FUNCTIONAL ROLES OF INVASIVE NON-INDIGENOUS PLANTS IN HURRICANE-AFFECTED SUBTROPICAL HARDWOOD FORESTS

CAROL C. HORVITZ, JOHN B. PASCARELLA, STEPHEN MCMANN, ANDREA FREEDMAN, AND RONALD H. HOFSTETTER

Department of Biology, P.O. Box 249118, University of Miami, Coral Gables, Florida 33124 USA

Abstract. Native forest species exhibit a well-known range of ecological roles with respect to natural disturbance regimes, from pioneer phase to mature phase, and they regenerate from a range of sources, including dormant seeds, seed rain, pre-established juveniles, and resprouts from damaged adults. In contrast, the ecological roles of invasive, non-indigenous species in forest communities after natural disturbances are not well understood. Some previous studies of invasive species have emphasized their weedy nature and their ability to colonize anthropogenic disturbances. Tropical hardwood hammock forests in southern Florida experience frequent disturbance by hurricanes. Our studies of forest regeneration during two years following a recent severe hurricane suggest that invasive non-indigenous forest species exhibit the same range of ecological roles as native forest species and compete with native species for particular kinds of regeneration opportunities.

To study ecological roles of non-indigenous species in regenerating forests after Hurricane Andrew, we set up four large study areas at each of three study sites that had differing amounts of hurricane-caused canopy disturbance. There were two pairs of 30 × 60 m research plots per site, and in each pair there was one control plot and one restoration plot; restoration areas were subject to an aggressive management program, focused on reducing non-indigenous vine cover. Within these study areas we subsampled vegetation in small study plots that were regularly spaced, and conducted vegetation censuses in April (the end of the dry season) and October (the end of the rainy season) for 2 yr, beginning in April 1993.

We found that the source of regeneration for forest species was dependent upon the amount of canopy disturbance, the time since disturbance, and the autecology of the constituent species. Overall, 28% of the 90 species were non-indigenous: 34% of the vines ($N = 32$) and 24% of other life-forms ($N = 58$). Non-indigenous vines seemed to have a special role; not only could they compete with native vines, but they could also negatively affect the regeneration of other natives from a diverse array of sources including pre-established juveniles and resprouts from damaged adults. Both native and non-indigenous vine cover in unmanipulated study areas increased following the hurricane. Non-indigenous vine species had higher cover than native vine species, and many species formed dense "blankets." Non-indigenous species in general (not just vines) did not differ significantly from native species in seed mass, nor were they restricted to the pioneer type of life history. Many non-indigenous species had invaded forests prior to hurricane disturbance and had their own banks of pre-established juveniles; others recruited from dormant seeds, seed rain, and/or resprouts from pre-established adults.

Based on information on source of regeneration and impact on native species, we propose a classification scheme for functional roles of non-indigenous invasive species in forests. To investigate whether non-indigenous taxa had roles in other geographic regions similar to those they had in Florida, we reviewed literature for 50 taxa belonging to genera that have species known to be invasive in southern Florida. We found that these taxa were invasive or had congeners that were invasive in other geographic regions (Western Australia, the Mariana Islands, Hawaii, the Mascarene Islands, and South Africa). We propose that taxa predominantly retain their invasive, functional-role type across regions. Thus, studies of ecological roles of invasive species with respect to natural disturbance regimes in one region may help us predict invasive roles in other regions.

Key words: biological invasions; exotic plants in forest communities; Florida (USA), subtropical forest regeneration; forest regeneration functional groups; Hurricane Andrew; invasive functional groups; non-indigenous plants; regeneration sources, comparisons; seed bank, seed rain vs. advance regeneration; subtropical hardwood hammocks; vertical forest strata; vine cover, native vs. non-indigenous.

INTRODUCTION

Forest regeneration in openings caused by natural disturbances occurs from many sources (Denslow 1980, Runkle 1989, Veblen 1989). The relative importance of these sources may vary with time since disturbance. Immediately following a disturbance, sources include dormant seeds, suppressed seedlings and juveniles, shrubs, small understory trees, thin-stemmed vines, and lianas (Putz and Brokaw 1989). In addition, fallen but living stems of canopy trees may produce new vertical shoots from root and stem sprouts, and snapped-off standing stems of canopy trees may produce lateral and vertical growth from lateral buds (Putz and Brokaw 1989). Seed rain from surrounding undisturbed areas by species that are fruiting at the time of disturbance may also occur (Putz and Brokaw 1989). Additional sources, such as seed rain from the regenerating patch itself or from surrounding vegetation, may become available only considerably after a disturbance.

The relative importance of sources may also vary with amount of disturbance (size and spatial distribution of openings), intensity of disturbance, and nature of disturbance; regeneration after individual treefalls, fires, and hurricanes can differ dramatically. The landscape context of regeneration as well as resilience to disturbance will differ among forests that differ in historical disturbance patterns. Gap regeneration in forests that have a history of openings caused by death or branchfalls of individual overstory trees has been well studied (Connell 1989, Whitmore 1989, Poulson and Platt 1996). The refilling of such gaps is time- and size-dependent. Soon after the disturbance, small gaps tend to be filled by the lateral growth of branches of surrounding trees; intermediate-sized gaps tend to be filled by the release of shade-tolerant juveniles; and large gaps tend to be filled by pioneer (colonizing) species that require high-light conditions for germination (Poulson and Platt 1989, Whitmore 1989). In contrast, the establishment of new seedlings of shade-tolerant canopy species occurs later (Whitmore 1989). Regeneration in openings of forests that have a history of frequent, low-intensity fires (e.g., pine-savannas) has a different pattern (Platt 1997). Forest canopies are often relatively sparse, both before and after fires. These fires do not generally kill overstory trees, but they do reduce or remove aboveground understory vegetation (Platt et al. 1988, Doren et al. 1993, Attiwill 1994, Grace and Platt 1995). Regeneration is frequently from newly arriving seeds, from newly released seeds of serotinous species, and from belowground stems.

Post-disturbance regeneration in forests that have a history of frequent hurricanes has a pattern distinct from that in either treefall-driven or fire-driven systems. These regional-scale disturbances open forest canopies by extensive defoliation, loss of major branches, snap-off of trunks, and multiple treefalls (Brokaw and Grear 1991, Brokaw and Walker 1991, Slater et al. 1995). Light and heat levels increase dramatically in the understory (Brokaw and Walker 1991, Fernandez and Fetcher 1991, Horvitz et al. 1995, Pascarella 1995), even when some adult trees remain standing (Slater et al. 1995). Vigorous resprouting is common in canopy trees as well as understory trees and shrubs (Walker 1991, Yih et al. 1991, Howard and Schokman 1995, Slater et al. 1995). Understory trees and shrubs have lower mortality than overstory trees (Pascarella 1995). In less severe hurricanes many trees remain standing; however, in intense hurricanes many trees are tipped up, snapped off, and/or killed (Horvitz et al. 1995), resulting in severe alteration of vertical structure (Armentano et al. 1995) in addition to a significantly more open canopy. The spatial extent and distribution of gaps following severe hurricanes result in a landscape that is distinct from that associated with small-scale treefalls or fires. Gaps are much larger and interconnected, and surrounding vegetation is also damaged; consequently, there may be a long lag-time in recovery of seed sources on a landscape level.

The ecological roles of invasive, non-indigenous species in forest ecosystems, in contrast to native species, are not well understood. Some analyses (e.g., Rejmanek and Richardson 1996) have suggested that non-indigenous species that are successful are those that have an r-selected, colonizing life history, characterized by small, widely dispersed seeds, and that they most frequently become established in a region in anthropogenically disturbed habitats (see Parker et al. 1993). In contrast to these views, we propose that successful invasion may occur through recruitment and persistence in natural habitats prior to disturbance followed by post-disturbance population expansion, as well as through recruitment in naturally caused openings. Some studies have explicitly compared establishment of native and non-indigenous species in natural openings (Weiss and Milton 1984, Weiss and Noble 1984a, b, Hobbs 1989, Attiwill 1994, Dean et al. 1994), but interactions between native and non-indigenous species in closed habitats, such as forest understories, are not well studied.

The terms "non-indigenous" and "invasive" require definition, as there is no standard usage. We define a non-indigenous species as one that has entered a new region of the world anthropogenically rather than by natural dispersal. Such movements of species by humans, both accidental and intentional, began to accelerate during Europe's age of exploration/conquest (15th century) and have continued to increase through the present. We define invasive, non-indigenous species as those that have become naturalized and abundant in natural ecosystems, having escaped from human-dis-

turbed areas (Elton 1958, Mack 1985, Drake et al. 1989).

A recent (1992) severe hurricane in southern Florida (Hurricane Andrew) provided the opportunity to study the dynamics of invasive non-indigenous species in the context of forest regeneration following a natural disturbance. All trees in the region most affected by this storm were stripped of leaves, fruits, flowers, and minor branches. Most trees in the region also lost major limbs and many trees were tipped up or snapped off. Structural alteration of forests was severe (Loope et al. 1994, Armentano et al. 1995). At the time of Andrew, this region had much more abundant non-indigenous vegetation (Gordon 1998) than it did the previous time a hurricane of similar magnitude occurred, during the 1920s (Simpson 1932). We empirically explored ecological roles of non-indigenous plants in the regeneration of subtropical hardwood forests. Preliminary evidence (Horvitz et al. 1995) and prior experience of land managers (Rob Line [Metro-Dade Parks Natural Areas], *personal communication*) indicated that non-indigenous vines were of special concern with respect to their potential negative effects on forest regeneration in tropical hardwood hammocks.

In this paper (1) we first examine vegetation dynamics, especially in relation to vertical structure, during 2 yr following Hurricane Andrew. We ask how abundant non-indigenous species are among species and among stems of different height classes, and we compare the vine cover of non-indigenous and native vines. (2) We assess which regeneration sources are most important, comparing among study sites that varied in amount of canopy disturbance and between censuses that represented different times after disturbance. (3) We then ask whether or not successfully invading non-indigenous species have regeneration sources similar to native species. Finally, (4) based on our information on regeneration sources, life-forms, and impacts on regeneration of particular groups of native species, we propose functional roles for invasive, non-indigenous species in southern Florida forests and consider whether these functional roles are similar in other geographic regions.

THE STUDY SYSTEM

Subtropical hardwood hammocks

Subtropical hardwood hammock forests are evergreen, broad-leaved forests that occur on limestone outcroppings in the Caribbean basin. They occur in the continental United States only in extreme southern Florida as tree islands within the more extensive pine savannas and sawgrass wetlands (Davis 1943, Alexander 1967, Craighead 1971, 1974, Tomlinson 1980, Snyder et al. 1990). The tropical plant families that characterize these forests are at the northern edge of their distributions; 130 (Tomlinson 1980) to 170 (Craighead 1974) species of woody plants have been

reported in these habitats. Despite the diversity observed across the system as a whole, any given hammock has a small subset of species. This likely results from the insular nature of hammocks, combined with the patchy nature of the many disturbances (hurricanes, fires, floods, freezes, and droughts) in the region (Phillips 1940, Olmsted et al. 1983, Horvitz et al. 1995, Slater et al. 1995).

Study sites

Three study sites are located within 24 km of one another (80–81° W and 25–26° N) and are managed as natural areas by Metro-Dade County (Florida, USA). Matheson Hammock Park (143 ha; at Southwest 96th Street and Old Cutler Road) consists of coastal hammock and mangroves, is adjacent to Fairchild Tropical Garden, and is surrounded by landscaped residential areas. Charles Deering Estate (150 ha; at Southwest 167th Street and Southwest 72nd Avenue) consists of coastal hammocks, mangroves, pine savanna, and salt marsh, and also is surrounded by landscaped residential areas. Castellow Hammock (22 ha; at Southwest 223rd Street and Southwest 162nd Avenue) consists of hammock and historical pine savanna and is surrounded by agricultural land, including tropical plant nurseries. Prior to Hurricane Andrew, these hammocks differed in species composition, including canopy dominants and abundance of non-indigenous species (Horvitz et al. 1995). For example, *Lysiloma latisiliquum* was a canopy dominant at Castellow, but it was absent from the other sites; *Sideroxylon foetidissimum* was a canopy dominant at Matheson, but was much lower in abundance at the other sites. The number and abundance of non-indigenous species was greatest at Matheson (C. C. Horvitz, *personal observation*).

Hurricane Andrew

Hurricane disturbance is expected to recur at 8–12 yr intervals in southern Florida (Simpson and Lawrence 1971, Chen and Gerber 1990, Pimm et al. 1994), although few are of a magnitude similar to Hurricane Andrew. Andrew was a small, but intense hurricane (category IV on the Saffir/Simpson hurricane scale [i.e., winds 131–155 miles/h, where 1 mile = 1.609×10^3 m]) that crossed southern Florida on 24 August 1992 (Mayfield et al. 1994) with maximum sustained wind speeds estimated between 230 km/hr (Mayfield et al. 1994) and 242 km/hr (Pimm et al. 1994), and with gusts up to 282 km/hr.

The effects of Hurricane Andrew on the study sites differed despite the small distances separating the three forests (Horvitz et al. 1995). Castellow and Deering were traversed by the northern eyewall, where the most intense winds occurred (Mayfield et al. 1994, Powell and Houston 1996), but Matheson was well to the north of the hurricane eyewall (eyewall = area of maximum wind speeds surrounding the relatively calm and fre-

quently clear eye). Canopy tree mortality (measured 8 mo after Andrew) and canopy openness (measured 4 mo after Andrew) was nearly twice as high at Castellow (67% mortality, 50% canopy openness) as at Matheson (32% mortality, 25% canopy openness) (Horvitz et al. 1995). The vertical structure of the forests also differed. The mean height of live standing stems (≥2 cm in diameter at breast height [1.37 m]) 8 mo after the hurricane was close to 2 m at Castellow and close to 4 m at Matheson (Horvitz et al. 1995). Deering was similar to Castellow in amount of canopy openness and height of living stems.

METHODS

Vegetation dynamics

Study areas and associated management activities.—After Hurricane Andrew, we set up four large study areas in each hammock, two pairs of 30 × 60 m research plots. In each pair, there was one control plot ("to-remain-untreated"; established September–December 1992) and one restoration plot ("to-be-restored"; established January–March 1993) (Horvitz et al. 1995). Restoration areas were subjected to Metro-Dade Parks Department's aggressive management program, focused on reducing non-indigenous vine cover. Management also restricted the study; our study areas were not in sections of the parks designated as the most heavily covered by non-indigenous vines. Our first vegetation census (8 mo post-hurricane) was carried out before the first restoration treatment, which occurred 13 mo post-hurricane. We include data from both types of plots to maximize the size of the data set. The goal of the present paper is to examine large-scale patterns in forest regeneration and the roles of non-indigenous species in forest regeneration, not to analyze effects of non-indigenous vine cover and its removal on native plants. Initial sources of regeneration are not dependent on restoration treatments. The abundance of non-indigenous stems in managed areas post-treatment was affected by restoration treatment only for targeted species, principally invasive vines. Where reported patterns are attributable directly to management activities, we explicitly state this.

Vegetation censuses.—Within large study areas we subsampled vegetation in small study plots that were regularly spaced. Vegetation censuses were conducted in April (near the end of the dry season) and October (near the end of the rainy season) for 2 yr beginning in April 1993. The vegetation was sampled at two scales: 5 × 5 m plots for stems ≥2 cm dbh, and adjacent to these plots, 2 × 0.5 m plots for all stems. There were 72 plots of each size, 12 per treatment within each hammock. Within these plots stems were identified to species whenever possible. For analyses of growth, survival, and recruitment, each stem that was separate at breast height in the large-stem plots and each stem that was separate at ground level in the all-stem plots was

tagged with an identification number. For clumps of rhizomatous plants (e.g., ferns and grasses), each clump was tagged. At each census, we recorded height and diameter of each stem (or clump), and we evaluated damage, recovery, and regrowth of each stem (or clump).

Native or non-indigenous origin of species.—To verify whether species were of native or of non-indigenous origin, we consulted the Metro-Dade County Parks plant checklists (R. Hammer, *unpublished data*). We also consulted the Florida Exotic Pest Plant Council's List (Florida EPPC 1995) of invasive non-indigenous plant species. We classified both native and non-indigenous species into "vine" and "non-vine" (trees, shrubs, and herbs) categories, because vines were of special concern to park managers with respect to their potential effects on forest regeneration.

The origin of *Carica papaya,* an abundant species, remained ambiguous; Metro-Dade Parks Department listed it as non-indigenous, but EPPC had not included it in its 1995 list. After library research and consultation with Dade County Archaeologist R. S. Carr, we concluded that occurrence of papaya in forest sites of southern Florida represents "escape" from cultivation after its introduction by Europeans (also see Austin 1980). *C. papaya* was already naturalized in Florida near the Saint John's River in 1774 (Bartram 1774, edited by Cruickshank 1986). That site is located in the same region of Florida as the early Spanish settlement of Saint Augustine. *C. papaya* is native to tropical America (Sturtevant 1919, Popenoe 1920, Stambaugh 1945, Prance 1984), having most likely evolved in the Andes (Prance 1984). Indigenous peoples of Mexico, Central America, South America, and the West Indies utilized this species prior to the arrival of the Spanish, and the Spanish disseminated papaya (as they did oranges) throughout the tropics and subtropics by the early 1600s (Nakasone 1975). Early Spanish explorers commented on the lack of agriculture by indigenous people of southern Florida (Scarry 1985), and papaya is not reported in lists of wild plants used by these peoples written by early Spanish explorers or lists compiled by archaeologists from recent analyses of plant remains in archaeological sites (Scarry 1985).

Forest regeneration: vine cover.—To compare roles of native and non-indigenous vine cover in forest regeneration, we categorized each 5 × 5 m plot according to percentage coverage by native vines and also by percentage coverage by non-indigenous vines. The categories were 0%, 1–5%, 6–25%, 26–75% and 76–100%, represented by cover-index values 0, 1, 2, 3, and 4, respectively. We report data on the untreated plots only. For native and for non-indigenous vine cover, we report three summary parameters: the number of plots that had vines, the percentage of these that were heavily covered (76–100% covered), and the mean cover index for each hammock for each of four censuses (8, 14,

20, and 26 mo post-hurricane). To analyze differences between native and non-indigenous vine occurrence we utilized G tests (SAS Institute 1989: FREQ procedure), to analyze the differences between native and non-indigenous vine cover we utilized nonparametric ANOVAs (SAS Institute 1989: RANK procedure followed by GLM procedure).

To compare vine cover among species and between native and non-indigenous species we recorded cover class of each species for each plot and census. Most species increased in cover over time (C. C. Horvitz, *unpublished data*). We report two summary parameters for the 26-mo post-hurricane census: the percentage of plots in which the species was present and the mean cover index.

Forest regeneration: number of stems and vertical structure.—To understand overall differences among sites and changes in forest structure during the first 2 yr, we pooled data on stems from all plots in restoration areas and all plots in control areas, respectively, at each hammock at each census. We tracked the dynamics of both native and non-indigenous stems, and we focused on changes between the first census (April 1993: 8 mo post-hurricane) and the fourth census (October 1994: 26 mo post-hurricane). The basic unit of analysis for this paper is a subset of data defined by cross-classifying observations on stems by hammock, type of treatment, and census date; there were 3 hammocks × 2 types-of-treatment for each of two census-dates.

We examined variation in the process of reassembly of vertical structure by analyzing changes at each site in the numbers of stems in each of seven vertical forest strata, defined by a logarithmic series (Terborgh 1985); (≤0.25 m, 0.25–0.5 m, 0.5–1.0 m, 1–2 m, 2–4 m, 4–8 m, and >8 m, measured as height above the forest floor). At each census the number of stems in a layer was given by the number of stems of corresponding height class; each stem was assigned to the highest layer it occupied. To investigate whether stem number in each stratum, as well as the numbers of non-indigenous and of native stems, varied significantly among sites or between censuses, we utilized Kruskal-Wallis tests (SAS Institute 1989:NPAR1WAY procedure). One-way (rather than multi-way) analyses were performed to look for overall trends through space or time.

Inasmuch as it is difficult to identify the particular source of regeneration for a particular stem, we confined our attempts to those stems contributing most to changes in forest structure during forest regeneration. In order to identify a subset of data for investigating the relative importance of regeneration sources to forest dynamics, we determined which layers of the forest were most actively changing. The percentage change was quantified separately for each subset of the data (cross-classifying observations by hammock and type-of-treatment area). Then, absolute values of changes were used to compute the average magnitude of change

for a layer, and differences among layers were analyzed with a Kruskal-Wallis test (SAS Institute 1989: NPAR1WAY procedure).

Relative importance of sources of regeneration

To investigate the relative importance of different regeneration sources of stems, we concentrated on the three most dynamic strata of the forest. In each of these, we further focused on the three (up to five, in the case of ties) most abundant species in each subset of the data (defined by hammock, type-of-treatment area, and census date). The extent to which a sample based on only the dominant species is representative of a population of stems is determined by whether a large a proportion of stems belongs to the dominant species. If it does, the sample reflects the main trends in the population of stems, even though rare species are not represented. For each stem belonging to one of the dominant species, we asked whether it was most likely to have arisen from a dormant seed, from "seed rain" (sensu Denslow and Gómez Diaz 1990: seeds that are not stored in a dormant seed pool, but germinate soon, <1 yr, after dispersal), from an "oskar" (sensu Silvertown 1987; a plant in a suppressed juvenile state in the understory of a forest), or as a resprout from a rhizome, a liana, a fallen stem, or a standing stem. Standing stems themselves were defined as having a "standing-stem-resprout" regeneration source. We examined whether the relative importance of regeneration sources varied by hammock and time since disturbance (census).

We used a number of criteria to determine a regeneration source for each stem. For some stems, the decision was based purely on its species—what we saw the species do frequently and what was in the literature. For example, all *C. papaya* stems appeared to come from dormant seeds because a few weeks after Andrew vast numbers of papaya seedlings appeared where no fruiting adults had been seen for years. These plants were in the ≥2 cm dbh class by our first census. The most abundant recruitment of papaya was in an area of very open canopy; papayas are known to have long-term dormancy, with germination stimulated by high light and heat (Simpson 1932, Craig 1993). Similarly, other species with long-lived dormant seeds that had abundant new seedlings soon after Andrew (but well in advance of any conspecific seed production) were presumed to have emerged from dormant seeds.

For some stems, our decision was based on our tagged-plant data combined with general knowledge of the landscape-level disturbance caused by Hurricane Andrew. For example, on a landscape level there was no seed rain during the first fall/winter after Andrew because all the leaves and flowers were stripped off every plant in the region. There was a hurricane-associated pulse in reproduction of understory trees the subsequent fall/winter (Pascarella and Horvitz 1998),

by which time many plants had recovered vegetatively. Thus, seedling-sized individuals that were present during the first spring (first census) of species that do not have dormant seeds and that fruit in the fall/winter were most likely oskars established prior to Andrew. In contrast, for the same species, new (=not yet tagged) seedlings that were first found the next spring (third census) were most likely derived from new seed rain. *Eugenia axillaris* is an example of this kind of species; we have observed that this species can germinate in shaded understory and persist as small plants (<5 cm in height) for several years in understory conditions without significant height growth.

For other stems, our decision was based primarily on our data from 7217 individual tagged plants. For example, during the first 2 yr post-Andrew, most of the vertical stems of *Coccoloba diversifolia* recruiting into the ≥2-cm-dbh class (thus forming part of our data on tagged plants), were resprouts from fallen stems.

Regeneration of native vs. non-indigenous species

Regeneration source of stems.—In addition to asking about the relative importances of regeneration source overall, we examined the representation of native and non-indigenous species in each regeneration source.

Seed mass.—To determine whether non-indigenous invasive species were mostly small seeded (as one might expect of a pioneer, colonizing species), we compared seed masses of non-indigenous and native species (Kruskal-Wallis test, SAS Institute 1989: NPAR1WAY procedure). Seed mass was measured for a subset of species, determined opportunistically by availability of seeds in two sources: a dried-seed collection (Buswell Herbarium, University of Miami, Miami, Florida, USA) and seeds collected from the field (air dried). Though not strictly a random sample of all native and non-indigenous species, our haphazard sample of species had no particular a priori bias with respect to the interaction of seed size with origin. For each species, 10 or 11 seeds were weighed to obtain mean seed mass. To place seed mass data in an ecological context, we classified native species as "shade tolerant" or "shade intolerant," based on our observations of their behavior in our study sites and life-history descriptions in the literature for these species in southern Florida and the Caribbean (Little and Wadsworth 1964, Little et al. 1974, Molnar 1990; M. S. Ross, J. F. Meeder, G. Telesnicki, and C. Weekley, *unpublished report* [1995] to U.S. Fish and Wildlife Service).

Proposed functional roles of invasive species in forests

We proposed functional roles for invasive, non-indigenous species in southern Florida forests based on our observations of regeneration sources, life-forms, and especially potential negative impacts on particular groups of native species. More species were included

than were in the stem-by-stem analysis of regeneration source of the most abundant taxa in the most dynamic layers.

One type of negative impact assumes that non-indigenous species that utilize a particular regeneration source and have a particular life-form might be more likely to impact native species with a similar source and life-form. The idea behind this assumption is that regeneration source coupled with life-form defines a suite of limiting resources, such as light, space, water, nutrients, and animal services. For example, species that require large gaps for regeneration may compete with each other for seed-bank space, or, more likely, for light during the early filling in of gaps. Species that regenerate in shade must have space available on the forest floor for establishment of seedlings; perhaps they compete for moisture as well. Fleshy-fruited species that require continual seed rain might compete for dispersers. Species that regenerate from standing stems may compete for canopy space. In addition to the competitive modes of interaction outlined here, a second type of negative impact is potentially presented by non-indigenous vines. By rapid growth in a variety of forest strata and by utilizing other species as trellises, vines may negatively impact species of a diverse array of regeneration sources and life-forms.

Finally, we propose that non-indigenous taxa in subtropical forests in other geographic regions might have functional roles similar to their roles in Florida. To test this hypothesis, we reviewed literature for fifty taxa, including genera that had invasive species in Florida as well as invasive species in other regions.

RESULTS

Vegetation dynamics

Native or non-indigenous origin of species.—Twenty-eight percent (N = 90) of the vascular plant species in our plots in these hardwood hammocks were non-indigenous, including 34% of vine species (N = 32) and 24% of other species (N = 58).

Forest regeneration: vine cover.—Both native and non-indigenous vines were present in most plots throughout the first 2 yr post-hurricane (Table 1). There was spatial and temporal variation in whether non-indigenous vine cover exceeded native vine cover (Table 1). Cover as well as frequency of heavily invaded plots was greater for non-indigenous than native vines at Matheson, but the reverse was true at Castellow (Table 1). At Deering, cover by non-indigenous vines exceeded cover by natives only at the last census, although frequency of heavily invaded plots was greater for non-indigenous than for native vines at all censuses (Table 1). The relative importance of non-indigenous vs. native vines appeared to increase with time at Matheson and Deering (Table 1). These data indicate native vines as well as non-indigenous vines may be an important part of the vegetation dynamics post-hurri-

TABLE 1. Vine frequency and cover during 2 yr post-hurricane (Hurricane Andrew, 24 August 1992) at three subtropical hardwood hammock forest study sites in southern Florida, USA.

		Frequency and coverage						Statistical comparison				
		Non-indigenous vines			Native vines							
Hammock	Census date (mo)†	No. of plots with vines	Plots heavily covered (%)	Cover index‡ (mean ± 1 SE)	No. of plots with vines	Plots heavily covered (%)	Cover index‡ (mean ± 1 SE)	% plots (G test)		Mean cover (ANOVA)		
								G^2	P	df_{err}	F	P
Castellow	8	7	14.3	2.3 ± 0.4	12	25.0	2.5 ± 0.3	0.32	NS	17	0.15	NS
	14	12	0.0	2.2 ± 0.2	12	16.7	2.6 ± 0.3	2.96	0.09	22	1.23	NS
	20	11	9.1	2.3 ± 0.2	12	25.0	2.8 ± 0.2	1.06	NS	21	2.74	NS
	26	12	8.3	2.2 ± 0.3	12	16.7	2.8 ± 0.2	0.32	NS	22	2.26	NS
Deering	8	8	25.0	2.3 ± 0.4	12	16.7	2.3 ± 0.3	0.2	NS	18	0.02	NS
	14	11	18.2	2.2 ± 0.4	12	0.0	2.6 ± 0.2	3.16	0.08	21	1.17	NS
	20	11	18.2	1.8 ± 0.4	12	0.0	2.8 ± 0.1	3.16	0.08	21	7.18	0.01
	26	12	41.7	2.7 ± 0.4	12	8.3	2.4 ± 0.3	3.81	0.05	22	0.28	NS
Matheson	8	12	8.3	2.4 ± 0.3	12	0.0	2.2 ± 0.3	1.43	NS	22	0.4	NS
	14	12	25.0	2.8 ± 0.3	12	16.7	2.2 ± 0.3	0.25	NS	22	2.75	NS
	20	12	25.0	3.0 ± 0.2	12	0.0	1.4 ± 0.2	4.6	0.03	22	30.31	0.0001
	26	12	8.3	2.8 ± 0.2	10	0.0	1.4 ± 0.2	1.2	NS	20	39.76	0.0003

Notes: Statistics compare non-indigenous to native vines at each hammock and census. Only plots from untreated areas are included. For plot (%) a G test (df = 1) was used; for mean cover an ANOVA on ranks was performed (treatment df = 1). NS at $P > 0.10$. Vegetation was censused in April (near end of the dry season) and October (near end of the rainy season) of 1993 and 1994. Untreated = study sites not being managed for restoration (i.e., not subject to Metro-Dade Parks Department's aggressive management program that focused on reducing non-indigenous vine cover).

† Number of months post-hurricane.

‡ Cover index varied from 1 to 4 (1 = 0% cover, 2 = 1–5%, 3 = 6–25%, 4 = 26–75%); cover index 5 (76–100%) = heavily covered.

cane, that relative effects of non-indigenous vs. native vines differ among sites, and that the relative effects of non-indigenous vines increased over time at some sites.

Individual vine species.—Comparison among vine species, including some native and some non-indigenous, illustrates differences in cover or occurrence. Mean cover index varied more than three-fold among selected species, from 0.8 to 2.8, and frequency of occurrence varied nine-fold among selected species, from 8.3% to 75% of plots (Table 2). Non-indigenous species generally exceeded native species in either cover or frequency (Table 2), and the species with the highest cover were non-indigenous (Table 2). Also, tropical taxa tended to have higher coverage than temperate taxa, and non-indigenous species were mostly tropical in origin (Table 2). In contrast to non-indigenous and native species belonging to tropical genera, native vines belonging to temperate genera (*Vitis* and *Parthenocissus*) occurred frequently but with low cover.

TABLE 2. Occurrence of selected vine species in untreated plots (N = 36) at 26 mo post-hurricane and mean cover at the same census in untreated plots in southern Florida.

Species	Latitude†	Plots present (%)	Cover index Mean ± SE	N	Family
Non-indigenous					
Jasminum dichotomum	Trop.	50.0	1.8 ± 0.2	20	Oleaceae
Jasminum fluminense	Trop.	75.0	1.4 ± 0.2	32	Oleaceae
Dioscorea bulbifera	Trop.	22.2	2.8 ± 0.4	8	Dioscoreaceae
Epipremnum pinnatum	Trop.	11.1	2.5 ± 0.9	4	Araceae
Rubus albescens	Trop./Temp.	8.3	2.7 ± 0.3	3	Rosaceae
Native					
Chioccoca alba	Trop.	22.2	2.0 ± 0.4	9	Rubiaceae
Gouania lupuloides	Trop.	30.5	1.5 ± 0.3	13	Rhamnaceae
Pisonia aculeata	Trop.	69.4	1.5 ± 0.2	27	Nyctaginaceae
Vitis rotundifolius	Temp.	47.2	1.3 ± 0.2	21	Vitaceae
Parthenocissus quinquefolia	Temp.	41.7	0.8 ± 0.1	21	Vitaceae
Ipomoea spp.	Temp./Trop.	52.7	1.0 ± 0.2	31	Convolvulaceae

Notes: Cover index varies from 0 to 4 (N for mean cover includes plots that had the species at any time up to and including that census). For additional site and analysis information see Table 1.

† Principal latitudinal distribution of the genus; Trop. = tropical, Temp. = temperate.

TABLE 3. Regeneration of forest strata, reporting how the numbers of non-indigenous, native, and total stems vary through space and time.

Forest stratum (m)†	Type of stems	Hammock			Census		
		χ^2	df	P	χ^2	df	P
<0.25	Non-indigenous	6.6	2	*	2.1	1	NS
	Native	2.9	2	NS	4.7	1	*
	All	1.9	2	NS	3.1	1	NS
0.25–0.5	Non-indigenous	7.2	2	*	0.9	1	NS
	Native	7.5	2	*	0.03	1	NS
	All	6.6	2	*	0.06	1	NS
0.5–1	Non-indigenous	2.8	2	NS	2.1	1	NS
	Native	2.9	2	NS	1.3	1	NS
	All	3.1	2	NS	0.03	1	NS
1–2	Non-indigenous	1.9	2	NS	3.7	1	*
	Native	7.5	2	*	0.03	1	NS
	All	2.8	2	NS	2.8	1	NS
2–4	Non-indigenous	8.1	2	*	0.8	1	NS
	Native	3.3	2	NS	4.7	1	*
	All	1.0	2	NS	6.2	1	*
4–8	Non-indigenous	1.6	2	NS	7.1	1	**
	Native	6.8	2	*	2.5	1	NS
	All	4.6	2	NS	5	1	*
>8	Non-indigenous	2.5	2	NS	0.3	1	NS
	Native	9.7	2	**	0.01	1	NS
	All	10.0	2	**	0	1	NS
Sum, all strata	Non-indigenous	6.3	2	*	1.6	1	NS
	Native	3.2	2	NS	3.7	1	*
	All	3.1	2	NS	2.6	1	NS

Notes: The table reports the Kruskal-Wallis chi-square statistic, indicating the significance of hammock and census on number of stems of different origins (where origin was defined for each species, and thus for each stem according to its species, as non-indigenous or native) and on total number of stems in subsets of the data (defined by cross-classifying the observations by hammock, type-of-treatment area, and census-date class) within each forest stratum. These analyses include both untreated and restored areas (see Table 1, *Notes*).
* $P < 0.05$, ** $P < 0.01$; NS indicates $P > 0.05$.
† Height above forest floor.

One native vine genus (common in both tropical and temperate regions), *Ipomoea*, was short-lived, germinating and growing rapidly, but not persisting; it was the only species that decreased markedly in its mean coverage (from 1.4 to 1.0) during the study.

Forest regeneration: number of stems and vertical structure.—The total number of stems, and of both non-indigenous and native stems, varied significantly among hammocks in several height classes of the forest (Table 3). Comparison of the site with the least structural damage (Matheson) to the sites with more structural damage revealed that it had more total stems in the highest stratum (Fig. 1G), attributable mostly to a large number of residual standing trees. This stand, which had more non-indigenous vegetation prior to Andrew, also had the most non-indigenous stems in the three lowest strata (Fig. 1A, B, and C), but the most native stems in middle and high strata (Fig. 1D, E, F, and G). A comparison of the two sites with a high degree of structural damage to each other shows that Deering had more non-indigenous stems in a middle stratum (2–4 m) (Fig. 1E), and this layer was quite dense in total, in contrast to Castellow (Fig. 1H). Castellow, particularly at the first census, had relatively few plants in this stratum (Fig. 1E). Thus, variation

among sites in both amount of hurricane-caused damage and species composition contributed to spatial variation in forest structure.

The total number of stems, and of non-indigenous and native stems separately, varied significantly between censuses in several strata of the forest (Table 3). First, stem number in the middle strata (2–4 m and 4–8 m), increased significantly (Fig. 1E and F). We also found a significant decrease of non-indigenous stems in the 1–2 m stratum coupled with increases in the 4–8 m stratum (Fig. 1D and F) resulting from rapid height growth (C. C. Horvitz, *unpublished data*). Significant increases of native stems in the middle layers (Fig. 1E and F) resulted mainly from recruitment into the ≥2-cm-dbh class (C. C. Horvitz, *unpublished data*). Second, the total number of stems in the lowest layer also greatly increased in most areas (Fig. 1A). These increases resulted from seedling recruitment—mainly natives at Deering, mainly exotics at Matheson, and a mix of both at Castellow (Fig. 1A). In summary, both native and non-indigenous species contributed substantially to increases in stem density in several forest strata, by germination and by growth, although there were site-specific differences in proportional contri-
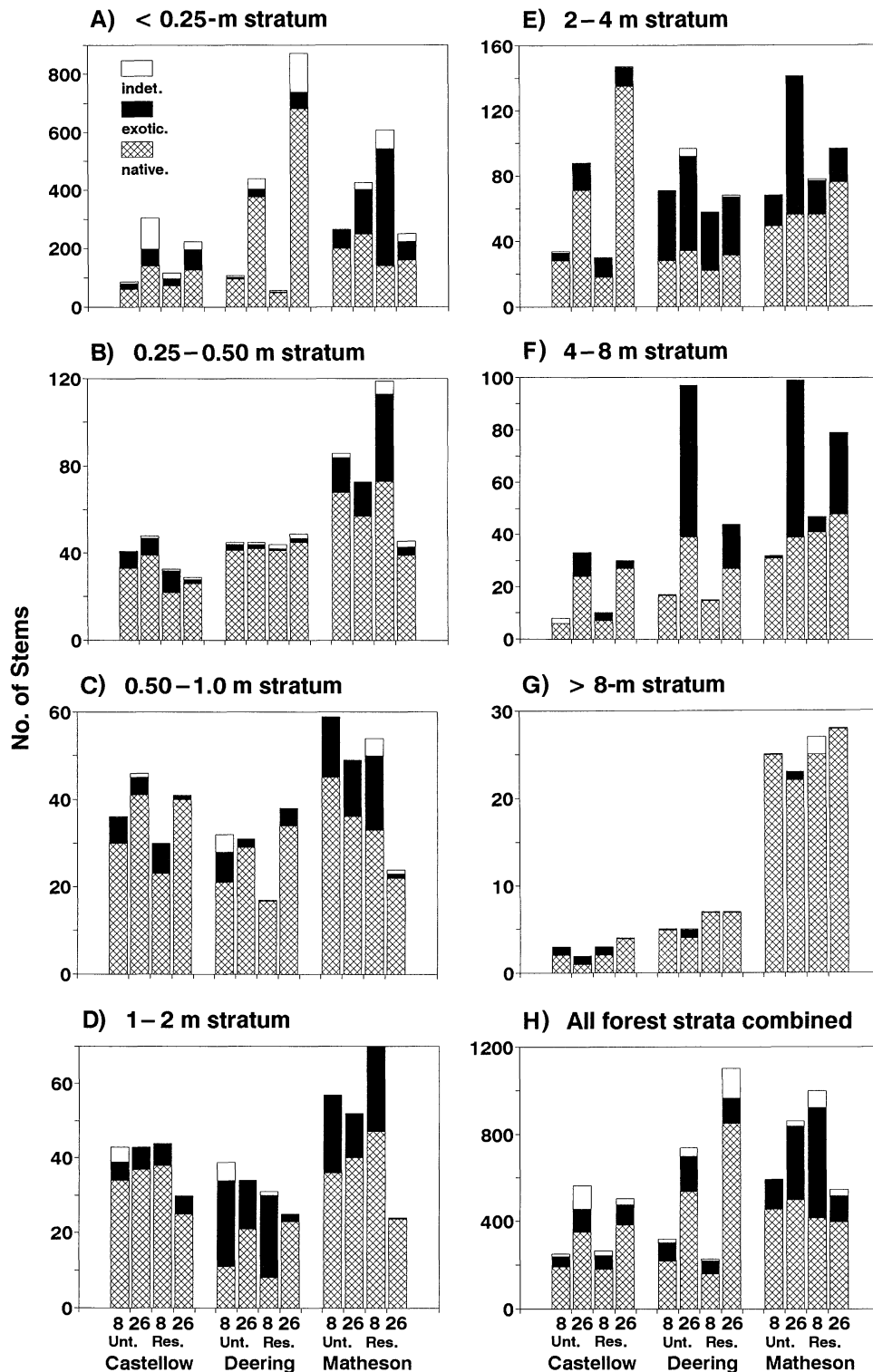
FIG. 1.   Regeneration of forest strata (after Hurricane Andrew) at three subtropical hardwood hammock forest study sites in southern Florida, including contributions of native and non-indigenous (=exotic) species. Only stems identified to species could be assigned an origin; some were indeterminate (indet.). Number of stems is shown for each subset of data defined by cross-classifying observations by hammock, type-of-treatment area, and census date within each forest stratum. Type-of-treatment area is denoted by "Unt." for untreated and "Res." for restored (or-to-be-restored) areas. The restoration treatment was not applied until 13 mo after the hurricane. Census date is denoted by "8" for the first census (8 mo post-hurricane) and "26" for the fourth census (26 mo post-hurricane).

TABLE 4. Regeneration of forest strata at three subtropical hardwood hammock forest sites in southern Florida, USA. Data are the percentage changes in stem density between the first and the fourth censuses (8 mo and 26 mo, respectively, post-hurricane).

Forest stratum (m)‡	Castellow		Deering		Matheson		Mean absolute value of change
	Untreated	Restored	Untreated	Restored	Untreated	Restored	
<0.25	243.8	90.7	303.7	1401.7	60.2	−58.7	359.8
0.25–0.50	17.1	−12.1	0.0	11.4	−15.1	−61.3	19.5
0.5–1	27.8	36.7	−3.1	123.5	−16.9	−55.6	43.9
1–2	0.0	−31.8	−12.8	−19.4	−8.8	−65.7	23.1
2–4	158.8	390.0	36.6	17.2	107.4	24.4	122.4
4–8	312.5	200.0	417.6	193.3	209.4	68.1	233.5
>8	−33.3	33.3	0.0	0.0	−8.0	3.7	13.1

Notes: The percentage change in the number of stems between the first and fourth censuses is defined as [(no. stems at 26 mo − no. stems at 8 mo)/(no. stems at 8 mo)] × 100. Also given is the mean of the absolute value of the percentage change ($N = 6$). For explanation of "untreated" and "restored," see Table 1, Notes.

‡ Height above forest floor.

butions of natives vs. non-indigenous species to these processes.

Changes in stem density in some forest strata were markedly larger than in others (Fig. 1A, E, and F compared with B, C, D, and G). The magnitude of change in stem number varied significantly among forest strata (Kruskal-Wallis chi-square = 24.7, df = 6, $P <$ 0.0004). The three strata with the largest change were designated "the most dynamic strata"; they were the <0.25-m, the 2–4 m, and the 4–8 m strata, with respective mean changes of 360%, 122%, and 234%. The other layers, 0.25–0.5 m, 0.5–1 m, 1–2 m, and >8 m, had respective mean changes of 19.5%, 43.9%, 23.1%, and 13.1% (Table 4; also Fig. 1).

Relative importance of sources of regeneration

We were able to hypothesize with reasonable certainty regeneration sources for an average of 70% (1 SD = 14%, range: 38%–100%,) of stems in each of the 36 subsets of the data (where data were cross-classified by hammock, type of treatment, census date, and height class). Details of species' contributions to these totals are shown in the Appendix (also see Table 5). Our sampling protocol documents regeneration patterns of the dominant species only, and likely underestimates diversity of regeneration patterns present owing to within-species consistency. Nonetheless, because ~70% of the stems were classified, the results are strongly indicative of the dominant modes of regeneration.

Among the strata examined, the lowest layer had more diverse sources—it was comprised of stems derived from seed bank, seed rain, oskars, and resprouts from both rhizomes and lianas (Fig. 2A), whereas the 2–4 m and 4–8 m strata of the forest were comprised of stems derived from seed bank and resprouts from both stems and lianas (Fig. 2B and C).

Hammocks differed in use of regeneration sources in the lowest and 2–4 m layers of the forest. In the lowest layer, seed bank was a more important source

of stems at both sites with very open canopy (50% open at 4 mo post-hurricane: Castellow and Deering), compared to the site with less open canopy (25% open at 4 mo post-hurricane: Matheson) (Fig. 2A). Conversely, oskars were a more important source of seedlings at the site with less open canopy (Matheson) than at the other sites (Fig. 2A). In the 2–4 m layer of the forest, seed bank was more important at Deering than at the other sites, particularly at the first census (Fig. 2B). Conversely stem sprouts were more important at Castellow and Matheson than at Deering (Fig. 2B). In summary, differences among sites in sources of plants in the lowest layer of the forest were associated with differences in canopy openness, but differences in sources in a middle layer of the forest were only partly associated with canopy openness.

Time since disturbance influenced regeneration source in the lowest layer and in the 4–8 m layer of the forest (Fig. 2B). In the lowest layer, seed rain was a more important source of stems 26 mo post-hurricane than it was 8 mo post-hurricane (Fig. 2A). In the 4–8 m layer of the forest, seed bank was a more important source of stems at 26 mo post-hurricane than at 8 mo post-hurricane (Fig. 2C), reflecting the time required for growth of seed bank recruits into this layer. There was also temporal variation in the 2–4 m later, but only for two sites (Fig. 2B); at both these sites the seed bank was a more important source of stems at the later date than the earlier date. In summary, regeneration sources differed with time since disturbance, reflecting the landscape-level recovery of seed rain for the lowest layer, and the time lag inherent in growth of seed-bank recruits into the middle and mid-upper layers.

Regeneration of native vs. non-indigenous species

Regeneration source.—Non-indigenous species were represented in each regeneration source (except rhizomes), although not necessarily in the same proportions as natives for a given layer and forest. Seed-bank recruits that were among the dominant species of the

TABLE 5. Regeneration of forest strata at three subtropical hardwood hammock study sites in southern Florida, 8 mo and 26 mo post-hurricane—a summary of origin (non-indigenous vs. native) and regeneration source of stems belonging to the most abundant taxa in the most dynamic layers of the forest.

Forest stratum (m)†	Origin‡	Regeneration source§	Castellow				Deering				Matheson			
			Untreated		Restored		Untreated		Restored		Untreated		Restored	
			8	26	8	26	8	26	8	26	8	26	8	26
<0.25-m stratum														
No. of stems			89	306	118	225	109	439	58	871	266	426	608	251
	N	Seedbank	24.7	14.4	14.4	22.7	38.6	40.1	12.1	63.2	0.0	0.0	0.0	0.0
	X	Seedbank	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	N	Rain	0.0	6.2	0.0	16.4	0.0	22.3	0.0	8.8	0.0	21.1	0.0	16.7
	X	Rain	0.0	11.8	0.0	20.9	0.0	0.0	0.0	0.0	0.0	20.4	0.0	25.5
	N	Oskar	0.0	0.3	0.0	0.0	8.3	1.1	0.0	0.2	50.4	25.8	18.4	23.5
	X	Oskar	18.0	5.2	19.5	10.2	0.0	0.0	0.0	0.0	21.4	13.4	64.8	0.0
	N	Rhizome	0.0	0.0	22.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	X	Rhizome	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	N	Liana	11.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	X	Liana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	N	Unknown	0.0	0.0	0.0	0.0	0.0	0.0	32.7	0.0	0.0	0.0	0.0	0.0
	X	Unknown	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2–4 m stratum														
No. of stems			34	86	30	147	71	98	58	68	68	141	78	97
	N	Seedbank	0.0	0.0	0.0	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	X	Seedbank	0.0	11.6	0.0	0.0	59.2	54.1	60.4	52.9	19.1	52.5	1.3	21.6
	N	Liana	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	X	Liana	0.0	0.0	13.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	N	Stem	38.2	33.7	30.0	32.7	12.7	13.2	20.7	20.6	47.1	28.4	46.2	61.9
	X	Stem	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4–8 m stratum														
No. of stems			8	33	10	30	17	88	15	44	32	99	47	79
	N	Seedbank	0.0	0.0	0.0	40.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	X	Seedbank	0.0	0.0	0.0	0.0	0.0	60.2	0.0	38.6	0.0	50.5	0.0	39.2
	N	Liana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	X	Liana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.6	0.0
	N	Stem	75.0	36.4	70.0	30.0	76.5	9.1	66.7	31.8	81.3	23.2	46.8	40.5
	X	Stem	0.0	15.2	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Notes: "Restored" refers to active management, begun 13 mo post-hurricane, to reduce non-indigenous vine cover. For each subset of data defined by cross-classifying observations by hammock, type of treatment, and census date, percentage of stems summed across species by regeneration source and by origin is given, where percentage is of the total number of stems in a subset of data class (see Appendix for how individual species contributed to these sums).
† Height above forest floor.
‡ X = non-indigenous, N = native species.
§ Regeneration sources were seedbank, seed rain, oskar layer (i.e., seedling bank), and resprouts from rhizomes, lianas, and stems (both standing and fallen).

2–4 and 4–8 m layer included both non-indigenous (Matheson and Deering) and native (Castellow at 26 mo) species, but seed-bank recruits among the dominant species of the <0.25-m layer (Castellow and Deering) were all native (Table 5). Seed-rain recruits and oskars that were among the dominant species included both non-indigenous and native species at Castellow and at Matheson, but only native species at Deering (Table 5). Liana resprouts that were among the dominant species included both native and non-indigenous species also (Table 5). Finally, stem resprouts that were among the dominant species were predominantly from natives (2–4 and 4–8 layers at all sites), but at Castellow there were some non-indigenous stem sprouts (Table 5). In summary, non-indigenous species that were among the dominant species used a wide range of regeneration sources.

Seed mass.—Seed masses of hammock plants varied over four orders of magnitude (Fig. 3). There was no significant difference in seed mass between the 12 non-indigenous species and the 29 native species for which we had seed-mass data (Kruskal-Wallis chi-square = 2.3, df = 1, NS) (Fig. 3). Many non-indigenous species had the larger seed sizes typically associated with shade tolerance in this system. Species that weighed >0.1 g in this data set for which we had independent information exhibit shade tolerance in our forest systems (Molnar 1990, Pascarella 1995; M. S. Ross, J. F. Meeder, G. Telesnicki, and C. Weekley, *unpublished report* [1995] to U.S. Fish and Wildlife Service; C. C. Horvitz and J. P. Pascarella, *personal observation*). Four non-indigenous vine species were shade tolerant to quite shade tolerant (*Abrus, Jasminum* spp., and *Merremia*). Of the non-indigenous species, only four tree species had seed sizes much smaller
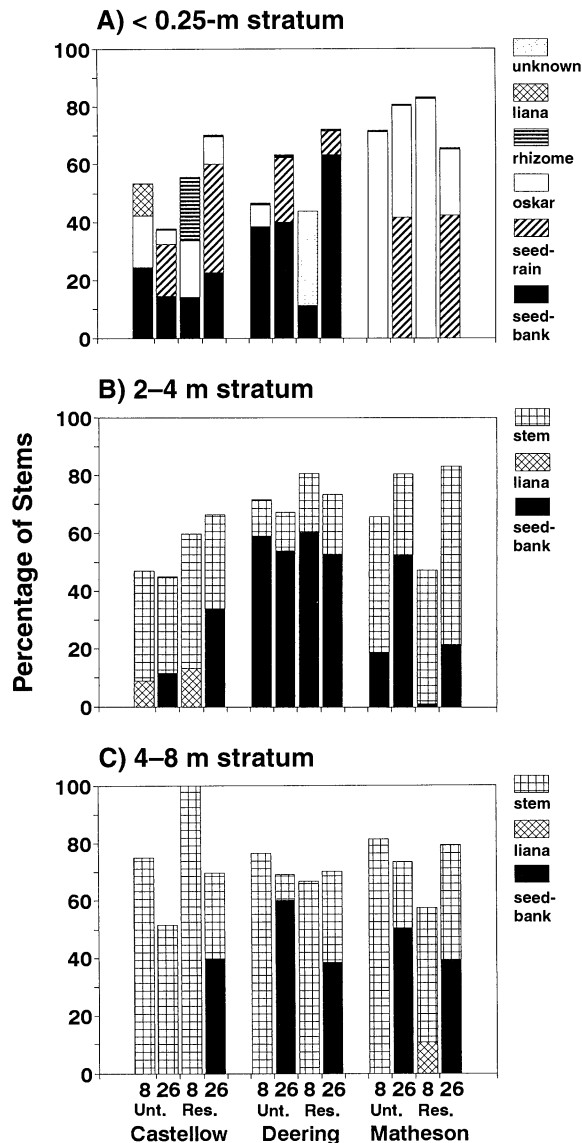
A) < 0.25-m stratum

B) 2–4 m stratum

C) 4–8 m stratum

FIG. 2. Regeneration of "the most dynamic forest strata" (i.e., the three vertical layers with the largest change in stem numbers), depicted in terms of regeneration source for stems of the dominant three species in the stratum at each census. Data are for three study sites in southern Florida, at 8 mo and 26 mo post-hurricane; Unt. = untreated, Res. = restored (see Fig. 1 caption and Table 1 footnote ‖ for explanation). Regeneration source was defined by the source of the stems: seed bank, seed rain, oskars, and resprouts from rhizomes, lianas, and stems. The percentage of stems belonging to each regeneration source (where percentage is of total number of stems in a forest stratum in a subset of the data defined by hammock, type-of-treatment area, and census date) is given. Table 5 gives these totals and percentages broken down by both origin and regeneration source; the Appendix shows details of how individual species contribute to these totals.

than 0.1 g on a logarithmic scale (Fig. 3A); these were probably shade intolerant. In summary, non-indigenous species were not restricted to being small-seeded colonizers; many had quite large seeds.

Comparison of sites.—In the lowest layer, differences among the three study sites may have been attributable to differences in canopy openness coupled with differences in species composition. At the first census, Matheson (the site with the least canopy disturbance but the highest level of non-indigenous vine cover) had the densest seedling layer (Fig. 1A), much of it comprised of the non-indigenous genus of vines, Jasminum (Table 5, Appendix). By the later date, the number of non-indigenous stems in the untreated areas had increased (Fig. 1A). The lowest layer at Deering (one of the sites with a quite-open canopy) was mostly native at the first census (Table 5, Appendix), but not especially dense (Fig. 1A). By the later date, Deering's lowest layer was much denser (Fig. 1A), still mostly native plants (Table 5), predominantly the shade-intolerant genera Petiveria and Rivina (Appendix). The lowest layer at Castellow (the other site with a quite-open canopy) was relatively low in density, with less change between dates than Deering (Fig. 1A), but also predominantly native: Psychotria at both censuses (Table 5, Appendix).

In the 2–4 m layer, the dynamics also differed among the three study sites (Figs. 1E and 2B), in large part because Carica papaya, a rapidly growing non-indigenous seed-bank recruit, figured prominently at two sites, but not at the third. At Matheson, the 2–4 m layer was initially dominated by native shrubs and small trees (Appendix), but by the 26-mo census, the non-indigenous papaya dominated the layer (Figs. 1E and 2B, Appendix). At Deering, the 2–4 m layer was dominated by non-indigenous papayas at both censuses (Figs. 1E and 2B, Appendix). Papayas grew much more rapidly at Deering (which was relatively more open) than at Matheson. Castellow was also a very open canopy site, but apparently papayas were not as abundant in the seed bank there as at the other two sites. In contrast, at Castellow native stems were more numerous than non-indigenous stems at both censuses (Fig. 1E). At the first census the stems consisted mostly of resprouts from fallen or damaged trees (principally Coccoloba) and released "oskars" (Simarouba) (Fig. 2B, Appendix), while at the 26-mo census many stems belonged to a native seed-bank recruit, Solanum (Fig. 2B, Appendix). These native pioneer recruits were in a very open area; nonetheless, they had grown less rapidly than the non-indigenous pioneer papayas of Deering. In summary, in this layer, as in the lowest layer, the differences among the three study sites appear attributable to differences in canopy openness coupled with differences in species availability.

Functional roles of invasive species in forests

For a cross section of species of hammock forests in southern Florida, regeneration sources present at the time
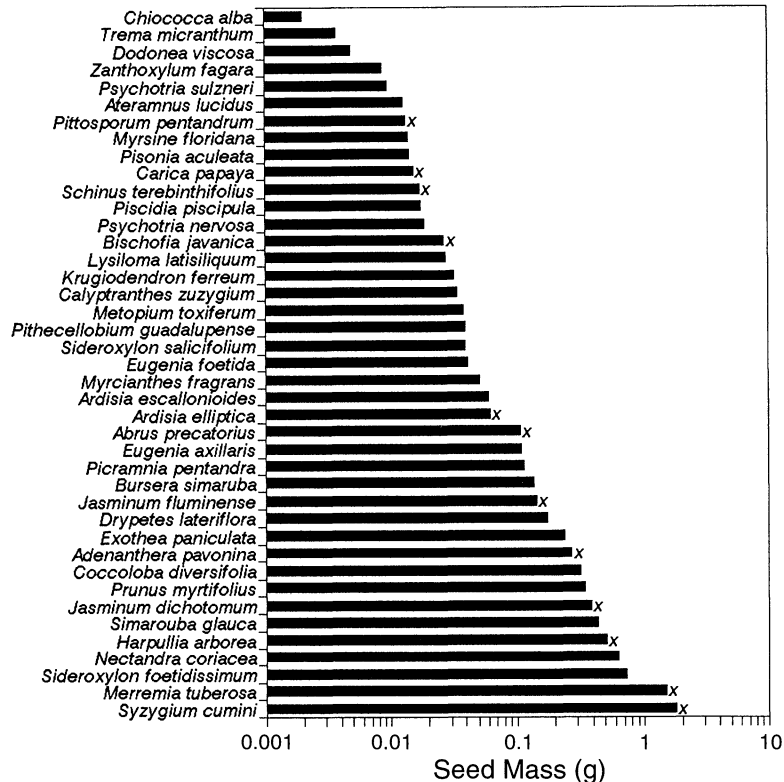
FIG. 3. Seed masses of trees, shrubs, and vines of south Florida subtropical hardwood forests (data are means). Those species that were non-indigenous (=exotic) are marked with an "×."

of the hurricane were seed bank, seed rain, oskars, res-prouts, and root suckers (Table 6). Lianas, thin-stemmed vines, and hemi-epiphytic aroids are separated in this table because they grow differently in the understory and they reach the canopy in distinct ways. Thirty-six examples of native species that used these sources are listed in Table 6. Non-indigenous species that may interfere with each of these groups of natives are also listed in Table 6. Twenty-one non-indigenous examples are listed for the sources that are available at the time of the hurricane. This table also proposes a non-indigenous invasive functional group (described in detail in Table 7) for each of these non-indigenous species.

Similarly, regeneration sources that appeared ≥1 yr after the hurricane were seed rain from surrounding areas, seed rain from a reproductive pulse in the understory, and seed rain from the canopy trees after they recovered vegetatively (Table 6). Eight native species exemplified regeneration from these sources, and six non-indigenous species are listed as examples of species that may interfere with these native sources of regeneration (Table 6).

Functional roles of invasive non-indigenous species were diverse. Non-indigenous species were by no means restricted to colonizing large new gaps through current seed rain by small, shade-intolerant seeds. We propose the following six functional groups of non-indigenous species: (1) seed-bank robbers, (2) seed rain-of-terror, (3) seedling- or juvenile-layer "oskar"-winners, (4) ground-level-resprout stealers, (5) canopy-layer thieves, and (6) vine blankets. The definitions of these groups (Table 7) emphasize how non-indigenous species may negatively impact particular groups of natives (Tables 6 and 7). The names of these groups are meant to suggest the negative impacts of these non-indigenous invasive species on particular ecological groups of native species, although "vine blankets" are likely to negatively impact several different groups of natives (Table 6). Overall, we proposed an invasive guild for 68% ($N = 25$) of the non-indigenous species in our data set.

Many taxa that invade natural habitats in southern Florida also invade subtropical or tropical forests throughout the world (Table 8). The geographic regions of invasion we examined included Western Australia, Pacific islands (the Mariana Islands and Hawaii), Indian Ocean islands (the Mascarene Islands east of Madagascar) and South Africa. We found data and/or observations on 50 taxa, spanning 23 genera, and we propose a non-indigenous invasive guild based on the available data for these taxa (Table 8). Some of these proposals are more well-grounded in data than others; we invite researchers familiar with other regions to consider our hypotheses summarized in this table.

TABLE 6. Regeneration sources of selected species of subtropical hardwood hammock forests. Some species had multiple sources of regeneration. For non-indigenous species, proposed functional groups are also indicated. Species are divided into (A) sources that are present at the time of hurricanes or that become available immediately following hurricanes and (B) sources that appear ≥1 yr after hurricanes.

| | | Non-indigenous | |
Regeneration source	Native species	Species	Functional group
A) Sources present at the time of hurricanes			
Seed bank (pioneers)	*Solanum erianthum*	*Carica papaya*	Seed-bank robber
	Trema micranthum		
	Rivina humilis		
	Petiveria alliacea		
	Psychotria spp.		
Seed rain from external sources			
Surrounding edge areas	*Myrsine floridana*	*Bischofia javanica*	Seed rain-of-terror
Intact forest areas	*Ximenia americana*	*Ardisia elliptica*	Seed rain-of-terror
		Jasminum spp.	Seed rain-of-terror
Suppressed seedling layer	*Simarouba glauca*	*Harpullia arborea*	Seedling-layer oskar-winner
	Eugenia axillaris	*Syzygium cumini*	Seedling-layer oskar-winner
	Nectandra coriacea	*Adenanthera pavonina*	Seedling-layer oskar-winner
	Exothea paniculata	*Jasminum* spp.	Seedling-layer oskar-winner
		Ardisia elliptica	Seedling-layer oskar-winner
		Eugenia uniflora	Seedling-layer oskar-winner
Shrub/small tree stem sprout	*Ardisia escallonioides*	*Ardisia elliptica*	layer oskar-winner
	Psychotria spp.	*Eugenia uniflora*	layer oskar-winner
	Eugenia axillaris		
	Calyptranthes pallens		
Liana sprout	*Pisonia aculeata*	*Jasminum* spp.	Ground-level-resprout stealer
	Vitis spp.		
	Gouania lupuloides		
Thin-stemmed vine sprout	*Ipomoea* spp.	*Paederia crudassiana*	Vine blanket
	Smilax spp.	*Dioscorea bulbifera*	Vine blanket
Aroids	None	*Epipremnum pinnatum*	Vine blanket
Canopy trees			
From seed bank	*Lysiloma latisiliquum*	*Alstonia macrophylla*	Canopy-layer thief
From root suckers	*Ficus aurea*	*Ficus microcarpa*	Canopy-layer thief
	Sideroxylon salicifolium		
	Quercus virginiana		
From fallen stems	*Sideroxylon foetidissimum*	*Bischofia javanica*	Canopy-layer thief
	Coccoloba diversifolia		
	Lysiloma latisiliquum		
From standing stems	*Bursera simaruba*	*Bischofia javanica*	Canopy-layer thief
	Roystonea elata	*Ptychosperma elegans*	Canopy-layer thief
	Ficus aurea	Other non-indigenous	Canopy-layer thief
	Magnolia virginiana	palms	
	Simarouba glauca		
	Nectandra coriacea		
	Coccoloba diversifolia		
	Quercus virginiana		
	Sideroxylon foetidissimum		
B) Sources that appear ≥1 yr after hurricanes			
Seed rain			
Surrounding edge areas	*Metopium toxiferum*	*Schinus terebinthifolius*	Seed rain-of-terror
Surrounding intact-forest areas	*Sideroxylon foetidissimum*	*Ardisia elliptica*	Seed rain-of-terror
		Jasminum spp.	Seed rain-of-terror
Within-site gap-dependent reproductive pulse in the understory			
Shrubs/treelets	*Eugenia axillaris*	*Eugenia uniflora*	Seed rain-of-terror
	Ardisia escallonioides	*Ixora arborea*	Seed rain-of-terror
Canopy trees post-disturbance regrowth-dependent reproduction	*Krugiodendron ferreum*	*Ptychosperma elegans*	Seed rain-of-terror
	Exothea paniculata		
	Ilex krugiana		
	Prunus myrtifolius		

TABLE 7. Proposed functional groupings of invasive non-indigenous plant species in forest communities, their effects on native forest species, and their similarity to invasive guilds of herbaceous communities (Newsome and Noble 1986).

Proposed invasive functional group for forests	Effect of non-indigenous species on native species	Similar invasive guild for herbaceous community
1) Seed-bank robber	Dominates seed bank Shades native pioneer seedlings	Gap-grabber
2) Seed rain-of-terror	Dominates seed rain from both internal and external native species	Swamper
3) Seedling- or juvenile-layer "oskar"-winner	Dominates oskar layer of forest Establishes in shade Outcompetes native shrubs and native suppressed seedlings	Competitor
4) Ground-level-resprout stealer	Shades native tree resprouts from roots and fallen stems Usually aggressive vines	(No equivalent)
5) Canopy-layer thief	Regrows new branches from damaged, standing trunk faster than damaged, standing native trees	Competitor
6) Vine blanket	Shades natives: the "oskar" layer, tree resprouts from roots and fallen stems, and regrowth of new branches from damaged standing stems Usually aggressive vines	(No equivalent)

Note: Group names were chosen to suggest the negative impacts the non-indigenous invasive species have on particular groups of native species.

DISCUSSION

Reasons for high proportions of non-indigenous species

Several causes may contribute to the high proportion of non-indigenous species at our study sites. First, these forests may be susceptible to invasion because of the high overall abundance of non-indigenous naturalized plants in the state of Florida. The proportion of species at our study sites that are non-indigenous (28%), is similar to the statewide pattern in Florida (27%) (Gordon 1998). One reason for this statewide phenomenon is that many (25,000) species have been introduced by humans into Florida (Gordon 1998); even if a small proportion of these become naturalized, a large number of successful, non-indigenous species would be likely in natural habitats.

Second, many subtropical forests, particularly on islands, have a large proportion of non-indigenous species. Examples include the Mascarene Islands (Lorence and Sussman 1986), the Mariana Islands (Craig 1993), and the Hawaiian Islands (Gerrish and Mueller-Dombois 1980). Extreme southern Florida is a subtropical island in a sense, bounded by water on three sides and frost on the north side. Sussman and Rakotozafy (1994) concluded the island effect was the main reason that the Mascarene Islands had a much higher proportion of non-indigenous species than did comparable forests on mainland Madagascar. This hypothesis, however, is not supported by most hammock forests within Everglades National Park (ENP), also located in the "island" of extreme southern Florida. After Hurricane Andrew, subtropical hardwood hammocks inside ENP had few non-indigenous species and stems (S. Koptur, S. Oberbauer, and K. Whelan, *unpublished data*; H. Slater and W. Platt, *unpublished data*).

Third, the location of the study hammocks as small-scale islands within anthropogenically altered landscapes appears likely to be important in the large proportion of non-indigenous species. The landscape surrounding the Dade County (Florida, USA) nature preserves contains urban and agricultural areas that have abundant, non-indigenous vegetation. Nature preserves in general are becoming increasingly fragmented, with many potentially invasive, non-indigenous species in surrounding landscapes (Janzen 1986, Loope and Mueller-Dombois 1989, Pimm 1989, Denslow and Gómez Diaz 1990, Hobbs and Huenneke 1992, Sussman and Rakotozafy 1994).

Our data do not indicate that hurricanes directly cause the high abundance of non-indigenous species, although they do indicate that hurricanes may accelerate invasions and alter the relative abundance of non-indigenous stems in some sites. Hurricane Andrew was not associated with the appearance of new non-indigenous species in Dade County Parks; Metro-Dade County Park plant lists compiled prior to the hurricane contained all the species found in our plots after the hurricane. However, the relative abundances and life-history-stage structures of both non-indigenous and native species changed following the hurricane. These changes, repeated over several cycles of natural disturbance, might result in long-term alteration of hammock structure and species composition.

TABLE 8. Functional groups proposed for species that belong to genera that are invasive in Florida and contain species that are invasive in other subtropical and tropical forests, based on descriptions of their ecological roles in each region of invasion. Observations from the cited literature on seed sizes and dormancy are also listed.

Species	Geographic region of invasion	Forest habitat invaded	Source[†]	Seed size (g)[‡]	Dormancy (yr)	Life-form	Proposed functional group
Acacia auriculiformis	Southern Florida	Sandy pine flatwoods	3, 19			Tree	Seed-bank robber
A. mearnsii	South Africa	Fynbos, forest, savanna, riverine	2	0.1	>50	Tree	Seed-bank robber
A. saligna	South Africa	Fynbos, forest, Evergreen coastal forests (margins and large gaps)	2 4	0.1	>10	Tree	Seed-bank robber
A. longifolia	South Africa	Fynbos, forest, Evergreen upland forests (margins to closed canopy)	2 4	0.1	>5	Tree	Seed rain-of-terror
A. melanoxylon	South Africa	Evergreen forests (invades gaps, becomes canopy)	2 4	0.1	>50	Tree	Seed-bank robber Canopy-layer thief
Albizia falcatorium	Oahu, Hawaii	Wet forest	5			Tree	Seed-bank robber
A. lebbeck	Southern Florida	Miami-Rockridge aggressive invader	13			Tree	
	Mariana Islands, Micronesia	Disturbed secondary forest on limestone substrate	1			Tree	
A. lophantha	South Africa	Fynbos, forest, riverine evergreen forests (margins and large gaps)	2 4	0.1	Yes	Tree	Seed-bank robber
Ardisia crenata	Northern Florida	Mesic temperate hard-wood forest	3, 19			Shrub	Seedling-layer oskar-winner
	Mauritius, Mascarene Islands	Forms thickets in wet forest	14				
	La Reunion, Mascarene Islands	Undisturbed primary forest	15				
	Oahu, Hawaii	Wet forest	5			Shrub	Seedling-layer oskar-winner
A. elliptica	Southern Florida	Bayhead forests	13			Shrub	Seedling-layer oskar-winner
		Subtropical hardwood hammocks	3, 10, 20				
Bauhinia variegata	Southern Florida	Disturbed forest margins	3, 19			Tree	Seed rain-of-terror
	South Africa	Evergreen forests (margins and large gaps)	4				
Bishofia javanica	Southern Florida	Disturbed forest margins	3, 19			Tree	Seed rain-of-terror
		Subtropical hardwood hammocks	10				
	Oahu, Hawaii	Wet forest	5				
Carica benghalensis	South Africa	Evergreen coastal forest (margins to large gaps)	4			"Tree"[§]	Seed-bank robber
C. papaya	Southern Florida	Subtropical hardwood hammocks post-hurricane	10, 16			"Tree"	Seed-bank robber
		Subtropical hardwood hammocks post-fire	18				
	Mariana Islands, Micronesia	Secondary limestone forests (typhoon indicator)‖	1				
	La Reunion, Mascarene Islands	Lava flows, near roadsides	15				

TABLE 8. Continued.

Species	Geographic region of invasion	Forest habitat invaded	Source†	Seed Size (g)‡	Dormancy (yr)	Life-form	Proposed functional group
Casuarina equisetifolia	Florida	(Not specified)	3			Tree	Seedling-layer oskar-winner
		Near planted areas	13				
	La Reunion, Mascarene Islands	Recent lava flows	15				
	South Africa	Evergreen coastal forests (margins and large gaps)	4				
Cinamonum camphora	South Africa	Evergreen forests (margins to closed canopy)	4			Shrub	Seedling-layer oskar-winner
	Florida	Temperate mesic forest	3, 19				
C. zeylanicum	Oahu, Hawaii	Tropical wet forest	5				Seedling-layer oskar-winner
Citrus reticulata	Mauritius, Mascarene Islands	Wet forest	14			Tree	Seedling-layer oskar-winner
Citrus spp.	Southern Florida	Subtropical hardwood hammock	10				
	South Africa	Evergreen upland forests (margins to closed canopy)	4				
Dioscorea bulbifera	Florida	(Not specified)	3			Vine	Vine blanket
		Subtropical hardwood hammocks	10				
	Oahu, Hawaii	Wet forest	5				
Lantana camara	Florida	Forest edges	3, 19			Shrub	Seed rain-of-terror
	Mariana Islands, Micronesia	Secondary limestone forests	1				
	Oahu, Hawaii	Wet forest	5				
	Hawaii	(Not specified)	17				
	La Reunion, Mascarene Islands	Tropical semi-dry forest, lava flows	15				
	South Africa	Fynbos, savanna, forest, karoo/desert	2	0.1	Yes		
		Evergreen coastal forests (margins and large gaps) especially post-fire	4				
Leucaena leucocephala	Florida	Forest edges	3, 19			Tree	Seed-bank robber
	Mariana Islands, Micronesia	Secondary limestone forests	1				
	La Reunion, Mascarene Islands	Tropical semi-dry forest (steep slopes)	15				
	South Africa	Evergreen forests (margins and large gaps)	4				
Ligustrum japonicum	Florida	Mesic temperate hardwood forest	3, 19			Shrub	Seedling-layer oskar-winner
	South Africa	Evergreen forests	4				
L. lucidum	Florida	(Not specified)	3				
L. robustum	Mauritius, Mascarene Islands	Wet forests (forms dense thickets)	14			Shrub	
	La Reunion, Mascarene Islands	Montane rain forest (small gaps and deep shade)	15			Shrub	Seedling-layer oskar-winner
Paederia crudassiana	Southern Florida	Subtropical hardwood hammocks	9, 11			Vine	Vine blanket
		(Not specified)	3				
P. foetida	Florida	Mesic temperate hardwood forest	3, 19			Vine	Vine blanket
	Oahu, Hawaii	Wet forests	5			Vine	

TABLE 8. Continued.

Species	Geographic region of invasion	Forest habitat invaded	Source†	Seed Size (g)‡	Dormancy (yr)	Life-form	Proposed functional group
Passiflora edulis	Southern Florida	Subtropical hardwood hammocks	10			Vine	Resprout stealers
	South Africa	Evergreen forests (margins to closed canopy)	4				
Pithecellobium dulce	Mariana Islands, Micronesia	Secondary limestone forests	1			Shrub	Seed-bank robber
Pittosporum pentandrum	Florida	Hardwood forest edges, pinelands	3, 19				
P. tobira	Florida	(Not specified)	3				
P. undulatum	South Africa	(Not specified)	12				
	South Africa	Fynbos, forest (germinates in shade, but not under itself)	2	0.1	Yes	Tree/ epiphyte	Seedling-layer oskar-winner
	South Africa	Evergreen forests (riverine margins to closed canopy)	4				
	West coast Australia	Forests	7			Shrub	
	Melbourne & Portland, Australia	Eucalyptus forests (rapidly forms dense canopy)	6			Tree	Seedling-layer oskar-winner
Psidium cattleianum	Oahu, Hawaii	Wet forest	5			Tree	Seed rain-of-terror
	Florida	Disturbed wet forest	3, 19				
	Mauritius, Mascarene Islands	Wet forest	14				
	La Reunion, Mascarene Islands	Tropical semi-dry forest and montane rain forest steep slopes, lava flows	15				
	South Africa	Evergreen coastal forests	4				
P. guajava	Oahu, Hawaii	Wet forest	5				
	Southern Florida	Miami Rockridge former pinelands	13			Tree	Seedling-layer oskar-winner
	Florida		3				
	La Reunion, Mascarene Islands	Human-disturbed forests	15				
	South Africa	Forest, savanna, riverine; especially after fire	2, 4	0.1	Yes		
Ricinus communis	Southern Florida	Subtropical hardwood hammock	10				
	South Africa	Savanna, riverine, karoo/desert	2	0.1	Yes	"Treelet"§	Seed-bank robber
		Evergreen coastal forests (margins to large gaps)	4				
Rubus alceifolius	La Reunion, Mascarene Islands	Tropical semi-dry forest post cyclones/ lava flows (climbs into canopy)	15			Liana	Vine blanket
R. cuneifolius	South Africa	Fynbos, savanna, forest, riverine (germinates in shade)	2	0.1	Some	Liana	
		Evergreen forest (gaps to closed forest)	4				
R. moluccanus	Mauritius, Mascarene Islands	Wet forest (forms dense thickets)	14			Shrub	Vine blanket
R. niveus	South Africa	Evergreen forest (margins and large gaps)	4			Shrub	Vine blanket
R. rosaefolius	Oahu, Hawaii	Wet forest	5			Trailing	Vine blanket
R. albescens	Southern Florida	Subtropical hardwood hammock	10			Trailing	

TABLE 8. Continued.

Species	Geographic region of invasion	Forest habitat invaded	Source†	Seed Size (g)‡	Dor-mancy (yr)	Life-form	Proposed functional group
Schinus terebinthifolius	Southern Florida	Disturbed hammocks pineland understory	8			Shrub	Seed rain-of-terror
		On rock-plowed substrate	13				
	Oahu, Hawaii	Wet forest, highly human-disturbed, and lava flows	5				
	Hawaii		17				
	La Reunion, Mas-carene Islands	Forest near human disturbance	15				
	South Africa	Forest, riverine	2	0.1	No		
		Evergreen coastal forest (margins and large gaps)	4				
Solanum auriculatum	La Reunion, Mas-carene Islands	Tropical semi-dry forest and montane rain forest (facilitated by cyclones)	15			Tree	Seed-bank robber
S. mauritianum	South Africa	Pine and wattle plantations	12				Seed-bank robber
		Fynbos, savanna, forest, riverine (germination in fluctuating temp./ high light)	2	0.1	>10	Treelet	
		Evergreen upland forests (margins to large gaps)	4				
S. torvum	Florida		3			Shrub	
S. viarum	Florida		3			Shrub	
S. diphyllum	Florida		3			Shrub	
Syzygium cuminii	Southern Florida	Subtropical hardwood hammocks	10			Tree	Seedling-layer oskar-winner
	Florida		3				
S. jambos	Florida		3			Tree	Seedling-layer oskar-winner
	Mauritius, Mas-carene Islands	Riparian wet forest	14				
	La Reunion, Mas-carene Islands	Tropical semi-dry forest	15				
Syzygium sp.	Southern Florida	Natural areas near Naples, Florida	8				

† Sources: (1) Craig 1993, (2) Dean et al. 1986, (3) Florida EPPC 1995, (4) Geldenhuys et al. 1986, (5) Gerrish and Mueller-Dombois 1980, (6) Gledow and Ashton 1981, (7) Groves 1986, (8) Gunderson 1983, (9) Horvitz 1994, (10) Horvitz et al. 1995, (11) Howard and Schokman 1995, (12) Kruger et al. 1986, (13) Loope and Dunevitz 1981, (14) Lorence and Sussman 1986, (15) MacDonald et al. 1991, (16) Simpson 1932, (17) Yoshioka and Markin 1991, (18) R. Hofstetter, *personal observation*, (19) J. B. Pascarella, *personal observation*, (20) R. Seavey and J. Seavey, *unpublished data.*

‡ Dean et al. (1986) defined seed size by orders of magnitude: m = 0.1 g; s = 0.01 g; vs = 0.001 g (also see Fig. 3 for additional data on seed mass); they also recorded notes on dormancy >1 yr, and the number of years, when known.

§ *Carica* and *Ricinus* are herbaceous, not woody, but are very large herbs that have the form of a tree and the ecological function of an early successional tree.

‖ Post-typhoon successional status.

An abundance of non-indigenous species characterizes other tropical cyclone-prone regions (Gerrish and Mueller-Dombois 1980, Lorence and Sussman 1986, MacDonald et al. 1991). For example, in the Mariana Islands the abundant non-indigenous papaya is considered an "indicator of storms" (Craig 1993). In one forest site on Mauritius, Lorence and Sussman (1986) observed that "non-indigenous invasion [was] accelerated by severe cyclone damage." Similarly, Gelden-

huys et al. (1986), studying evergreen forests of South Africa, found that some non-indigenous species use cyclone-opened areas as establishment sites. Moreover, MacDonald et al. (1991) reported that non-indigenous species in the Mascarene Islands were less adapted to cyclones than native species, so that as forests become dominated by non-indigenous species they became more susceptible to severe canopy damage.

In summary, the insular nature of the region and the

hammocks themselves within the region predispose Florida's hardwood hammocks to invasion by non-indigenous plants, but the proximity of seed sources influences the number and speed of arrival of species to a particular forest. Hurricanes may simply increase turnover of individuals and thereby accelerate ongoing changes in species composition.

Life histories, regeneration sources, and canopy disturbance

Non-indigenous species in hammock forests ranged from small seeded to large seeded, for trees as well as shrubs and vines. Our results contrast with those of Rejmanek and Richardson (1996) who concluded that small-seeded species were more successful invaders than large-seeded species, at least in the genus *Pinus* in pine-savanna/forest systems. The forest system that we studied is shadier (except after hurricanes) than the system that they studied, a feature that may be significant. In tropical hardwood forest systems with dense canopies, large seeds are generally associated with shade-tolerant germination and small seeds are associated with high-light germination (Silvertown 1987, Whitmore 1989). Thus, small seed size is characteristic of pioneers that recruit in large canopy gaps and form seed banks, and large seed size is characteristic of shade tolerants that recruit in smaller canopy gaps and form seedling banks. Other studies of invasion into forests have found that, in mature forest preserves, shaded understory conditions restrict invasion to shade-tolerant, non-indigenous species (Geldenhuys et al. 1986, Harty 1986), whereas shade-intolerant, non-indigenous species are restricted to infrequent large gaps or forest edges.

In our study, amount of canopy disturbance was associated with the relative importance of non-indigenous and native species and with different sources of regeneration in post-hurricane stem dynamics. Castellow and Deering hammocks had considerably more canopy damage than did Matheson (Horvitz et al. 1995), and recruitment from dormant seeds was much more important at the former two sites immediately after Andrew. Negative impacts of non-indigenous seed-bank species on native seed-bank species may occur only under conditions of very open canopy. Seed-bank species have relatively small seeds, and do not germinate in shaded conditions. Matheson had much less canopy disturbance, and oskars were a more important source of stems. But Matheson also had higher pre-hurricane abundances of non-indigenous oskar seedlings of vine, tree, and shrub species. Negative impacts of non-indigenous oskar species on native oskar species and on other species using shade-tolerant advance regeneration could occur in forests with relatively less open canopy.

The particular hammocks that we studied included two sites that were in the most intense winds of a very severe hurricane. It is likely that most other hammocks affected by Andrew were less damaged than these two sites. For example, the many subtropical hammock forests in ENP that were affected by Andrew had wind speeds (Powell and Houston 1996) and tree mortality (Loope et al. 1994, Slater et al. 1995, and S. Koptur, S. Oberbauer, and K. Whelan, *unpublished data*) more similar to Matheson than to Deering or Castellow (Horvitz et al. 1995). ENP hammocks, because they were more similar to Matheson in canopy openness than to Deering or Castellow, may have been more at risk (following Andrew) of negative impacts by large-seeded, shade-tolerant, non-indigenous species than by small-seeded, colonizing, non-indigenous species.

Regeneration sources and functional roles of invasive species

Newsome and Noble (1986) also have proposed functional groups for invasive species. Some of their groups, based on studies of herbaceous communities, are similar to our groups of invasive species of forest communities. Our seed-bank robber and seed rain-of-terror groups are similar to their "gap-grabber" and "swamper" groups (Table 7). Similarly, our oskar-winner and canopy-thief groups are similar to their "competitors" (Table 7); the greater vertical structural complexity of forests seems to require a separation of competitors in the understory from competitors in the canopy. Finally, vine blankets, composed of aggressive vines in forests, appear not to have a parallel in herbaceous communities, at least according to Newsome and Noble's scheme (Table 7).

We attempted to match regeneration sources of native species with regeneration sources of non-indigenous species to understand the ecological roles of non-indigenous species in the regeneration process. Toward this end, we assigned more than two thirds of the non-indigenous species in our data set to invasive guilds. This kind of matching suggests which non-indigenous species are likely to compete with which native species, and at which life-history stages the significant interactions may occur. Four examples serve to focus discussion on how non-indigenous invasive species sometimes interact with natives.

Seed-bank robbers.—There are several causes and effects of non-indigenous species taking over the seed bank of a native community. Dean et al. (1986) suggested an advantage after a disturbance for species that numerically dominate seed banks; species that become more numerous in the seed bank may recruit more seedlings. In addition, non-indigenous seed-bank species may displace natives through competition for light after germination. The seed-bank robber *Carica papaya* may be competitively superior to native pioneers at the seedling stage. The seedlings of this species rapidly form a large umbrella-shaped plant that can shade the smaller seedlings of native seed-bank species like *Solanum* and

Trema. Since only large gaps and high heat (J. B. Pascarella, *unpublished data*) stimulate germination of papaya, and only strong hurricanes create such large gaps, the takeover of the seed bank may occur only after several cycles of intense disturbance.

Non-indigenous pioneers may or may not be equivalent to native pioneers with respect to gap-phase succession that occurs following disturbances (Geldenhuys et al. 1986). Papayas are advocated for "use" in forest restoration projects in southern Florida to create shade, one reason they were not targeted by the Dade County Parks Non-indigenous-Removal Program (G. Gann, *personal communication*). Non-indigenous plants that take over the natural seed bank may profoundly alter subsequent forest dynamics by changing the type and longevity of initial shade produced after disturbances. Native pioneers *Trema* and *Solanum* are 3–4 times longer-lived and create a broadly branched canopy ~3 yr after germination. In contrast, papayas die at about that age and are mostly unbranched, thus providing shade over a smaller area for a shorter period of time.

Species that are seed-bank robbers in Florida appear to play a similar role in other regions. Papaya is one example. Other examples include hard-seeded legumes with dormant seeds (e.g., *Acacia, Albizia*). They may be non-indigenous analogues of the native hard-seeded legume with dormant seeds, *Lysiloma*; perhaps this native species is at risk of being displaced over the long term from its characteristic habitat, hammock forests that are surrounded by pine forests, by these genera that have been successful seed-bank robbers elsewhere.

Seed rain-of-terror.—There are several causes and effects of non-indigenous seeds assuming dominance of the seed rain over native seeds. One kind of effect may be purely numerical; more of them may reach the forest floor and thereby swamp out native recruitment by sheer numbers. In addition, they may find and occupy recruitment sites by more efficient dispersal. Such seed rain-of-terror species as *Schinus, Bischofia,* and *Eugenia uniflora* produce large seed crops attractive to animal dispersers. Data from mist-netted birds in ENP indicate that a native frugivore, the Grey Catbird (*Dumetella carolinensis*), readily consumes both native and non-indigenous fruits in subtropical hardwood hammocks (C. C. Horvitz, T. H. Fleming, R. Seavey, and J. Seavey, *unpublished data*). It is not known whether frugivores prefer non-indigenous fruits over native fruits, whether some non-indigenous fruit resources affect the population dynamics of frugivores, or whether frugivores provide better seed dispersal for non-indigenous than for native plants. Because hurricanes open forest canopies, resulting in a pulse of fruit production by both native and non-indigenous understory shrubs, seed-rain effects may increase in importance following hurricanes. An increase in frugivore activity in hammocks ~1.5 yr post-Andrew (C. C. Horvitz, T. H. Flem-

ing, R. Seavey and J. Seavey, *unpublished data*) may have increased the risk of new invasions of hammocks by fleshy-fruited non-indigenous species.

Among the taxa that we reviewed both in Florida and in other tropical and subtropical forests, *Schinus terebinthifolius* seems to be the global champion in the seed rain-of-terror category. In southern Florida, pine savannas and hammock margins (especially where fires have been eliminated), abandoned agricultural areas that have altered substrate, and mangrove edges are more often invaded by this species than are hammocks. Nevertheless, this species invades ENP hammocks, especially after fires (W. J. Platt, *personal communication*).

Other examples of seed rain-of-terror species can be found among temperate forest species. The annual herb *Impatiens glandulifera* invades temperate forest interiors in the Czech Republic after natural flooding of nearby rivers and streams (Pysek and Prach 1993) and disperses copious seed rain into the forest understory. The herb *Alliaria petidata,* which disperses numerous seeds into temperate forests (presumably into gaps) from the forest edge (Robinson et al. 1994), also appears to belong to this group.

Seedling- or juvenile-layer "oskar"-winners.—There may be several causes and effects of the seedling or juvenile layer becoming dominated by non-indigenous species. Geldenhuys et al. (1986:123) observed that "alien plants able to reproduce and establish in the closed forest are ... likely to become problem plants ... in forest biomes." Seedling- or juvenile-layer oskar-winners are shade-tolerant, non-indigenous species (e.g., *Ardisia elliptica, Jasminum* spp.) that germinate, grow, and reproduce in undisturbed forest. They may be the biggest threat to hurricane-prone forests, in which much regeneration occurs from understory sources. We propose that oskar-winners have a negative effect on native tree species that have a seedling or juvenile bank, such as *Eugenia axillaris* or *Simarouba glauca*. Also, they might outcompete seedlings of native shrubs such as *Ardisia escallonioides*. Monospecific clumps of non-indigenous, shade-tolerant species may be more likely to arise than monospecific clumps of natives, because non-indigenous species may be relatively free of biotic enemies (Elton 1958, Forcella 1985, Gray 1986). A diverse native understory may be taken over entirely by such monospecific stands of enemy-free, non-indigenous species. Such was the case in a human-altered bayhead forest in ENP that was near Royal Palm Hammock. *A. elliptica* spread from the bayhead to the hammock, where it was beginning to dominate the understory by the mid-1980s, until it was removed by management (R. Seavey and J. Seavey, *unpublished data*).

The oskar-winner guild was frequent among those Dade County taxa that occur in other tropical regions of the world, suggesting that advance regeneration into

forest communities by non-indigenous species is common in subtropical and tropical forests. There are also examples of oskar-winners in temperate forests. *Euonymous alatus* is an understory shrub that might be acting as an oskar-winner in temperate upland oak forests in Illinois (Harty 1986). Shade-tolerant *Rhododendron ponticum* may be playing a similar role in the oakwood forests of southwestern Ireland (Cross 1981), even if it does not maintain suppressed seedlings of its own, in that any species that forms dense, mono-specific clumps in shaded understory may prevent native oskar species from regenerating.

Vine-blankets.—Non-indigenous vines may negatively influence forest regeneration through competition with native vines and with fallen as well as standing, damaged native trees. In addition to preempting resources, they also may strangle native tree seedlings and juveniles by host phloem constriction (Hegarty 1991, Putz 1991). Also, non-indigenous vine tangles may create greater inter-tree connection, causing more trees to tip up during wind storms (Lorence and Sussman 1986, MacDonald et al. 1991, Putz 1991).

The extent to which non-indigenous vines negatively influence forest regeneration depends on species-specific morphological and ecophysiological traits. For example, lianas have shade-tolerant, self-supporting seedlings that can climb small to medium supports (Gentry 1991). In contrast, shade-intolerant herbaceous vines are limited to thin-stemmed hosts and require large gaps for seed germination and seedling survival (Gentry 1991, Hegarty and Caballe 1991). These species are often ephemeral. Adventitious root climbers (hemi-epiphytic aroids, e.g., *Epipremnum*) may dominate local patches of forest, forming dense mats of stems and leaves, both on the ground as well as in canopies.

Pre-Andrew species composition influenced the importance of both native and non-indigenous vines in post-Andrew forest dynamics; both were common in all sites post-hurricane. Matheson (the site with the most abundant non-indigenous vines pre-hurricane) had high (and increasing) post-hurricane abundance of non-indigenous vines, and a correspondingly low (and decreasing) abundance of native vines as compared with other sites, which suggests that non-indigenous vines have negative impacts on native vines. Non-indigenous vine species tended to have higher plot cover than native vine species, which suggests distinct impacts of non-indigenous vines on forest dynamics.

Caribbean forests, including the subtropical hammocks of Florida, are low in native vine numbers compared with other kinds of tropical forests. This observation leads to the "empty-niche" hypothesis: that non-indigenous vines readily invade hammocks because native vines have not filled all potential vine niches. Another observation is that native vines are primarily temperate in origin, but non-indigenous vines

are tropical in origin. Tropical vines may be more shade-tolerant than native vines; in this case a long-term effect of their dense cover may be greater ablility to recruit under their own dense shade better than native vines. Moreover, the absence of biotic enemies, as with other non-indigenous species, may allow the non-indigenous vines to become dense.

Post-disturbance invasion by non-indigenous vines has also been noted in other forests. *Lonicera japonica* invades temperate deciduous forests after natural disturbances, such as treefalls from wind or disease, although it does not require a gap for germination or spread (R. K. Peet, *personal communication*). After gap formation, native shrubs and saplings are crushed or strangled by its rapid vegetative growth, and native trees may be affected by root or moisture competition (Woods 1993, Robinson et al. 1994). This liana might be acting as a vine blanket. A similar role is played by *Fuchsia magellanica* in montane, mixed-evergreen rain forests in La Reunion, Mascarene Islands (MacDonald et al. 1991).

CONCLUSIONS

There have been two opposing views on the success of invasive species. First, invaders may displace natives from their own niches, either stochastically or by superior competitive ability (Elton 1946, Lack 1947, Hutchinson 1959). Second, invaders may occupy niches not occupied by natives (Mooney and Drake 1989, Rejmanek 1989). The second view applies to the success of non-indigenous species in human-altered habitats. Non-indigenous organisms may be expected to establish readily in highly anthropogenically disturbed areas (Elton 1958) such as roadsides, agricultural fields, pastures, and urban areas (Ramakrishnan and Vitousek 1989, Ghersa and Rousch 1993), especially those with highly altered substrates (Doren and Whiteaker 1990), fire regimes (Ewel 1986, Groves 1989), drainage patterns (Alexander 1967, Alexander and Crook 1975), or grazing intensities (Mack 1985). Human disturbance may create new, unoccupied niches free of native species (Hobbs 1989) and susceptible to invasion by colonizing species. Most significantly, such disturbance may create conditions that are not similar to those for which native species are adapted (Gerrish and Mueller-Dombois 1980, Noble and Slatyer 1980, Weiss and Milton 1984, Noble 1989, Doren and Whiteaker 1990). In contrast, the former view emphasizes the displacement of native species by non-indigenous species within areas that are relatively free of anthropogenic disturbance; this type of invasion is a more complex process and an intrinsically more serious threat to biodiversity conservation. Such invasions imply that nature preserves may not be "safe" havens for conservation of native species and of native ecological processes (Janzen 1986, Ramakrishnan and Vitousek 1989).

Our proposed functional roles for invasive species

emphasizes the negative impacts of non-indigenous on native species. Our concept of invasive functional groups clarifies the diversity of life histories of non-indigenous plants with respect to natural-disturbance regimes and focuses on the potential for interactions between subsets of native and non-indigenous species. Understanding the roles of life-history characteristics of non-indigenous species in the dynamics of natural forests may also provide clues to managers about which life-history stages of particular invasive species require the most control.

LITERATURE CITED

Alexander, T. R. 1967. A tropical hammock on the Miami (Florida) limestone—a twenty-five-year study. Ecology 48: 863–867.

Armentano, T. V., R. F. Doren, W. J. Platt, and T. Mullins. 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. Journal of Coastal Research (Special Hurricane Andrew Issue) 21: 111–144.

Attiwill, P. M. 1994. Ecological disturbance and the conservative management of eucalypt forests in Australia. Forest Ecology and Management 63:301–346.

Austin, D. F. 1980. Historically important plants of southeastern Florida. Florida Anthropologist 33:17–31.

Brokaw, N. V. L., and J. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo mountains, Puerto Rico. Biotropica 23:386–392.

Brokaw, N. V. L., and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23:442–447.

Chen, E., and J. F. Gerber. 1990. Climate. Pages 11–34 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Connell, J. H. 1989. Some processes affecting the species composition in forest gaps. Ecology 70:560–562.

Craig, R. J. 1993. Regeneration of native Mariana Island forest in disturbed habitats. Micronesica 26:99–108.

Craighead, F. C., Sr. 1971. The trees of South Florida. University of Miami Press, Coral Gables, Florida, USA.

———. 1974. Hammocks of South Florida. Pages 53–59 in P. J. Gleason, editor. Environments of South Florida: present and past. Memoir 2. Miami Geological Society, Miami, Florida, USA.

Cross, J. R. 1981. The establishment of Rhododendron ponticum in the Killarney Oakwoods, SW Ireland. Journal of Ecology 69:807–824.

Cruickshank, H. G. 1986, editor. William Bartram in Florida, 1774. The adventures of the great American explorer, artist. Florida Federation of Garden Clubs, Florida, USA.

Davis, J. H., Jr. 1943. The natural features of Southern Florida, especially the vegetation, and the Everglades. Florida Geological Survey, Geological Bulletin Number 25. State of Florida Department of Conservation, Tallahassee, Florida, USA.

Dean, S. J., P. M. Holmes, and P. W. Weiss. 1986. Seed biology of invasive alien plants in South Africa and South West Africa/Namibia. Pages 157–170 in I. A. W. MacDonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Proceedings of the National Synthesis Symposium on the ecology of biological invasions. Oxford University Press, Cape Town, South Africa.

Dean, W. R. J., S. J. Milton, P. G. Ryan, and C. L. Moloney. 1994 The role of disturbance in the establishment of indigenous and alien plants at Inaccessible and Nightingale Islands in the South Atlantic Ocean. Vegetatio 113:13–23.

Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46:18–21.

Denslow, J. S., and A. E. Gómez Diaz. 1990. Seed rain to treefall gaps in a neotropical rain forest. Canadian Journal of Forest Research 20:642–648.

Doren, R. F., W. J. Platt, and L. D. Whiteaker. 1993. Density and size structure of slash pine stands in the everglades region of south Florida. Forest Ecology and Management 59:295–311.

Doren, R. F., and L. D. Whiteaker. 1990. Comparison of economic feasibility of chemical control strategies on differing age and density classes of Schinus terebinthifolius. Natural Areas Journal 10:28–34.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson. 1989. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Elton, C. S. 1946. Competition and the structure of ecological communities. Journal of Animal Ecology 15:54–68.

———. 1958. The ecology of invasions by animal and plants. John Wiley & Sons, New York, New York, USA.

Ewel, J. J. 1986. Invasibility: lessons from South Florida. Pages 214–230 in H. A. Mooney and J. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Fernandez, D. S., and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. Biotropica 23:393–399.

Florida EPPC [Exotic Pest Plant Council]. 1995. Florida nonindigenous pest plant council's 1995 list of Florida's most invasive species. Florida EPPC Newsletter 5:5.

Forcella, F. 1985. Final distribution is related to rate of spread in alien weeds. Weed Research 25:181–191.

Geldenhuys, C. J., P. J. le Roux, and K. H. Cooper. 1986. Alien invasions in indigenous evergreen forest. Pages 119–131 in I. A. W. MacDonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Proceedings of the National Synthesis Symposium on the ecology of biological invasions. Oxford University Press, Cape Town, South Africa.

Gentry, A. H. 1991. The distribution and evolution of climbing plants. Pages 3–53 in F. E. Putz and H. A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Gerrish, G., and D. Mueller-Dombois. 1980. Behavior of native and non-native plants in two tropical rainforests on Oahu, Hawaiian Islands. Phtyocoenologia **8**:237–295.

Ghersa, C. M., and M. L. Roush, 1993. Searching for solutions to weed problems. BioScience **43**:104–109.

Gledow, R. M., and D. H. Ashton. 1981. Invasion by *Pittosporum undulatum* of the forest of central Victoria. I. Invasion patterns and plant morphology. Australian Journal of Botany **29**:705–720.

Gordon, D. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications **8**:975–989.

Grace, S. L., and W. J. Platt, 1995. Effects of adult tree density and fire on the demography of pre-grass stage juvenile longleaf pine (*Pinus palustris* Mill.) Journal of Ecology **95**:75–86.

Gray, A. J. 1986. Do invading species have definable genetic characteristics? Philosophical Transactions of the Royal Society London **B 314**:655–674.

Groves, R. H. 1986. Plant invasions of Australia: an overview. Pages 137–149 *in* R. H. Groves and J. J. Burdon, editors. Ecology of biological invasions. Cambridge University Press, Sydney, Australia.

―――. 1989. Ecological control of invasive terrestrial plants. Pages 437–461 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions, a Global Perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Gunderson, L. H. 1983. Status of exotic woody species in Big Cypress National Preserve. Report SFRC-83/07. South Florida Research Center, Everglades National Park, Homestead, Florida, USA.

Harty, F. M. 1986. Exotics and their ramifications. Natural Areas Journal **6**:20–26.

Hegarty, E. E. 1991. Vine–host interactions. Pages 357–377 *in* F. E. Putz and H. A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Hegarty, E. E., and G. Caballe. 1991. Distribution and abundance of vines in forest communities. Pages 313–337 *in* F. E. Putz and H. A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasion. Pages 389–405 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Hobbs, R. J., and L. F. Huenneke, 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324–337.

Horvitz, C. C. 1994. Hammocks and hurricanes: a surprisingly diverse array of non-indigenous plants threaten the natural regeneration of hardwood hammocks after hurricanes. Box 3.7.a *in* D. C. Schmitz and T. C. Brown, editors. An assessment of invasive non-indigenous species in Florida's public lands. Technical Report Number TSS-94-100. Florida Department of Environmental Protection, Tallahassee, Florida, USA.

Horvitz, C. C., S. McMann, and A. Freedman. 1995. Exotics and hurricane damage in three hardwood hammocks in Dade County Parks, Florida. Journal of Coastal Research (Special Hurricane Andrew Issue) **18**:145–158.

Howard, R. A., and L. Schokman. 1995. Recovery responses of tropical trees after Hurricane Andrew. Harvard Papers in Botany **6**:37–74.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why there are so many kinds of animals? American Naturalist **93**:145–159.

Janzen, D. H. 1986. The eternal external threat. Pages 286–303 *in* M. E. Soulé, Editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Kruger, F. J., D. M. Richardson, and B. W. van Wilgen. 1986. Processes of invasion by alien plants. Pages 145–155 *in* I. A. W. MacDonald, F. J. Kruger and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Proceedings of the National Synthesis Symposium on the ecology of biological invasions. Oxford University Press, Cape Town, South Africa.

Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge, UK.

Little, E. L., Jr., and F. H. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. Agriculture Handbook Number 249. USDA Forest Service, Washington, D.C., USA.

Little, E. L., Jr., R. O. Woodbury, and F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands. Second Volume. Agricultural Handbook Number 449. USDA Forest Service, Washington, D.C., USA.

Loope, L., M. Duever, A. Herndon, J. Snyder, and D. Jansen. 1994. Hurricane impact on uplands and freshwater swamp forest. BioScience **44**:238–246.

Loope, L. L., and V. L. Dunevitz. 1981. Impact of fire exclusion and invasion of *Schinus terebinthifolius* on limestone rockland pine forests of southeastern Florida. U.S. National Park Service Report T-645. South Florida Research Center, Homestead, Florida, USA.

Loope, L. L., and D. Mueller-Dombois. 1989. Characteristics of invaded islands, with special reference to Hawaii. Pages 257–280 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Lorence, D. H., and R. W. Sussman. 1986. Exotic species invasion into Mauritius wet forest remnants. Journal of Tropical Ecology **2**:147–162.

MacDonald, I. A. W., C. Thebaud, W. A. Strahm, and D. Strassberg. 1991. Effects of alien plant invasions on native vegetation remnants on La Reunion (Mascarene Islands, Indian Ocean). Environmental Conservation **18**:51–61.

Mack, R. N. 1985. Invading plants: their potential contribution to population biology. Pages 127–142 *in* J. White, editor. Studies in plant demography: a festschrift for John L. Harper. Academic Press, London, UK.

Mayfield, M., L. Avila, and N. Rappaport. 1994. Atlantic hurricane season of 1992. Preliminary report (updated 2 March 1993) Hurricane Andrew 16–28 August 1992. Monthly Weather Review **122**:517–538.

Molnar, G. 1990. Successional dynamics of a tropical hardwood hammock on the Miami rockridge. Thesis. Florida International University, Miami, Florida, USA.

Mooney, H. A., and J. A. Drake. 1989. Biological invasions: a SCOPE program overview. Pages 491–506 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions, a Global Perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Nakasone, H. Y. 1975. About our cover. Horticultural Science (Calcutta) **10**:198.

Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. Pages 1–20

in R. H. Groves and J. J. Burdon, editors. Ecology of biological invasions. Cambridge University Press, Sydney, Australia.

Noble, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. Pages 301–313 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5–21.

Olmsted, I. C., W. B. Robertson, Jr., and O. L. Bass, Jr. 1983. The vegetation of Long Pine Key, Everglades National Park. Report SFRC-83/05. South Florida Research Center, Homestead, Florida, USA.

Parker, I. M., S. K. Mertens, and D. W. Schemske. 1993. Distribution of seven native and two exotic plants in tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist 130:43–55.

Pascarella, J. B. 1995. The effects of Hurricane Andrew on the population dynamics and the mating system of the tropical understory shrub Ardisia escallonioides (Myrsinaceae). Dissertation. University of Miami, Coral Gables, Florida, USA.

Pascarella, J. B., and C. C. Horvitz, 1998. Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis. Ecology 79: 547–563.

Phillips, W. S. 1940. A tropical hammock on the Miami (Florida) limestone. Ecology 21:166–175.

Pimm, S. L. 1989. Theories of predicting species success and impact of introduced species. Pages 351–367 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Pimm, S. L., G. E. Davis, L. E. Loope, C. T. Roman, T. J. Smith III, and J. T. Tilmant. 1994. Hurricane Andrew. BioScience 44:224–229.

Platt, W. J. 1998. Southeastern pine savannas. *In* R. C. Anderson, J. S. Fralish, J. Baskin, editors. The savanna, barren and rock outcrop communities of North America. Cambridge University Press, Cambridge, UK, *in press*.

Platt, W. J., G. W. Evans, and S. L. Rathburn. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). American Naturalist 131:491–525.

Popenoe, W. 1920. Manual of tropical and subtropical fruits. Macmillan, New York, New York, USA.

Poulson, T., and W. J. Platt. 1989. Gap light regimes influence canopy tree diversity. Ecology 70:553–555.

Poulson, T., and W. J. Platt. 1996. Replacement patterns of beech and sugar maple in Warren Woods. Ecology 77: 1234–1253.

Powell, M. D., and S. H. Houston. 1996. Hurricane Andrew's landfall in South Florida. Part II. Surface wind fields and potential real-time applications. Weather and Forecasting 11:329–349.

Prance, G. T. 1984. The Pejibaye, *Guilielma gasipaes* (HBK) Bailey, and the Papaya, *Carica papaya* L. Pages 85–104 *in* D. Stone, editor. Pre-Columbian Plant Migration. Papers of the Peabody Museum of Archaeology and Ethnology, Volume 76, Harvard University Press, Cambridge, Massachusetts, USA.

Putz, F. E. 1991. Silvicultural effects of lianas. Pages 493–

503 *in* F. E. Putz and H. A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Putz, F. E., and N. V. L. Brokaw. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. Ecology 70:508–512.

Pyšek, P., and K. Prach. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central europe. Journal of Biogeography 20:413–420.

Ramakrishnan, P. S., and P. M. Vitousek. 1989. Ecological-level processes and the consequences of biological invasions. Pages 281–300 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York, USA.

Rejmanek, M. 1989. Invasibility of plant communities. Pages 369–388 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions, a global perspective. Scientific Committee on Problems (SCOPE) of the Environment of International Council of Scientific Unions (ICSU). John Wiley & Sons, New York, New York USA.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1660.

Robinson, G. R., M. E. Yurlina, and S. N. Handel. 1994. A century of change in the Staten Island flora: ecological correlates of species losses and invasions. Bulletin of the Torrey Botanical Club 121:119–129.

Runkle, J. R., 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree diversity. Ecology 70:546–547.

SAS Institute. 1989. SAS user's guide, release 6.09 Edition. SAS Institute, Cary, North Carolina, USA.

Scarry, C. M. 1985. Paleoethnobotany of the Granada Site. Pages 181–248 *in* J. W. Griffin, S. B. Richardson, M. Pohl, C. D. McMurray, C. M. Scarry, S. K. Fish, E. S. Wing, L. J. Loucks, and M. K. Welch, editors. Excavations at the Granada Site. Volume I. Florida Divisions of Archives, History and Records Management, City of Miami, Florida, USA.

Silvertown, J. W. 1987. Introduction to plant population ecology. John Wiley & Sons, New York, New York, USA.

Simpson, C. T. 1932. Florida wildlife. Observations on the flora and fauna of the state and the influence of climate and environment on their development. Macmillan, New York, New York, USA.

Simpson, R. H., and M. B. Lawrence. 1971. Atlantic hurricane frequencies along the U.S. coastline. NOAA Technical Memorandum **NWS SR-58**.

Slater, H. H., W. J. Platt, D. B. Baker, and H. A. Johnson. 1995. Effects of Hurricane Andrew on damage and mortality of trees in subtropical hardwood hammocks of Long Pine Key, Everglades National Park, Florida, USA. Journal of Coastal Research (Special Hurricane Andrew issue) 18: 197–207.

Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida rockland. Pages 230–277 *in* R. L. Myers, and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Stambaugh, S. U. 1945. The papaya: a fruit suitable for S. Florida. State of Florida Department of Agriculture New Series Number **90**.

Sturtevant, E. L. 1919. Sturtevant's notes on edible plants. New York Agricultural Experiment Station, Geneva, New York.

Sussman, R. W., and A. Rakotozafy. 1994. Plant diversity

and structural analysis of a tropical dry forest in south-western Madagascar. Biotropica **26**:241–254.

Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. American Naturalist **126**:760–776.

Tomlinson, P. B. 1980. The biology of trees native to tropical Florida. P. B. Tomlinson, Allston, Massachusetts, USA.

Veblen, T. T. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology **70**:541–543.

Walker, L. R., 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica **23**:379–385.

Weiss, P. W., and S. Milton. 1984. *Chrysanthemoides monilifera* and *Acacia longifolia* in Australia and South Africa. Pages 159–160 *in* B. Dell, editor. Proceedings of 4th International Conference on Mediterranean Ecosystems. Botany Department, University of Western Australia, Nedlands, Perth, Western Australia, Australia.

Weiss, P. W., and I. R. Noble. 1984*a*. Status of coastal dune communities invaded by *Chrysanthemoides monillifera*. Australian Journal of Ecology **9**:93–98.

Weiss, P. W., and I. R. Noble. 1984*b*. Interactions between seedlings of *Chrysanthemoides monilifera*. Australian Journal of Ecology **9**:107–115.

Whitmore, T. C. 1989. Canopy gaps and two major groups of forest trees. Ecology **70**:536–537.

Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. American Midland Naturalist. **130**:62–74.

Yih, K., D. H. Boucher, J. H. Vandermeer, and N. Zamora. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. Biotropica **23**: 106–111.

Yoshioka, E. R., and G. P. Markin. 1991. Effects of biological control of Christmas Berry (*Schinus terebinthifolius*) in Hawaii. Pages 377–387 *in* T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers, and L. D. Whiteaker, editors. Proceeding of the Symposium on Exotic Pest Plants. Technical Report NPS/NREVER/MRTR-91/06. National Park Service, Washington, D.C., USA.

APPENDIX

Origin and regeneration source of the most abundant taxa in the three most dynamic layers of the forest. "Origin" is defined as native (N) or non-indigenous (X), according to species. Data are from three subtropical hardwood hammock forest study sites in southern Florida, USA; censuses are 8 mo and 26 mo post-hurricane. "Untreated" = study sites not being managed for restoration; "restored" = subject to aggressive management, begun 13 mo post-hurricane, to reduce non-indigenous vine cover. For each subset of data, defined by cross-classifying observations by hammock, type of treatment area, and census date, the percentage of stems representing a particular taxon and regeneration source is given (N = total no. of stems in a hammock by type-of-treatment-area by census-date class). For each column (subset of data) only the three most abundant taxa are given (except in the case of ties). Note that some taxa have more than one regeneration source.

Species	Origin	Regeneration source†	Castellow Untreated 8	26	Castellow Restored 8	26	Deering Untreated 8	26	Deering Restored 8	26	Matheson Untreated 8	26	Matheson Restored 8	26
A) <0.25-m stratum														
No. of stems			89	306	118	225	109	439	58	871	266	426	608	251
No. of taxa counted			3	3	3	3	3	3	3	3	3	3	3	3
Species														
Celtis laevigata	N	Unknown	···	···	···	···	···	···	10.3	···	···	···	···	···
Eugenia axillaris	N	Rain	···	6.2	···	16.4	···	22.3	···	8.8	···	21.1	···	16.7
E. axillaris	N	Oskar	···	0.3	···	···	···	1.1	···	0.2	30.8	19.2	9.7	23.5
E. uniflora	X	Rain	···	···	···	···	···	···	···	···	···	···	···	6.4
Jasminum spp.	X	Rain	···	11.8	···	20.9	···	···	···	···	···	20.4	···	19.1
Jasminum spp.	X	Oskar	18.0	5.2	19.5	10.2	···	···	···	···	21.4	13.4	64.8	···
Nectandra coriacea	N	Oskar	···	···	···	···	8.3	···	···	···	19.5	6.6	8.7	···
Nephrolepis exaltata	N	Rhizome	···	···	22.0	···	···	···	···	···	···	···	···	···
Parthenocissus quinquefolia	N	Unknown	···	···	···	···	···	···	22.4	···	···	···	···	···
Petiveria alliacea	N	Seedbank	···	···	···	···	30.3	21.2	12.1	16.5	···	···	···	···
Pisonia aculeata	N	Liana	11.2	···	···	···	···	···	···	···	···	···	···	···
Psychotria spp.	N	Seedbank	24.7	14.4	14.4	22.7	8.3	···	···	···	···	···	···	···
Rivina humilis	N	Seedbank	···	···	···	···	···	18.9	···	46.7	···	···	···	···
Sum most abundant			53.9	37.9	55.9	70.2	46.9	63.6	44.8	72.3	71.8	80.8	83.2	65.7
Sum others			46.1	62.1	44.1	29.8	53.1	36.4	55.2	27.7	28.2	19.2	16.8	34.3
B) 2–4 m stratum														
No. of stems			34	86	30	147	71	98	58	68	68	141	78	97
No. of taxa counted			3	3	4	3	3	3	5	3	4	3	3	3
Species														
Ardisia escallonioides	N	Stem	···	···	···	···	···	···	6.9	···	···	···	···	···
Bischofia javanica	X	Stem	···	···	16.7	···	···	···	···	···	···	···	···	···
Carica papaya	X	Seedbank	···	11.6	···	···	47.9	54.1	48.3	52.9	19.1	52.5	1.3	21.6
Calyptranthes pallens	N	Stem	···	···	···	···	···	···	6.9	13.2	···	···	···	···
Coccoloba diversifolia	N	Stem	20.6	23.3	16.7	27.2	12.7	7.1	···	···	10.3	8.5	17.9	21.6
Eugenia axillaris	N	Stem	···	···	···	···	···	···	6.9	···	26.5	19.9	28.2	40.2
Ficus aurea	N	Stem	···	···	···	···	···	···	···	···	10.3	···	···	···
Jasminum spp.	X	Liana	···	···	13.3	···	···	···	···	···	···	···	···	···
Magnolia virginiana	N	Stem	···	···	···	···	···	6.1	···	···	···	···	···	···
Nectandra coriacea	N	Stem	···	10.5	···	5.4	···	···	···	7.4	···	···	···	···
Pisonia aculeata	N	Liana	8.8	···	···	···	···	···	···	···	···	···	···	···
Ricinus communis	X	Seedbank	···	···	···	···	11.3	···	12.1	···	···	···	···	···
Simarouba glauca	N	Stem	17.6	···	13.3	···	···	···	···	···	···	···	···	···
Solanum erianthum	N	Seedbank	···	···	···	34.0	···	···	···	···	···	···	···	···
Sum most abundant			47.1	45.3	60.0	66.7	71.9	67.3	81.1	73.5	66.2	80.9	47.4	83.5
Sum others			52.9	54.7	40.0	33.3	28.1	32.7	18.9	26.5	33.8	19.1	52.6	16.5
C) 4–8 m stratum														
No. of stems			8	33	10	30	17	88	15	44	32	99	47	79
No. of taxa counted			4	3	4	3	4	3	3	4	4	3	3	3
Species														
Annona glabra	N	Stem	···	···	···	···	11.8	···	···	···	···	···	···	···
Ardisia escallonioides	N	Stem	···	···	···	···	···	···	20	···	···	···	···	···
Bischofia javanica	X	Stem	···	15.2	20.0	···	···	···	···	···	···	···	···	···
Bursera simaruba	N	Stem	···	12.1	···	···	···	···	···	···	···	···	···	···
Carica papaya	X	Seedbank	···	···	···	···	···	54.5	···	38.6	···	50.5	···	39.2

APPENDIX. Continued.

Species	Origin	Regeneration source†	Castellow Untreated 8	Castellow Untreated 26	Castellow Restored 8	Castellow Restored 26	Deering Untreated 8	Deering Untreated 26	Deering Restored 8	Deering Restored 26	Matheson Untreated 8	Matheson Untreated 26	Matheson Restored 8	Matheson Restored 26
Calyptranthes pallens	N	Stem	···	···	···	···	17.6	···	···	9.1	···	···	···	···
Coccoloba diversifolia	N	Stem	12.5	···	60.0	20.0	35.3	9.1	26.7	13.6	21.9	8.1	25.5	22.8
Eugenia axillaris	N	Stem	···	···	···	···	···	···	20	···	40.6	15.2	21.3	17.7
E. uniflora	X	Stem	···	···	10.0	···	···	···	···	···	···	···	···	···
Ficus aurea	N	Stem	···	···	10.0	10.0	···	···	···	···	···	···	···	···
Jasminum spp.	X	Liana	···	···	···	···	···	···	···	···	···	···	10.6	···
Lysiloma latisiliquum	N	Stem	12.5	···	···	···	···	···	···	···	···	···	···	···
Sideroxylon foetidissimum	N	Stem	···	···	···	···	···	···	···	···	9.4	···	···	···
Nectandra coriacea	N	Stem	···	···	···	···	11.8	···	···	9.1	9.4	···	···	···
Quercus virginiana	N	Stem	12.5	···	···	···	···	···	···	···	···	···	···	···
Ricinus communis	X	Seedbank	···	···	···	···	···	5.7	···	···	···	···	···	···
Simarouba glauca	N	Stem	37.5	24.2	···	···	···	···	···	···	···	···	···	···
Solanum erianthum	N	Seedbank	···	···	···	40.0	···	···	···	···	···	···	···	···
Sum most abundant			75.0	51.5	100.0	70.0	76.5	69.3	66.7	70.4	81.3	73.7	57.4	79.7
Sum others			25.0	48.5	0.0	30.0	23.5	30.7	33.3	29.6	18.8	26.3	42.6	20.3

† Regeneration source is defined by the source of the stems: seedbank, seed rain, oskar layer (seedling bank), and resprouts from rhizomes, lianas, and stems (both standing and fallen).