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ORIGINAL PAPER

Decline in exotic tree density facilitates increased plant diversity: the experience from *Melaleuca quinquenervia* invaded wetlands

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Abstract The Australian tree *Melaleuca quinquenervia* (melaleuca) formed dense monocultural forests several decades after invading parts of Florida and the Caribbean islands. These dominant forests have displaced native vegetation in sensitive wetland systems. We hypothesized that native plant diversity would increase following recent reductions in density of mature melaleuca stands in south Florida. We therefore examined data on changes in melaleuca densities and plant species diversity derived from permanent plots that were monitored from 1997 to 2005. These plots were located within mature melaleuca stands in nonflooded and seasonally-flooded habitats. Two host-specific biological control agents of melaleuca, *Oxyops vitiosa* and *Boreioglycaspis melaleucae*, were introduced during 1997 and 2002, respectively. Also, an adventive rust fungus *Puccinia psidii* and lobate-lac scale *Paratachardina pesudolobata* became abundant during the latter part of the study period. Overall melaleuca density declines in current study coincided with two to four fold increases in plant species diversity. The greatest declines in melaleuca density as well as the greatest increases in family importance values and species diversity indices occurred in nonflooded as compared to seasonally-flooded habitats. Most pioneer plant species in study sites belonged to Asteraceae, Cyperaceae, Poaceae, and Ulmaceae. The rapid reduction in melaleuca density and canopy cover during the study period may be attributed to self-thinning accelerated by the negative impact of natural enemies. Densities of other woody plants, particularly *Myrica* and *Myrsine*, which were sparsely represented in the understory by a few suppressed individuals also declined during the same period, possibly due to infestation by the generalist lac-scale. These findings indicate that natural-enemy accelerated self-thinning of melaleuca densities is positively influencing the native plant diversity and facilitating the partial rehabilitation of degraded habitats.

Keywords Basal area · Biological control · Family importance value · Invasive plants · Natural enemies · Psyllid · Rust fungus · Species diversity · Weed · Weevil

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Introduction

Invasion of native plant communities by exotic organisms threatens the integrity of many natural systems (OTA 1993; Wilcove et al. 1998; Myers and Bazely 2003). An alarming number of invasive plants have invaded natural communities on both local and regional scales (D'Antonio and Vitousek 1992). Important effects of invasive weeds include

diminished biodiversity (Braithwaite et al. 1989; Malecki et al. 1993) coupled with alteration of nutritional, hydrological, and fire regimes (Vitousek et al. 1997; D'Antonio and Vitousek 1992). In Florida USA, for instance, 39% of invasive plants are capable of modifying geomorphology and 77% of altering biotic communities (Gordon 1998). Evidence suggests that invading vines (Gorchov and Trisel 2003), shrubs (Baker and Van Lear 1998), and trees (Brown et al. 2006a; Nagaike et al. 2006) behaving as dominant species have successfully reduced the density, diversity, and abundance of native plants. Aggressive invaders develop dense thickets (Baker and Van Lear 1998; Rayamajhi et al. 2006a) and change forest floor properties through accumulation of slowly decomposing litter (White 1994; Rayamajhi et al. 2006a). Litter accumulation may inhibit seedling establishment and growth not only through shading but also through mulching effects, which over time alters the forest floor physiography (White 1994; Rayamajhi et al. 2006a).

Forest managers have observed that increased stem densities of a dominant plant species often results in reduced plant species diversity in the overstory and increased species replacement in the understory (Nagaike et al. 2006). Additionally, the role of forest canopy gaps in the maintenance of plant species diversity has been well recognized in many systems (Denslow 1987). Mitigation and ultimately restoration of weed invaded habitats will typically involve suppression of the target-weed (Gordon 1998). Therefore, one would logically assume that greater plant diversity could be realized in invasive plant dominated communities by reducing density and canopy cover of the invader thereby increasing light penetration to the forest floor (Baker and Van Lear 1998) and reducing mulching effects (Gordon 1998).

Very few published examples exist that quantify the influence of reductions in exotic tree densities on plant species diversity in natural areas (Brown et al. 2006a; Baker and Van Lear 1998). It is essential to understand the effects of density reductions in a dominant invasive tree and the type of plant species (native versus non native) which may colonize the space vacated by the invader in order to formulate management strategies. To investigate this phenomenon, we studied the dynamics of mature *Melaleuca quinquenervia* (Cav.) Blake (Family, Myrtaceae; hereafter "melaleuca") stands and their impact on other associated plant species in the community over time and space (habitat).

The noxious weed melaleuca has been introduced to many parts of the world (Holliday 1989) including Florida (Dray et al. 2006) and is recognized as one of the most invasive weeds of the southeastern United States and the Caribbean islands (Bodle et al. 1994; Hofstetter 1991; Pratt et al. 2005, 2006a, b, 2007). Melaleuca has become a pernicious invader of wetland systems in the Florida Everglades (Browder and Schroeder 1981; Woodall 1982) due in part to its competitive superiority over native vegetation and development of dense stands (Turner et al. 1998; Dray et al. 2006) and canopy closure. These stands often appear as domes characterized by larger founder trees up to 20 m tall mixed with co-dominant and suppressed trees near the center and tapering progressively towards smaller trees at the periphery (Hofstetter 1991; Rayamajhi et al. 2006a). The melaleuca invasion ultimately affected ecosystem structure and dynamics by causing a 60–80% loss in graminoid marsh communities (Austin 1978) and other understory vegetation through shading and soil accretion (White 1994). Melaleuca also invaded pine-cypress ecotones and displaced well established pond cypress (*Taxodium ascendens* Brong.) stands (Myers 1975, 1983; Ewel 1986). Thus, diverse natural communities have been replaced by monoculture thickets and forests of close-canopied melaleuca trees (Rayamajhi et al. 2006a) which are of negligible wildlife value (Laroche 1994; O'Hare and Dalrymple 1997). Similar incidence of decreased species richness with increased canopy coverage has also been reported for other systems such as abandoned chestnut (*Castanea sativa*) stands (Romane et al. 2001).

Recently, however, marked reductions in melaleuca tree densities have been reported in southern Florida. Rayamajhi et al. (2007), for instance, demonstrated that changes in stand densities are due primarily to the combined effects of density-dependent (self-thinning) and density-independent (natural-enemy mediated) factors that result in tree mortality. They implied that the intentionally introduced and adventive natural enemies inflicting damage to trees have enhanced the level of melaleuca tree mortality that formerly resulted from density dependent mortality factors acting alone (Rayamajhi et al. 2007). Intentionally introduced melaleuca natural enemies

include the weevil *Oxyops vitiosa* Pascoe (a foliage feeder) and the psyllid *Boreioglycaspis melaleucae* Moore (a sap-feeder), which were imported from Australia to southern Florida during 1997 and 2002, respectively. Both arthropods are well established in most melaleuca populations of Florida (Center et al. 2000; Center et al. 2006; Pratt et al. 2003). An outbreak of a polyphagous scale-insect *Paratachardina pseudolobata* (Kondo and Gullan 2007) was first observed attacking melaleuca and other trees in south Florida during 2002 (Pemberton 2003). Additionally, an unidentified sooty mold (indiscriminately covering foliage and green stems) was also associated with heavy infestations of this lac-scale. An adventive rust fungus, *Puccinia psidii* G. Wint originally reported from allspice plants (*Pimenta* sp.), also causes damage to new foliage and succulent tips by distorting, defoliating, and inducing localized swellings on twigs which cumulatively results in dieback of *M. quinquenervia* tips (Rayachhetry et al. 1997; Rayamajhi et al. 2006b). As reported by Rayamajhi et al. (2007) weevil and rust damaged melaleuca leaves in leaf-litter increased from 4.7% in 1997 to 38.7% in 2005 and 4.1%, in 2004 to 8.0% in 2005 which is indicative of substantial weevil damage in the canopy.

While investigating the density-dependent and density-independent causes of melaleuca tree mortalities, Rayamajhi et al. (2007) determined that overall tree damage was greatest (2.82 at the scale of–5; 1 = up to 1%, 2 = 1.1–25%, 3 = 25.1–75% 4 = 75.1–100% of the total leaves are damaged or defoliated, and 5 = the plant was completely killed) among small versus large individuals. Highest levels of herbivory were also observed on trees of smaller dimensions, which corroborates with the accelerated rate of melaleuca tree mortality. However, basal area coverage decline, an indication of the mortality of larger trees, was also evident (Rayamajhi et al. 2007). A combination of density reduction and canopy opening due to mortality of both smaller as well as larger trees was visually discernable and this phenomenon was expected to facilitate recruitment of non-melaleuca species as long as the competitive ability of melaleuca remains checked through top-down population regulation (Rayamajhi et al. 2007). Experimental evidence has further proven the weevil's (Pratt et al. 2005) and the psyllid's ability to reduce melaleuca flowering and kill newly recruited seedlings (Franks et al. 2006). These abilities of the natural enemies to inflict leaf-damage, defoliation, twig dieback, and ultimately mortality of melaleuca trees (Pratt et al. 2003, 2004, 2005; Franks et al. 2006; Morath et al. 2006; Rayamajhi et al. 2007, 2008) will presumably continue to open up forest gaps allowing non-melaleuca plant diversity to increase over time in south Florida.

Here, we hypothesized that this decline in melaleuca densities would facilitate increases in non-melaleuca plant species richness and diversity. We tested this hypothesis through temporal and spatial monitoring of mature melaleuca stands in southern Florida (1997 through 2005) by quantifying: (a) melaleuca density as a dominant species, (b) number of plants of each non-melaleuca species, and (c) indirect indications of natural-enemy damage on melaleuca canopies during our study periods.

Materials and methods

Study sites and species

The study system included melaleuca stands that proliferated in and around fresh water marshes where surface water depths fluctuate in accordance with topography and the wet-dry seasonality of south Florida, USA (Kushlan 1990). Melaleuca stands at two sites in nonflooded habitats and two sites in seasonally-flooded habitats were included in this study. Sites designated as "nonflooded" remained inundated intermittently for a few hours to several days during or following periods of heavy rain but were not continuously flooded nor flooded every year, whereas "seasonally-flooded" sites remain inundated for variable periods every year (Rayamajhi et al. 2006a). The nonflooded and seasonally-flooded sites were located in the Holiday Park area (N26°02′59.0″, W80°26′22.6″; N26°02′58.2″, and W80°26′21.8″) within Broward County, and along Krome Avenue (N25°55′49.5″, and W80°27′1.9″) within Miami-Dade as well as in the Clewiston area (N26°47′4.2″, and W80°57′13.7″) of Palm Beach County. Soil types in all study sites were poorly drained Histosols as described by Brown et al. (1990) and Kushlan (1990).

Melaleuca plots selected for this study were located at or near the center of the stands within sites, referred to as "interior or mature stands". These

were composed primarily of mature trees mixed with sparsely scattered suppressed trees and saplings. Four 10 × 10 m plots were established at each site (i.e., four replications per site). The forest floors in these plots were nearly devoid of vegetation or, if present, the vegetation was sparsely confined to a few plants occurring sporadically under canopy gaps and at the invasion fronts of developing melaleuca stands. The forest floors in the sites were generally blanketed by thick layers of litter. Baseline data describing litterfall, biomass, and stem density in these plots have been reported for an early phase characterized by little or no herbivory (before 2001) followed by a later phase (2002–2005) of intense herbivore pressure on melaleuca populations (Rayamajhi et al. 2006a, 2007).

Canopy damage

Melaleuca trees at the sites were tall so it was impractical to monitor leaf-damage and defoliation at the upper canopy levels. We assumed that the causes and the intensity of natural-enemy damage in the canopy would be reflected in the percentages of damaged leaves among the total number of leaves collected in litter traps under the trees in the melaleuca stands. Therefore, an indirect approach was employed which involved collecting the fallen leaves in litter-traps placed on the forest floor. Two litterfall collection traps were randomly placed in each study plot. These consisted of square wooden frames (0.5 × 0.5 m) with 16 cm high sides, and copper wire screened bottoms (2 mm mesh) to provide drainage. The traps were raised 24 (on inverted plastic container at the four corners) or 70 cm (on wooden legs at the four corners) above the forest-floor to minimize litter-wetness and decomposition between collections. The traps in all plots were emptied at monthly intervals from July 1997 to June 2005.

Melaleuca leaf-litter samples were oven-dried at ca. 70°C to constant weight and separated into non-damaged and natural-enemy (weevil and rust fungus) damaged (leaves with weevil feeding scars and rust pustules) fractions. Numbers of leaves in each fraction were counted and the percentages of weevil, *O. vitiosa* and rust-fungus, *P. psidii* damaged leaves were determined for each sample.

Stand density

All plants (melaleuca and non-melaleuca) within permanent plots were counted regardless of size to determine the absolute density of each species. Initial enumeration of melaleuca and non-melaleuca plants was performed during March–April 1997. These measurements were then repeated once in 2000 and every year thereafter during the same time period until 2005. Permanent plots in the seasonally-flooded areas were lost to aerial herbicidal treatment after spring 2005, just after making the DBH measurement but before recording non-melaleuca plants in the plots.

Plant diversity

All prominent macrophytes (psilophytes, pteridophytes, gymnosperms, and angiosperms) with discernable characteristics within the plots were identified in the field to the lowest taxonomic level possible or sampled and later identified from herbarium specimens. Plant lists were prepared for each habitat. Family and species richness were determined from these lists. None of the non-melaleuca plants, especially the perennial dicots and gymnosperms, were at least 1 cm diameter at 1.3 m height from the base and so DBH could not be measured for those species.

Family importance values (FIV) were calculated based on the method described by Mori et al. (1983). These values were used to compare the relative contribution of each plant family to the community composition of each habitat type. Calculations were performed as follows:

Relative family diversity = (Number of species in family/Total number of species in the habitat) × 100.

Relative family density = (Number of plants per ha in family/Total number of plants per ha in the habitat) × 100.

The sum of these two values (Relative family diversity + Relative family density) for each family provided the FIV for each habitat.

Plant species diversity presented herein was based on Simpson's reciprocal index (Krebs 1999) as follows: $1/D = 1/\sum p_i^2$ where D = Simpson's original index, p_i (proportion of individuals of species in the community) = number of individuals of a

species enumerated in a plot divided by the summation of the individuals of all the species in the plot.

Statistical analysis

The effects of habitat, year, and stand position within a given stand on melaleuca density, basal area coverage, number of families and species per plot, and Simpson's Reciprocal Index (1/*D*) for species diversity were analyzed using repeated measures analysis of variance (ANOVA). Mean percentages and standard errors of the proportion of damaged leaves were determined for nonflooded habitats. Means and standard errors of density and the numbers of families and species per plot were determined for plots in both habitat types. Mean separations for density was carried out using Duncan's Multiple Range Test. Fisher's protected least significant difference test (LSD) was used to compare the means of the species and family richness and species diversity. Number of plant species/plot during our 7 year data collection period was regressed against the proportion of weevil and rust damaged leaves in the corresponding year to quantify the relationship between herbivory and changes in species diversity. Correlation between the level of damage on melaleuca canopies (proportion of damaged leaves) and the number of plant species/plot was determined using Pearson's Correlation Coefficient test.

Results

Melaleuca density

At the onset of the experiments, mean (±SE) melaleuca density in the permanent plots was similar ($P = 0.9589$) in nonflooded (28,513 ± 5,331trees/ha) and seasonally-flooded (27,200 ± 5,390 trees/ha) habitats but the effects of years (1997–2005) within habitats were highly significant ($P < 0.0001$). Overall, the density tended to decline over time in both habits (Fig. 1). The annual rate of decline in melaleuca density during the 8 year (1997–2005) study period was 9.1 and 8.6% per year for nonflooded and seasonally-flooded habitats, respectively. As reported in Rayamajhi et al. (2007), most of the loss was due to mortality among smaller trees and the tree

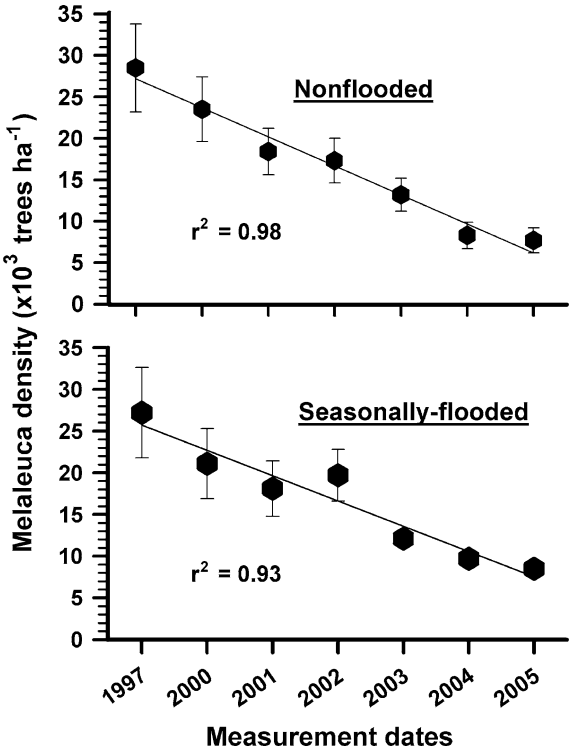

Fig. 1 Absolute density changes in *M. quinquenervia* tree populations in southern Florida

mortality rate increased with natural-enemy impact, i.e., after year 2001.

Plant families

Diversity of plant families increased in both habitats while melaleuca densities decreased. Habitat and year both affected ($P < 0.0001$) family richness, which decreased during the first phase (1997–2001) then gradually increased during the second phase (2002–2005) of the study period (Fig. 2). The mean (±SE) numbers of families during 1997 and 2005 in nonflooded habitats were 9.0 (±1.0) versus 16.7 (±0.7), respectively. In seasonally-flooded habitats during 1997 and 2004, the numbers were 4.1 (±1.0) versus 10.25 (±1.3), respectively. The fewest and the most plant families (family richness) existed in seasonally-flooded (13 in 1997 and 15 in 2004) and nonflooded (15 in 1997 and 26 in 2005) habitats, respectively (Table 1). In terms of FIV, Myrtaceae, Cyperaceae, and Asteraceae ranked first, seond, and third, respectively, in both habitats and during both

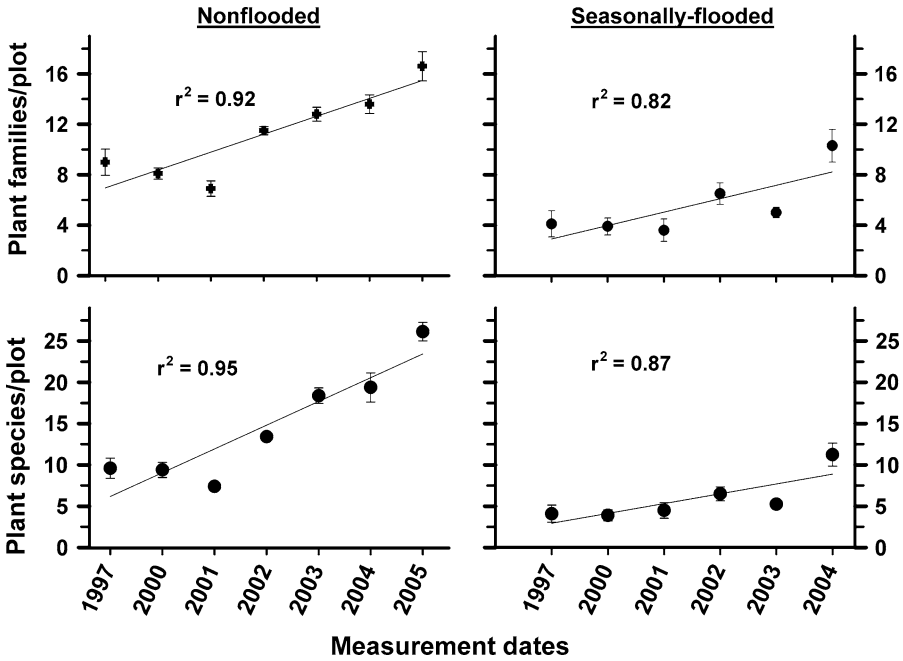

Fig. 2 Family and species richness in nonflooded and seasonally-flooded *M. quinquenervia* dominated stands in south Florida. Note that the study plot dimensions were 100 m^2 (0.01 ha) and plant species enumeration years have only up to 2004 in seasonally flooded habitat due to the loss of plots from herbicide

years (Table 1). The FIV increased over time within habitats for some plant groups but others declined. Although the decline in the FIV of Myrtaceae was much more rapid in nonflooded habitats (from 61.6 in 1997 to 15.8 in 2005) compared to seasonally-flooded habitats (from 96.2 in 1997 to 69.0 in 2004), family richness in the latter habitat was documented only up to the year 2004. Interestingly, the FIV of Asteraceae, Cyperaceae, and Poaceae increased in both habitat types but on different scales (Table 1). As shown in Table 1, more new families were documented during 2004/2005 compared to 1997.

Plant species

Simpson's reciprocal diversity-index differed between habitats ($P = 0.0512$) and among years ($P < 0.0001$) within a given habitat. There was a slight declining trend in the mean diversity index during 1997–2001 in both nonflooded and seasonally-flooded habitats (Fig. 3). However, the diversity index increased ca four-fold (2.76–9.8) in nonflooded habitats during 2001–2005 and two fold (1.6–2.4) in seasonally-flooded habitats during 2001–2004 (Fig. 3). These indices reflect differences in the magnitude of species diversity changes during three time periods (Fig. 3).

Habitat and year affected species richness ($P < 0.0001$) in the permanent plots. Species richness decreased between 1997 and 2001 and then gradually increased from 2002 to 2005 (Fig. 2). This trend was similar to that observed for family richness. The mean (±SE) numbers of species in the plots were 9.6 (±1.2) versus 26.1 (±1.2) during 1997 versus 2005 in nonflooded and 4.1 (±1.0) versus 11.3 (±1.3) during 1997 versus 2004 in seasonally-flooded habitats. Cumulative plant species enumerated within habitats showed greater numbers of species in nonflooded than in seasonally-flooded habitats (Table 2). Native plant species in nonflooded habitats during 1997 and 2005 comprised 88 and 83% of the total flora, respectively. In seasonally-flooded habitat, these percentages were 78 and 77% during 1997 and 2004, respectively. The majority of species were native, both at the onset of the experiment and at the final evaluation, although melaleuca and/or sawgrass were the dominant species in both habitats.

Major perennial plant species enumerated in permanent plots (Table 2) showed differences in their densities. The order of the density of major plant species in 1997 was *M. quinquenervia* (melaleuca) > *C. jamaicense* (sawgrass) > *M. cerifera* (wax myrtle) in mature melaleuca stands in both nonflooded and seasonally-flooded habitats. Melaleuca

Table 1 Habitat-wise (from all plots within habitat) family importance value (FIV), comparing the relative contribution to the plant species composition in mature stands of *Melaleuca quinquenervia* in south FL

Plant families	Nonflooded[a]		Seasonally flooded[a]	
	1997[b]	2005[b]	1997[b]	2004[b]
Anacardiaceae	5.3	3.7	10.8	12.6
Annonaceae	–	2.3	–	12.7
Aquifoliaceae	–	2.9	–	–
Araliaceae	–	5.9	–	–
Asteraceae	18.9	35.0	–	16.3
Bromeliaceae	5.3	–	–	–
Casurinaceae	–	2.2	–	–
Convolvulaceae	–	2.4	–	–
Cucurbitaceae	–	5.5	–	–
Cyperaceae	20.9	32.5	15.1	18.0
Euphorbiaceae	–	2.5	–	–
Fabaceae	–	–	–	7.4
Lauraceae	5.3	2.4	10.1	6.0
Malvaceae	–	–	–	6.0
Moraceae	5.3	2.4	10.2	6.0
Myricaceae	10.9	3.2	10.2	–
Myrsinaceae	5.8	3.2	–	–
Myrtaceae	61.6	15.8	96.2	69.0
Orchidaceae	5.3	17.0	10.1	–
Osmundaceae	13.6	11.4	–	–
Poaceae	10.7	22.2	10.0	10.8
Psilotaceae	8.8	5.9	–	7.7
Pteridaceae	6.6	2.8	–	–
Rubiaceae	5.3	2.3	10.2	–
Schizaeaceae	–	2.3	–	–
Thelypteridaceae	6.6	7.0	17.1	–
Ulmaceae	–	2.4	–	7.4
Urticaceae	–	2.2	–	7.5
Vitaceae	–	2.6	–	–

[a] Habitat types

[b] Year vegetation surveyed

density in the non-flooded habitats declined by 36% during the period between 1997 and 2001 as compared to a decline of 58% between 2001 and 2005; the melaleuca density in seasonally flooded habitats declined by 33% during the earlier phase as compared to 47% during the later time period. The density of wax myrtle in non-flooded habitats declined by 82% during the period between 1996 and 2001 but increased by 140% during 2001 to

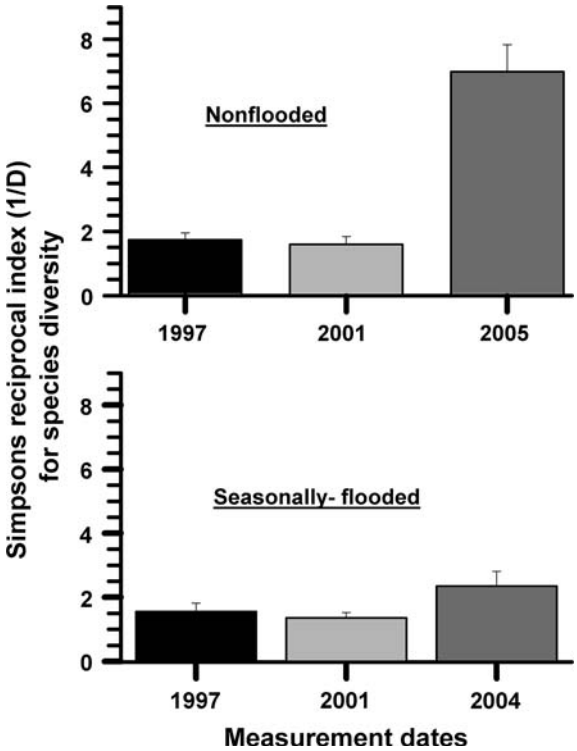

Fig. 3 Simpson's reciprocal index (1/*D*) for overall species diversity (richness + abundance) in *M. quinquenervia* dominated forest stands of south Florida. Note that the plant species enumeration years have only up to 2004 in seasonally flooded habitat due to the loss of plots to herbicide drift. *Error bars* represent stand error of the mean; columns sharing a common letter within a given year are not significantly different at $P = < 0.1$ level using Fisher's protected least significant difference (*LSD*) test

2005; wax-myrtle density decline in seasonally-flooded habitat was 24 and 100% for the 1996–2001, and 2001–2004, respectively. Sawgrass density in nonflooded habitats declined by 60% between 1996 and 2001 but increased by 118% between 2001 and 2005 whereas in seasonally flooded habitats it declined by 48% during the early phase as compared to only 3% during the later phase. The plant species that colonized and proliferated after melaleuca density declines, especially in the nonflooded habitats, consisted mainly of several native woody species (*Annona glabra, Cephalanthus occidentalis, Ficus aurea, Ilex cassine, Myrsine floridana, Persea palustris,* and *Trema micranthum*), shrubs (*Baccharis glomerulifolia*, *Eupatorium* sp.), vines (*Mikania scandens* and *Vitis* sp.), sedges (*Cladium jamaicense* and *Rhyncospora* spp.), grasses, and ferns

Table 2 Cumulative list (from all plots) of plant species showing densities (ha^{-1}) in two *M. quinquenervia* dominated habitats as recorded during four (1997, 2001, 2004, and 2005) observation dates

Species/status[a]	Habitat/observation dates					
	Nonflooded			Seasonally flooded		
	1997	2001	2005	1997	2001	2004
Annona glabra L./native	–[b]	125 (25)[c]	63 (50)	–	25 (25)	1050 (100)
Baccharis glomerulifolia Pers./native	1138(75)	536 (75)	5375 (100)	–	13 (13)	300 (75)
Bischofia javanica Blume/exotic	–	–	188 (50)	–	–	–
Bletia purpurea (Lam.) DC /native	25 (25)	13 (13)	75 (25)	25 (25)	25 (25)	–
Boehmeria cylindrica (L.) Sw. /native	–	–	13 (13)	–	–	250 (75)
Casuarina sp./exotic	–	–	13 (13)	–	–	–
Catopsis sp./native	13 (13)	–	–	–	–	–
Centella asiatica (L.) Urb/native	–	2488 (63)	–	–	13 (13)	100 (25)
Cephalanthus occidentalis L./native	25 (13)	–	38 (13)	50 (13)	100 (13)	–
Circium sp./native	38 (13)	–	25 (25)	–	–	–
Cladium jamaicense Crantz /native	6913 (100)	2763 (75)	3238 (100)	1600 (50)	825(50)	800(50)
Cyperus sp./unknown	–	–	813 (38)	–	–	–
Desmodium sp./native	–	–	225 (100)	–	–	–
Eleocharis sp./native	–	–	175 (13)	–	–	–
Eugenia uniflora L./exotic	–	–	25 (13)	–	–	–
Eupatorium capillifolium (Lam.) Sm. Ex Porter & Britton/native	–	–	613 (88)	–	–	–
Ficus aurea Nutt./native	25 (25)	150 (25)	113 (50)	63 (25)	50 (25)	25 (25)
Habenaria sp. 1/native	–	–	75 (13)	–	–	–
Habenaria sp. 2/native	–	–	6863 (100)	–	–	–
Ilex cassine L./native	–	–	438 (88)	–	–	–
Ipomoea sagittata Poir./native	–	–	125 (25)	–	–	–
Lygodium microphyllum (Cav.) R.Br./exotic	–	–	25 (13)	–	–	–
Melaleuca quinquenervia /exotic	28513 (100)	18400 (100)	7650 (100)	27200 (100)	18113 (100)	9675 (100)
Mikania scandens (L.) Willd./native	–	–	388 (63)	–	–	–
Momordica sp./exotic	–	–	688 (13)	–	–	–
Myrica cerifera L./native	2638 (100)	463 (75)	650 (100)	50 (25)	38 (25)	–
Myrsine floridana A.DC. /native	263 (50)	213 (25)	650 (100)	–	–	–
Oplismenus hirtellus (L.) P.Beuv. /native	–	–	1700 (38)	–	–	–
Osmunda regalis L./native	3888 (50)	4650 (75)	6213 (88)	–	–	–
Panicum ripens L./exotic	–	–	–	–	–	750 (25)
Panicum sp.[d]	–	–	4050 (100)	–	–	–
Passiflora sp./native	–	–	625 (88)	–	–	25 (25)
Persea palustris (Raf.) Sarg. /native	25 (13)	13 (13)	113 (38)	38 (13)	–	25 (25)
Pluchea sp./native	263 (25)	–	2688 (100)	–	–	–
Psilotum nudum (L.) P. Beuv./native	1675 (50)	338 (38)	2513 (100)	–	–	275 (75)
Pteris sp.[d]	638 (50)	–	375 (63)	–	–	–
Rhyncospora sp. 1/native	–	–	5500 (100)	–	–	–
Rhyncospora sp. 2/native	–	–	2275 (88)	–	–	150 (100)
Rhyncospora sp. 3/native	–	–	950 (63)	–	–	–
Schinus terebinthifolius Raddi/exotic	38 (13)	–	975 (100)	250 (50)	138 (25)	1025 (100)

Table 2 continued

Species/status[a]	Habitat/observation dates					
	Nonflooded			Seasonally flooded		
	1997	2001	2005	1997	2001	2004
Thelypteris sp./native	638 (75)	112 (25)	3250 (100)	2250 (50)	2488 (50)	–
Trema micranthum (L.) Blume/native	–	–	113 (38)	–	–	225 (50)
Urena lobata L./exotic	–	–	–	–	–	25 (25)
Vitis sp./native	–	–	275 (13)	–	–	–
Known native species	14	10	31	7	9	13
Pteridophyte (uncertain native/exotic status)[d]	1	–	1	–	–	–
Monocot (uncertain native/exotic status)[d]	0	–	1	–	–	–
Known exotic species	2	1	7	2	2	4
Total number of species	17	11	40	9	11	17

[a] Exotic and native status of plants was determined based on Wunderlin and Hansen (2003)

[b] Species not present in permanent plots

[c] Number of plants/ha, i.e., density of the given species; numbers in parenthesis indicate the percentage of permanent plots in which the species occurred

[d] Plant species whose exotic and native status could not be determined

(*Thelypteris* sp. and *Osmunda regalis*) (Table 2). Also, some prominent exotic species of concern invaded the site and proliferated, but to a lesser extent than the species of native trees and shrubs. These exotic species of concern were mainly *Schinus terebinthifolius* (Brazilian pepper tree), *Lygodium microphyllum* (Japanese climbing fern), and *Bischofia javanica*.

Melaleuca canopy damage and plant species richness

The number of species per plot (species richness per plot) recorded annually increased concomitantly with natural-enemy damaged leaves during 1997–2005 ($r^2 = 0.8196$) (Fig. 4). Spearman's correlation coefficient also showed positive correlation (Correlation coefficient = 0.905, $P = 0.00503$) between the proportion of damaged leaves in the litter trap and the species richness within the plots. The increase in proportion of damaged leaves falling prematurely may have accelerated melaleuca canopy thinning, which led to increased number of plant species per plot as a result of increased light penetration to the forest floor.

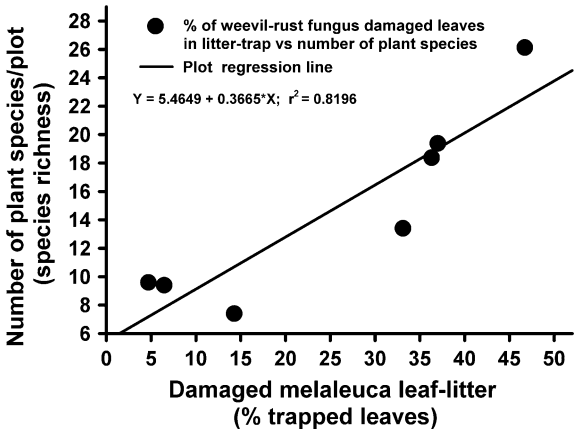

Fig. 4 Linear regression of natural-enemy-damaged *M. quinquenervia* leaves and plant species richness in nonflooded forest stands of south Florida

Discussion

Natural area managers of south Florida were making efforts to develop plans for halting further advance of melaleuca invasions while simultaneously reducing the existing populations (Bodle et al. 1994). They proposed deployment of mechanical and chemical means to remove mature tree populations and classical

biological control to prevent reproduction and recruitment, thereby constraining the expansion and regeneration of this noxious species (Bodle et al. 1994; Turner et al. 1998). This strategy aimed to reduce existing populations and densities of melaleuca, in order to facilitate the diversification of plant communities, as native plants re-colonized infested areas. The current study documents the increased diversity of non-melaleuca species in mature melaleuca stands reported by Rayamajhi et al. (2007) to be subjected to self-thinning and chronic damage by foliovorous weevils, sap-feeding psyllids and lac-scales, and a rust fungus. The accelerated mortality of melaleuca seedlings and saplings in south Florida caused primarily by the psyllid *B. melaleucae* has been documented by Franks et al. (2006). Similar phenomena have been reported in a general purpose model developed by Polyakov et al. (2008) for other systems.

Our findings show that declines in melaleuca densities coincide with overall increases in understory regeneration and subsequent increases in plant species diversity even though melaleuca is still occupying the topmost vertical layer in the community. This was expected since others have reported similar increases in understory recruitment and overall diversity with decreased stem density of dominant trees in other systems (Thomas et al. 1999; Nagaike et al. 2006). The family Myrtaceae, for instance, had the highest FIV in both habitats at the inception of our study in 1997 due primarily to the density and canopy dominance by *M. quinquenervia*. By 2005, however, FIV of Myrtaceae was reduced by 74 and 28% in nonflooded and seasonally-flooded habitats, respectively. The decrease in FIV of melaleuca in nonflooded habitat coincides with an increased FIV of Asteraceae, Poaceae, and Orchidaceae by $\geq$100% between 1997 and 2005. Such an increase in the FIV of these three families in melaleuca vacated gaps may be attributed to the availability of resource mother plants in areas adjacent to our study areas (personal observation) and the seed attributes (small-sized anemophilous seeds). Ohtsuka (1999) studied colonization of abandoned cropland and reported the marked success of pioneer plant species in Asteraceae (*Galinsoga*, *Crassocephalum*, *Conyza* and *Eupatorium* species), Poaceae (*Imperata* sp.) and a member of Ulmaceae (*Trema* sp.). He attributed successful colonization of abandoned sites by members of Asteraceae and Poaceae to smaller seed size and dispersive capabilities (Ohtsuka 1999). Similarly, members of Asteraceae (represented by *Baccharis*, *Eupatorium, Mikania*, and *Pluchea* species), Poaceae (represented by *Panichum* and *Oplismenus* species) and Cyperaceae (represented by *Cladium*, *Cyperus*, and several species of *Rhyncospora* species), all with small seeds, have rapidly colonized the forest floor gaps caused by the mortality or thining of melaleuca trees. Increased FIV of Poaceae, Asteraceae, Cyperaceae, and Orchidaceae in these gaps is not surprising since these four families are most abundantly represented by 124, 81, 53, and 42 species, respectively, out of ca 1,000 species cataloged in the Everglades National Park (Brown et al. 2006b) located adjacent to our study sites. Other notable groups of plants taking advantage of the gaps, especially around decomposing melaleuca stumps, are fern species (*Thelypteris, Osmanda* and *Lygodium* species) that recruit sporophytic adults as other ferns do through germination of anemophilous (Cobb et al. 2005) haploid spores. The increase in populations of the members of Orchidaceae (*Bletia* sp. and *Habenaria* spp.) also followed a trend similar to that reported in Ohtsuka (1999). Overall, it appeared that forest-floor and canopy gaps created due to mortality of melaleuca tree in both nonflooded and seasonally flooded habitats in our study have been colonized early by plants bearing smaller regenerative units that are easily wind dispersed. However, this dynamic is expected to change over time with the recruitment of tree and shrub species. As a result, we predict that species diversity will decrease over time because of the codominance of more stable perennial tree and shrub species. This prediction is supported by the reports in other systems where annuals have been replaced by woody plants during later phase of succession (Ohtsuka 1999).

The comparative FIV of some woody plant families, such as Myricaceae (*M. cerifera*) and Myrsinaceae (*M. floridana*), was represented by fewer suppressed understory saplings at the onset of the study (during 1997) and their FIV was slightly decreased at final evaluation (in 2004/2005). Their decreased FIV may be attributed to herbivory from the lac scale as members representing these families are susceptible to this arthropod (Pemberton 2003) and their populations in south Florida peaked during 2002 (Rayamajhi et al. 2007). Therefore, any increase in the FIV of non-melaleuca plants can primarily be

attributed to the decreased FIV of Myrtaceae represented by melaleuca rather than to the declines in the density of other plant species in the stand. On the other hand, new (that were not recorded at the onset of the study in 1997) woody plant species (*T. micranthum*, *I. cassine, Casuarina* sp.) appeared both in nonflooded and seasonally-flooded habitats in our study; others (Brokaw 1985; Ohtsuka 1999; Kwit et al. 2000) have reported one (*Trema*) of the above three genera as a pioneer tree species in gaps of other forest systems.

Positive correlation between the increase in the level of melaleuca canopy damage and the subsequent increase in plant species richness was apparent in our study. This supports the assumption that the natural enemies, by reducing competitive dominance of an exotic plant species, can promote the development of plant communities with higher plant diversity. This assumption is further supported by Center et al. (2005) who reported that the herbivory from introduced natural enemies reversed the competitive dominance of the invasive aquatic host, *Eichhornia crassipes*, and resulted in its replacement by the weaker competitor *Pistia stratiotes*. Similar abilities of herbivores to alter plant species richness and ecosystem processes have been experimentally demonstrated by Mulder et al. (1999).

Does this melaleuca density decline represent a shift from melaleuca monoculture to a complex of desired native species or rather to a group of equally invasive exotic species? Of the 17 and 40 plant species documented for nonflooded habitat in 1997 and 2005, two (*M. quinquenervia* and *S. terebinthifolius*) and four (*E. uniflora, M. quinquenervia, Momordica* sp., and *S. terebinthifolius*) species, respectively, were exotic. Similarly, out of 9 and 17 species recorded in seasonally-flooded habitats during 1997 and 2004, two (*M. quinquenervia* and *S. terebinthifolius)* and four (*M. quinquenervia* and *S. terebinthifolius, Panicum* sp. and *U. lobata*) species, respectively, were exotic. Hence, the spaces vacated by melaleuca in nonflooded and seasonally-flooded habitat are mostly colonized by native plants.

Summary

A landscape level Everglades restoration program has been initiated in hopes of returning the degraded systems to a semblance of their historic ecological condition. Restoring the system to its former state, however, is improbable if not economically impossible. Restoration of areas previously occupied by gramineous vegetation (White 1994; Turner et al. 1998), for instance, has proven problematic because of the alteration of physiography (White 1994) and soil characteristics due to decades of melaleuca occupation (Rayamajhi et al. 2006a). Rehabilitation of such degraded or derelict ecosystems will require reduction of the existing population densities of melaleuca and inhibition of further recruitment and invasion. Recently, reduced stand densities due to density-dependent (self-thinning) and density-independent (natural-enemy impact) factors (Rayamajhi et al. 2007, 2008), reduced reproductive potential (Pratt et al. 2005; Rayamajhi et al. 2008) and suppression of growth (Pratt et al. 2005; Center et al. 2007) in the stands has been documented. It has been reported that reduction in melaleuca density and canopy coverage can be accelerated through the chronic impact of defoliating agents (Rayamajhi et al. 2007, 2008). Our findings indicated that sites dominated by melaleuca can gradually be rehabilitated through reduction of its canopy coverage and stem density. The current study has documented a two to four-fold increase in non-melaleuca plant diversity in study sites within our 8 year period which may decrease or increase in future owing to the community succession. It may also be noted that the sites degraded by invasive plants may only be partially rehabilitated by passive means, such as natural regeneration of non-melaleuca plants. This may require more active restoration efforts like continued mechanical or chemical removal of larger stands and direct seeding or replanting of desired vegetation where deemed ecologically and economically feasible.

References

Austin DF (1978) Exotic plants and their effects in southeastern Florida. Environ Conserv 5:25–35

Baker TT, van Lear DH (1998) Relations between density of rhododendron thickets and diversity of riparian forests. For Ecol Manage 109:21–32. doi:10.1016/S0378-1127(98)00259-X

Bodle MJ, Ferriter AP, Thayer DD (1994) The biology, distribution, and ecological consequences of *Melaleuca quinquenervia* in the Everglades. In: Davis SM, Ogden JC

(eds) The Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, pp 341–355

Braithwaite RW, Lonsdale WM, Estbergs JA (1989) Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. Biol Conserv 48:89–210. doi:10.1016/0006-3207(89)90118-3

Brokaw NVL (1985) Gap-phase regeneration in a tropical forest. Ecology 66:682–687. doi:10.2307/1940529

Browder JA, Schroeder PB (1981) Melaleuca seed dispersal and perspectives on control. In: Geiger RK (Compiler) Proceedings of Melaleuca symposium. Florida Department of Agriculture and Consumer Services, Division of Forestry, Tallahassee, pp 17–21

Brown RB, Stone EL, Carlisle VW (1990) Soils. In: Myers RL, Ewel JJ (eds) Ecosystems of Florida. University of Central Florida Press, Orlando, pp 35–69

Brown KA, Scatena FN, Gurevitch J (2006a) Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. For Ecol Manage 226: 145–152

Brown MT, Cohen MJ, Bardi E, Ingwersen WW (2006b) Species diversity in the Florida Everglades, USA: a systems approach to calculating biodiversity. Aquat Sci 68:254–277. doi:10.1007/s00027-006-0854-1

Center TD, Van TK, Rayachhetry MB, Buckingham GR, Dray FA, Wineriter SA, Purcell MF, Pratt PD (2000) Field colonization of the melaleuca snout beetle (*Oxyops vitiosa*) in south Florida. Biol Control 19:112–123. doi:10.1006/bcon.2000.0856

Center TD, Van TK, Dray FA, Franks SJ, Rebelo T, Pratt PD, Rayamajhi MB (2005) Herbivory alters competitive interactions between two invasive aquatic plants. Biol Control 33:173–185. doi:10.1016/j.biocontrol.2005.02.005

Center TD, Pratt PD, Tipping PW, Rayamajhi MB, Van TK, Wineriter S, Dray FA (2006) Field colonization, population growth, and dispersal of *Boreioglycaspis melaleucae* Moore, a biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.). Biol Control 39:363–374. doi:10.1016/j.biocontrol.2006.08.009

Center TD, Pratt PD, Tipping PW, Rayamajhi MB, Van TK, Wineriter S, Dray FA (2007) Initial impacts and field validation of host range for *Boreioglycaspis melaleucae* Moore (Hemeptera: Psyllide), a biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake (Myrtales: Myrtaceae: Leptospermoideae). Environ Entomol 36(3):569–576

Cobb B, Farnsworth E, Lowe C (2005) A field guide to ferns and their related families: Northeastern and Central North America, vol 2. Houghton-Miflin Company, Boston

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycles and global change. Annu Rev Ecol Syst 23:63–87

Denslow JS (1987) Tropical rain forest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451. doi:10.1146/annurev.es.18.110187.002243

Dray FA Jr, Bennett BC, Center TD (2006) Invasion history of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida. Castanea 71:210–225. doi:10.2179/05-27.1

Ewel JJ (1986) Invasibility: lesions from south Florida. In: Mooney HA, Drake HA (eds) Ecology of biological invasions of North America and Hawaii ecological study vol 58. Springer, New York

Franks SJ, Kral AM, Pratt PD (2006) Herbivory by introduced insects reduces growth and survival of *Melaleuca quinquenervia* seedlings. Environ Entomol 35:366–372

Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecol Appl 8:975–989. doi:10.1890/1051-0761(1998)008[0975:EOINIP]2.0.CO;2

Gorchov L, Trisel DE (2003) Competitive effect of invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecol 166:13–24. doi:10.1023/A:1023208215796

Hofstetter RH (1991) The current status of *Melaleuca quinquenervia* in south Florida. In: Center TD, Doren R, Hofstetter RL, Myers RL, Whiteaker LW (eds) Proceedings of the symposium on exotic pest plants. US Dept Interior, Nat Park Service,Washington, pp 159–176

Holliday I (1989) A field guide to Melaleucas. Hamlyn Publishing Group, Sydney

Kondo T, Gullan PJ (2007) Taxonomy review of the lac insect genus Paratachardina Balachowsky (Hemiptera Coccoidea, Kerriidae), with a revised key to genera of Kerridae and description of two species. Zootaxa 1617:1–41

Krebs CJ (1999) Ecological methodology, 2nd edn. Addison Wesley, New York

Kushlan JA (1990) Freshwater Marshes. In: Myers RL, Ewel JJ (eds) Ecosystems of Florida. University of Central Florida Press, Orlando, pp 324–363

Kwit C, Platt WJ, Slater HH (2000) Post-hurricane regeneration of pioneer plant species in south Florida subtropical hardwood hammocks. Biotropica 32:244–251

Laroche FB (1994) Melaleuca management plan for Florida, 2nd edn. Exotic Pest Plant Council of Florida, West Palm Beach

Malecki RA, Blossy B, Hight SD, Schroeder D, Kok LT, Coulson JR (1993) Biological control of purple loosestrife. Bioscience 43:680–686. doi:10.2307/1312339

Morath S, Pratt PD, Silvers CS, Center TD (2006) Herbivory by *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae) accelerates foliar degradation and abscission in the invasive tree *Melaleuca quinquenervia*. Environ Entomol 35:1372–1378. doi:10.1603/0046-225X(2006)35[1372:HBBMHP]2.0.CO;2

Mori SA, Boom BM, de Carvalino AM, dos Santos TS (1983) Ecological importance of Myrtaceae in an eastern Brazilian wet forest. Biotropica 15:68–70. doi:10.2307/2388002

Mulder PH, Koricheva J, Huss-Danell K, Högberg P, Joshi J (1999) Insects affect relationships between plant species richness and ecosystems processes. Ecol Lett 2:237–246. doi:10.1046/j.1461-0248.1999.00070.x

Myers RL (1975) The relationship of site conditions to the invading capability of *Melaleuca quinquenervia* in southwest Florida. MS Thesis. University of Florida, Gainesville

Myers RL (1983) Site susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. J Appl Ecol 20:645–658. doi:10.2307/2403532

Myers JH, Bazely DR (2003) Ecology and control of introduced plants. Cambridge University Press, Cambridge

Nagaike T, Hayashi A, Masako K, Kazuaki T, Midori A, Nobumasa A (2006) Changes in plant species diversity over years in *Larix kaempferi* plantations and abandoned coppice forests in central Japan. For Ecol Manage 236:278–285

O'Hare NK, Dalrymple GH (1997) Wildlife in southern Everglades wetlands invaded by melaleuca (*Melaleuca quinquenervia*). Bull Fl Mus Nat Hist 41:1–68

Ohtsuka T (1999) Early stages of secondary succession on abandoned cropland in north-east Borneo Island. Ecol Res 14:281–290. doi:10.1046/j.1440-1703.1999.143304.x

OTA US Congress Office of Technology Assessment (1993) Harmful non-indigenous species in the United States. OTA-F-565, US Government printing office, Washington, 397pp

Pemberton RW (2003) Invasion of *Paratachardina lobata* (Hemiptera: Kerriidae) in south Florida. Fla Entomol 86:373–377. doi:10.1653/0015-4040(2003)086[0373:IOPLLH]2.0.CO;2

Polyakov M, Majumdar I, Teeter L (2008) Spatial and temporal analysis of the anthropogenic effects on local diversity of forest trees. For Ecol Manage 255:1379–1387

Pratt PD, Slone DH, Rayamajhi MB, Van TK, Center TD (2003) Geographic distribution and dispersal rate of *Oxyops vitiosa* (Coleoptera: Cruculionidae), a biological control agent of the invasive tree *Melaleuca quinquenervia* in South Florida. Environ Entomol 32:397–406

Pratt PD, Rayamajhi MB, Van TK, Center TD (2004) Modeling the influence of resource availability in population densities of *Oxyops vitiosa* (Coleoptera: Curculionidae), a biological control agent of the invasive tree *Melaleuca quinquenervia*. Biocontrol Sci Technol 14:51–61. doi:10.1080/09583150310001638539

Pratt PD, Rayamajhi MB, Van TK, Center TD (2005) Herbivory alters resource allocation and compensation in the invasive tree *Melaleuca quinquenervia*. Ecol Entomol 15:443–462

Pratt PD, Rayamajhi MB, Bernier LS, Center TD (2006a) Geographic range expansion of Boreioglycaspis melaleucae (Hemiptera: Psyllidae) to Puerto Rico. Fla Entomol 89:529–531. doi:10.1653/0015-4040(2006)89[529:GREOBM]2.0.CO;2

Pratt PD, Quevedo V, Bernier L, Sustache J, Center TD (2006b) Invasions of Puerto Rican wetlands by the Australian tree *Melaleuca quinquenervia*. Caribb J Sci 41:42–54

Pratt PD, Rayamajhi MB, Silvers CS (2007) Naturalization and biomass allocation of the invasive tree *Melaleuca quinquenervia* in wetlands of the Bahamas. J Aquat Plant Manage 45:8–16

Rayachhetry MB, Elliot ML, Van TK (1997) Natural epiphytotic of a rust fungus (*Puccinia psidii*) on *Melaleuca quinquenervia* in Florida. Plant Dis 81:831. doi:10.1094/PDIS.1997.81.7.831A

Rayamajhi MB, Van TK, Pratt PD, Center TD (2006a) Temporal and structural effects of stands on litter production in *Melaleuca quinquenervia* dominated wetlands of south Florida. Wetlands Ecol Manage 14:303–316. doi:10.1007/s11273-005-1481-7

Rayamajhi MB, Van TK, Pratt PD, Center TD (2006b) Interactive association between *Puccinia* psidii and *Oxyops vitiosa*, two introduced natural enemies of *Melaleuca quinquenervia* in Florida. Biol Control 37:56–67. doi:10.1016/j.biocontrol.2005.10.013

Rayamajhi MB, Van TK, Pratt PD, Center TD, Tipping PW (2007) *Melaleuca quinquenervia* dominated forests in Florida: analyses of natural-enemy impacts on stand dynamics. Plant Ecol 192:119–132. doi:10.1007/s11258-006-9231-3

Rayamajhi MB, Pratt PD, Center TD, Tipping PW, Van TK (2008) Above-ground biomass of an invasive tree (*Melaleuca quinquenervia*) before and after herbivory by adventive and introduced natural enemies: a temporal case study in Florida. Weed Sci 56:451–456. doi:10.1614/WS-07-152.1

Romane F, Gondard H, Grandjanny M, Grossmann A, Renaux A, Shater Z (2001) Measuring and managing plant species diversity in the chestnut (*Castanea sativa* Mill.) ecosystems of the Cevennes. For Snow Landsc Res 76:493–497

Thomas SC, Halpern CB, Falk DA, Liguori DA, Austin KA (1999) Plant diversity in managed forests: understory responses to thinning and fertilization. Ecol Appl 9:864–879. doi:10.1890/1051-0761(1999)009[0864:PDIMFU]2.0.CO;2

Turner CC, Center TD, Burrows DW, Buckingham GR (1998) Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, USA. Wetlands Ecol Manage 5:165–178. doi:10.1023/A:1008205122757

Vitousek PM, D'Antonio CMD, Loope LL, Rejmanek M, Westbrooke R (1997) Introduced species: a significant component of human-caused global change. N Z J Ecol 21:1–16

White PS (1994) Synthesis: vegetation pattern and process in the Everglades Ecosystems. In: Davis SM, Ogden JC (eds) The Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, pp 445–458

Wilcove DS, Rothsein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615. doi:10.2307/1313420

Woodall SL (1982) Seed dispersal in *Melaleuca quinquenervia*. Fla Sci 46:65–71

Wunderlin RP, Hansen BF (2003) Guide to the Vascular Plants of Florida, 2nd edn. University Press of Florida, Gainesville