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13. Invasibility: Lessons from South Florida

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13.1. Introduction

South Florida contains more conspicuous introduced plants and animals than any other region in the continental United States. At the same time the region also encompasses one of the largest contiguous complexes of preserved ecosystems in the eastern U.S. (Fig. 13.1.). Everglades National Park, dedicated in 1947, covers about 2500 (terrestrial) km^2; the Big Cypress National Preserve, established only a decade ago, occupies 2300 km^2; and the Fakahatchee State Preserve, whose acquisition by the State of Florida began in 1974, contains about 200 km^2. An additional 3600 km^2 are included in the three diked basins with modified hydroperiods controlled since 1949 by the South Florida Water Management District. Most of the introduced species that cause concern in South Florida were present before government agencies gained control of these lands.

Naturalized species represent a large fraction of the total number of species in a wide range of taxonomic groups (Table 13.1.). I will focus on invasions by tree species, and I will begin with an introduction to the flora, environment, and ecosystems of South Florida.

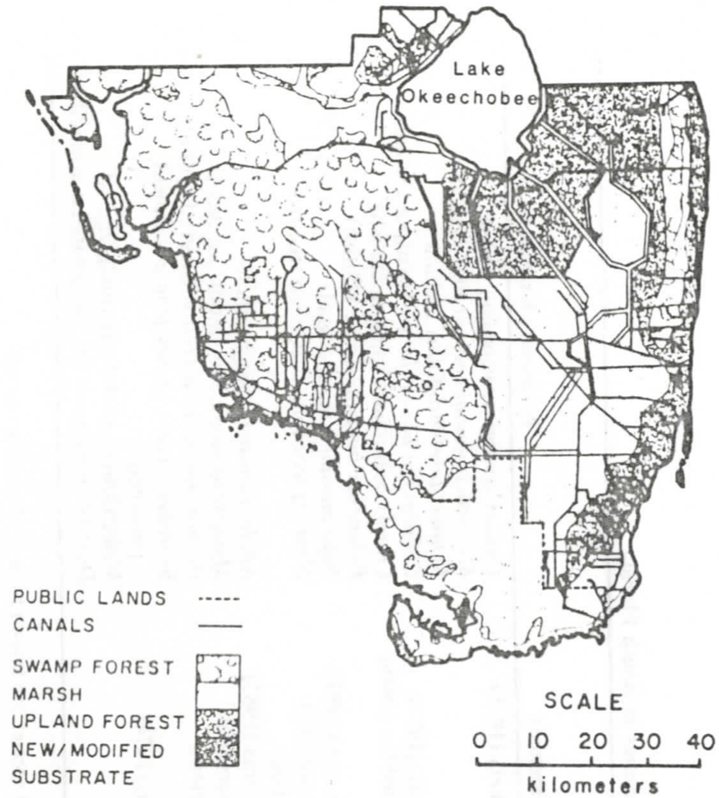

Figure 13.1. South Florida's ecosystems, protected public lands, and major canals and dikes.

13.2. Phytogeography of South Florida

The flora of South Florida, which includes nearly 1650 species, has originated from two main sources (Long and Lakela 1971; Long 1974). About 1000 species (61%) are of tropical origin, and most of these (91%) are "landed immigrants" that reached Florida from the West Indies. These are species—many of which happen to be bird-dispersed pioneers in more tropical settings—that make the region's flora so unique when compared to that of the rest of the mainland.

A second suite of about 642 species, accounting for 39% of the flora, colonized from the temperate north (Long 1974). The animals of South Florida differ strikingly from the plants in this regard. Most of the region's depauperate native fauna consists of temperate-zone taxa: for example, 88% of the breeding land birds are northern species (Robertson and Kushlan 1974).

There are nearly 300 naturalized introduced species in South Florida and they account for approximately 18% of the flora (Ewel and Conde 1979 based on descriptions in Long and Lakela 1971). All of South Florida's naturalized

Table 13.1. Numbers of native and naturalized exotic species in South Florida

Taxonomic Group	Total Number of Species	Number of Exotics	References	Notorious Examples
Plants	1647	±250	Long and Lakela (1971)	*Casuarina* spp. (Australian pines) *Melaleuca quinquenervia* (melaleuca) *Schinus terebinthifolius* (schinus)
Fish[a]	80	13	Courtenay et al. (1984); Loftus and Kushlan (1986)	*Cichlosoma bimaculatum* (twospot cichlid) *Clarius batrachus* (walking catfish) *Pelonesox belizanus*(pike killifish)
Amphibians	18	4	Wilson and Porras (1983); W.F. Loftus (personal communication)	*Bufo marinus* (marine toad) *Hyla septentrionalis* (Cuban tree frog)
Reptiles	52	22	Wilson and Porras (1983)	*Anolis equestris* (knight anole)
Birds	296[b]	±15	Owre (1973, personal communication), Robertson and Kushlan (1974)	*Myiopsitta monachus* (monk parakeet) *Pycnonotus jocosus* (red-whiskered bulbul) *Brotogeris versicolurus* (canary-winged parakeet) *Melopsittacus undulatus* (budgerigars)
Mammals	44	10	Layne (1974)	*Dasypus novemcinctus* (nine-banded armadillo)

[a] Includes freshwater species only.
[b] Of these, 116 species breed in South Florida; an additional 83 species are known from < 10 credible records.

tree species were introduced intentionally, some as ornamentals, some for fruit, and some to afforest the Everglades marshes.

13.3. The South Florida Environment

Few sea-level land areas at latitudes of 25° to 27° receive as much rainfall as South Florida (Fig. 13.2.). Mean annual rainfall averages about 1400 mm, and most of it falls between May and October.

Most rainfall in the region is convectional and accompanied by thunderstorms. The incidence of lightning strikes is among the world's highest, and fires are common, even when the soil is flooded. Fire is important to almost every ecosystem in South Florida (Wade et al. 1980) and often influences the success or failure of species' invasions.

South Florida's landscape is one of the geologically youngest on the North American continent; much of it has probably been above sea level for less than 5000 years (Fairbridge 1974; but see Robbin 1984). Its young flora, although species-rich, may not fully occupy all resources. This undersaturation may explain, in part, why so many introduced species have successfully colonized the region.

The southern extremity of peninsular Florida is a limestone platform that barely emerges above sea level. In some places it is covered with a veneer of sand, marl, or peat; elsewhere the limestone itself is the substrate for plant growth. Much of southern Florida floods during the summer rainy season. The water flows slowly southward in sheets over the surface, and well-defined stream channels are almost nonexistent. Therefore its hydrology—and its vegetation—

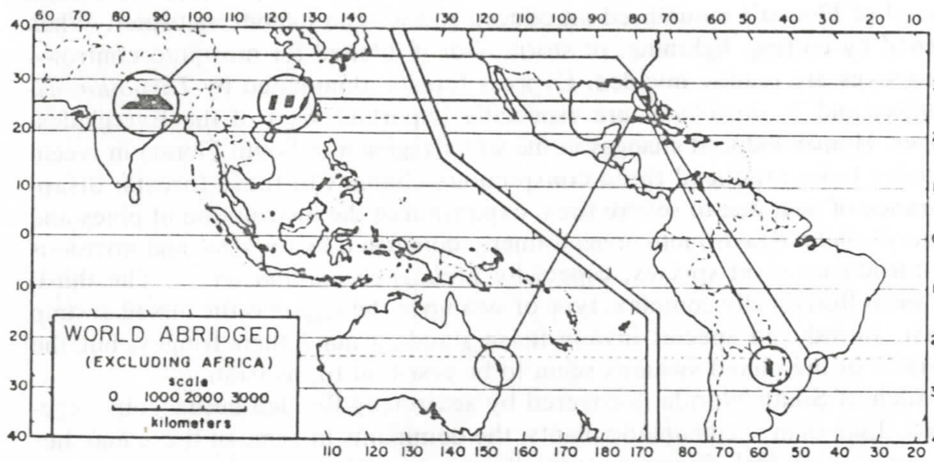

Figure 13.2. World distribution of areas with latitude, elevation, and amounts of rainfall similar to South Florida. Africa has contributed relatively few species (except some important grasses) to South Florida's non-native flora because its climates at comparable latitudes and altitudes are drier than Florida's.

are very susceptible to drainage modifications at distant locations. Ditching and diking were common land-reclamation procedures in South Florida from the 1880s until the late 1940s, dubbed the "Age of Rapacious Drainage" by Gleason (1984).

13.4. The Ecosystems of South Florida

Several detailed treatments of the plant communities of South Florida have been published (e.g., Davis 1943; Egler 1952; Craighead 1971). Four broad groups of communities that reflect major differences in physiognomy, floristics, and environment—upland forests, swamps, marshes, and human-created communities—are delineated in Figure 13.1.

There are two main kinds of upland forest in South Florida, pine forests (dominated by *Pinus elliottii* var. *densa*) and mixed-broadleaved forests (dominated by trees of West Indian origin). Introduced species invade the pinelands readily, especially if they are not burned regularly or if they are severely burned. The mixed broadleaved forests, locally called tropical hammocks, rarely flood and seldom burn. Although they occupy little area in South Florida, their unique and rich species composition has made them important targets for ecological studies and conservation efforts. In urban areas they become havens for many introduced species, but in preserves non-natives usually play a relatively unimportant role.

There are three main types of swamps in South Florida: mangroves, cypress forests, and mixed-species swamp forests. Florida contains most of the mangrove swamps of the U.S., and the Everglades National Park alone contains 1500 km^2, or about two-thirds of the statewide total. Intact mangrove communities are relatively resistant to invasion by introduced species, even though several of Florida's naturalized introduced species can tolerate saltwater. When opened by cutting, lightning, or storms—or if ditched for mosquito control—mangroves are readily invaded. Cypress forests, dominated by *Taxodium ascendens* and *T. distichum*, are especially important west of the Everglades-proper. Human-induced changes in the water regimen of South Florida in recent decades have produced three conspicuous changes in these forests: disappearance of peat due to severe fires, expansion of the distribution of pines and palms (*Sabal palmetto*) into areas formerly dominated by cypress, and invasions by introduced plant species, especially *Melaleuca quinquenervia*. The third, and most floristically complex, type of swamp in the region is the mixed swamp forest. Introduced species invade these stands around their fringes, but the interiors of the mixed swamps seem to be resistant to invasion.

Much of South Florida is covered by seasonally flooded herbaceous vegetation. Like many semiaquatic plants, the dominants in some of these marshes are not mycorrhizal. Sawgrass (actually a sedge, *Cladium jamaicense*) covers vast areas and dominates what may be one of the world's most extensive nonmycorrhizal, monospecific communities. When water regimens change the soil sometimes becomes better oxygenated. This permits mycorrhizal plants—including several notorious aliens—to invade habitats from which they would normally be excluded.

The sands, marl, and limestone that support most South Florida ecosystems are not especially good substrates for plant growth. When people modify these substrates they unwittingly create new habitats, unlike any that occur naturally in the region. Farming increases soil fertility and aeration. Dredging creates canals (now inhabited by introduced species of fishes and plants) in a land that had few ponds and streams; the spoil banks become dry islands surrounded by marshes. Bulldozing and road construction create topography in a landscape that is otherwise billiard-table flat. These new substrates are not colonized by the same assemblages of plants that originally blanketed South Florida. Instead, new species combinations—frequently dominated by introduced species—grow there. The new substrates themselves occupy thousands of hectares. More importantly perhaps, they harbor dense concentrations of introduced species, so become the staging areas from which these aliens disperse into natural communities. The effectiveness of these new ecosystems as facilitators of introduced-species invasions is enhanced by their shape. Because many of them result from canal and road construction, they are long and narrow, so have a high edge-to-area ratio. Introduced species that colonize such habitats therefore penetrate well inside unmodified ecosystems so their seeds must travel only short distances to reach large areas of native communities.

13.5. Two Successful Introduced Species

Of the dozens of species that have become naturalized in the nonagricultural ecosystems of South Florida, I selected the two best-studied and most conspicuous ones for discussion here: *Melaleuca quinquenervia* (hereafter melaleuca) and *Schinus terebinthifolius* (hereafter schinus). Both species have undergone dramatic range expansions in recent decades and they are still expanding rapidly. Thus, they offer a unique opportunity to study colonization and invasion while they are occurring, rather than after the fact. Both species are evergreen, subtropical trees that were intentionally introduced into Florida within the past century and both have become dominants in landscapes that were formerly treeless, or nearly so. Their northward migration up the Florida peninsula is checked by frost.

There are important differences between melaleuca and schinus, and a comparison of their ecological and life-history traits should prove instructive. They differ with respect to their relationships to fire and water regimens and they tend to invade different communities. They also differ in their degree of dependence on human modification of natural conditions to facilitate invasion. Regardless of each of their impacts on local ecosystems, neither species seems to be a strong competitor of the other. Good invaders that they are, they seem to have divided the spoils fairly equitably.

13.5.1. Melaleuca

Melaleuca quinquenervia (Cav.) Blake (called melaleuca, cajeput, or punk tree) is a myrtaceous tree native to Australia, New Caledonia, and New Guinea. In its native habitat it grows in coastal lowlands where it forms open, nearly monospecific stands that burn regularly. It was introduced into southeastern and southwestern Florida around the turn of the century as a prospect for afforesting the Everglades. It has been the object of many studies in Florida, the most detailed of which were by Meskimen (1962) and Myers (1983, 1984).

Once established, melaleuca tolerates a broad range of site conditions. It becomes established more readily on sand than on marl, but can survive on almost any soil in South Florida. It tolerates extended flooding, moderate drought, and some salinity.

Melaleuca is almost perfectly adapted to fire. It has thick, spongy bark that insulates the cambium. The outer layers of bark are flaky and burn vigorously. This conducts flame into the canopy, igniting the oil-laden foliage. The leaves and small branches are killed, but dormant lateral buds on the trunk germinate within weeks. This prolific resprouting greatly increases the surface area of small branches and therefore the tree's reproductive potential. Furthermore, melaleuca can flower within weeks after a fire.

Each serotinous capsule on a melaleuca contains about 250 tiny seeds (36,000 per g), and these are released after a burn, frost, or any other event that severs the vascular connections to the fruit. A burned melaleuca can release millions of seeds, which are dispersed short distances by wind and water. A melaleuca colony frequently consists of a series of annulae of even-aged trees surrounding a clump of founders. With its within-capsule seed bank, melaleuca can potentially reproduce any time during the year.

13.5.2. Schinus

Schinus terebinthifolius Raddi (schinus, Florida holly, Brazilian pepper, Christmas berry) is a member of the Anacardiaceae native to Brazil, Paraguay, and Argentina. In its natural habitat it is a sparse species and never dominates the landscape as it does in South Florida. It has dark green foliage and produces copious quantities of bright red drupes in late December. Schinus was introduced as an ornamental to South Florida more than 100 years ago, but did not begin to explode across the landscape until the 1950s.

Like melaleuca, schinus grows on a broad range of sites in South Florida, ranging from mangroves to pinelands. It thrives on disturbed soils and in the newly created habitats that result from drainage and farming. It is more exclusively ruderal than melaleuca and tends to prefer better-drained sites.

The relationship of schinus to fire is very different from that of melaleuca. Whereas melaleuca is a tall, slender-crowned tree, schinus is short and squat (Fig. 13.3.). The broad crowns of adjacent schinus trees intertwine. This creates a dense shade and results in almost no herbaceous understory vegetation that might burn. Because schinus produces new leaves throughout the year, and

Figure 13.3. *Melaleuca quinquenervia* (left) and *Schinus terebinthifolius* (right) in South Florida. (Courtesy of J.R. Snyder.)

because its litter decomposes quickly (J.R. Snyder, unpublished) little leaf litter builds up on the forest floor. When schinus does burn (as it frequently does when it colonizes open pinelands), the above-ground parts are killed, but the tree promptly resprouts from the base.

Another important contrast between melaleuca and schinus concerns their reproduction. Schinus flowers synchronously in October and is pollinated by a native syrphid fly, *Palpada vinetorum*. Its fruits ripen in December through February and the pea-sized drupes are dispersed long distances by mammals and birds. Most dispersal is effected by the huge flocks of robins *(Turdus migratorius)* that periodically (but not annually) congregate in South Florida during the winter. Introduced species, such as the red-whiskered bulbul, *Pyononotus jocosus*, also disperse their seeds (Owre 1973). During the late winter months when schinus seeds are dispersed, there is little reproductive activity by native trees. This exploitation of a different time of reproduction may help to explain schinus' success in South Florida.

13.6. Invasibility

Invasibility is a measure of a community's susceptibility to colonization by a particular species. Thus, a given community might have high invasibility with respect to one prospective colonist and low invasibility with respect to another.

It is often argued that most undisturbed communities have low invasibility with respect to almost all newcomers. Before examining the evidence that supports this contention (and an example that refutes it) we should consider the commonly held view that introduced species invasions are determined primarily by species' abilities to gain access to new communities.

13.6.1. Invasions as a Problem of Site Access

The reasoning associated with this view usually goes something like this: A new species is introduced (usually by people) to a region from which it was previously excluded by geographical barriers. It aggressively invades the local community, outcompeting the native species. It is an especially effective competitor because the biological controls that kept it in check at home did not get transferred with it. There are two ways to contain this invader: (1) attack it with all the weapons available, killing as many individuals as possible, and (2) study the species in its native habitat so that the herbivores and diseases that attack it there can be identified, screened, and eventually introduced into its new territory.

By this view, successful invaders are regarded as a disease, rather than a symptom. Sometimes a community has high invasibility because its biota has been disrupted or because the site has been devegetated. Frequently, however, the weakening is more subtle and results from environmental changes that are not readily perceptible to casual observation. Changes in hydrology due to

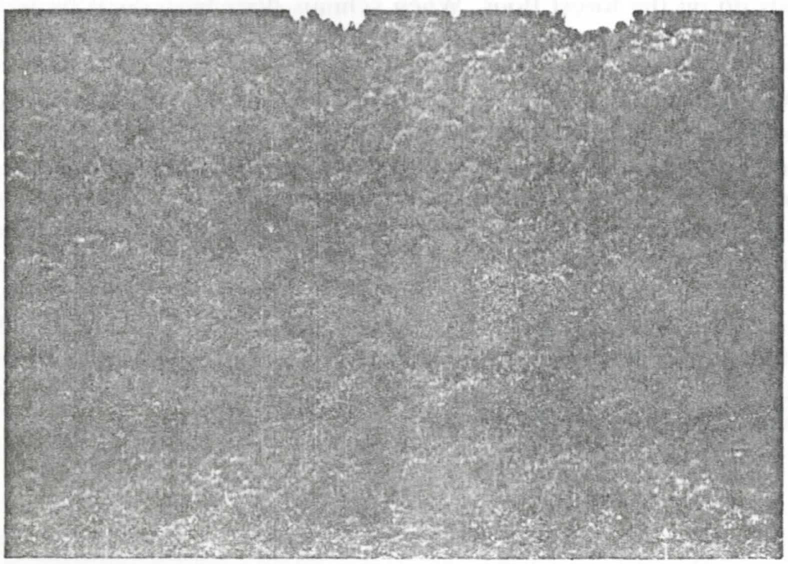

Figure 13.4. Kudzu *(Pueraria lobata)* blanketing a plantation of sugi cedar *(Cryptomeria japonica)*, both in their native Japan. (Courtesy of K. Hara.)

drainage or dike construction in the northern reaches of the Everglades' marshes is one such example; the slow eutrophication of the Great Lakes is another.

Furthermore, it is not true that naturalized species are invariably kept under control in their native habitats by local competitors, herbivores, and parasites. Witness, for example, the growth of that scourge of the southeastern U.S., kudzu *(Pueraria lobata)*, on a sugi cedar *(Cryptomeria japonica)* stand in its native Japan (Fig. 13.4.).

Admittedly, many introduced species have successfully invaded presumably pristine ecosystems. Examples might include the circumglobal introductions of pigs, goats, and rats by early explorers onto uninhabited islands as well as some of the early bird introductions on the Hawaiian Islands (see Moulton and Pimm 1983 and this volume). Most cases involve species-poor communities, such as those on remote islands (or peninsulas, such as Florida, which jut into a climatic zone different from that of the continent from which they protrude). Some localities commonly cited in the literature on introduced species invasions, e.g., Great Britain and New Zealand, probably reflect both circumstances: a depauperate biota and disturbed native communities. Few, if any, introduced mammals or trees have become naturalized in the mature forests of the Amazon Basin, Zaire, or Borneo.

13.6.2. Tests of Invasibility

Invasibility can be inferred a posteriori by observing communities and the species they contain. One danger of this approach is that it is subject to unintentional bias. Observers tend to be more likely to generalize from a few observations of successful invasion into a community type than from many observations of communities that have not been invaded.

Invasibility can also be tested experimentally, and this is the approach I and my co-workers have taken in studying melaleuca and schinus in South Florida. We conduct these tests by introducing seeds of the potential invader into an array of communities representing various successional stages, degrees of disturbances, hydroperiods, fire regimens, and soil types. Seeds are introduced at intervals throughout the year to test ecosystem invasibility during as many conditions as possible. Myers (1983), for example, introduced at least 2 million melaleuca seeds into each of eight communities over a 2-year period. In the Everglades National Park we introduced more than 20,000 schinus seeds into each of nine communities over a 2-year period (Ewel et al. 1982).

The results of those seed introductions led to similar conclusions regarding both species: introduced seeds yielded more seedlings in disturbed communities than in mature ones (Table 13.2.). In some cases seed germination was higher in a mature community (e.g., the dwarf cypress forest studied by Myers), but in no case did the numbers of surviving seedlings in the mature communities approach those in the disturbed communities. In many communities the seed introductions were complete failures and yielded no surviving seedlings.

Suppose, however, that the timing of the seed-introduction experiments did not coincide with the chance juxtaposition of conditions required to ensure

Table 13.2. Germination of the seeds of two exotic trees introduced into mature and disturbed ecosystems in South Florida

Exotic Species	Total No. Seeds Introduced	Mature Communities		Disturbed Communities	
		Number[a]	Germination (%)	Number[a]	Germination (%)
Schinus terebinthifolius	200,000	5	1.27	14	2.62
Melaleuca quinquenervia	22,000,000	6	0.01	2	0.14

Data for *M. quinquenervia* are summarized from Myers RL (1983) J Appl Ecol 20:645–658.
[a] Number of communities into which introductions were made.

both germination and seedling establishment? To guard against this possibility, both Myers (1983) and Ewel et al. (1982) bypassed the crucial germination and early survival phases and planted seedlings of melaleuca and schinus in the same communities that seeds of these two species had been sown in.

Melaleuca and schinus responded differently (Fig. 13.5.). The outplanted melaleuca seedlings had lower than 50% survivorship in five of the eight communities. Survivors grew best in two disturbed ecosystems (a severely burned pine-cypress ecotone and a drained cypress forest) and one undisturbed community (a dwarf cypress forest).

Schinus, on the other hand, survived everywhere it was planted. The outplanted seedlings grew best in disturbed, open communities, but mortality was low in even the most diverse and dense communities studied. Furthermore, schinus seedlings that looked like they were barely surviving in dense shade proved capable of responding to altered environmental conditions when gaps were formed. A schinus seedling, once established, is a potential canopy tree in almost any forest in South Florida.

13.6.3. Displacement of Cypress by Melaleuca

It is clear that, as postulated earlier, disturbance facilitates invasion. But is it an essential prerequisite? The answer, of course, is "not always," and the work of Myers (1984) on the invasion of malaleuca into the ecotone between pine and cypress forests demonstrates this nicely.

Pond cypress, *Taxodium ascendens*, is one of those native species that colonized South Florida from the north temperate zone. Myers (1984) argues that because there are few trees in South Florida that are well adapted to both fire and flooding, cypress underwent ecological release and occupies habitats from which it might otherwise be competitively excluded. One such habitat lies be-

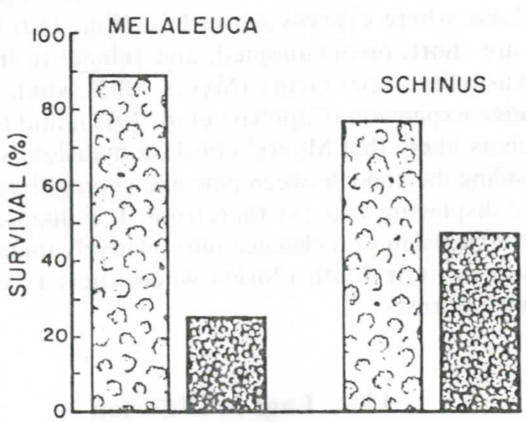

Figure 13.5. Survival of outplanted seedlings of two introduced species of trees, *Melaleuca quinquenervia* and *Schinus terebinthifolius*, in disturbed (open shading) and mature (dense shading) communities in South Florida. [Data on *M. quinquenervia* are from Myers (1983)].

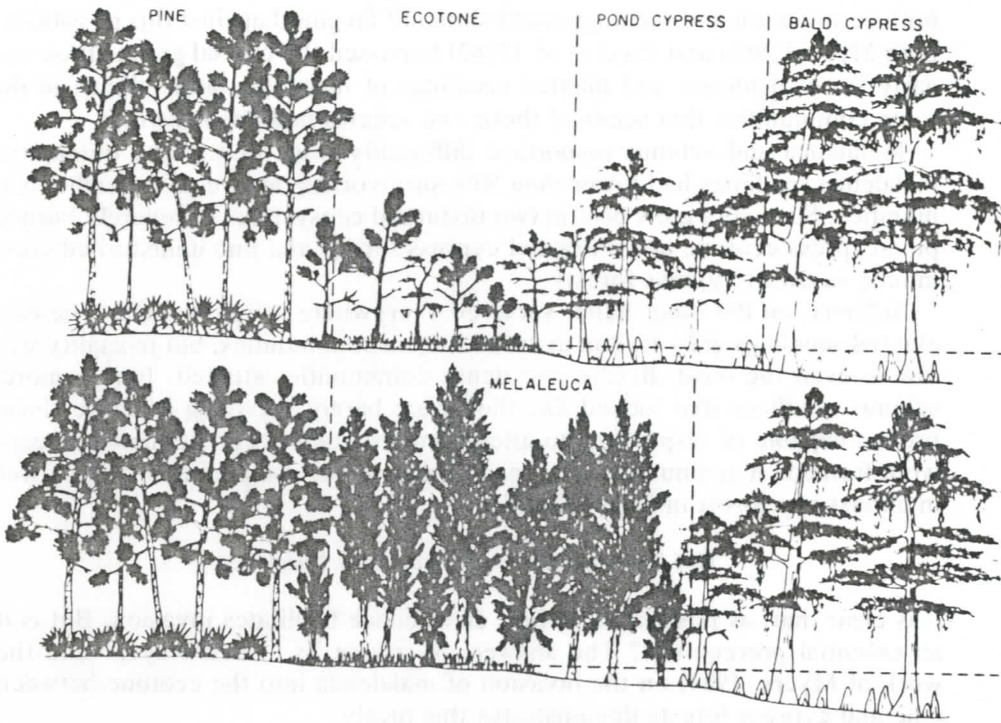

Figure 13.6. Invasion of the ecotone between pine and cypress forests in South Florida by *Melaleuca quinquenervia*. [From Myers RL (1984) In: Ewel KC, Odum HT (eds), Cypress Swamps. Reproduced with permission of University of Florida Press.]

tween pinelands and swamps on soils that are too wet for good growth of pines yet drier than those where cypress grows best (Fig. 13.6.). Cypress stands in these ecotones are short, open-canopied, and subject to frequent fires.

Based on invasibility experiments (Myers 1983), studies of melaleuca distribution and range expansion (Capehart et al. 1977), and a decade of field observations, it seems likely that Myers' (1984) conclusion is correct. Melaleuca is capable of invading the zone between pine and cypress forests in South Florida and successfully displacing cypress therefrom. It is likely, then, that we can anticipate further expansion of melaleuca into relatively undisturbed ecosystems, especially in southwestern South Florida where there is an extensive mosaic of pine and cypress forests.

13.7. Lags in Diffusion

Both schinus and melaleuca were present in Florida long before they became conspicuous elements in the landscape, a phenomenon that is well known with respect to invasions of many other introduced species. What accounts for the long lag between the time these species were introduced and the time their populations became noticeable? There are at least four possible explanations.

First, schinus and melaleuca may have been introduced during a time when South Florida's ecosystems were more pristine—and therefore more invasion-resistant—than they are today. These two aliens may have exploded across the landscape in response to drainage, farming, and urbanization.

Second, these species may have been undergoing rapid—yet unnoticeable—expansion. An exponentially growing population appears to undergo a long lag phase of initial buildup before its numbers escalate so dramatically that it becomes a conspicuous element in the landscape. The same phenomenon may be occurring today with more recently arrived plants such as downy rosemyrtle *(Rhodomyrtus tomentosus)* and colubrina *(Colubrina asiatica)*.

Two other possible explanations for the long time lag between introduction and population explosion concern new ecosystems as reservoirs of potential invaders. Disturbed areas colonized by introduced species may be staging areas from which invading species shower the surrounding landscape with seeds. A second idea is that populations occupying disturbed habitats eventually produce genetic variants adapted to invasion of undisturbed local communities.

It may have taken several decades for melaleuca and schinus to build up populations large enough to have significant reproductive potential (or "infection pressure," sensu Salisbury 1961). A small population would have dispersed relatively few propagules, and until those seeds hit the right combination of conditions for germination, survival, growth, and reproduction, there would have been no range expansion. The probability of hitting the right combination of environmental conditions increases with time and with the number of propagules dispersed. Colonization of heavily disturbed habitats may have permitted schinus and melaleuca to establish pockets of infestation from which large numbers of seeds were dispersed into healthier communities. Eventually, populations became established there, too. The end result may have been inevitable, but its occurrence may have been hastened by the establishment of island-like populations from which infection could radiate outward.

Baker (1965) suggested an alternative to Salisbury's "infection pressure" explanation of the lag often observed in the colonization pattern of a new invader. He suggested that a new colonist might be confined to restricted habitats until appropriate genotypes become available through recombination or introgression. Although no genetic studies of schinus or melaleuca in Florida have been done, this seems a likely possibility, especially in the case of schinus, which is comprised of four varieties (Barkley 1944). Schinus has many of the characteristics listed by Baker (1965) as attributes of an ideal weed, yet it also has many traits more typical of mature-system species, including high tolerance of shade. Its behavior is analogous to that of a sit-and-wait predator: it becomes established in the understory of dense forests, then captures the site when gaps occur in the canopy. This makes it an unusually formidable species to control. To what extent its physiological characteristics are shared by all genotypes in South Florida is unknown, but it seems likely that there is substantial variation within the population.

13.8. Conclusions

There are few areas in the world with climate–soil combinations similar to those of South Florida. In spite of this paucity of equivalent landscapes likely to act as species donors, naturalized introductions comprise 15 to 25% of most major taxonomic groups in South Florida, giving the region the continent's most exotic-laden biota. Although its geological youth and depauperate fauna may be related to the success of many introductions, its rich flora argues against undersaturation as a major factor in the colonization of thousands of hectares by introduced trees such as melaleuca and schinus.

Species invasions often reflect the condition of the community being invaded rather than uniquely aggressive traits of the invader. Human modification of South Florida's ecosystems has made them especially susceptible to invasions for two reasons. First, some human activities cause changes in community structure that lower the competitiveness of natives and facilitate invasions by introduced species. Land clearing is an obvious example, but more subtle changes induced by aseasonal burning or modest changes in hydroperiods can be equally important. Second, new habitats have been created by drainage, ditching, diking, and farming, and introduced species are often better adapted than native species to these new environments.

On new substrates we can expect to see new communities develop, comprised of combinations of native and introduced species. Naturalized species often develop mutualistic interactions with indigenous species. Schinus, for example, provides food for native organisms that pollinate its flowers and disperse its seeds. It is likely that South Florida's canals, spoil banks, and anthrosols will always support vegetation in which introduced species are important.

This does not mean that resource managers must relinquish intact, native ecosystems to introduced species. However, to be successful a management program must be tailored to fit both the invader and the invadee: i.e., the autecological and life-history attributes of the species as well as the biotic and abiotic attributes of the ecosystem being protected.

For example, schinus is such a well-dispersed invader of ruderal habitats that it is almost impossible to keep it off of well-drained, abandoned farmland in South Florida. The risk of massive invasion of relatively undisturbed forests, however, can probably be reduced substantially by ferreting out individuals that colonize naturally occurring gaps and by burning pine forests frequently.

Melaleuca requires a different approach. It colonizes relatively wet sites, thrives on fire, and is capable of invading some undisturbed communities. It is probably the limited mobility of melaleuca seed that has confined its invasion thus far. Resource managers might be well advised to concentrate on eliminating seed sources nearest the pine-cypress ecotones into which melaleuca is preadapted to spread, rather than expending their resources on pockets of melaleucas near other, less susceptible habitats.

In considering introduced species in South Florida, we must recognize that: (1) some permanent changes in species composition resulting from species introductions are inevitable; (2) invasions often involve intricate—and perhaps positive—interactions between introduced and native species; and (3) an intact native ecosystem is often the best prophylactic against exotics. To consider only the invading species themselves in developing management programs or in recommending regulatory actions is tantamount to curing symptoms and not disease.

13.9. Acknowledgments

Field work on melaleuca and schinus in South Florida was supported by the U.S. Department of the Interior. Several scientists provided me with information on the status of introduced species in specific taxonomic groups: W.R. Courtenay (fish), J.N. Layne (mammals), W.F. Loftus (fish and herps), and O.T. Owre (birds). I owe special thanks to J.R. Snyder and R.L. Myers for helpful reviews of the manuscript plus many stimulating discussions on species' introductions and South Florida's ecosystems over the past several years.

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