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EFFECTS OF INVASIVE, NON-INDIGENOUS PLANT SPECIES ON ECOSYSTEM PROCESSES: LESSONS FROM FLORIDA

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Abstract. Individual plant species that modify ecosystem properties have traditionally been thought to be uncommon in natural systems. I hypothesize that many invasive non-indigenous species do alter these properties at several scales. The non-indigenous plant species in Florida considered the most invasive by the Florida Exotic Pest Plant Council are examined for this capability through review of the available literature. Out of 31 species total, 12–20 (39–64%) potentially alter the ecosystem properties of geomorphology, hydrology, biogeochemistry, and disturbance. When population-level properties that indicate superior competitive ability of the invading species are examined, 13–24 (42–77%) of the species are included, with the majority of species showing traits capable of modifying natural systems at both ecosystem and community/population scales. This review suggests that ecosystem alteration may be relatively common among invasive non-indigenous species. However, much of the current information is anecdotal. Empirical studies directly examining the effects of species on ecosystem and smaller-scale processes are necessary, and highly invasive species may be particularly appropriate for such research. Further, as non-indigenous species homogenize the global flora, they may also homogenize the local flora by increasing the representation of ruderal species. Where ecosystem processes have been altered, site restoration likely will require both control of the invader(s) and recovery of processes.

Key words: *competitive effects; ecosystem processes; exotics, effect on ecosystem properties and competition; Florida, invasive plants; global flora; invasive species effects; non-indigenous plant species.*

INTRODUCTION

The characteristics and effects of non-indigenous (i.e., exotic) invasive species have received increasing attention from ecologists, conservationists, and land managers. Until relatively recently, non-indigenous plant species invading agricultural systems and waterways received primary focus. However, an increasing number of plant species that colonize natural areas, potentially threatening the diversity and interactions of native species, have been recognized and have become the subject of ecological dialogue and experimentation over the last two decades (Mooney and Drake 1986, Drake et al. 1989, Soulé 1990, Pyšek 1995). The traits of species that result in successful invasion of natural areas—sometimes resulting in shifts in community dominance, and alteration of ecosystem processes or competitive regimes—are among the topics that have received attention. The latter topic of system alteration is the primary focus of this review. If species are not only competitive enough to invade, but also able to alter the habitat, they are likely to modify the structure,

composition, and habitat quality of native plant communities significantly (D'Antonio and Vitousek 1992).

While non-indigenous animals have long been recognized to create disturbances that can result in changes in resources and ecosystem processes (Elton 1958, Greenway 1967, Simberloff 1981, Drake et al. 1989, Ramakrishan and Vitousek 1989, Coblenz 1990), plants have traditionally been thought to invade only exogenously disturbed sites (Fox and Fox 1986, Drake et al. 1989, Hobbs and Huenneke 1992). Theories of plant community composition and resource partitioning have focused on structuring of vegetation by competition and herbivory; new species have been hypothesized to invade only when resources were released or if they were superior competitors for the available resources (Orians 1986, Case 1990). Clear evidence of successful invasion of islands was explained by their depauperate flora, in which unoccupied niches remained available (Elton 1958, Pimm 1993, Woodward 1993). Similar arguments have been invoked to explain the large numbers of naturalized and invasive plant species in peninsular Florida (Ewel 1986, Myers and Ewel 1990).

While some types of habitats are invaded more easily than others (Usher 1988, Rejmánek 1989), few habitats

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appear invulnerable to invasion (Johnstone 1986, Crawley 1987, di Castri 1990). Increasing evidence from autecological research on a number of non-indigenous species around the world provides examples of plant species that are able to invade continental and island habitats without clear exogenous disturbances (Bazzaz 1986, Hobbs and Atkins 1988, Usher 1988, Binggeli 1990, Huenneke 1991, Lodge 1993, Horvitz et al. 1998). The natural disturbance factors that maintain native species also allow invasion by species that historically have been excluded by biogeographic barriers and ecological constraints, but now are present because of human-mediated transport (di Castri 1990, Roy et al. 1991, Hobbs and Huenneke 1992).

Theoretical and empirical evidence would predict that the most successful non-indigenous species, those that are capable of displacing native species and sometimes communities, would have one or more of several characteristics. These include (1) effective reproductive and dispersal mechanisms; (2) competitive ability superior to that of the natives in the original or modified system; (3) few to no herbivores or pathogens, especially in herbivore-controlled communities; (4) ability to occupy a "vacant niche"; and (5) capability of altering the site by either significantly changing resource availability or disturbance regimes or both. The relative roles of the first four of these characteristics have received much attention in the literature (e.g., Elton 1958, Baker 1974, Bazzaz 1986, Herbold and Moyle 1986, Johnstone 1986, Coblenz 1990, Bond 1993). Recently, however, more examples of the last characteristic have been documented, causing reassessment of the frequency with which invading plant species modify natural systems (Versfeld and van Wilgen 1986, Braithwaite et al. 1989, Macdonald et al. 1989, Soulé 1990, Vitousek 1990, D'Antonio and Vitousek 1992).

Several authors have identified the types of processes that may be modified by non-indigenous plant species (Vitousek 1986, Macdonald et al. 1989, Westman 1990, D'Antonio and Vitousek 1992). At the ecosystem level, these include alteration of geomorphological processes, biogeochemical or hydrological cycling, and disturbance types and regimes (Table 1). At the community and population levels, stand structure, recruitment rates of natives, and resource competition may be altered (Table 1). Novel growth forms or phenologies, as well as rapid growth rates relative to the natives, might support these types of changes (Vitousek 1986). While population- and community-level effects of invaders have been documented better than have ecosystem effects (D'Antonio and Vitousek 1992), smaller-scale processes acting across large areas will result in ecosystem-level modification as well (Versfeld and van Wilgen 1986, Binggeli 1990, Vitousek 1990).

The best-known examples of ecosystem-level effects of invasive non-indigenous plant species include ni-

TABLE 1. Types of effects caused by invasive, non-indigenous species at three scales (after Macdonald et al. 1989).

Ecosystem-level effects	
Altered geomorphological processes	
	Erosion rate
	Sedimentation rate
	Elevation
	Water channels
Altered hydrological cycling	
	Water-holding capacity
	Water-table depth
	Surface-flow patterns
Altered biogeochemical cycling	
	Nutrient mineralization rate
	Nutrient immobilization rate
	Soil or water chemistry
Altered disturbance regime	
	Type
	Frequency
	Intensity
	Duration
Community/population-level effects	
Altered stand structure	
	New life form
	Vertical structure
Altered recruitment of natives	
	Allelopathy
	Microclimate shift
	Physical barrier
Altered resource competition	
	Light absorption
	Water uptake
	Nutrient uptake
	Space preemption

trogen-fixers and species that modify disturbance regimes. For example, *Myrica faya* (myrica) colonizes young volcanic soils and modifies nutrient cycles, invertebrate populations, and plant community composition and structure (Vitousek 1990, Walker and Vitousek 1991). Invasive grasses have been demonstrated to modify natural fire regimes and species composition in several sites (D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992). *Tamarix* spp. (salt-cedar) alters fluvial geomorphology, nutrient cycling, fire regimes, and native species regeneration rates (D'Antonio and Vitousek 1992).

The effects of changes in resource availability and disturbance types and frequencies on interactions among native species potentially could reduce both species richness and connectance, and create novel selection pressures (D'Antonio and Vitousek 1992, Pimm 1993). All of these modifications may increase the competitive advantage of the invading species, which may be better adapted to the new conditions and thus be able to dominate large areas (Johnstone 1986, Vitousek 1986, D'Antonio and Vitousek 1992).

Most non-indigenous species do not become established in the new habitats to which they are introduced (Williamson and Brown 1986, Crawley 1987, di Castri 1990, Lodge 1993). Additionally, most of those that are able to persist or invade in the new location do not

TABLE 2. Florida's Category I "most invasive plant species" (Austin 1993), and date of introduction or first record of the introduction when available (Gordon and Thomas 1997).

Species	Common name	Family	Introduction to Florida
<i>Abrus precatorius</i>	Rosary pea	Fabaceae	pre-1932
<i>Acacia auriculiformis</i>	Earleaf acacia	Fabaceae	by 1932
<i>Ardisia elliptica</i> (= <i>A. humilis</i>)	Shoebuttan ardisia	Myrsinaceae	by 1900
<i>Casuarina equisetifolia</i> (= <i>C. litorea</i>)	Australian pine	Casuarinaceae	1887
<i>Casuarina glauca</i>	Suckering Australian pine	Casuarinaceae	1890
<i>Cinnamomum camphora</i>	Camphor tree	Lauraceae	pre-1933
<i>Colubrina asiatica</i>	Lather leaf	Rhamnaceae	pre-1933
<i>Cupaniopsis anacardioides</i>	Carrotwood	Sapindaceae	1968†
<i>Dioscorea bulbifera</i>	Air potato	Dioscoreaceae	1905
<i>Eichhornia crassipes</i>	Water hyacinth	Pontederiaceae	1884
<i>Ficus microcarpa</i> (= <i>F. nitida</i> = <i>F. retusa</i> var. <i>nitida</i>)	Laurel fig	Moraceae	pre-1912; [wasp c. 1975]
<i>Hydrilla verticillata</i>	Hydrilla	Hydrocharitaceae	1950–51
<i>Ipomoea aquatica</i>	Water spinach	Convolvulaceae	pre-1950
<i>Jasminum dichotomum</i>	Gold Coast jasmine	Oleaceae	pre-1947
<i>Lantana camara</i>	Lantana	Verbenaceae	1804
<i>Lonicera japonica</i>	Japanese honeysuckle	Caprifoliaceae	1875
<i>Lygodium microphyllum</i>	Old World climbing fern	Schizaeaceae	pre-1958
<i>Melaleuca quinquenervia</i>	Melaleuca	Myrtaceae	1906
<i>Melia azedarach</i>	Chinaberry	Meliaceae	c. 1830 South Carolina and Georgia
<i>Mimosa pigra</i>	Cat claw mimosa	Fabaceae	1926
<i>Neyraudia reynaudiana</i>	Burmareed; cane grass	Poaceae	1916†
<i>Paderia foetida</i>	Skunk vine	Rubiaceae	1897
<i>Panicum repens</i>	Torpedo grass	Poaceae	1920s
<i>Pistia stratiotes</i>	Water lettuce	Araceae	pre-1765
<i>Pueraria montana</i> (= <i>P. lobata</i>)	Kudzu	Fabaceae	1899
<i>Rhodomyrtus tomentosus</i>	Downy rose myrtle	Myrtaceae	?
<i>Sapium sebiferum</i>	Chinese tallow tree; popcorn tree	Euphorbiaceae	pre-1784 South Carolina, 1900s Florida
<i>Scaevola taccada</i> var. <i>sericea</i> (= <i>S. frutescens</i> = <i>S. sericea</i>)	Scaevola; half flower	Goodeniaceae	?
<i>Schefflera actinophylla</i> (= <i>Brassaia actinophylla</i>)	Schefflera	Araliaceae	1927
<i>Schinus terebinthifolius</i>	Brazilian pepper	Anacardiaceae	1840s
<i>Solanum viarum</i>	Tropical soda apple	Solanaceae	c. 1985

† Earliest plant introduction date in Miami as listed by the U.S. Department of Agriculture; not necessarily the date of first introduction.

become dominant in that system. For example, at least 25 000 species and cultivars are estimated to have been cultivated in Florida (D. Hall, *personal communication*), where native species richness is reported to be 2523 (Ward 1990). When the 925 naturalized non-indigenous species are included in Florida's flora, the number of species increases to 3448, resulting in an estimated 27% of the flora being non-indigenous (Ward 1990). However, the Florida Exotic Pest Plant Council (EPPC) lists only 95 plant species as current or potential serious invaders of the state's natural systems (Austin 1993). Thus, fewer than 4% of the introduced taxa currently are identified as naturalized, with 10% of those, invasive.

It seems likely that the subset of invasive species that are known to become community dominants will be predominantly those with the potential to modify ecosystem properties. Those species that invade and establish viable populations without becoming dominants are probably less likely to alter larger-scale pro-

cesses. While these, too, are successful invaders, they appear not to displace native species over the short term. Conversely, species that become community dominants appear likely to change environmental conditions and resource availability over larger areas than they occupy, or create a new community structure. Because the non-indigenous species essentially has changed the conditions under which the indigenous species evolved, the invader is able to increase in abundance relative to indigenous species. In this paper I explore the hypothesis that highly invasive species in Florida alter ecosystem and community processes. While my original intent was to compare whether these species more frequently become community dominants because of this system alteration than because of their superior competitive ability, this review revealed that insufficient data were available for such an analysis.

METHODS

I reviewed published and unpublished data on the list of the 31 most invasive plants in Florida developed

TABLE 3. Documented ecological effects of the 31 most invasive non-indigenous plant species in Florida, USA. Numbers indicate references in the list at the end of the table. A “?” indicates a likely effect that has not been examined.

Species	Ecosystem-level effects								
	Geomorphology			Hydrology		Biogeochemistry			Disturbance regime
	Erosion	Soil elevation	Water channel	Water table depth	Surface flow	Nutrient mineralization	N-fixation	Water chemistry	
<i>Abrus precatorius</i>	25†	...	?
<i>Acacia auriculiformis</i>	...	27§	43§	27†
<i>Ardisia elliptica</i>
<i>Casuarina glauca</i>	26
<i>C. equisetifolia</i>	7	1
<i>Cinnamomum camphora</i>
<i>Colubrina asiatica</i>
<i>Cupaniopsis anacardioides</i>	?
<i>Dioscorea bulbifera</i>	?
<i>Eichhornia crassipes</i>	...	38§	4	...	9§	38	...
<i>Ficus microcarpa</i>
<i>Hydrilla verticillata</i>	9§	38	...
<i>Ipomoea aquatica</i>	?	...
<i>Jasminum dichotomum</i>	?
<i>Lantana camara</i>
<i>Lonicera japonica</i>
<i>Lygodium microphyllum</i>	36§
<i>Melaleuca quinquenervia</i>	...	20§	...	45§	20§	13§	29
<i>Melia azedarach</i>
<i>Mimosa pigra</i>	22	...	22	...	22†
<i>Neyraudia reynaudiana</i>	37§
<i>Poederia foetida</i>	?
<i>Panicum repens</i>	41§
<i>Pistia stratiotes</i>	38§	...	40, 38	38	...
<i>Pueraria montana</i>	44†	...	?

References:

- | | | |
|--|----------------------------|-------------------------------|
| 1) Abdel Wahab (1980) | 8) Doren and Jones (1994) | 17) Horvitz et al. (1998) |
| 2) D. F. Austin, personal communication [1993] | 9) Duever et al. (1986) | 18) Jones and McLeod (1989) |
| 3) Binggeli (1990) | 10) Ewel et al. (1982) | 19) Jubinsky (1993) |
| 4) Bogart (1949) | 11) Fairchild (1947) | 20) Laroche (1994) |
| 5) Cameron and Spencer (1989) | 12) Gann and Gordon (1998) | 21) Leatherman (1955) |
| 6) Carter and Teramura (1988) | 13) Greenway (1994) | 22) Lonsdale et al. (1989) |
| 7) Craig et al. (1978) | 14) Gunderson (1983) | 23) Loope and Durevitz (1981) |
| | 15) Gunn (1969) | 24) Martin (1974) |
| | 16) Haller (1994) | |

† Legume.

‡ Twining vine.

§ Statement made without accompanying data within the citation(s) listed.

Table 3. Extended.

Community-/population-level effects								
Stand structure		Recruitment of natives				Resource competition		
New life form	Vertical structure§	Decreased recruitment	Allelopathy	Micro-climate	Physical barrier	Light	Water uptake	Nutrient uptake
‡	15§	25§
...
...	...	17, 39§	39§
8§ 26	8 26
...	...	7	9§	7
...
...	37	34	34
...	33	?	...	33§	?	...
‡	42	42§	42§	...	24
16	...	38	...	38	...	38	38	38
...	30§	30§
16	...	38	38	38	...	38	...	38
...	...	?	...	?	...	?	?	?
‡	11	11§	11§
...	3	3§	3§
6‡	32	21	21	6
...	35	31§
...	14	20	29§	29§	14	...
...
...	22	22	22	22§	...
...	...	2§	2§
‡	12	12	12§
...	...	41§
...	...	38§	...	38	...	38§	38	38
‡	44	44	44

25) Morton (1976)	34) Olmstead et al. (1981)	40) Sharma (1984)
26) Morton (1980)	35) Rejmánek (1989)	41) Smith et al. (1992)
27) Morton (1985)	36) Roberts (1994)	42) TNC (1993)
28) Mullahey et al. (1993)	37) Schmitz (1994)	43) Versfeld and van Wilgen (1986)
29) Myers (1983)	38) Schmitz et al. (1993)	44) Winberry and Jones (1974)
30) Nadel et al. (1992)	39) R. Seavey and J. Seavey (unpublished report [1993] to Everglades National Park Resource Management, Homestead, Florida, U.S.A.)	45) Woodall (1981)
31) Nauman and Austin (1978)		
32) Nyboer (1992)		
33) Oliver (1992)		

TABLE 3. Continued.

Species	Ecosystem-level effects								Disturbance regime
	Geomorphology			Hydrology		Biogeochemistry			
	Erosion	Soil elevation	Water channel	Water table depth	Surface flow	Nutrient mineralization	N-fixation	Water chemistry	
<i>Rhodomyrtus tomentosus</i>
<i>Sapium sebiferum</i>	5§	?	5
<i>Scaevola taccada</i> var. <i>sericea</i>	2§
<i>Schefflera actinophylla</i>
<i>Schinus terebinthifolius</i>	...	?	10
<i>Solanum viarum</i>

by the Exotic Pest Plant Council (EPPC) (Table 2). These species are listed as Category I invaders, defined as widespread in Florida, with a recognized potential to invade and disrupt native plant communities (Austin 1993). While including the 64 Category II species (invasive but not community dominants in Florida, but highly invasive elsewhere in the world) would strengthen this analysis, review of the Category I species provides an initial assessment of the hypothesis. Further, the paucity of data available, even on the most invasive group, suggests that little more can be learned by expanding the list at this time.

At least 25% of the 31 species are documented as invasive in other southeastern states. Some, like *Lonicera japonica*, *Lantana camara*, and *Eichhornia crassipes* (common names are in Table 2) are highly invasive across the region. Most of the 25 plant families on the list are represented by only one species. However, 13% (4) are legumes. Four of the species are obligately aquatic; most invade mesic to wet habitats. Neither the Asteraceae nor the Pinaceae, families with high numbers of invasive species in other areas (Heywood 1989), are represented on either Florida's or other southeastern states' lists of most invasive species. Only one species in the Asteraceae, *Wedelia trilobata* (wedelia), is included in the expanded Florida EPPC list of 95 species (Austin 1993).

I conducted literature searches on all species to examine evidence for their ability or potential to alter ecosystem and community-level processes. Research effort has been applied unevenly across these species; little is known about several, and much of the information in the literature is anecdotal (as indicated in Table 3). No data were available on four of the species (*Cinnamomum camphora*, *Melia azedarach*, *Rhodomyrtus tomentosus*, and *Schefflera actinophylla*), but all percentages were calculated using the total number of 31 species for added conservatism in the analysis. Throughout this paper, the lower

value in the range of percentages reported is supported by data, while the higher value represents species whose effects have been suggested or observed but not measured. Potential effects were extrapolated from autecological information when no larger-scale data were available (e.g., nitrogen fixers potentially modify nitrogen dynamics where they dominate large areas). The results are summarized in the categories identified in Table 1 where data were found. Patterns presented need to be interpreted cautiously because few of the data available are the result of empirical efforts to examine ecosystem-level effects and much of the data are anecdotal. Autecological and empirical research are necessary before this hypothesis can be tested rigorously.

RESULTS AND DISCUSSION

Ecosystem-level changes: geomorphology

Overall, 6–22% of the species listed (2 demonstrated plus 5 more with anecdotal effects = 7 species out of 31 total) are reported to alter geomorphological processes (Table 3). Three to six percent (1–2 species) increase erosion rates, and 0–13% (4 species) increase sedimentation rates or increase soil elevation. At least 6–13% (2–4 species) impact the effective geometry or configuration of water channels.

Casuarina equisetifolia modifies geomorphological processes by causing shoreline erosion and steepening, resulting in beach-width reduction (Craig et al. 1978, Deaton 1994). This erosion is thought to be accelerated indirectly by the exclusion of soil-stabilizing grasses (Johnson 1994). Litter deposition of at least 5 cm under *Melaleuca quinquenervia* modifies soils and topography in the flat, shallow wetlands of south Florida (Flowers 1991, OTA 1993). *Schinus terebinthifolius* also appears to cause soil development and elevation increases in the shallow soil systems it colonizes (D.

TABLE 3. Continued, extended.

Strand structure		Community-/population-level effects						
		Recruitment of natives				Resource competition		
New life form	Vertical structure§	Decreased recruitment	Allelopathy	Micro-climate	Physical barrier	Light	Water uptake	Nutrient uptake
...
...	5	19	18	5†	5
...
...
...	10	23	10	23§
...	28	28§

Gordon, *personal observation*). *Mimosa pigra* has caused sediment accumulation and disruption of waterways in Australia and Thailand (Lonsdale et al. 1989). *Eichhornia crassipes* and *Pistia stratiotes* can increase siltation rates by slowing water flows (Schmitz et al. 1993); *Panicum repens* may also modify water channels by stabilizing lake and stream edges (Smith et al. 1992).

Ecosystem-level changes: hydrology

Species that alter geomorphological features also are likely to influence hydrological systems. In total, 6–22% (2–7) of the species alter hydrological cycling, with up to 10% (3 species) altering water table depth, and 6–19% (2–6 species) altering surface-flow patterns (Table 3).

Non-indigenous species with evapotranspiration rates higher than those of the native flora may significantly alter hydrological regimes and lower water tables. Tree species invading herbaceous communities, like *Melaleuca quinquenervia* and, potentially, *Sapium sebiferum*, generally have been demonstrated to modify rainfall interception, surface flow, evapotranspiration rates, and possibly water-table levels (Versfeld and van Wilgen 1986, Vitousek 1986). For example, field evapotranspiration of *M. quinquenervia* has been estimated to be higher than that of the native *Cladium jamaicense* (sawgrass) (Alexander et al. 1977, cited in Woodall 1981). The hypothesized enhanced net evapotranspiration is based on the higher leaf area of *M. quinquenervia* compared to many native herbs, as well as its evergreen growth habit, differing from the deciduous tree species native to the system (Woodall 1981). This higher net evapotranspiration, along with increases in substrate elevation associated with this species, may change both the distance to the water table and the direction and rate of surface water flow. As a result, distributions of native species are altered in ar-

reas invaded by *M. quinquenervia* (see *Resource competition*, below).

Two aquatic species, *Pistia stratiotes* and *Eichhornia crassipes*, have evapotranspiration rates that exceed open-water evaporation rates by ten- and three- to six-fold, respectively (Schmitz et al. 1993). Whether these high rates can result in regional hydrological modifications in Florida's shallow water bodies and surface flow has not been investigated. *E. crassipes* (Bogart 1949) and *Hydrilla verticillata* (Duever et al. 1986) have been suggested to impede water flow in canals. Duever et al. (1986) suggest, however, that reductions in water flows caused by *E. crassipes* may locally negate the high evapotranspiration loss caused by this species.

The changes in surface flow and water-table height likely influence frequency, duration, and scale of both drought and inundation, although I found no quantification of these effects. Fire frequency and intensity also are influenced in hydrologically altered systems (Wade et al. 1980). As discussed below (see *Disturbance*), species like *M. quinquenervia* have been demonstrated to alter fire regimes.

Ecosystem-level changes: biogeochemistry

Aside from the aquatic species, whose effects are relatively well studied, few measurements of nutrient modification exist for the species examined. If all the nitrogen-fixing species are assumed to have significant impacts where they are dominant, a total of 32–39% (10–12) of the species are likely to alter biogeochemical cycles (Table 3). Twenty-two to twenty-six percent (7–8) of the species affect soil nutrient availability, and 10–13% (3–4 species) significantly alter water chemistry.

Three of the four aquatic species (*E. crassipes*, *H. verticillata*, and *P. stratiotes*), but not *Ipomoea aquatica* have been demonstrated to modify water chem-

istry significantly. Dissolved O₂, pH, and phosphorus decrease, while dissolved CO₂, turbidity, and water color increase with these species (Schmitz et al. 1993). The modified water chemistry and shading caused by these species have resulted in loss of native submerged vegetation. Phytoplankton abundance decreases because of low phosphorus and low-light conditions.

Many soil types in Florida are highly weathered, acidic, and have high leaching rates (Brown et al. 1990). As a result, nitrogen levels are generally low. The four legumes (*Abrus precatorius*, *Acacia auriculiformis*, *Mimosa pigra*, and *Pueraria montana*) are nitrogen fixers, as are both *Casuarina equisetifolia* and *C. glauca*, which are actinorhizal. Where such species form large stands, local nitrogen cycling may be altered significantly (Vitousek 1986). Mycorrhizal associations have been suggested to result in both higher concentrations of nitrogen and phosphorus in leaves of non-indigenous *Acacia* spp. invading South African fynbos and in enriched soil-nutrient levels (Versfeld and van Wilgen 1986). These data suggest that *A. auriculiformis* might increase phosphorus availability when it invades low-nutrient habitats in Florida.

Data on nutrient mobilization and immobilization are almost non-existent. At least six species have been suggested to alter litter accumulation (*A. auriculiformis*, *C. equisetifolia*, *E. crassipes*, *M. quinquenervia*, and *Schinus terebinthifolius*) or decomposition (*Sapium sebiferum*) rates in the communities they invade. Under stands of *C. equisetifolia*, leaf and branch litter is often 5–10 cm thick (Fernald and Barnett 1981). High detritus-deposition rates under *E. crassipes* can cause anoxia, rapid phosphorus releases, and large-scale plant and animal mortality (Schmitz et al. 1993). In Australia, *M. quinquenervia* has high C:N and C:P ratios (60:1 and 1400:1, respectively, for litter >5 mm) and low rates of litter decay. Both decay-resistant lignins and anti-bacterial phenolics in leaves are suggested to explain the slow decay rates (Greenway 1994). *Sapium sebiferum* leaves increase Ca, N, K, Mg, and P levels over concentrations found in soil under native Gulf Coast vegetation as a result of both higher initial leaf concentrations and higher litter-decay rates. Thus, the species has been hypothesized to alter soil nutrient distributions and enhance productivity where it has invaded (Cameron and Spencer 1989).

Ecosystem-level changes: disturbance

Both native and non-indigenous species in south Florida appear to survive hurricanes (Armentano et al. 1995). Nonetheless, non-indigenous species can shift both competitive interactions and system resilience to subsequent hurricanes (Horvitz et al. 1998). At shorter temporal and spatial scales, hydrological alteration is likely to result in shifts in disturbance regimes associated directly or indirectly with water levels (Myers 1983; see *Hydrology*, above). Similarly, shifts in fire

frequency should alter litter accumulation rates, with associated effects on biogeochemical cycles (Versfeld and van Wilgen 1986), but I found no documentation of these types of changes. As a result, species' effects in Table 3 are associated only with fire and do not represent a novel type of disturbance. Depending on whether vines reduce fire frequency (see below), 6–29% (2–9) of the species may alter fire frequency, intensity, or both.

Fire frequency and intensity may be shifted by some of these species with unmeasured impacts on the native species. While many of the invaded communities are pyric, fuel accumulation increases with colonization of grasses like *Neyraudia reynaudiana* (Schmitz 1994). Additionally, *M. quinquenervia* (Myers 1983) and *Schinus terebinthifolius* taller than 1 m (Loope and Du-nevitz 1981) are significantly more fire tolerant than are other woody species in colonized hardwood hammocks. Fuels provided by *M. quinquenervia*'s flammable leaves and shaggy bark likely increase fire frequency, intensity, and spread where it has invaded (Flowers 1991); the tree disperses its seeds before any other woody species following dormant-season fire (Myers 1983). The bark of this species (Wade et al. 1980), like the leaves of *Lygodium microphyllum* (Roberts 1994), has been suggested to increase the probability of canopy tree-killing crown fires that are uncommon in the native communities. Conversely, once *S. terebinthifolius* forms dense stands, the high moisture retained by its litter and low fine-fuel levels in the understory may reduce the fire frequency in pyric pine rocklands (Wade et al. 1980). Invasion of vines into fire-evolved systems also can impede or preclude fire movement into those communities by creating a moist vegetative barrier ("vine-blankets" of Horvitz et al. [1998]) and increasing relative humidity levels, especially during the growing season when natural fire ignitions occurred most frequently in Florida (F. Putz *personal communication* 1994).

Community-level changes: stand structure

Overall, 13–58% (4–18) of the species appear to alter native stand structure, either by adding an infrequent or new life-form (13–32%; 4–10 species) or by changing vertical structure of the vegetation (48%; 15 species), with some overlap between the categories (Table 3). Thirty-two percent (10) of the species on the list are vines or viney shrubs. Several, like *Lonicera japonica*, *Lygodium microphyllum*, *Dioscorea bulbifera*, and *Pueraria montana* have twining growth forms, differing from most native vines, which generally climb large stems by adhering to the bark and do not as readily link tree canopies. Twining increases the probability that the supporting plants will eventually collapse under the weight of the climber, resulting in a significant change in vertical structure of the community (Hardt 1986). As a result, the combined effect of several non-

indigenous plant species in south Florida tropical-hardwood hammocks is to reduce the overall stature of the canopy and create canopy openings (Horvitz et al. 1998; see *Recruitment of natives*, below).

Species with phenologies significantly different than those of the natives represent a different type of life-form in the systems they invade (Vitousek 1986). Almost all of the non-indigenous vine species are of tropical origin, in comparison to the predominantly temperate native vines; this may result in species with physiological advantages over the natives in Florida's sub-tropical environment (Horvitz et al. 1998). The evergreen to semi-evergreen growth of *L. japonica*, coupled with its low photosynthetic light compensation point, partially explains its advantage over the predominantly deciduous communities that it invades, shades, and topples (Carter and Teramura 1988). In aquatic systems, both *Eichhornia crassipes* and *Hydrilla verticillata* have novel growth forms. The former species is a floating form that, unlike the native aquatic species, is cold tolerant and can occupy open waterways (Haller 1994). *H. verticillata* is a submerged plant capable of using light levels below the light compensation points of native submerged species. As a result, *H. verticillata* not only can grow in deeper water than can the natives, where it forms a continuous canopy and reduces light penetration, but also can outcompete the natives at shallower depths. High growth rates enable the invader to reach the surface of the water before the natives (Haller 1994). Similar to *L. japonica*, *H. verticillata*'s low light compensation point also extends its growing season beyond that of the natives it replaces (Schmitz et al. 1993).

Several of the non-indigenous tree species invade predominantly herbaceous (wetland, coastal prairie, dune, etc.) or shrub (coastal strand) communities, adding an infrequent or new life-form to those communities and changing the vertical structure of the vegetation. These include *Mimosa pigra*, *Melaleuca quinquenervia*, *Schinus terebinthifolius*, and *Cupaniopsis anacardioides*. *Sapium sebiferum* converts herbaceous coastal prairie into closed-canopy woodlands within a decade in Texas (Bruce et al. 1995). Some of these species also invade hardwood floodplain forests. Alterations of structure by *M. pigra* are well documented in Australia (Lonsdale et al. 1989). Both *Casuarina equisetifolia* and *C. glauca* can change beach, dune, and coastal scrub communities into closed-canopy forests with little understory (Johnson 1994).

Like the trees that add vertical structure rare in the communities they invade, some shrub species (*Ardisia elliptica* and *Solanum viarum*) colonize prairies. Similarly, the viney shrub *Colubrina asiatica* can invade communities from beach dune to tidal marshes (Schmitz 1994), and *Scaevola taccada* var. *sericea* colonizes dunes (Johnson 1994).

Community-level changes: recruitment of natives

Bond (1993) named those invaders that suppress the seedlings of other species "keystone weeds." Several species on the EPPC (Florida's Exotic Pest Plant Council) list appear to prevent the recruitment of native species. While patterns of altered native-species establishment in invaded stands appear clear, the mechanisms causing inhibition or shifts in recruitment generally have not been investigated. Reduced numbers of seedlings of native species have been documented (32%; 10 species) or observed (23%; 7 species) in stands of invading non-indigenous species (Table 3). At least 6–13% (2–4) of the non-indigenous species have allelopathic properties. Because microclimate modifications only have been documented for the aquatic species, the estimate of 10–13% (3–4 species) is likely low. Generally, conversion of more open stands to low-light, closed-canopy systems should be accompanied by higher humidities, lower temperatures, and other environmental and biological changes, while conversion of closed stands to open systems should have the opposite effect (Sarukhan et al. 1985, Hobbs and Mooney 1986). Ten to twenty-two percent (3–7) of the species present a physical barrier to growth of native species. Overall, 42–74% (13–23) of the species show evidence of altering native species recruitment (Table 3).

The causes of this alteration are variable. They include allelopathic effects demonstrated for *Schinus terebinthifolius* (Gogue et al. 1974, Ewel et al. 1982), *Melaleuca quinquenervia* (DiStefano cited in Myers [1983], but see Duever et al. [1986]), *H. verticillata* (Kulshreshtha and Gopal 1983), and potentially *Abrus precatorius* (Gunn 1969). Other mechanisms reducing establishment of natives include inhospitable environmental changes, like higher water temperatures caused by the aquatic species (Schmitz et al. 1983), and physical suppression of seedling establishment. High rates of litterfall by species like *E. crassipes* (Schmitz et al. 1993) and, potentially, *Casuarina equisetifolia* (Duever et al. 1986), suppress recruitment of other species. *Lonicera japonica* (Leatherman 1955, Sasek and Strain 1990), *Pueraria montana* (Winberry and Jones 1974), and *Paederia* spp. (Gann and Gordon 1998) physically constrict, or bend and topple saplings. *Paederia crudasiana* (sewer vine) (combined with skunk vine in the EPPC list) causes complete canopy opening, forming a multi-layered monoculture above the remaining vegetation (Horvitz et al. 1998). In one Dade County, Florida site, the mean depth of stem layers of this vine at ground level was 20.2 cm (1 SD = 10.4 cm). On average, 0.4 stems/m² of other species were found growing under this mat (Gann and Gordon 1998), compared to 27–82 stems/m² in uninvaded areas at the same site (D. R. Gordon and G. Gann, unpublished data).

Non-indigenous species may also increase the species richness of native communities over the short term,

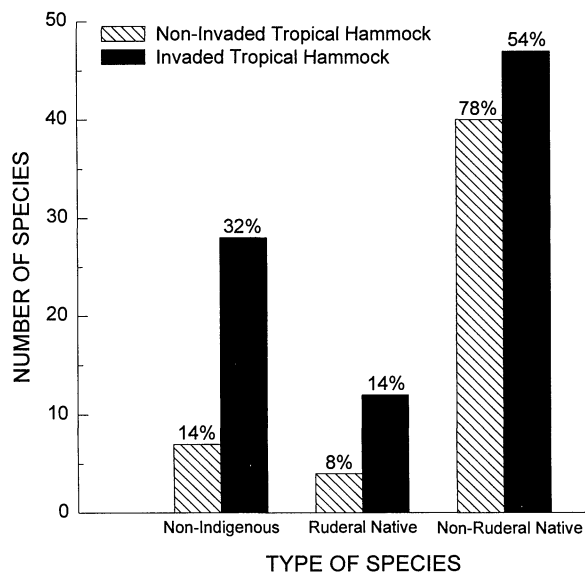


FIG. 1. Percentages of non-indigenous and native species in tropical hammock and invaded tropical hammock in Dade County, Florida, USA (adapted from Molnar 1990). "Non-indigenous" species are those identified as "exotic" by Molnar (1990); "ruderal native" are those characteristic of disturbed areas (Long and Lakela 1971) or described as pioneer species by Molnar (1990); and "non-ruderal native" are the remaining species listed for the relatively intact and invaded tropical hammock sites (Molnar 1990). For a description of sites, see *Results and discussion: . . . Recruitment of natives*.

although the species involved may indicate degradation of the natural community. Data that support this hypothesis come from the examination of species composition in adjacent stands of either relatively intact or invaded tropical hammock in Castello Hammock, Dade County, Florida (Molnar 1990). The intact stand was described as mature closed-canopy hammock with indistinct vertical strata and a relatively open understory with low herbaceous cover and low light levels. This area could be identified from aerial photographs taken in 1940, 1964, and 1984 (Molnar 1990). The invaded stand was part of the same mature hammock in 1940 and 1964, but by 1984 was "a dense, virtually impenetrable, thicket growth of exotic and native herbaceous, vining, and shrubby species [with] . . . a paucity of regenerative trees and virtually no canopy layer" (Molnar 1990: 39). Changes in stand composition and structure over the 45-yr period were hypothesized to have resulted from site fragmentation, local disturbance, lowered water table, and modification of the natural fire regime. Twenty percent of the importance values for trees and shrubs was comprised of non-native shrubs in the invaded sites, which also had high non-indigenous vine cover (Molnar 1990). Despite the higher species richness in the invaded hammock, a higher percentage of the total species in that site was represented by native ruderal species (Fig. 1). That higher number of species represents a shift from mature ham-

TABLE 4. 1984 tree sizes and densities in adjacent 1-ha stands of tropical hammock without and with non-indigenous plant species, Dade County, Florida, USA (adapted from Molnar 1990). Aerial-photograph interpretation suggested that stands were homogeneous in 1940 (Molnar 1990). For description of sites see *Recruitment of natives*.

Hammock type	Total basal area (m ² /ha)	Mean height (m)	Total density (no. stems/ha)
Tropical	661.2	3.91	115 783
Invaded tropical	101.3	1.90	5000

mock tree species to herbaceous species in the invaded site, resulting in 4–5 times the richness and an order of magnitude higher density of herbs present in the uninvaded site. Further, basal area, mean height, and density of tree stems were reduced in the invaded site (Table 4). As a result, the richness increase in the invaded sites is at the expense of canopy species and reflects a degradation of the hammock community, not only because of invading non-indigenous species but also because of altered stand structure. Additionally, the non-indigenous vines now appear to be affecting the ability of the canopy to recover following hurricane-caused canopy damage (EPPC 1992, Horvitz et al. 1995, 1998).

Another example of shifts in species composition caused by non-indigenous species is also from subtropical hammock sites in Dade County. In this case, three sites from two county parks had 15–100% *Dioscorea bulbifera* cover. Eighteen percent of the 77 species recorded within 30 × 30 m plots were non-indigenous (D. Gordon and G. Gann, unpublished data). Twenty-five percent of the 63 natives present were ruderal species (as defined in Fig. 1 legend) that were colonizing vine-maintained openings in the tree canopy. This proportion, almost double that in Molnar's (1990) plots, may reflect both spatial and temporal differences; our data were collected 7 yr after those of Molnar (1990). Both studies demonstrate a shift to ruderal species in vine-invaded stands, however.

Population-level changes: resource competition

Overall, 32–71% of the non-indigenous species have been documented (10 species) or suggested (12 species) to alter resources for which competition is likely (Table 3), although empirical analyses of competition have been conducted for only a few of the species. More specifically, 26–71% of the species (8–22 species) reduce light availability, 10–22% (3–7 species) have high water-uptake rates, and 13–23% (4–6 species) alter nutrient availability.

Non-indigenous species with high productivity that change community structure, resulting in reductions in light availability, have higher evapotranspiration rates than the native vegetation or fix nitrogen. Thus, they are likely to modify competitive interactions. Addi-

tionally, several species, including *Lonicera japonica* (Nyboer 1992), *Jasminum dichotomum* (Horvitz et al. 1998), and *Casuarina equisetifolia* (Abdel Wahab 1980), can outcompete the native vegetation (Table 3). For example, *Sapium sebiferum* is competitively superior to the native *Nyssa aquatica* (water tupelo) under flooded conditions (Jones and Sharitz 1990) and to *Platanus occidentalis* (sycamore) and *Quercus pagoda* var. *pagodifolia* (cherrybark oak) under low light (5%) conditions (Jones and McLeod 1989). Similarly, *Mimosa pigra* in Australia can form monospecific stands over several hectares, under which photosynthetically active radiation may be reduced to 1–5% of incident radiation (Lonsdale et al. 1989). *Hydrilla verticillata* can form dense canopies at the water surface from depths of 15 m, unlike any of the native species (Schmitz et al. 1993). In 1983, a statewide population reduction of native *Vallisneria* spp. (eelgrass) was attributed primarily to competition with *H. verticillata* (van Dijk 1985).

Schinus terebinthifolius dominates the understory of unburned pine rockland by growing more rapidly and shading the competing native shrubs and herbs. In portions of the Everglades where fire had been suppressed, this species was found to comprise 40% of the trees that reached at least 2 m in height, and 66% of the trees reaching 5 m or more (Loope and Dunevitz 1981). Those authors concluded that neither the pines nor many of the herbaceous species would persist in unburned rocklands dominated by *S. terebinthifolius*.

Other studies provide additional indirect support for the competitive impacts of these invasive species by examining native species composition and richness patterns in invaded communities. Both plant and wildlife diversity in several native Australian communities are reduced following *M. pigra* invasion (Braithwaite et al. 1989). Plant species richness in wet prairie is reduced by 60–80% when *Melaleuca quinquenervia* is present (Gurney 1971, unpublished data, as cited in Austin [1978:27]). Pine rocklands dominated by *S. terebinthifolius* contained ~50% of the species richness of uninvaded sites (Loope and Dunewitz 1981). Additional examples are discussed under *recruitment of natives*, above.

Ecosystem process change vs. competitive ability

Evaluation of whether these non-indigenous species are more likely to either modify environmental and disturbance regimes or to outcompete the native species is difficult because neither these main effects nor their interaction have been empirically compared. However, most of the species analyzed here appear to have both types of main effects. If only the ecosystem properties of geomorphology, hydrology, biogeochemistry, and disturbance are examined, 39–64% (12–20) of the species potentially have impacts. Adding alteration of stand structure increases that proportion supported by

data to 42% of the species (13). The remaining two categories from Table 1 are related to competitive ability; 42–77% (13–24) of the species are suggested to alter variables within these categories. Two species, *Ardisia elliptica* and *Ficus microcarpa*, likely modify only competitive regimes without having larger ecosystem effects, while three species, *Acacia auriculiformis*, *Casuarina glauca*, and *Scaevola taccada* var. *sericea* likely have ecosystem effects but no observed competitive advantage (Table 3).

Overall, these data suggest that at least half of the most invasive non-indigenous species in Florida may alter ecosystem processes, changing the resource availability and selective pressures on the native community and often modifying native species composition. The numbers of non-invasive species with potential for this effect are roughly equivalent to those with traits conferring high competitive ability; most of these invasive species seem to have both types of traits. Again, however, without clear empirical tests of the relative individual and combined importances of these effects, the mechanisms behind the dominance of these species over natives cannot be differentiated.

IMPLICATIONS FOR MANAGEMENT

The results of this review suggest that the potential for individual species to modify ecosystem properties is more prevalent than many ecologists have suspected. Invasive species may provide some of the clearest examples of ecosystem-altering taxa across a variety of phylogenetic groups and physiological and growth-form attributes (Vitousek 1990). Insufficient data on the species composition of invaded vs. relatively intact stands were available for identification of patterns of species remaining in these invaded and altered sites. However, if the species composition shifts documented by Molnar (1990) are characteristic of other invaded sites, then we should expect communities with environments modified by non-indigenous species to also contain higher proportions of ruderal species. Thus, as non-indigenous species homogenize the global flora (Lodge 1993), it seems likely that they will have the additional effect of homogenizing the local flora by increasing the representation of ruderal species. The responses of other native species to the invader should depend on interactions among the shifts in resource availability, stand structure, and disturbance regimes. The variety and complexity of potential effects of invaders hampers our ability to make predictions about their long-term impacts on native biodiversity and to prioritize research and management efforts.

Where ecosystem properties have been altered by a non-indigenous species, it is likely that both control of the species and restoration of properties will be necessary if a return to pre-invasion communities is desired. In California, removal of non-indigenous *Eucalyptus* spp. (eucalyptus) without restoration of the

native community can result in erosion, flooding and inundation, and changes in the dynamics of carbon fixation, causing further modifications of the site (Westman 1990). In Florida, removal of the litter accumulated under *Schinus terebinthifolius* invading pine rockland appears necessary if rockland, rather than hammock restoration is desired (G. Gann, *personal communication*; D. Gordon, *personal observation*). The same has been suggested for *Melaleuca quinquenervia* tree islands in the sawgrass prairie of south Florida (Laroche 1994). Not all species will require this level of post-removal site management; e.g., water tables and native species appear to recover without further action when *Tamarix* spp. are removed (Vitousek 1986). However, the potential for long-lasting alteration of ecosystem processes demonstrated by many of the species included in this review suggests that development of techniques for restoring invaded sites will require substantial research in most communities. Prevention of species translocation, especially those already demonstrated to be invasive outside their native ranges, would likely be more tractable and far less expensive.

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