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Forest Ecology and Management 190 (2004) 145–161
Forest Ecology and Management
www.elsevier.com/locate/foreco

Emerging forests on abandoned land: Puerto Rico's new forests

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Received 8 June 2003; received in revised form 24 August 2003; accepted 24 September 2003

Abstract

The species composition of forests change continuously as the earth's biota evolves and adjusts to environmental change. Humans are accelerating the rate of species turnover by moving species around the planet and dramatically changing environmental conditions. Our focus is on new forests in Puerto Rico that emerge naturally on abandoned lands previously converted to agriculture and degraded. These forest stands have combinations of species that are new to the island's landscapes. New forests exhibit high species dominance during forest establishment, which includes dominance by alien tree species. These alien tree species establish and maintain forest cover, which may facilitate regeneration of native tree species. Landscape analysis and literature review revealed that these emerging stands are highly fragmented (60% were <1 ha in 1991), function as refugia for native organisms, and at 60–80 years old have similar species richness and structural features as native stands of similar age. However, the island's new forests exhibit important differences from mature native forests on unconverted forestlands. New forests have fewer endemic species and fewer large trees ($\geq$55 cm dbh) than mature native forests; they have higher soil bulk density and lower soil carbon and litter stocks; and they accumulate aboveground biomass, basal area, and soil carbon more slowly than native forests of similar age. We suggest that new forests will become increasingly prevalent in the biosphere in response to novel environmental conditions introduced to the planet by humans.
Published by Elsevier B.V.

Keywords: Puerto Rico's forest; Species turnover; Unconverted forestlands; Tropical forests; Succession; Degraded lands; Alien species

1. Introduction

The species composition of forest ecosystems changes continually as the earth's biota evolve and adjust to environmental changes. Over time, the cumulative result of this slow rate of change is the formation of a different community from the original one (Behrensmeyer et al., 1992).

Today, humans are accelerating the rate of this process by dramatically changing the conditions under which forests develop. In the tropics, deforestation, land cover change, and expansion of agricultural activities are examples of anthropogenic disturbances that are transforming the landscape and changing familiar forest ecosystems. Anthropogenic disturbances are responsible for a legacy of millions of hectares of abandoned landscapes with unfamiliar forest ecosystems (Grainger, 1988). Although there is significant scientific attention on the processes of change, ecologists have so far not focused as much attention on the forest ecosystems that are naturally emerging after abandonment of converted lands. Are these emerging forests different from those present before? If yes, how so and what are the ecological implications of the differences?

The Caribbean basin is an ideal region to assess the interplay between anthropogenic disturbance and

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0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2003.09.012

nature's response through emerging ecosystems. The region has a long history (millennia) of human activity and a high density of human population (>300 km^{-2}). Caribbean islands have experienced multiple cycles of deforestation and recovery of forests at landscape scales (Lugo et al., 1981), and it is possible to evaluate today's forests to assess anthropogenic effects.

In this paper, we (1) highlight landscape changes in Puerto Rico that have led to emerging forest formation and (2) review available literature on Puerto Rico's forest attributes to compare these emerging forests (defined below) with native ones, i.e., those forests on lands that have not been previously converted to agriculture or other non-forest land cover. Native tree species dominate native forests. When present, alien tree species comprise a very small fraction of the total importance value of native forests. Finally, we compare the changes taking place in Puerto Rico with those in New England where similar land use and land cover dynamics are in process, and discuss the implications of this case study for forest conservation. We do not address the species extinction issue, already summarized for Puerto Rico by Lugo (1988), nor the long-term evolution of landscape fragmentation discussed by Lugo (2002).

2. Methods

For the purposes of this paper, we differentiate between four types of forest succession in Puerto Rico (Fig. 1). Type I succession occurs after natural disturbances, e.g., hurricanes, in primary forests of the Luquillo Mountains. Type II occurs after natural disturbances in mature native secondary forests where the size of past clearings relative to the forest matrix is small. The native pioneer *Cecropia schreberiana* L. dominates the early stages of type I and type II succession in wet forests, and there are few if any alien species in the various forest seres (Smith, 1970). Alien species are those non-native species introduced to Puerto Rico by humans.

Type III succession occurs after abandonment of forestlands that have experienced the cycle of deforestation, agricultural use, and abandonment. The succession on these lands is a natural succession, but native pioneer species are uncommon. Alien species dominate the early stages of type III succession in the most extensive ecological zone in Puerto Rico. Alien species also dominate type IV succession, which occurs on lands that are in a state of arrested succession or are so degraded after human use, that trees must be planted to jump-start succession (Parrotta and Turnbull, 1997). Mature forest stands develop under all four types of succession. However, they can have different species composition, because they developed under different conditions, including different levels of propagule availability. We define mature stands as those whose rate of change of structural state variables approach steady state, irrespective of species composition. In this paper, we focus on type III succession. Appendix A contains a list of all forest types mentioned in this manuscript with notations of their origin and species dominance.

For the specific case of Puerto Rico, we use the term "emerging forest" to mean a forest that regenerates naturally on lands abandoned after deforestation and degradation, i.e., forests developed under succession types III and IV (Fig. 1). We will show that these emerging forests depend on alien species for their establishment, and we will refer to them as "new forests" because they exhibit species combinations that are new to the landscapes of the region. While the definition of new forests includes forests with intact canopies invaded by alien species, we focus on the post-agricultural new forests that develop through succession, because insufficient data are available to evaluate the changes that follow invasion of intact canopies of native forests by alien species.

We evaluated Puerto Rico's forested landscape by mapping forests and estimating the forest patch size distribution present in 1991. We used a Landsat Thematic Mapper image-derived vegetation map with 30 m resolution (Helmer et al., 2002). By forest, we mean a closed canopy woody vegetation stand $\geq$0.27 ha. We combined all upland and wetland forest classes from 1991 into a single forest class. We excluded the mixed class that largely contained active coffee and other agriculture but included the mixed class composed of active as well as abandoned shade coffee and secondary forest. A subsequent contiguity analysis (ERDAS, 1999), in which a connected neighboring pixel could include any of the eight pixels surrounding a focal pixel, yielded the sizes of forest patches. In summarizing the distribution of patch sizes, we included all patches $\geq$0.27 ha, or three pixels.

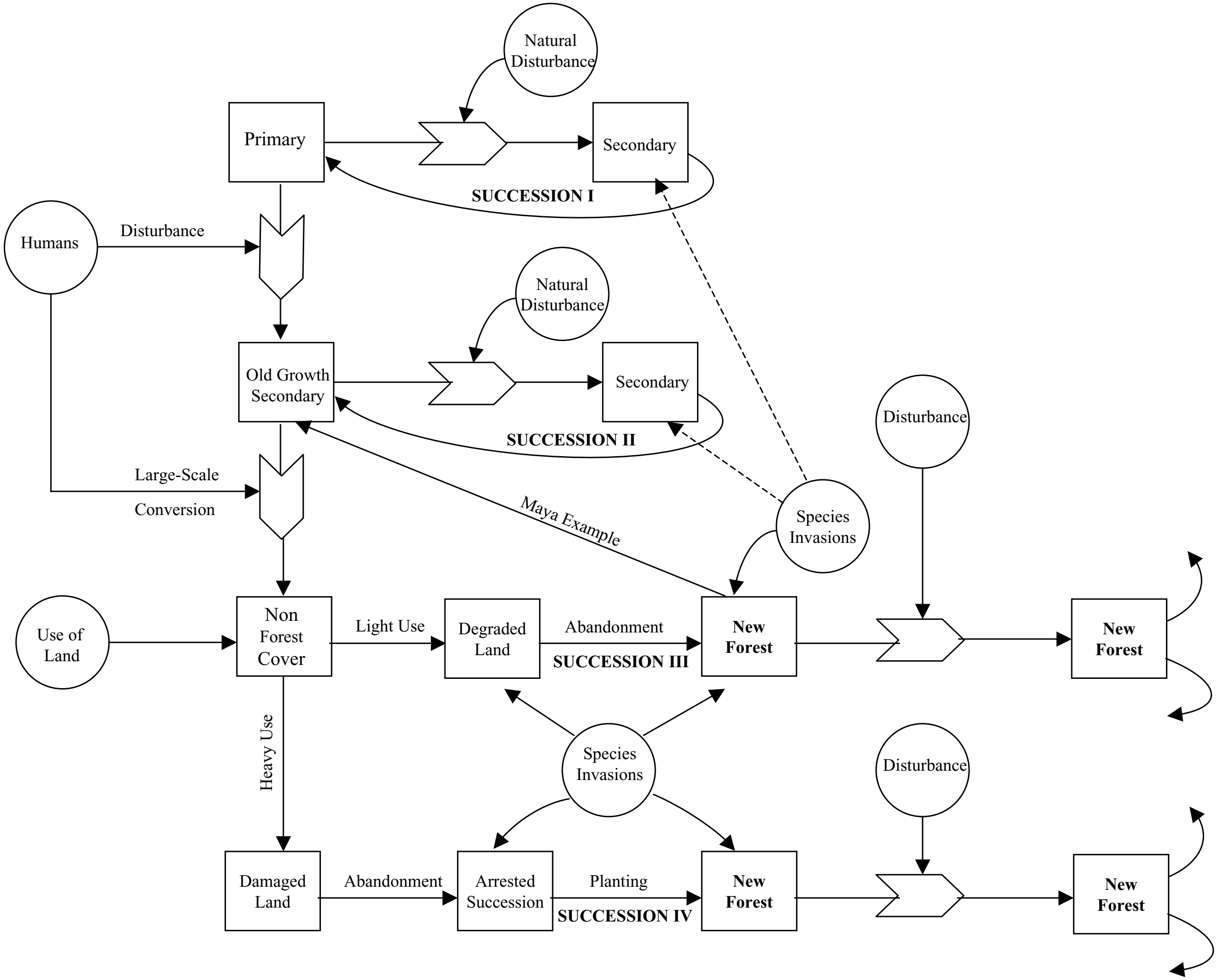

Fig. 1. Conceptual diagram showing four types of forest succession in Puerto Rico. Boxes are forest states, circles are external forcing functions, and lines represent the progression of succession or species invasions. Dotted lines represent low levels of species invasions. The arrow-shaped symbol identifies the interaction between external forces and changes in forest states. The future states of forests identified as new are not known, thus, the lines are not connected. The four succession types are described in the text.

We performed a similar contiguity analysis for urban lands after converting 1994 vector data from López et al. (2001) to a raster image with 30 m cell resolution. Urban lands are built-up lands with intensive use and mostly covered with structures. This analysis gave us the patch size distribution of urban or built-up land cover throughout Puerto Rico. The 3-year interval between the images used for forest (1991) and urban (1994) cover determinations should not significantly affect our conclusions about their interaction.

To assess the attributes of emerging forests, we summarized available literature on these stands and compared them with native stands. When making comparisons, we took the precaution of comparing stands in similar Holdridge life zones with similar topographic features and elevation. We focused our attention both on state variables (e.g., stand structure, tree species composition, soil organic matter, and loose litter stocks) and functional, or rate variables (i.e., the processes).

We obtained island-wide data on the structure and species composition of emerging forests from two forest inventories (Birdsey and Weaver, 1982; Franco et al., 1997). These inventories focused on commercial forestlands and excluded alluvial regions and dry forest life zones. They also excluded the highest mountains with excessive rainfall and slopes. These excluded forestlands have watershed value and usually contain the largest areas of mature native forests. Although not inventoried, our observations indicate that at these elevations the native tree fern *Cyathea arborea* (L.) J.E. Smith is an important pioneer in pastures reverting to forests. The location of plots was random within a grid laid over forest lands considered suitable for timber production. Plots were inventoried in 1980 and 1990 and their area was 0.07 ha. Measurements in 1990 included forested plots that in 1980 were non-forest. The inventories included three forest types that roughly represent a time sequence from the time of conversion to non-forest cover:

- Active shade coffee—a multistory, multi-crop system used principally for the production of coffee. An upper story of shade trees is characteristic.
- Abandoned shade coffee—secondary forests resulting from the abandonment of coffee production under shade trees.
- Secondary forest—forests resulting from the abandonment of cropland or pasture, and from the regeneration of previously cutover or disturbed stands. This forest type excludes abandoned shade coffee.

Secondary forest types included young (<10 years in 1980 and <20 years in 1990) and old (>20 years in 1980 and >30 years in 1990) stands. They also included *reverted* forest stands on lands on which agricultural use had ceased mostly from pasture, since the inventory conducted in 1980. All stands were recovering from past land use—mostly for agriculture because Puerto Rico was mostly an agricultural island during the first half of the 20th century (Roberts, 1942).

We summarized the following information from the inventory data: total number of tree species, including the number of native, alien, and endemic species; basal area, tree density, and volume by species and/or forest type; and species importance values. Importance value was the sum of relative density (percent of the stand's total density) and relative basal area (percent of the stand's total basal area) divided by 2 (Curtis and McIntosh, 1951). Minimum diameter at breast height (dbh) for larger trees was 12.5 and 2.5 cm for regenerating trees. We estimated basal area growth by the difference in basal area between 1990 and 1980 divided by the time interval. Birdsey and Weaver (1982) and Franco et al. (1997) contain detailed methodology for the tree inventory as well as the statistical analysis. The botanical authority for scientific names was from Little et al. (1974) and Francis and Liogier (1991).

Weaver et al. (1987) collected soil to a depth of 23 cm and standing litter in 129 inventory locations in 1980. Sampling included all forest types included in the tree inventory of Birdsey and Weaver (1982). Laboratory analysis of these soil and litter samples included soil bulk density, soil organic matter, and litter standing stock. Weaver et al. (1987) contains the detailed methodology used in the analyses as well as the statistical analysis.

3. Results and discussion

3.1. A landscape of fragmented forests: the consequence of human activity in Puerto Rico

The high-resolution map of Puerto Rico's forests shows few areas of continuous forest cover and a predominance of forest patches surrounded by either urban or other land cover (Fig. 2). The number of forest fragments $\geq$0.27 ha in 1991 was about 24,000 (Fig. 3). Sixty-four percent of these fragments were smaller than 1 ha. Scattered among these forest patches are urbanized areas, which in 1994 covered 14.4% of Puerto Rico (López et al., 2001) and reflect an island-wide population density of 450 people $\cdot$ km^{-2}. We counted 9000 urban fragments, 84% of which were <10 ha (Fig. 3). Such a high level of urban and forest fragmentation indicates that human influences on Puerto Rico's forests are dispersed throughout the island.

3.2. *Emerging forest stands*

3.2.1. *Forest structure*

For the area covered by the forest inventories, wood volume, tree density, and basal area increased between 1980 and 1990 (Table 1). These patterns of structural change are typical of forest succession. As a forest stand matures, basal area and tree volume increase. Increased tree density and number of species reflect the expanding area of regenerating forests in abandoned agricultural fields.

For forests of known past land use, basal area, tree density, and species richness were lower in active shade coffee than in abandoned shade coffee or secondary forests (Table 2). Tree density decreased in all three forest types between 1980 and 1990, reflecting stand thinning with age. The highest tree density was in secondary forests. Basal area peaked in abandoned shade coffee as compared with active shade coffee and secondary forests, and it increased in all forest types between 1980 and 1990. Basal area also increased from reverted lands (8.3 m^2/ha) to young (<30 years) secondary forests (14.6 m^2/ha) and older (>30 years) ones (22.6 m^2/ha) (Chinea and Helmer, 2003).

3.2.2. *Large trees*

Forest stands that reverted from agriculture between 1980 and 1990 had 0.2% of their stems with diameters $\geq$55 cm—the largest size class distinguished during the inventory (Franco et al., 1997). In active shade coffee, the percentage of this size class was 1.2%, followed by 0.4 and 0.1% in abandoned shade coffee and secondary forests. This size class reaches 1.2% of the stems in mature native forests in the same life zone (Briscoe and Wadsworth, 1970). Active shade coffee has a low tree density (Table 2) and old shade trees that are remnants of past land uses. For this reason, active shade coffee has a similar percentage of large trees as the mature native forests.

3.2.3. *Species composition*

3.2.3.1. Species richness. The number of tree species increased from active to abandoned shade coffee (Table 2). The number of tree species decreased between 1980 and 1990 in active and abandoned shade coffee, but increased in secondary forests. This increase was due to an increase in species richness of secondary forest stands older than 10 years. Reverted forests exhibited similar species richness as active shade coffee (5.5 species per plot in reverted vs. 5.7 species per plot in active shade coffee; Chinea and Helmer, 2003). However, the species richness of secondary forest (minus reverted forests) was higher than that of the other forest types (11.8 and 14.3 species per plot for young, and older secondary forests, respectively; Chinea and Helmer, 2003). Alien tree species composed a large fraction of forest stands of all types (Table 2), but decreased in importance as the total number of species increased and as forests matured from active shade coffee to secondary forest.

3.2.3.2. The contribution of alien species. The eight most abundant tree species in the two inventories were the same, although their ranking varied somewhat: *Spathodea campanulata* Beauv.*, *Guarea guidonia* (L.) Sleumer, *Inga vera* Willd, *C. schreberiana*, *Andira inermis* (W. Wright) H.B.K., *Tabebuia heterophylla* (DC.) Britton, *Syzygium jambos* (L.) Alst.*, and *Inga fagifolia* (L.) Willd (alien species with asterisk). Birdsey and Weaver (1982) noted that humans commercially used 9 of the 10 most abundant species in the island-wide inventory. Stand management has favored tree species that have commercial value. Consistent with this finding are research results that show that previous land use has a significant effect on present forest structure and species composition (García Montiel and Scatena, 1994; Zimmerman et al., 1995; Foster et al., 1999; Molina Colón, 1998; Chinea, 2002; Thompson et al., 2002).

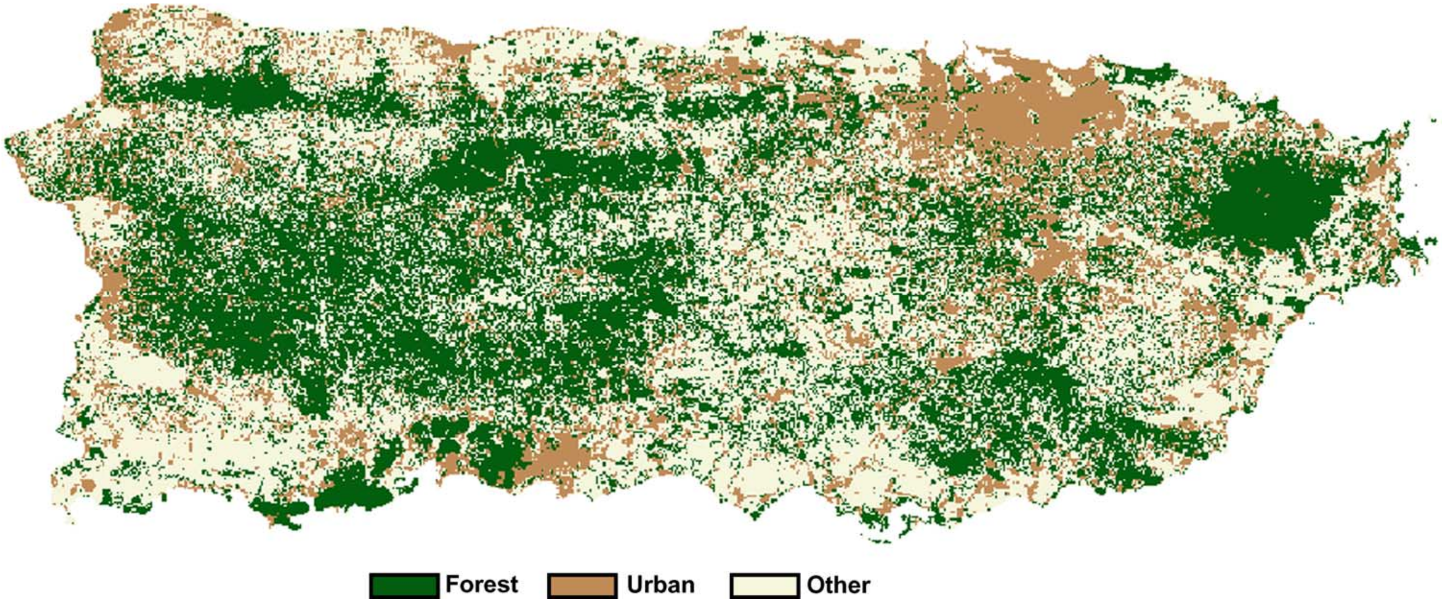

Fig. 2. Map of forest and urban fragments in Puerto Rico. Forest fragments are from Helmer et al. (2002) and correspond to 1991. Urban fragments are from López et al. (2001) and correspond to 1995.

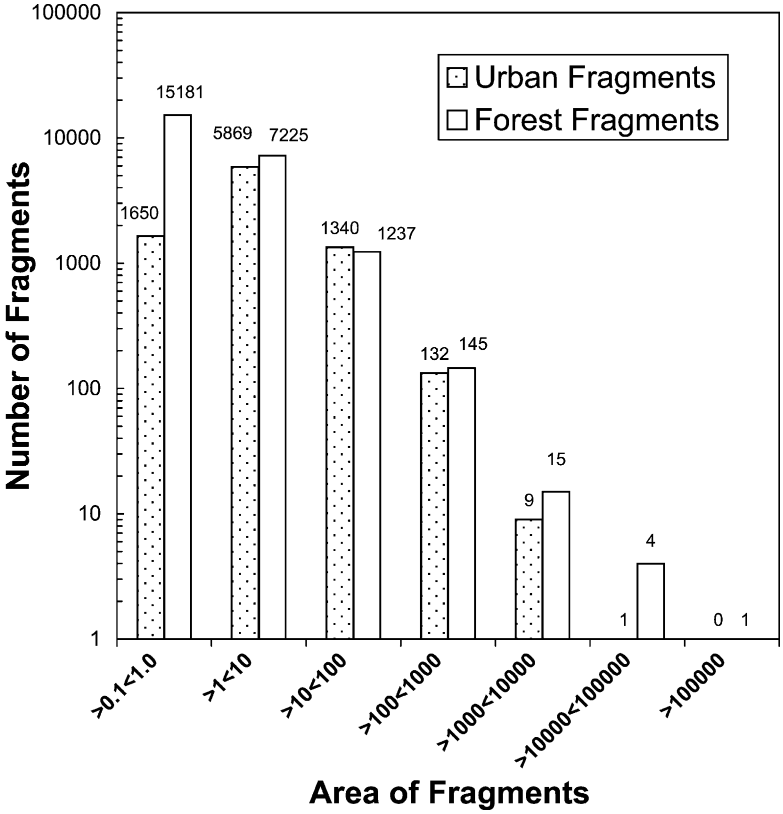

Fig. 3. Frequency histograms of forest and urban fragments by area of patch in Puerto Rico. Urban areas are from López et al. (2001) and forest areas are from Helmer et al. (2002). The numbers over the bars are the number of fragments of the area represented by the particular bar. Note the logarithmic scale.

The percentage of a stand's density or basal area attributed to alien species was higher than expected from the percent of the total number of species classified as alien (Table 2). For example, in 1980, alien species accounted for 11.7 and 10.7% of the density and basal area of secondary forests, but only 2.3% of the total number of species. Alien species accounted for a higher fraction of the density and basal area in active shade coffee than in the other two forest types. The contribution of coffee trees to these data was negligible. The percentage of a stand's tree density and basal area contributed by alien species decreased from active shade coffee to secondary forests. It is possible that with the passing of time, the influence of alien species decreases due to the regeneration of native species in these stands

Table 1
Change in the properties of emerging forest stands in Puerto Rico between 1980 and 1990[a]

Parameter and unit of measure	1980	1990
Area of new forests (ha)[b]	118800	143932
Density of trees (trees/ha)	1985	2086
Basal area (m^2/ha)	12.0	14.8
Timber volume (m^3/ha)	42.1	77.7
Number of tree species[c]	189	209

[a] Inventories covered 130,500 and 148,100 ha of forest lands considered suitable for timber production in 1980 and 1990, respectively (Birdsey and Weaver, 1982; Franco et al., 1997). Data are for trees with dbh $\geq$5 cm.

[b] Active and abandoned shade coffee, forest reverted from croplands, and young and old secondary forest. Excludes non-stocked areas.

[c] Correspond to all inventoried forests in Puerto Rico.

Table 2
Species richness, tree density, and basal area and percent of each that corresponds to alien tree species for trees with dbh >5 cm in emerging forest stands in Puerto Rico (data from Birdsey and Weaver, 1982; Franco et al., 1997)[a]

Year	Active shade coffee		Abandoned shade coffee		Secondary forests[b]		All forests	
	Total	% alien	Total	% alien	Total	% alien	Total	% alien
Number of Species								
Stand								
1980	44	20.0	81	7.4	172	2.3	189	4.7
1990	25	32.0	71	9.9	187	3.2	209	5.7
Common species								
1980	20	45.0	20	30.0	25	16.0	48	18.8
1990	25	32.0	30	20.0	65	18.5	65	18.5
Tree density (trees/ha)								
Stand								
1980	1393	65.3	1728	23.0	2752	11.7	1985	21.8
1990	942	30.8	1694	33.9	2248	13.0	2086	21.1
Common species								
1980	1249	72.9	1214	32.7	1479	21.8	1457	29.7
1990	942	30.8	1193	48.2	1372	21.3	1750	25.2
Basal area (m^2/ha)								
Stand								
1980	10.2	22.4	14.0	18.8	13.8	10.7	12.0	16.8
1990	12.5	35.4	16.1	16.9	15.1	20.6	14.8	23.5
Common species								
1980	9.4	24.4	11.8	22.3	8.4	17.5	10.2	19.9
1990	12.5	35.4	14.9	21.6	10.7	29.0	13.5	25.8

[a] Common species are those for which the authors report basal area and density data.

[b] Secondary forests include forests reverted from agriculture since 1980 plus secondary forests >10 years old.

(Wadsworth and Birdsey, 1985). However, long-term time series data are needed on the same plots to verify this trend.

3.2.3.3. Endemic species. The percentage of endemic species in the 1980 and 1990 forest inventories of trees with dbh >12.5 cm was 6.5 and 4.6, respectively (Birdsey and Weaver, 1982; Franco et al., 1997). Both inventories found the same three endemic species (*Roystonea borinquena* O.F. Cook, *Thouinia striata* Radlk., and *Montezuma speciossima* Sessé & Moc.), but because the 1990 inventory reported more species, the percent of endemics declined. Molina Colón (1998) found that 5.8 and 6.5% of the species of plants and trees (respectively) of emerging forests in the dry limestone region of Guánica were endemic. For Puerto Rico's flora as a whole, the percent of endemic plant species is 9.9, whereas for trees (including aliens) it is 19.6 (). These comparisons suggest that endemic species representation in emerging forests is below average when compared with native forests island-wide.

3.2.4. Ranked species importance value curves

The ranked species importance value curves by forest type (Fig. 4) resulted in two patterns. First, the slope of the curves was steeper for active shade coffee, followed by abandoned shade coffee, and lastly by secondary forests. The slope for the ranked importance value curves of secondary forests was relatively shallow. The second pattern was that the importance value of the top ranked species decreased with forest type along the same gradient: active coffee shade, abandoned coffee shade, and secondary forest. The difference in importance value between

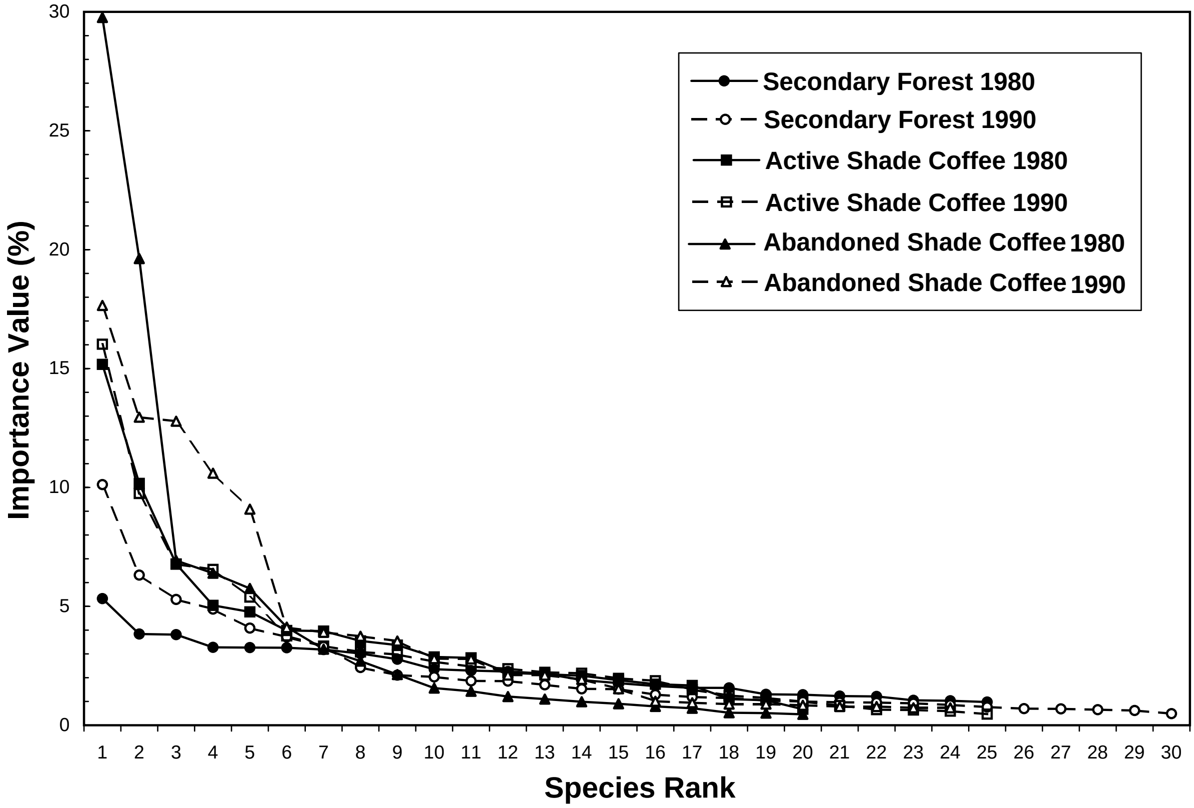

Fig. 4. Importance value of dominant species in emerging forest stands in Puerto Rico. Data include changes over time and with land use intensity based on island-wide forest inventories (Birdsey and Weaver, 1982; Franco et al., 1997). The year in the legend corresponds to the date of measurement. The date of abandonment of coffee shade production is unknown.

the top ranked species and species in the tail of the ranking is much greater in active and abandoned shade coffee than in secondary forests. In short, a small percentage of the species exert high dominance over stands. However, during the 10-year interval between inventories, forests on each of the three categories, exhibited a reduction in the importance value of the top ranked species. The slope of the ranked species importance value curves decreased. This suggests that the enrichment of species at these sites results in a lower degree of dominance and a redistribution of space and resources among species.

3.2.5. *Persistence of alien species*

We analyzed the importance value of all species recorded during the 1980 and 1990 island-wide inventories (Birdsey and Weaver, 1982; Franco et al., 1997) and found the following. (1) The identity of species did not change among the top 20 ranked species in terms of importance values. Only *Cupania americana* L., which ranked 20th in importance value in 1990, was not among the top 20 species in 1980. (2) Some species exhibited wide fluctuations in importance value, both increases and decreases. *S. campanulata*, an alien species, emerged as the species with the highest importance value in 1990 from a ranking of 8th in 1980. This dramatic increase was probably due to the presence of this species in pastures that reverted to forest between 1980 and 1990 Chinea and Helmer (2003). (3) Forty-five percent of the top 11 tree species were alien, and they remained among the most important in spite of the larger number of species recorded

Table 3
Percent of alien species in species counts in Puerto Rico (PR)

Type of count	Area sampled[a] (ha)	Alien species	Source
Trees of Puerto Rico	Island-wide	27	Little et al. (1974), Francis and Liogier (1991)
Secondary forests of PR[b]	113600		Chinea and Helmer (2003)
Reversion		26	
Young secondary		15	
Secondary		15	
Abandoned shade coffee in PR	23400	21	Chinea and Helmer (2003)
Active shade coffee in PR	7000	33	Chinea and Helmer (2003)
Top 11 species in secondary forests of PR	113600	45	Birdsey and Weaver (1982), Franco et al. (1997)
Abandoned Baseball Park[c] in a dry forest, Guánica, PR	0.2	36	Molina Colón (1998)
Abandoned farmlands[c] in a dry forest, Guánica, PR	0.2	27	Molina Colón (1998)
Abandoned houses[c] in a dry forest, Guánica, PR	0.2	55	Molina Colón (1998)
Abandoned charcoal pits[c] in a dry forest, Guánica, PR	0.2	2	Molina Colón (1998)

[a] From Franco et al. (1997) and Molina Colón (1998).
[b] Averages on a per plot basis.
[c] After 45 years of abandonment.

in 1990. In fact, alien species constitute a substantial proportion of the flora of Puerto Rico (Table 3).

These results suggest that either the alien species persist as emerging forests age, or continued disturbances maintain their dominance. A combination of both explanations is more likely. From these data, we conclude that the emerging forests of Puerto Rico are new forests because their species composition and dominance relationships are different from those of native forests. The high importance value and persistence of alien tree species in these forests is the main reason why these forest stands are new forests. Obviously native forests evolved isolated from these alien species, which now dominate the emerging landscapes that result from human activities.

3.2.6. The forest floor and soil

We observed poor development of the interface between the mineral soil, the humus layer, and the litter layer of new forests. The interface is abrupt and lacks the rich organic matter horizon that is typical of mature native forest. In 1980, Weaver et al. (1987) studied the same stands in Birdsey and Weaver (1982) and found higher bulk densities in younger forests than in older ones. They found an average bulk density of 0.95 g/cm^3 in new forest stands (by our definition) in the wet forest life zone. However, in mature native wet forests, Lugo and Scatena (1995) found over 80% of the samples with a bulk density of between 0.2 and 0.85 g/cm^3, which is lower than the value reported by Weaver et al. (1987) for new forests. These differences are due to soil compaction while the site was in use by humans. We do not know how much time is required to reverse this soil compaction.

Weaver et al. (1987) also reported litter stocks in new forests of 4–6 Mg/ha. In comparison, litter stocks in mature native forests are higher, reaching as much as 35 Mg/ha, and 70% of the samples had >6 Mg/ha (Lugo and Scatena, 1995). Similarly, Weaver et al. (1987) found that soil organic matter in new forests averaged between 3 and 4% in inventoried stands, while mature native forests in the Luquillo Mountains contain between 5 and 7% organic matter in the A horizon (Lugo, 1992), and 8 and 47% in the top 15 cm (Odum, 1970). Silver et al. (2000) demonstrated depleted soil carbon pools in new forests on former agricultural land, and slow but steady recovery of pools after abandonment. The soil organic matter content of four types of new forests in the wet life zone increased with time after abandonment from 6 to 10 kg/ha to 23 cm soil depth (Weaver et al., 1987).

3.2.7. Forest function

As they age, new forests exhibit fast turnover rates of species (Aide et al., 1996) and are carbon sinks (Silver et al., 2000). Silver et al. (2000) found that new forests exhibited a net carbon sink in both aboveground and soil compartments over periods of 80–100 years after abandonment of agricultural activity. All secondary forests share the carbon-sink capability found in new forests (Brown and Lugo, 1990). However, a major difference between new forests and native ones is the velocity of processes. Rates vary depending on the process. Silver et al. (2000) showed that aboveground biomass production and soil carbon accumulation in new forests on abandoned land was a function of past land use. Biomass production was fastest on abandoned agricultural land, slower in abandoned pastures, and slowest in cleared land with arrested succession. All of these rates are slower, however, than those measured rates in native forest successions (Aide et al., 1995; Silver et al., 2000). In contrast, Molina Colón (1998) found that litterfall rates were not significantly different in new vs. mature native forests in the Guánica limestone region.

The rate of tree basal area growth per unit area between the 1980 and 1990 by forest type (estimated from data in Table 2) was higher for dominant species in active and abandoned shade coffee (0.31 m^2 ha^{-1} per year) and lowest in secondary forests (0.23 m^2 ha^{-1} per year). These values are low compared to those of mature native forests in the Luquillo Mountains, which range between 1 and 2 m^2 ha^{-1} per year (Lugo, 1992; Fu et al., 1996).

No data were available to evaluate if new forests can, or will eventually, function effectively as habitat for species that depend on old-growth forest structural characteristics. Some evidence indicates that native forest fragments without a history of clearing can support wildlife species that, thus far, post-agricultural forests do not (Glor et al., 2001). Nevertheless, the ecological importance of shade coffee and other types of new forests for sustaining populations of arthropods, birds, lizards, and other vertebrates was documented for Puerto Rico (Torres, 1984; Wunderle and Latta, 2000; Wunderle and Waide, 1993; Carlo Joglar, 1999; Genet, 1999a,b).

3.3. Is Puerto Rico's experience with new forests unique?

The results of this study established several defining characteristics for Puerto Rico's new forests. First, they have novel species composition due to the establishment of alien species in the forest canopy. The complement of endemic species is small in new forests in comparison to native forests. The new forests are typically young, originate in a highly fragmented landscape, are structurally simple (low basal area and low species richness) and contain few large trees. Soil organic matter is low and bulk density is high. While processes of soil organic matter and above ground biomass accumulation are slow in comparison with those of native forests, the new forest is dynamic and exhibits high turnover of species. With time, native species regenerate in these forests, species richness increases, and the presence and high dominance of alien species declines. However, alien species prevail in the mature phases of forest development. In terms of overall stand physiognomy and canopy structure, new forests are similar to native secondary forests.

The formation of novel forest ecosystems is not unique to Puerto Rico. New forest ecosystems appeared naturally everywhere in geological time (Behrensmeyer et al., 1992) and anywhere today due to human activity (e.g., Moravcík, 1994). Unfortunately, landscape-level analysis such as is available for Puerto Rico is not readily available for other tropical countries. However, the landscape changes that occurred in Puerto Rico closely parallel those documented for New England, USA (Fig. 1 in Foster and Motzkin, 1998; Fig. 4 in Foster et al., 1998; Foster, 2002).

The changes in land use and land cover in New England had significant effects on forests, including the following:

- Anthropogenic forces became the primary factors determining forest community composition while climate variation became less important as a correlate of vegetation composition and distribution (Foster et al., 1998; Fuller et al., 1998).
- The tree species present are the same today as in pre-colonial time, but species' abundances and

distributions changed significantly (Table 4 in Foster et al., 1998; Fuller et al., 1998; Cogbill et al., 2002; Hall et al., 2002).

- The species combinations of today's forests differ from those in colonial forests (Foster et al., 1997), reflecting a landscape undergoing continuous human disturbance (Foster, 1992; Foster et al., 1998).
- The types of forest wildlife species changed along with land cover and land use (Fig. 4 in Foster and Motzkin, 1998).
- There is no evidence to show that forest composition is returning to pre-colonial conditions (Foster and Motzkin, 1998; Fuller et al., 1998).

A major difference between New England and Puerto Rico is that alien tree species are not as predominant in New England's new forests as they are in Puerto Rico. The aliens that invade New England new forests include pests, pathogens, and herbaceous plants (Bellemare et al., 2002; Orwig, 2002). Alien species in New England have not invaded the canopy of its forests. The tree species present before anthropogenic disturbance still grow on today's landscape after human abandonment of past land uses. They form new forests because their distribution, relative importance, and dominance changed after forestlands were converted to agriculture and abandoned.

In Puerto Rico, human activity is intense, pervasive, and fragments natural habitats (Figs. 1 and 2). Consequently, alien species find suitable niches in the landscape, dominate under certain conditions, and remain as components of mature forest stands (Tables 2 and 3; Aide et al., 1995, 1996, 2000; Marcano Vega et al., 2002; Molina Colón, 1998). Puerto Rico's new forests contain a different group of species than the original, and they experience changes in species importance values over time (Fig. 4). As in New England, there is no evidence that these forests reestablish their original species composition and importance values after 60–80 years of succession (Aide et al., 1996). Despite compositional differences, 30–45 years after abandonment of human activity, the density, basal area, species number, and species diversity of new forests is not distinguishable from those of native undisturbed forests nearby (Fig. 2 in Aide et al., 1996; Fig. 3 in Aide et al., 2000; Fig. 2 in Marcano Vega et al., 2002; Molina Colón, 1998). These new forests also approach steady state values in aboveground biomass and soil carbon (Silver et al., 2000).

If species composition fails to return to original conditions after almost a century, are they likely to return in the future? The regeneration of the aliens *S. jambos* in native wet forests (Smith, 1970), and *Swietenia mahagony* (L.) Jacq. in native dry forests (Molina Colón, 1998), is a harbinger of irreversible change in species composition due to human activity in Puerto Rico. However, of greater weight is the argument of increased anthropogenic disturbance in the future. The predictions of Gómez-Pompa and Vázquez-Yanes (1974), that it would take millennia for original species composition to return in disturbed sites, might be correct with the caveat: that significant disturbances do not interrupt forest growth and development. In such scenarios, shade tolerant species with large seeds might eventually recolonize forests. However, continuous disturbances, such as those expected of a fragmented forest landscape (Fig. 2), preclude any possibility of stands having sufficient time to return to pre-Colombian conditions.

The Mayan forest described by Gómez-Pompa and Bainbridge (1995) is a dramatic example of how humans promote the formation of new tropical forests without apparently reducing their structural complexity or altering their functioning. The Maya either introduced species or altered their distribution to suit their needs. They favored *Brosimum alicastrum* Swartz, *Manilkara* sp., *Calocarpum* sp., *Cordia* sp., and *Sabal* sp. and created favorable conditions for *Swietenia macrophylla* G. King (Lamb, 1966). These species formed new forests throughout Central America that today many consider primary, when in fact they are products of human activity.

3.4. Implications for forest conservation

Formation of the new forest ecosystems described or mentioned here occurred through natural interactions between species. Human intervention was limited to favoring certain species and creating conditions suitable for species invasion. Natural processes were responsible for most of the seed dispersal, species sorting, and tree growth that permitted establishment and growth of alien species. At least six implications for forest conservation emerge from the Puerto Rico case study. These supplement rather than substitute for conservation efforts designed to reduce the spread of alien species, establish reserves for preserving genetic material, and mitigate negative consequences from invasive species, which cannot be ignored. However, in our study we found no evidence of chronic invasiveness among the alien species that we studied. While they could invade abandoned sites in high numbers, the species that we studied eventually stabilized at low numbers in mature forests.

1. *Environmental change is inevitable*. Most ecologists recognize the importance of disturbances to ecosystem structuring and function (Sousa, 1984). Biota appear to have evolved in the context of environmental change, either gradual or punctuated (Behrensmeyer et al., 1992). Change in the conditions that regulate ecosystems leads to change in species composition and new ecosystems. As humans become the predominant force of change in the world, species composition will naturally change in response to the new anthropogenic forces. Opportunities exist to take advantage of new forest attributes or coax them to develop and sustain ecosystem functions and species that we value. Research could focus on management strategies that are economically viable for increasing new forest functionality, resilience, and contribution to landscape sustainability. Valuable combinations of species, for example, might result in new forests that (a) develop old-growth structural and functional characteristics or (b) are richer in native species.
2. *Alien species have a role*. Species have always dispersed across biogeographic regions but anthropogenic change is different from most natural change in its rapidity, unpredictability of actions, abruptness, and duration. Humans create novel conditions under which many native species cannot grow, and alien species—assuming we seek tree cover—can contribute to forest reestablishment on degraded lands. The lesson from Puerto Rico is not to dismiss alien tree species a priori, because they played an important role in reversing forest fragmentation and deforestation (Lugo, 2002) without yet causing extinction of the island biota (Lugo, 1988).
3. *The importance of self-organization*. Self-organization is a natural mechanism for sorting species according to their functioning in ecosystems and reaching homeostasis at community and landscape scales (Odum, 1989). Allowing species sorting may increase chances for developing stable new forests. Learning to guide the species sorting might be an ecologically sound strategy for managing forests—much as the Maya did in Central America (Gómez-Pompa and Bainbridge, 1995).
4. *There is a time lag to recovery of degraded lands*. In spite of the impressive establishment of new forests on Puerto Rico's degraded lands, a long time must pass before stand conditions approach those of primary forests. After 60–80 years of growth, new forests lag behind primary forests in endemic species, large trees, and soil structure. We still do not know how long the time lag will last; mature new forests could reflect the level of complexity that is possible in degraded lands. However, if restoring old-growth characteristics and composition of primary forests requires >100 years, we know that the path to those stands may be through these new forests. Such a path may be the inevitable requirement of repairing degraded lands.
5. *Small forest fragments have ecological value*. Turner and Corlett (1996) recognized the value of small mature forest fragments (<100 ha). In Puerto Rico, even smaller forest fragments (<1 ha) predominate on the landscape ranging across a wide spectrum of ages (from <10 to >100 years). They support well-structured forest communities with a high density of tree and animal species. Small forest fragments are seed sources for regenerating forests on deforested lands (Helmer, 2000). These small forest patches are critical for reversing landscape fragmentation and deforestation.
6. *New forests provide lessons for coping with global change*. If natural processes result in new forest ecosystems that are structured and

> function in ways similar to native forests in spite of altered species composition, we can learn a lesson from that experience. By focusing on the functioning of forests, we can nudge succession in directions that are adaptive to conditions in the Homogeocene. Without losing momentum towards the goal of preservation of all species, we can take advantage of self-organization to design new ecosystems that are useful to humans.

The recombination of species to form new ecosystems that can function in human-altered environments suggests that restoring "old ecosystems" is very difficult. Old ecosystems are those with species combinations that function in the environments of the past. The recurrence of past environments that allow reestablishment of past species combinations is unlikely. This view does not preclude the preservation of primary forests. These systems are coping with current conditions, and their preservation is imperative. However, preserving primary forests and primary forest patches do not preclude learning how to manage new forests and landscapes so that they will sustain ecosystem functions.

Acknowledgements

This study is in collaboration with the University of Puerto Rico (UPR). It is part of the USDA Forest Service contribution to the National Science Foundation Long-term Ecological Research Program at the Luquillo Experimental Forest (Grant BSR-8811902 to the Institute for Tropical Ecosystem Studies of the UPR and the International Institute of Tropical Forestry, USDA Forest Service); and the NASA-IRA Grant NAG8-1709, under UPR subcontract 00-CO-11120105-011. We thank H. Nunci, G. Reyes, G. Sánchez, and M. Alayón for their help in the production of the manuscript. We also thank N. Brokaw, S. Brown, B. Bryan, J.D. Chinea, C. Domínguez Cristóbal, J.J. Ewel, G. González, E. Medina, R. Ostertag, F.E. Putz, F.N. Scatena, J.M. Wunderle, and nine anonymous reviewers for their reviews of the manuscript.

Appendix A

Checklist of forest types used in this manuscript in relation to type of succession (Fig. 1).

Type of succession and forests	Origin of stands in this study	Abundance of native species	Abundance of alien species
Type I: *Dacryodes excelsa* Vahl. Primary forest	By natural events	Dominate succession	None
Type II: *D. excelsa* old secondary and dry forest old secondary	By light logging and thinning for charcoal	Dominate succession	Only *Zyzygium jambos* at low density and *S. mahagony* in the dry forest
Type III: active shade coffee	A multistory, multi-crop system used principally for the production of coffee. An upper story of shade trees is characteristic	Few species in the overstory	Predominate
Abandoned shade coffee	Secondary forests resulting from the abandonment of coffee production under shade trees	Increase number relative to active shade coffee	Predominate
Secondary forest	Forests resulting from the abandonment of cropland or pasture, and from the regeneration of previously cutover or disturbed stands. Excludes abandoned shade coffee	Many species	Still important
Young secondary forest	Secondary forest less than 30 years old	Increase number relative to active shade coffee	Predominate
Old secondary forest	Secondary forest more than 30 years old	Many species	Still important
Reverted secondary forest	Abandoned after 1980	Few species in the overstory	Predominate
Dry limestone forest	Abandoned after mixed uses	Predominate	Few species
Moist volcanic forest	Abandoned after agricultural use	Predominate	Few species but high importance
Type IV: tree plantations	Planted and managed by humans	Invade the understory	Tend to dominate the canopy

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