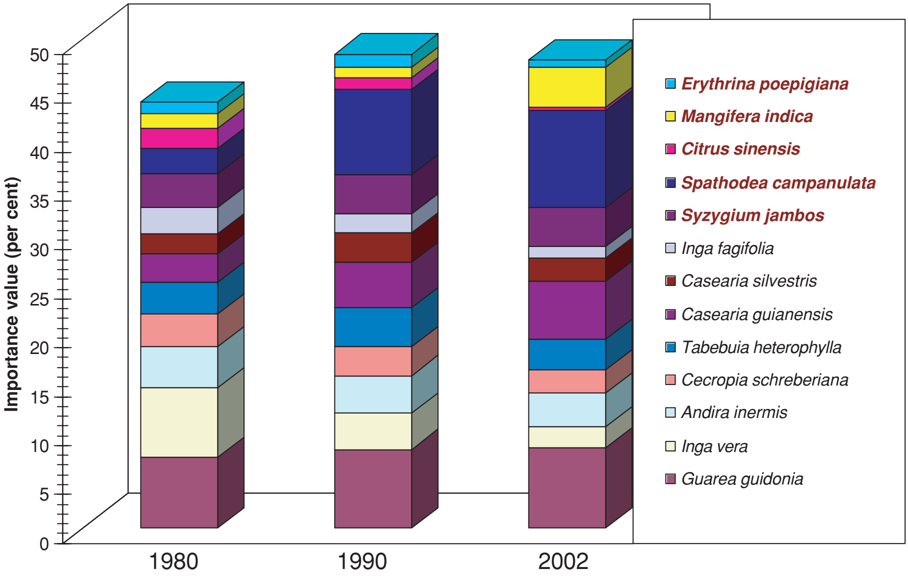

Figure 20.4 Temporal variation in the importance value of the dominant species in inventoried forests of Puerto Rico. The first five species on the top of the list are alien species.

Temporal change

Over the 22-year interval between the first and third forest inventory, the percentage of alien species remained relatively constant in shade coffee (about 20 per cent) but increased in all moist and wet secondary forests from 13 to 20 per cent (Table 20.5). These alien species accounted for 28 per cent of the importance value of forest stands, a slight increase from 1980 values. In shade coffee, *G. guidonia* had a large increase in importance value while *I. vera* decreased by 2002. In the secondary forest, *S. campanulata* increased its importance value.

The aggregation of all inventory data shows that alien species increased in their share of the importance value island-wide. However, when compared with urban forests, both the proportion of alien species in the tree flora and their share of the importance values were much lower than in the urban. The trend by species (Fig. 20.4) shows both increases and decreases of both native and alien species that appear more dependent on the history of land use. For example, the alien *Citrus sinensis* and the native *I. vera*, two species common in actively managed coffee shade, decreased, while the alien *Mangifera indica*, a favoured fruit tree, and the native *G. guidonia*, which thrives in abandoned shade-grown coffee and agricultural land, increased in importance value.