

# Modeling the long-term effects of introduced herbivores on the spread of an invasive tree

Bo Zhang · Donald L. DeAngelis · Min B. Rayamajhi · Daniel Botkin

Received: 13 March 2016 / Accepted: 7 April 2017  
© Springer Science+Business Media Dordrecht 2017

## Abstract

**Context** *Melaleuca quinquenervia* (Cav.) Blake (hereafter melaleuca) is an invasive tree from Australia that has spread over the freshwater ecosystems of southern Florida, displacing native vegetation, thus threatening native biodiversity. Suppression of melaleuca appears to be progressing through the introduction of insect species, the weevil, *Oxiops vitiosa*, and the psyllid, *Boreioglycaspis melaleucae*.

**Objective** To improve understanding of the possible effects of herbivory on the landscape dynamics of

melaleuca in native southern Florida plant communities.

**Methods** We projected likely future changes in plant communities using the individual based modeling platform, JABOWA-II, by simulating successional processes occurring in two types of southern Florida habitat, cypress swamp and bay swamp, occupied by native species and melaleuca, with the impact of insect herbivores.

**Results** Computer simulations show melaleuca invasion leads to decreases in density and basal area of native species, but herbivory would effectively control melaleuca to low levels, resulting in a recovery of native species. When herbivory was modeled on pure melaleuca stands, it was more effective in stands with initially larger-sized melaleuca. Although the simulated herbivory did not eliminate melaleuca, it decreased its presence dramatically in all cases, supporting the long-term effectiveness of herbivory in controlling melaleuca invasion.

**Conclusions** The results provide three conclusions relevant to management: (1) The introduction of insect herbivory that has been applied to melaleuca appears sufficient to suppress melaleuca over the long term, (2) dominant native species may recover in about 50 years, and (3) regrowth of native species will further suppress melaleuca through competition.

---

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10980-017-0519-6](https://doi.org/10.1007/s10980-017-0519-6)) contains supplementary material, which is available to authorized users.

---

B. Zhang (✉)  
Department of Biology, University of Miami, 1320 S  
Dixie Hwy, Coral Gables, FL 33146, USA  
e-mail: bo@bio.miami.edu

D. L. DeAngelis  
Wetlands and Aquatic Research Center, U. S. Geological  
Survey, 7920 NW 71st Street, Gainesville, FL 32653,  
USA

M. B. Rayamajhi  
USDA-ARS Aquatic Weed Research Laboratory, 3205  
College Avenue, Fort Lauderdale, FL 33314, USA

D. Botkin  
Department of Ecology, Evolution, and Marine Biology,  
University of California, Santa Barbara, Santa Barbara,  
CA 93106, USA

**Keywords** Invasive plant · Insect herbivory ·  
Individual-based model · JABOWA-II forest

simulator · *Melaleuca quinquenervia* · Native species recovery

## Introduction

*Melaleuca quinquenervia* (Cav.) Blake (common names: melaleuca, paper bark, punk tree; Family, Myrtaceae, referred to as melaleuca thereafter) is a large (25–30 m tall) native Australian tree introduced into the Florida landscape during the late 19th century for pulp production and ornamental purposes (Dray 2003). It has strong invasive attributes, such as ecological fire adaptation and high reproductive potential. A single 10-m tall open-grown tree can store over 20 million seeds in its capsules at any given time (Myers 1983). By the end of the 1900s melaleuca had spread over 200,000 ha of ecologically sensitive freshwater ecosystems of southern Florida (Dray et al. 2006) displacing native vegetation such as slash pine (*Pinus elliottii* Engelm.) and pond cypress (*Taxodium ascendens* Brong.), threatening native biodiversity (Serbesoff-King 2003; Martin et al. 2009, 2011). Melaleuca invasion has caused adverse economic and environmental impacts to southern Florida (Center et al. 2007), with the loss valued, 16 years ago, at nearly \$30 million per year (Center et al. 2000).

The difficult work of making predictions of the establishment and spread of invading species such as melaleuca has important ecological and economic implications (e.g., Williamson 1999; Rai 2015a, b; Elliott-Graves 2016). Modeling has been applied to make predictions of future spread in many cases, including both niche modeling (e.g., Bradley et al. 2010) and mechanistic models (e.g., Higgins and Richardson 1996). Various control methods have been applied, including the use of biocontrol agents that are natural enemies of the pest species. Because use of both biocontrol and other methods of control are costly, prediction of the efficacy of control is needed. The long-term success of biocontrol is still uncertain, so modeling has been used in a number of cases of invasive species, including plant species (e.g. Maines et al. 2013; Krug and Richardson 2014).

Our objective is to apply modeling to melaleuca, for which biocontrol has been attempted. A program to suppress melaleuca, begun in 1997 with insect herbivore agents, including the melaleuca weevil *Oxyops vitiosa* Pascoe and the psyllid *Boreioglycaspis*

*melaleucæ* Moore (Myers and Bazely 2003; Tipping et al. 2008, 2009; Balentine et al. 2009; Center et al. 2012), appears to be highly successful. The introduced biological control agent *O. vitiosa* feeds exclusively on the foliar biomass while the sap-sucking psyllid feeds on foliage and stems (Pratt et al. 2005). The combined effects of these herbivores cause losses of leaves, forcing melaleuca to switch resource allocation from seed production to production of new, often unseasonal growth (Tipping et al. 2008). Field studies (Tipping et al. 2009) show that melaleuca weevils attack new lead tissue preferentially and relentlessly, thereby contributing to continuous defoliation and re-foliation cycles. Because complete recovery of leaf tissue is rare, the usual temporary reallocation of plant assimilates to leaf production may become permanent under this sustained herbivory. As a result, formerly pure stands of melaleuca are being re-colonized by native species (Tipping et al. 2012).

Through applications of insect herbivore agents, combined with mechanical removal and chemical treatments, melaleuca is now being removed from most public lands (Center et al. 2012). However, the extent to which melaleuca can be controlled to low levels primarily through biocontrol is important to estimate, because of the costs of mechanical and chemical methods. Also, what the long-term recovery of native plant communities will be as melaleuca is gradually suppressed remains unknown. To investigate such possibilities, we used a modeling approach, made possible because a substantial amount of information is available on the melaleuca and stand dynamics for the period prior to the release of insect herbivores (Meskimen 1962; Myers 1983; Greenway 1994; Rayachhetry et al. 1998, 2001; Van et al. 2000, 2002; Kaufman and Smouse 2001; Serbesoff-King 2003). More recently, additional information has become available on the negative impact on melaleuca due to chronic damage inflicted by the insect agents (Pratt et al. 2005; Rayamajhi et al. 2007; Tipping et al. 2008, 2009; Martin et al. 2010). Information from these published data is sufficient to parameterize a well-known individual-based forest modeling platform, JABOWA-II (Botkin et al. 1972; Botkin 1993; Ngugi and Botkin 2011).

In JABOWA-II, establishment, growth and mortality of individual trees on small patches of land are simulated as functions of biotic factors (competition for available light) and abiotic factors (climate and

soils) (Bugmann 2001). JABOWA-II and similar modeling platforms link environmental parameters to demographics and growth (Acevedo et al. 1996), and have provided successful simulations of forest succession in hundreds of cases around the world (Pausas et al. 1997). Given the compatibility of the data needed for JABOWA-II with the information available on melaleuca, JABOWA-II is well positioned to provide both understanding and forecasts on the dynamics of melaleuca-invaded forest stands in Florida. Below we describe the model and apply it to two types of swamps that have been invaded by melaleuca, to project the long-term effects of continued control through herbivory.

## Methods

Here we use the Overview, Design Concepts, and Details (ODD) approach of Grimm et al. (2006, 2010) to describe the individual-based JABOWA-II model (Botkin 1993). After that, we describe the scenarios and data analysis.

## Overview

### Purpose of the model

The purpose of using JABOWA-II in this study is to (1) simulate scenarios for two habitat types, Florida cypress swamp and bay swamp, including native species that are affected by melaleuca invasion, without and with the application of insect herbivory, (2) simulate scenarios of pure melaleuca stands (no native species are included) following the introduction of insect herbivory, and (3) project extended future changes that might occur over successional time scales in the scenarios of cypress and bay swamp.

### Entities, state variables and scales

The entities of the model are individual trees. Besides melaleuca, these are slash pine (*Pinus elliotti*), pond cypress (*Taxodium ascendens*), dahoon holly (*Ilex cassine* L.), sweet bay (*Magnolia virginiana* L.) and loblolly bay (*Gordonia lasianthus* L.). Insect herbivores were not simulated explicitly; a constant effect level of herbivory on each melaleuca tree was

assumed, by decreasing the melaleuca reproduction rate by 49% and the growth rate by 83% based on empirical measurement in Tipping et al. (2008), which represented the maximum levels.

There are two types of variables. First there are the characteristics of the environment, which are the site variables. In this case, the light environment at different heights above ground is the main environmental state variable. Each tree is assumed to be able to affect the light environment of every other tree in the plot, through shading, depending on a combination of the relative heights of the trees and individual tree species' leaf area index. Hence, the only resource for which there is competition in JABOWA-II is light. The belowground resources, such as water and nutrients, are specified for a site. These affect plant growth but are not assumed to be affected by feedback from the tree communities, and are summarized in the  $f_i(\text{environment})$  factor of the growth equation (see "Growth submodel" section).

The second set of variables, the state variables, consists of the characteristics of the trees; in JABOWA-II, the diameter at breast height (DBH) is the key state variable. All other variables, such as height, vertical leaf profile, etc., are deduced from stem diameter via allometric relationships.

### Processes

JABOWA-II simulates plant succession on yearly time steps for up to 600 years in a 0.01 hectare plot, using the life history characteristics (see Table 1 for the characteristics in the model) and environmental preferences of several woody plants and a set of environmental conditions. Each tree is simulated individually from the sapling stage. JABOWA-II includes the following basic features: establishment, growth, and mortality.

### Establishment

A maximum limit on the possible number of new saplings that can be established is determined for each year. The actual number is modified by site conditions, including the light environment, and depends also on the degree of shade tolerance of the species. For less tolerant species the number of saplings would be limited, depending on light available. Within those limits, a uniformly distributed random number is used

**Table 1** Definitions of key parameters in the model

Notation	Definition
$S$	Shade tolerance. This is input as categorical values; 1 (intolerant), 2 (moderately tolerant), or 3 (tolerant)
$N$	Tolerance to low nitrogen availability. This is input as categorical values; 1 (intolerant), 2 (moderately tolerant), or 3 (tolerant)
SAP	Maximum number of saplings of species that can be added in any one year to the 0.1 hectare plot
$R$	Maximum possible relative growth rate of tree
$C$	Relationship between total foliage weight, $W$ , and diameter at breast height, $D$
$D_{\max}$	Maximum possible diameter at breast height (dbh)
$H_{\max}$	Maximum possible height of tree
$A_{\max}$	Maximum age tree can reach
$A_{\text{INC}}$	Minimum diameter growth in a year that a tree can grow and still be considered healthy
$DD_{\min}$	Minimum growing degree days for species
$DD_{\max}$	Maximum growing degree days for species
$D_T$	Maximum depth of water table possible for species to persist
$WLT_{\max}$	Maximum wilt possible for species
$LT_{\min}$	Minimum light (as a fraction of full sunlight) under which a tree can grow

to determine the actual number of saplings established in a given year.

### Growth

Diameter growth,  $D$ , is modeled as a deterministic process on an annual time step, based on a consideration of the maximum possible growth rate ( $G$ ) at a given size under optimal conditions.  $D$  is reduced according to the canopy volume (leaf area index) and stand volume (as woody biomass) (Smith and Urban 1988), which affect available light, as well as by environmental factors. Growth is described further under “[Growth submodel](#)”.

### Mortality

Tree mortality is modeled as a stochastic process and is assumed to consist of two components: (1) a background mortality that allows on average only 2% of the trees to survive to maximum tree age (a model parameter) where annual mortality probability is constant across tree life, and (2) a stress-related mortality that acts when diameter increment is less than 0.01 cm for any given year and species. For stress-related mortality, a tree has a 1% chance of surviving 10 stress years; as soon as there is no stress, the stress-related mortality ceases to be effective.

Hence, it is assumed that there are no lags between the occurrence of stress and the associated mortality, and that stress tolerance is not species-specific.

## Design concepts

### Emergence

The dynamics of tree species composition and size distribution are computed in each simulation scenario, and are emergent phenomena of the competition for light.

### Adaptations

The tree species have different adaptations to shading ( $S$ ), nitrogen availability ( $N$ ) and ground water table depth ( $DT$ ), quantified as indices of tolerance to each environmental factor.

### Fitness

The fitness of a tree is defined in terms of its growth over its past several years. The greater the growth, the more fit the tree is, both in terms of competitive fitness (height advantage) and avoidance of stress-related

mortality, the chance of which increases when growth decreases below 0.01 cm per year.

### Interaction

The interactions between trees occur through shading. Each tree is assumed able to affect every other tree in the plot, through shading, depending on the relative heights of the trees and their leaf area indices.

### Stochasticity

JABOWA-II is a Monte Carlo simulation model. Stochasticity is incorporated into establishment and mortality processes; that is, how many new saplings of each species will be added to the plot and both yearly natural mortality and stress-related mortality.

## Details

### Site description

We simulated two types of swamp habitat in Florida affected by melaleuca invasion, Florida cypress swamp and bay swamp, for which information on environment and plant demography are available from studies of two sites (Casey and Ewel 2006). Although the information used here is from cypress and bay swamps in northern Florida, we believe these are reasonable surrogates for the similar swamp types in southern Florida, which is the focal area for our simulations. These two habitats are similar to field sites used in Tipping et al. (2008, 2009).

In this region, the mean annual rainfall is about 1331 mm to 1364 mm (NOAA 1968–1977), most of which occurs from June through September. Mean monthly temperature ranges from 14.4 to 28.3 °C (NOAA 1968–1977).

Cypress swamps are relatively deep (standing water depth = 20 cm), while bay swamps represent shallower (standing water depth = 8 cm), peaty swamp (Penfound 1952; Ewel 1990). Cypress swamp has standing water for at least part of the year and is dominated by pond cypress (Mitsch et al. 1979; Deghi et al. 1980). The vegetation communities in cypress habitats vary along a hydrologic gradient. Cypress

swamp generally forms in poorly drained to permanently wet depressions in areas of pine flatwood. Cypress-hardwood associations are defined as communities in which cypress grows in association with species such as red maple (*Acer rubrum* L.), ash (*Fraxinus* sp.), cottonwood (*Populus heterophylla* L.) and water oak (*Quercus nigra* L.). A cypress-pine association is indicative of severely drained conditions, which allow slash pine (*Pinus elliottii*) and sweet bay (*Magnolia virginiana* L.) to invade cypress (Brown 1981). Cypress in pure stands generally indicates continuous high water (Mitsch and Ewel 1979).

At least 50% of the tree species in bay swamp are broad-leaved evergreen trees growing on acid soils high in organic matter and subjected to seasonal flooding. Canopy species include red bay (*Persea borbonia* L. (Spreng.)) and swamp bay (*M. virginiana*), as well as dahoon holly (*Ilex cassine*) and pond apple (*Annona glabra* L.) (Monk 1966, 1968).

In JABOWA-II, the main implemented differences in environmental conditions between cypress swamp and bay swamp are soil depth and standing water depth. Parameter values are listed in Supplementary Information (SI): Table S1. We selected five native species: slash pine, pond cypress, dahoon holly, sweet bay and loblolly bay, for which most information on key parameters for JABOWA-II is available (Table 1). Another reason for selecting those five native species is that pond cypress and slash pine are the dominant canopy trees, with 77% of total relative frequency in cypress swamp. Loblolly bay and sweet bay together dominate bay swamp with 76% relative frequency (Casey and Ewel 2006). All five species are present in both cypress and bay swamp.

### Submodels

Only the “[Growth submodel](#)” section is described here, as the other submodels are described in sufficient detail under “[Processes](#)” section.

#### *Growth submodel*

In JABOWA-II, diameter at breast height of the tree ( $D$ ) is the key state variable. The growth equation is:

$$\delta D = \frac{\{G_i D [1 - [D(137 + b_{2,i} D - b_{3,i} D^2) / (D_{\max,i} H_{\max,i})]]\} * f_i(\text{environment})}{274 + 3b_{2,i} D - 4b_{3,i} D^2}, \quad (1)$$

where  $\delta D$  is the annual growth increment and  $D_{\max,i}$  = maximum diameter of tree of species  $i$   $H_{\max,i}$  = maximum height of tree of species  $i$   $G_i$  = maximum growth rate parameter  $b_2$ ,  $b_3$  = parameters in height versus diameter relationship and where  $f_i(\text{environment})$  ( $<1$ ) incorporates the effects of environment, causing  $\delta D$  to decrease from the value it would have under optimal environmental conditions. Specifically,

$$f_i(\text{environment}) = f_i(\text{AL}) * Q_i * s(\text{BAR}), \quad (2)$$

where available light,  $f_i(\text{AL})$ , is a function of leaf area index (AL) and  $Q_i$  measures site quality, which depends on the effects of several factors;

$$Q_i = \text{TF}_i * \text{WiF}_i * \text{WeF}_i * \text{NF}_i, \quad (3)$$

where  $\text{TF}_i$  is the effect of temperature on tree growth as a function of growing degree-days during current year at site (DEGD),  $\text{WiF}_i$  is the effect of soil moisture on tree growth, or the wilting factor for effect of drought, and  $\text{WeF}_i$  is the wetness factor for the effect of soil wetness, including flooding. In particular,  $\text{WiF}_i$  is related to water depth and  $\text{WeF}_i$  is related to the height of the water table tolerable for the species.  $\text{NF}_i$  is the nitrogen factor for the effect of soil nitrogen, which is based on the species-specific concentration of nitrogen in leaves and the concentration of available nitrogen in the soil. The function  $s(\text{BAR})$  represents the density-dependent limitation on the total basal area of the stand.

## Parameterization of model

Key life cycle parameters used for each species in JABOWA-II are listed with definitions in Table 1, and values are in SI: Table S2. The values of all the parameters are from literature, based on field studies (see SI: Table S3); for example, the studies of Rayachhetry et al. (2001), Serbesoff-King (2003) and Tipping et al. (2013) were used for the melaleuca parameterization. All parameters in JABOWA-II can be adjusted to apply to a particular situation. We assigned all parameter values for which data could be

found for the cases modeled here, but a few that were not known were left as default values of JABOWA-II.

## Initialization

The initialization for each type of simulation is noted in the scenario descriptions.

## Descriptions of scenarios

The scenarios that are evaluated by model simulations are designed to both show the effects of melaleuca on the native forest, which can be compared with data, and project how the impact of herbivory may reverse these effects and allow the native forest to recover. We begin by simulating the cypress swamp and bay swamp forests without melaleuca to help calibrate the model. We then simulate the invasion of melaleuca in both forest types over 600 years, along with simulations in which biocontrol is added at year 300. We also simulate the effects of herbivory on pure melaleuca stands, as there are short-term empirical data that can be used for comparison. Finally, we do a sensitivity analysis by assuming the herbivory is less efficient than the estimates we used based on empirical data.

*Scenario 1* This scenario was used for calibration with densities and size distributions of native species in cypress and bay swamps without melaleuca, based on Casey and Ewel (2006). (More description, see SI, Appendix S1).

*Scenario 2* These simulations started with a cypress swamp community with the size distributions of native species in cypress swamps after 300 years from scenario 1. We allowed melaleuca to invade this community at year 1 and simulated its invasion for 600 years. The simulation provided a test of whether the model agrees with recently observed effects of melaleuca on the native community, and projected the effects of melaleuca with no herbivory on the native community 600 years into the future. In an accompanying simulation, insect herbivory was added beginning at 300 years, via decreasing the melaleuca reproduction rate 49% and the growth rate 83%, based on empirical measurement in Tipping et al. (2008).

*Scenario 3* These simulations were the same as scenario 2, but simulated bay swamp.

*Scenario 4* These simulations projected the long-term effects of herbivory (600 years) on the pure melaleuca stands (i.e., no other species were included in the simulation), starting from saplings. There were four sub-scenarios; no herbivory impact; the addition of herbivory on melaleuca-dominated stands starting with small-sized ( $54 \text{ cm}^2/\text{m}^2$  in basal area); with medium-sized ( $76 \text{ cm}^2/\text{m}^2$  in basal area); and with large-sized trees ( $134 \text{ cm}^2/\text{m}^2$  in basal area). We compared model simulation with empirical data (Rayamajhi et al. 2007).

### Sensitivity analysis

Sensitivity analysis was applied to two parameters regarding the effectiveness of herbivory; SAP (maximum number of saplings of species that can be added in any one year to the 0.01 hectare plot) and  $G$  (maximum growth rate of tree of species) in pure mature-grown melaleuca stands. In scenario 4, reductions in SAP and  $G$  were 49 and 83% respectively, here, we reduced these to 25 & 40 and 10 & 10%.

### Data analysis

All simulations were replicated 50 times. The relative proportion of each species in both cypress swamp and bay swamp was calculated directly as (the number of stems by species/the total number of stems in all the species)  $\times 100$ .

## Results

### Scenario 1

The results of scenario 1 simulations showed the model's expected dynamics of native species without melaleuca's invasion under the current climate, which agreed with field measurements (Fig. 1, note a log scale is used). For more description, see Appendix S1.

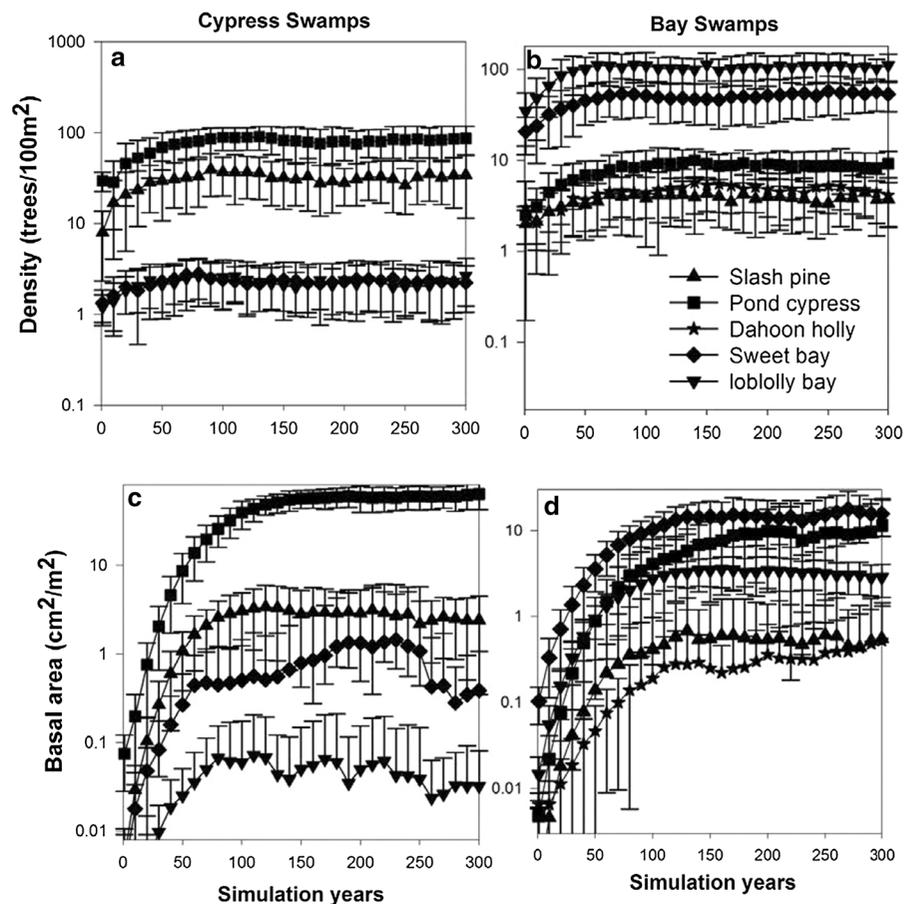
### Scenario 2

Simulations of melaleuca's invasion in cypress swamp without and with herbivory were started with the densities of the mature cypress swamp community

projected in scenario 1. We first describe the simulation without herbivory, shown for a typical simulation with solid data markers in Fig. 2a, b. External input of melaleuca, as saplings, started from year 1 and continued until the melaleuca in the site were large enough to reproduce. The simulation demonstrated that melaleuca stem density grew from 100 to 350 trees/100  $\text{m}^2$ , then dropped to 50 trees/100  $\text{m}^2$  due to intraspecific competition (self-thinning) and interspecific competition from native species, especially pond cypress (Fig. 2a; error bars shown in Fig. S1a). Melaleuca recovered, with oscillations, toward a steady state density of about 200 trees/100  $\text{m}^2$  (filled circles). Overall, melaleuca had greater stem density of individuals than the other species, including pond cypress. Slash pine lost half its original density due to melaleuca invasion in the simulations (Fig. 2a, filled trianglesup). Pond cypress was able to maintain dominance in basal area over melaleuca during most of the 600-year simulation without herbivory, though melaleuca slightly exceeded cypress in basal area for several decades (Fig. 2a), roughly years 120–200, when large numbers of melaleuca saplings were growing in size. After that period, melaleuca's basal area decreased from 40 to 25 due to interspecific competition with cypress and mortality of larger, older trees (Fig. 2b, filled circles).

At year 300, insect herbivory was added in the simulation, by decreasing the melaleuca reproduction rate by 49% and growth rate by 83%. In contrast with the simulated case without the herbivores (Fig. 2a, filled circles), melaleuca stem density declined from 80 to 30 trees/100  $\text{m}^2$  within 50 years of herbivory application (Fig. 2a, unfilled circles), and thereafter melaleuca's density remained below 100 trees/100  $\text{m}^2$ . Pond cypress started to rapidly increase in basal area, due to decreased competition for light, so existing cypress individuals were able to grow larger in size and accumulate greater basal area, although stem density changed little. Melaleuca's basal area decreased from its previous level of 30 to very low levels ( $2\text{--}3 \text{ cm}^2/\text{m}^2$ ) (Fig. 2b, unfilled circles). Although there was some increase in melaleuca stem density from its low by 600 years, its basal area did not recover. In order to make it easier to see the values of slash pine, sweet bay and loblolly bay, which are at very low levels, their densities and basal areas are plotted separately at a finer scale in Fig. 2c, d. We found the three species all had higher basal area

**Fig. 1** **a** The stem densities and **b** the basal areas of the four woody plant species included in modeling in cypress swamp without melaleuca. **c** Projected densities and **d** projected basal areas of the five woody plant species included in modeling in bay swamp without melaleuca



(unfilled line) after insect herbivory was applied, compared to without herbivory (filled line).

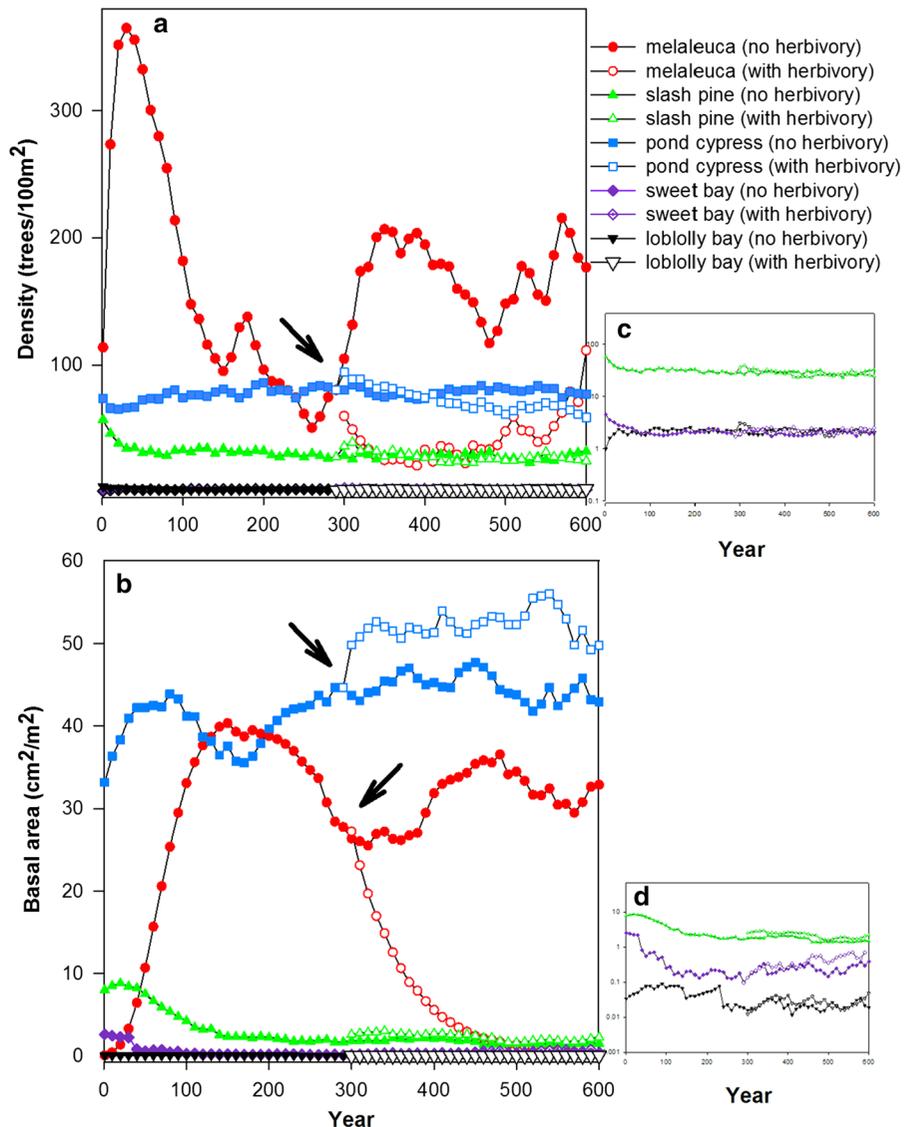
### Scenario 3

As in the cypress swamp scenarios, we first considered the 600-year simulations without herbivory impact, starting with the mature bay swamp community projected from scenario 1, which was dominated by understory trees or shrubs (sweet bay and loblolly bay) beneath the cypress canopy. Compared with cypress swamp, melaleuca rapidly invaded bay swamp, due to its stronger competitive capacity in bay swamp than cypress swamp, as shown in a typical simulation (Fig. 3a; and finer scale in Fig. 3c; error bars in Fig. S2a). Melaleuca reached a peak density (saplings plus trees) of about 2800 trees/100 m<sup>2</sup> (Fig. 3a, filled circle line) by year 50. Its density then dropped to 200 trees/100 m<sup>2</sup> by year 200, mainly due to intraspecific competition (self-thinning), and then oscillated around

400–800 trees/100 m<sup>2</sup>. Melaleuca basal area increased to a high of 90 cm<sup>2</sup>/m<sup>2</sup> at year 100 (Fig. 3b; error bars in Fig. S2c), and then decreased to roughly 55 cm<sup>2</sup>/m<sup>2</sup> at year 250 (Fig. 3b, filled circles). The native species survived at lower densities in the simulations (Fig. 3a, filled triangles up, stars, diamonds and triangles down) and all decreased in basal area during the first 100 years, in response to melaleuca's increase (Fig. 3b, filled triangle up, stars, diamonds and triangles down).

The addition of herbivory on melaleuca at year 300 suppressed melaleuca's reproductive rate by 49% and growth rate by 83%. Melaleuca declined in density from 700 to 100 trees/100 m<sup>2</sup> at year 320, though it then recovered to about 200 trees/100 m<sup>2</sup> (Fig. 3a, unfilled circles) by year 400. This stem density was close to the simulated density without herbivory, but these were very small stems, as the results for basal area (below) show. Meanwhile, dominant native species in bay swamp, especially loblolly bay, started to grow back after melaleuca growth was restricted by

**Fig. 2** Results of scenario 2. **a** Densities, **b** basal area of woody plant species in melaleuca-invaded cypress swamp of Florida with and without insect herbivory. *Arrows* show when herbivory starts to be applied. Because slash pine, sweet bay, and loblolly bay are difficult to see in this plot, they are plotted separately in **c** densities and **d** basal areas at a finer scale. (This figure is shown with *error bars* for 50 simulations in the SI: Fig. S1a–d.)



herbivory. Compared to loblolly bay, the density of sweet bay was still low even when herbivory was applied, because it is less shade-tolerant than loblolly bay. Slash pine also dropped its density because of its low reproduction rate and perhaps shading. With herbivory the basal area of melaleuca declined rapidly from 45 to less than 5 cm<sup>2</sup>/m<sup>2</sup> in 100 years, as the application of herbivory killed larger trees through chronic damage to leaves (Fig. 3b, unfilled circle line) and melaleuca did not grow back as sizable trees. After melaleuca lost its dominant position, native species that had been suppressed started to grow back in numbers and basal areas, reaching their typical

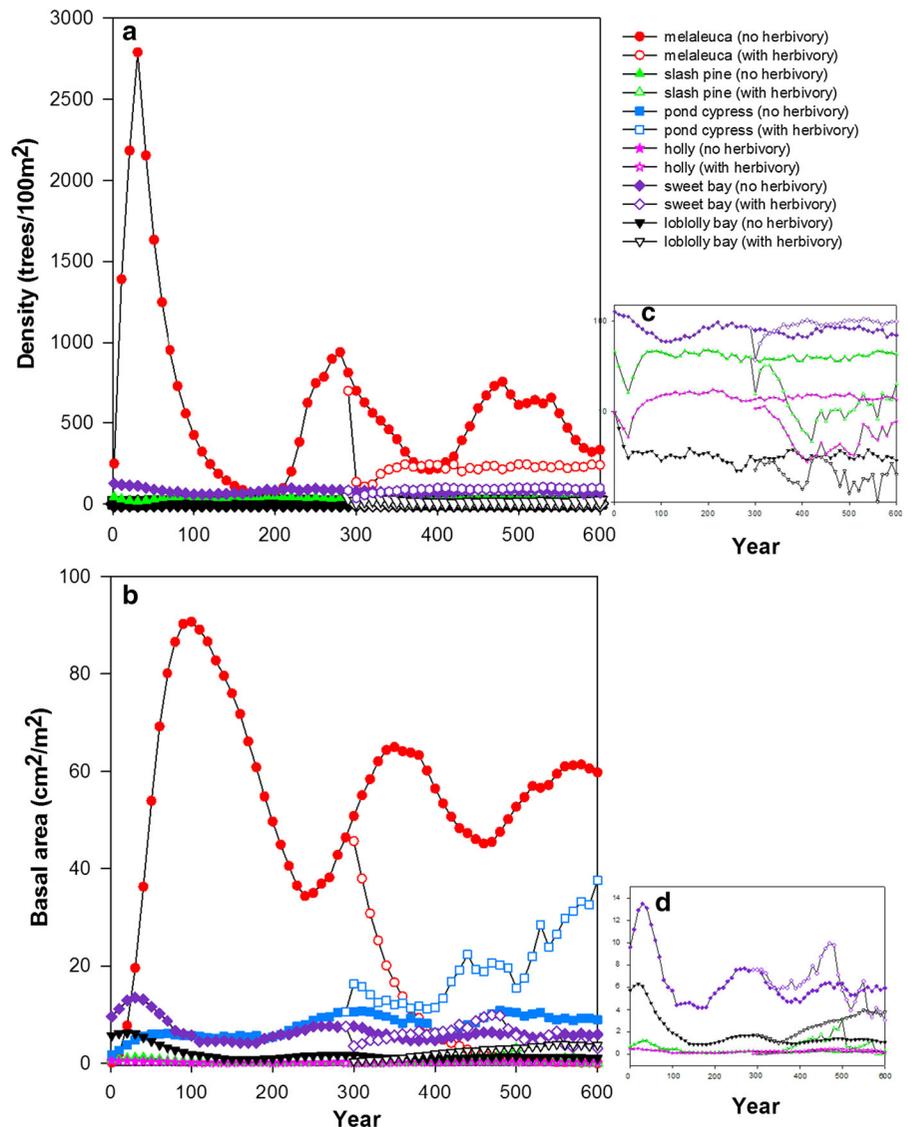
observed levels in stands without melaleuca in about 100 years (Fig. 3b, d, unfilled trianglesup, stars, diamonds and trianglesdown).

No empirical data are available to compare with these long-term effects of herbivory for either cypress or bay swamp, which suggests that it is important to continue long-term field observations of the impact of herbivory to further test and improve the model.

#### Scenario 4

This 600-year simulation was started from a plot with only melaleuca saplings. Starting with an external

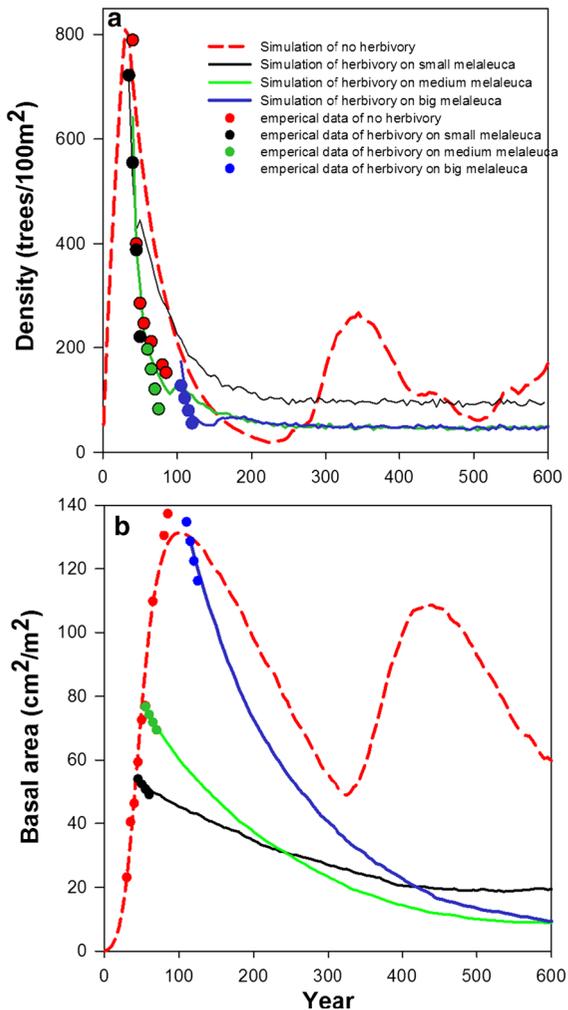
**Fig. 3** Results of scenario 3. **a** Densities, **b** basal area of woody plant species in melaleuca-invaded bay swamp of Florida with and without herbivory. *Arrows* show when herbivory starts to be applied. The density and basal area of slash pine, dahoon holly, sweet bay, and loblolly bay are plotted separately in (c) and (d) at a finer scale (This figure is shown with *error bars* for 50 simulations in SI: Fig. S2a–d.)



input of saplings during the first few decades, there was a continuous increase of melaleuca density until it reached a maximum of about 800 trees/100 m<sup>2</sup> at year 50, followed by a sharp decrease due to both self-thinning and mortality of old-aged trees (Fig. 4a, red dashed line; error bars in Fig. S3a), then an oscillating recovery towards a steady state of between 100 and 200 trees/100 m<sup>2</sup>. Concomitant with the increase in stem density, the melaleuca increased in basal area during the first 100 years, to the maximum amount of 135 cm<sup>2</sup>/m<sup>2</sup> (Fig. 4b, red dashed line; error bars in Fig. S3b). Then basal area declined with stem density from 130 to 45 cm<sup>2</sup>/m<sup>2</sup> during the next 200 years, and

began an oscillating trend towards a steady state. Empirical data from Rayamajhi et al. (2007) in three study sites in southeastern Florida were available for a melaleuca-dominated site without insect herbivory, shown as red dots in Fig. 3a, b. The model followed the increase in basal area very well over about 60 years (Fig. 4b), but did not fit the observed rapid decline in stem density, which declined faster than the simulated density.

Empirical data from Rayamajhi et al. (2007) were also collected following herbivory in nearly pure melaleuca stands. We attempted to match these empirical data, with points in time along our



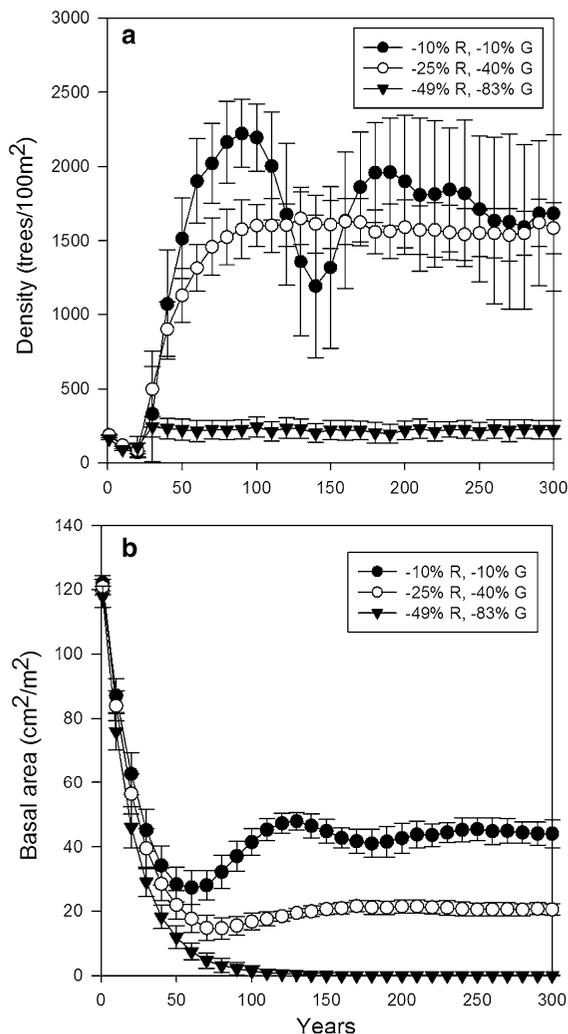
**Fig. 4** Result of scenarios 4. **a** Densities, **b** basal area of pure melaleuca stand with and without herbivory. *Arrows* show when herbivory began to be applied. (Figures are shown with *error bars* in the SI: Fig. S4.a,b.)

simulation that corresponded to stands of approximately the same ages and basal areas as when those studied in the field were affected by herbivory. These empirical data points are shown as blue, purple, and green dots in Fig. 4a, b. Herbivory in the simulation was applied by decreasing the melaleuca reproduction rate by 49% and the growth rate by 83%, in each of three different melaleuca stands, having basal areas of roughly 50, 80, and 130  $\text{cm}^2/\text{m}^2$  (black arrows in Fig. 4b). We concentrate here on Fig. 4b, as the model fits basal area better than stem density. Note that the rate at which the basal area declines following

introduction of herbivory in the simulation depends on the initial basal area of the stand. In the model it is possible that older, larger individuals are more strongly affected by the herbivory (perhaps because they are already stressed from competition), which slowed their rate of growth and increased their mortality rate, so that the stand with larger basal area (i.e., larger trees) experienced a greater rate of decline (Fig. 4b, blue and green solid lines). Simulated impact of herbivory caused slowest decline in stands with younger, smaller individuals (Fig. 4b, black solid line). During the course of the simulation, herbivory decreased melaleuca's basal area from both the 135  $\text{cm}^2/\text{m}^2$  (Fig. 4b blue solid line) and 80  $\text{cm}^2/\text{m}^2$  (Fig. 4b, green solid line) starting values down to 5  $\text{cm}^2/\text{m}^2$ , when applied to stands with larger trees. However, during the same period, the simulated melaleuca stand starting from a basal area of 45  $\text{cm}^2/\text{m}^2$  declined only to 25  $\text{cm}^2/\text{m}^2$  (Fig. 4b, black solid line). We did not observe recovery of melaleuca from these low values in any of the three sub-scenarios simulations, and herbivory significantly decreased melaleuca's basal area compared to stands without its application (Fig. 4b, red dashed line). All three sub-scenario simulation results fit field data from Rayamajhi et al. (2007) well (Fig. 4b, blue, green and black dots), although these field data span too short a time interval to be a strong test of the model. Similar results were found in the changes of melaleuca stem density with application of herbivory on different size stages (Fig. 4a), though they are not as clear as in the case of basal area densities.

#### Scenario 5

The sensitivity analysis results showed that a mere 10% decrease of both reproduction rate (SAP) and growth rate (G) lead to lack of control melaleuca's invasion (Fig. 5). In fact, density and basal area levels were found to be the same as the field observations of uncontrolled melaleuca now. A 25% reduction of reproduction rate (R) and a 40% decrease of the growth rate were shown to keep melaleuca somewhat lower than the non application of herbivory case. But we found that only application of herbivory impacts much closer to a 49% reduction of reproduction rate (R) and a 83% decrease of the growth rate (G) were able to control melaleuca to a very low level.



**Fig. 5** Results of sensitivity analysis. **a** The stem density, **b** the basal area of pure melaleuca stands with different levels of biocontrol

## Discussion

### Effects of the biological control agent on recovery of native woody plant communities

The model projects substantial herbivory-mediated reduction in survival and reproductive potential of melaleuca. Introducing herbivory in our simulations led to large reductions of stem density and basal area of melaleuca. This agrees with Rayamajhi's et al. (2007) field measurements. Native plants are projected to recover basal area and stem density comparable to the pre-melaleuca invasion state (although slash pine and sweet bay did not completely recover in bay

swamp). The simulations also show that as native plants recolonize the habitat, melaleuca is further suppressed, since melaleuca trees are rendered less competitive due to chronic damage inflicted by insect herbivores. Because of the short time available for field observations following the introduction of specialized herbivores, no significant recolonization by natives has been recorded. However, Rayamajhi (unpublished data) found increases in native plant diversity and abundance following herbivore-mediated declines for melaleuca growing in wetter, higher organic soils.

This relates to the problem of specialist biocontrol agents in general. These require some persistent population of their host species to remain as effective control agents (Murdoch and Briggs 1996; Ewel et al. 1999; Fagan et al. 2002; Symondson et al. 2002; Stiling and Cornelissen 2005). A general strategy in such cases has been the augmentation of the biocontrol agents through periodic mass rearing and reintroduction (DeBach 1974), Reduction of melaleuca to a relatively minor component of future tree communities could also facilitate application of other methods (e.g., mechanical removal and chemical treatment) to reduce it further.

### Effects of biological control agent on different size staged pure melaleuca stands; management implications

Simulation results (Fig. 4a, b) showed good fits to empirical data, especially basal area, when no herbivory was applied to these stands. Projections show that without control melaleuca has higher stem density and basal area in pure stands than when it is mixed in cypress- and bay-swamps (Figs. 2, 3), due to the lack of interspecific competition with native species. Oddly, the introduction of herbivory to the early-age pure melaleuca stand (starting at 54 cm<sup>2</sup>/m<sup>2</sup> in basal area) did not reduce basal area as much as its application to older stands (starting at larger than 76 cm<sup>2</sup>/m<sup>2</sup> in basal area) (Fig. 4b). This greater reduction of the older stands may reflect that these are already under stress due to high basal area density.

The sensitivity analysis shows a large drop in effectiveness of control would occur if negative effects of herbivory on growth and reproduction (such as only 10% decrease of both reproduction rate and growth rate) were appreciably less than estimated

from empirical data. This suggests that managers should attempt to maintain reductions on reproduction and growth as close to the levels of 49 and 83%, respectively, as possible, to have the level of effects shown in our simulations.

Three conclusions relevant to management can be drawn from our model findings: (1) The introduction of insect herbivory applied to melaleuca is sufficient to suppress melaleuca to a low density and basal area level over the long term. (2) It takes about 50 years for native species to recover in the system and gain higher basal area. Thereafter, the density of melaleuca remains lower than if there are no native species in cypress swamp, suggesting that cypress will aid control by shading the melaleuca saplings. (3) Fostering native species reinvasion will help control melaleuca through competition.

#### Model limitations

Parameters of both plants and environment are limited by the available field measurements and observations. We have not included all the species and environmental conditions in southern Florida. We have only been able to test the model's usefulness on a small set of selected species, and the effect of herbivory on melaleuca-dominated stands. We could improve the model via recoding JABOWA-II to include more site variables, such as available phosphorus. One model conclusion that needs further consideration is that pond cypress maintained dominance over melaleuca in the cypress swamp simulation (Fig. 2a), as melaleuca has been found to take over in some cases (K. C. Ewel, personal communication). Absence of fire in the model is one possible explanation. Another limitation of the present simulations is that the climate is assumed constant, which is unlikely over the 600-year scenarios. Our future plan is to use 100-year climate projections to refine model output.

Implications of using an individual based forest model on other invasive plant issues

Biological control offers long-term, economically viable management potential, by reducing the rate of spread, vitality and growth rate of plants, thus rendering them more vulnerable to other environmental stresses and other control methods (Turner et al. 1998). Models that can accurately predict the long-

term impact of such control on performance of native species in melaleuca-invaded habitats will be especially useful for freshwater systems that were previously dominated by melaleuca.

**Acknowledgements** This work is the product of collaboration with researchers from USDA-ARS Aquatic Weed Research Laboratory, for which we are grateful. In particular, we thank Dr. Carol Horvitz and her lab, and Dr. Philip Tipping for their useful discussions; Rob Burgess for help compiling JABOWA-II. Comments from Jiang Jiang and Orou Gaoue greatly improved the quality of this paper. We gratefully acknowledge the comments from Dr. Julien Martin, Dr. Geoff Wang, and two anonymous reviewers. The USGS's Greater Everglades Priority Ecosystem Science provided funding for supporting Ms. Bo Zhang's research. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

#### References

- Acevedo MF, Urban DL, Shugart HH (1996) Models of forest dynamics based on roles of tree species. *Ecol Model* 87:267–284
- Balentine KM, Pratt PD, Dray FA, Rayamajhi MB, Center TD (2009) Geographic distribution and regional impacts of *Oxyops vitiosa* (Coleoptera: Curculionidae) and *Boreioglycaspis melaleuca* (Hemiptera: Psyllidae), biocontrol agents of the invasive tree *Melaleuca quinquenervia*. *Environ Entomol* 38:1145–1154
- Botkin DB (1993) *Forest dynamics: an ecological model*. Oxford University Press, Oxford, p 309
- Botkin DB, Janak JF, Wallis JR (1972) Some ecological consequences of a computer model of growth. *J Ecol* 60:849–872
- Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH (2010) Predicting plant invasions in an era of global change. *Trends Ecol Evol* 25:310–318
- Brown S (1981) A comparison of the structure, primary productivity and transpiration of cypress ecosystems in Florida. *Ecol Monogr* 51:403–427
- Bugmann H (2001) A review of forest gap models. *Clim Change* 51:259–305
- Casey WP, Ewel KC (2006) Patterns of succession in forested depressional wetlands in north Florida, USA. *Wetlands* 26:147–160
- Center TD, Pratt PD, Tipping PW, Rayamajhi MB, Van TK, Wineriter SA, Dray FA (2007) Initial impacts and field validation of host range for *Boreioglycaspis melaleuca* Moore (Hemiptera: Psyllidae), a biocontrol agent of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake. *Ecol Monogr* 36:569–576
- Center TD, Purcell MF, Pratt PD, Rayamajhi MB, Tipping PW, Wright SA, Dray FA Jr (2012) Biological control of *Melaleuca quinquenervia*: an Everglades invader. *Biocontrol* 57:151–165
- Center TD, Van TD, Rayachhetry M, 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
- DeBach P (1974) Biological control by natural enemies. Cambridge University Press, Cambridge, p 323
- Deghi GS, Ewel KC, Mitsch WJ (1980) Effects of sewage effluent application on litter fall decomposition in cypress swamps. *J Appl Ecol* 17:397–408
- Dray FA Jr (2003) Ecological genetics of *Melaleuca quinquenervia* (Myrtaceae): population variation in Florida and its influence on performance of the biocontrol agent *Oxyops vitiosa* (Coleoptera: Curculionidae). PhD dissertation, Florida International University, Miami, FL
- Dray FA Jr, Bennett BC, Center TD (2006) Invasion history of *Melaleuca quinquenervia* (Cav.) S. T. Blake in Florida. *South Appalach Bot Soc* 71:210–225
- Elliott-Graves A (2016) The problem of prediction in invasion biology. *Biol Philos* 31:373–393
- Ewel JJ, O'Dowd D, Bergelson J, Dachler CC, D'Antonio CM, Gomez LD, Gordon D, Hobb RJ, Holt A, Hopper KR, Hughes CE, LaHart M, Leakey RRB, Lee WG, Loope LL, Lorence DH, Louda SV, Lugo AE, McEvoy PB, Richardson DM, Vitousek PM (1999) Deliberate introductions of species: research needs. *Bioscience* 49:619–630
- Ewel KC (1990) Multiple demands on wetlands. *Bioscience* 40:660–666
- Fagan WF, Lewis MA, Neubert MG, van den Driessche P (2002) Invasion theory and biological control. *Ecol Lett* 5:148–157
- Greenway M (1994) Litter accession and accumulation in a *Melaleuca quinquenervia* (Cav.) S. T. Blake wetland in Southeastern Queensland. *Aust J Mar Fresh Res* 45:1509–1519
- Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz S, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Peer G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi S, Stillmann R, Vabø R, Visser U, DeAngelis DL (2006) A standard protocol for describing individual-based and agent-based models. *Ecol Model* 198:115–126
- Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF (2010) The ODD protocol: a review and first update. *Ecol Model* 221:2760–2768
- Higgins SI, Richardson DM (1996) A review of models of alien plant spread. *Ecol Model* 87:249–265
- Kaufman SR, Smouse PE (2001) Comparing indigenous and introduced populations of *Melaleuca quinquenervia* (Cav.) Blake: response of seedlings to water and pH levels. *Oecologia* 127:487–494
- Krug RM, Richardson DM (2014) Modelling the effect of two biocontrol agents on the invasive alien tree *Acacia cyclops*—flowering, seed production and agent survival. *Ecol Model* 278:100–113
- Maines A, Knochel D, Seastedt T (2013) Biological control and precipitation effects on spotted knapweed (*Centaurea stoebe*): empirical and modeling results. *Ecosphere* 4:1–14
- Martin MR, Tipping PW, Reddy KR, Daroub SH, Roberts KM (2010) Interactions of biological and herbicidal management of *Melaleuca quinquenervia* with fire: consequences for ecosystem services. *Biol Control* 54:307–315
- Martin MR, Tipping PW, Reddy KR, Madiera PT, Fitzgerald D (2011) An evaluation of the impact of *Melaleuca quinquenervia* invasion and management on plant community structure after fire. *Aquat Bot* 95:287–291
- Martin MR, Tipping PW, Sickman JO (2009) Invasion by an exotic tree alters above and belowground ecosystem components. *Biol Invas* 11:1883–1894
- Meskimen GF (1962) A silvicultural study of the melaleuca tree in south Florida. Master's thesis, University of Florida, Gainesville, FL
- Mitsch W, Ewel KC (1979) Comparative biomass and growth of cypress in Florida wetlands. *Am Midl Nat* 101:417–426
- Mitsch WJ, Dorage CL, Wiemhoff JR (1979) Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. *Ecology* 60:1116–1124
- Monk CD (1966) An ecological study of hardwood swamps in north-central Florida. *Ecology* 47:649–654
- Monk CD (1968) Successional and environmental relationships of the forest vegetation of north central Florida. *Am Midl Nat* 79:441–457
- Murdoch WW, Briggs CJ (1996) Theory for biological control: recent developments. *Ecology* 77:2001–2013
- Myers JH, Bazely DR (2003) Ecology and control of introduced plants. Cambridge University Press, Cambridge
- Myers RL (1983) Site susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. *J Appl Ecol* 20:645–658
- Ngugi MR, Botkin DB (2011) Validation of a multispecies forest dynamics model using 50-year growth from Eucalyptus forests in eastern Australia. *Ecol Model* 222:3261–3270
- Pausas JG, Austin MP, Noble IR (1997) A forest simulation model for predicting eucalypt dynamics and habitat quality for arboreal marsupials. *Ecol Appl* 7:921–933
- Penfound WT (1952) Southern swamps and marshes. *Bot Rev* 18:413–445
- Pratt PD, Rayamajhi MB, Van TK, Center TD (2005) Herbivory alters resource allocation in the invasive tree *Melaleuca quinquenervia*. *Ecol Entomol* 30:316–326
- Rai PK (2015a) Paradigm of plant invasion: multifaceted review on sustainable management. *Environ Monit Assess* 187:1–30
- Rai PK (2015b) What makes the plant invasion possible? Paradigm of mechanisms, theories and attributes. *Environ Skep Crit* 4:36e66
- Rayachhetry MB, Van TK, Center TD (1998) Regeneration potential of the canopy-held seeds of *Melaleuca quinquenervia* in south Florida. *Int J Plant Sci* 159:648–654
- Rayachhetry MB, Van TK, Center TD, Laroche F (2001) Dry weight estimation of the aboveground components of *Melaleuca quinquenervia* trees in southern Florida. *For Ecol Manag* 142:281–290
- 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
- Serbesoff-King K (2003) Melaleuca in Florida: a literature review on the taxonomy, distribution, biology, ecology, economic importance, and control measures. *J Aquat Plant Manag* 41:98–112

- Smith TM, Urban DL (1988) Scale and resolution of forest structural pattern. *Vegetatio* 74:143–150
- Stiling P, Cornelissen T (2005) What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. *Biol Control* 34:236–246
- Symondson WO, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Ann Rev Entomol* 47:561–594
- Tipping PW, Martin MR, Nimmo KR, Smart MD, White E, Madeira PT, Center TD (2009) Invasion of a West Everglades wetland by *Melaleuca quinquenervia* countered by classical biocontrol. *Biocontrol* 48:73–78
- Tipping PW, Martin MR, Pierce R, Center TD, Pratt PR, Rayamajhi MB (2012) Post-biocontrol invasion trajectory for *Melaleuca quinquenervia* in a seasonally inundated wetland. *Biocontrol* 60:163–168
- Tipping PW, Martin MR, Pratt PD, Center TD, Rayamajhi MB (2008) Suppression of growth and reproduction of an exotic invasive tree by two introduced insects. *Biocontrol* 44:235–241
- Tipping PW, Martin MR, Pratt PD, Rayamajhi MB, Center TD (2013) An abundant biocontrol agent does not provide a significant predator subsidy. *Biocontrol* 67:212–219
- Turner CE, Center TD, Burrows DW, Buckingham GR (1998) Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, U.S.A. *Wetl Ecol Manag* 5:165–178
- Van TK, Rayachhetry MB, Center TD (2000) Estimating above-ground biomass of *Melaleuca quinquenervia* in Florida, USA. *J Aquat Plant Manag* 38:62–67
- Van TK, Rayachhetry MB, Center TD, Pratt PD (2002) Litter dynamics and phenology of *Melaleuca quinquenervia* in South Florida. *J Aquat Plant Manag* 40:22–27
- Williamson M (1999) Invasions. *Ecography* 22:5–12