

Quantifying the Adventive Geographic Distribution and Dispersal Rate of *Oxyops vitiosa*, a Biological Control Agent of the Invasive Tree *Melaleuca quinquenervia*

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Introduction

The primary objective of most weed biological control programs is to suppress a pest plant population below an ecological threshold, ultimately resulting in the replacement of the target weed with more desirable vegetation (McEvoy and Rudd 1993). Although the realization of this objective has been described anecdotally for multiple programs, rarely are impacts on the target weed quantified after release of the biological control agent (McFadyen 1998; McEvoy and Coombs 1999). The paucity of post release evaluations may be due, in part, to limited financial support, inadequate scientific know how or lack of a cohesive framework from which these evaluations can be made (McEvoy and Coombs 1999). With respect to the latter obstacle, Parker et al. (1999) suggest that ecological impacts of introduced species can be evaluated as a function of 1) the organism's geographic distribution, 2) its population densities and 3) the suppressive effect per individual. In early stages of a weed biological control program calculation of the first parameter, geographic distribution, is generally limited to initial release localities. However, as target weeds deteriorate or otherwise become unsuitable, the agent is forced to disperse and its distribution increases. Therefore, evaluating the biological control agent's rate of spread is integral to assessing its potential geographic distribution and for quantifying its impacts on the targeted weeds in space and time. Herein we assess the distribution and rate of spread of *Oxyops vitiosa* (Pascoe), a classical weed biological control agent of the Australian tree *Melaleuca quinquenervia* (Cav.) S.T. Blake.

Melaleuca quinquenervia (melaleuca), first introduced into south Florida (U.S.) by horticulturists in the late 1800's, remained innocuous for nearly half a century (Dray and Bennet, in press). More recently, however, melaleuca invasion rates have increased to average 2,850 ha/yr or approximately 7.8 ha/d over the past century (Laroche and Ferriter 1992; Center et al. 2000). *Melaleuca quinquenervia* now occupies approximately 200,000 ha of graminoid/herbaceous wetlands, including portions of the Everglades National Park (Turner et al. 1998). Heavily infested sites consist of closed-canopy swamp forests comprised of melaleuca stands of up to 132,000 saplings and trees/ha (Rayachhetry et al. 2001). Transitional stages of the invasion include savannahs with scattered, individual trees and mature dense melaleuca heads surrounded by relatively pristine marshes that contain moderate to low levels of melaleuca (O'Hare and Dalrymple 1997).

To limit invasion and provide a biologically-based approach to the control of melaleuca, a classical weed biological control program was initiated in 1986 (Balciunas et al. 1994). Explorations for natural enemies of melaleuca in eastern Australia resulted in the enumeration of >450 associated herbivorous arthropod species (Burrows and Balciunas 1999). One of the most promising candidates, the melaleuca snout beetle (*O. vitiosa*), was the first species selected for quarantine-based host specificity testing (Purcell and Balciunas 1994). These tests showed the weevil to be host specific and

predicted that it would exploit a very narrow range of plant species (Balciunas et al. 1994). Therefore, in 1997 *O. vitiosa* was released at 13 melaleuca-infested locations in south Florida (Center et al. 2000). Nascent populations established at 9 of the original 13 release sites and closely monitored redistribution efforts were instigated thereafter.

This is the first in a series of reports that evaluates the impacts of *O. vitiosa* on *M. quinquenervia* populations. Specific objectives of this study were to: 1) quantify the current geographic distribution of *O. vitiosa* in southern Florida, 2) document the rate of spread of the weevil, 3) identify specific factors that influence dispersal rates, and 4) model the spread of *O. vitiosa* as a management tool for redistribution efforts.

Materials and Methods

Geographic distribution of *Melaleuca quinquenervia* and *Oxyops vitiosa*. The distribution of *M. quinquenervia* in south Florida was estimated from habitat maps provided by the South Florida Water Management District and U.S. Geological Survey (Florida Gap Analysis Project). The first source was developed by observing from a fixed-wing aircraft the presence and abundance of melaleuca at timed intervals spaced evenly along east-west transects established in southern Florida (Laroche 1999). Transects were spaced at 4 km intervals and ranged from the northern rim of Lake Okeechobee to the Florida Keys. The second source was developed by multispectral classification of LANDSAT satellite imagery. These data sources were combined, then the resulting map was compared with ground-truthed data to find additions or deletions. Clusters of data points, representing many discrete melaleuca stands in close proximity to each other, were integrated into a single continuous stand. This technique overestimates the area invaded by melaleuca but accurately quantifies the area over which *O. vitiosa* must disperse to locate distant plants. In addition, melaleuca has invaded areas north of Lake Okeechobee, with sustainable populations occurring near Orlando, Orange County, FL; however distribution data are not available for this region. We therefore restricted our analysis and subsequent inferences to the areas south of the northern rim of Lake Okeechobee.

The current geographic distribution of *O. vitiosa* was determined by fixing the location of each release site using real-time differential global positioning (GPS; Trimble Pathfinder Pro XR: Trimble Navigation Limited, Sunnyvale, CA 94086). Only releases made from the spring 1997 (first introduction) through July 2001 were included in the analysis. Data at each release site were collected in decimal degrees with resolution accuracy to the fourth decimal place. We allowed for 5 min of averaging to occur for each GPS reading before recording the coordinates. Data were imported into the georeferenced software ArcView GIS version 3.0a (Environmental Systems Research Institute, Inc., Redlands, CA 92373) and graphical output was in the Mercator projection type.

Rate of Spread and Spatial Patterns of *Oxyops vitiosa*. To estimate the rate of spread of *O. vitiosa*, we randomly selected 4 release sites from among the first 14 release locations (Center et al. 2000) and quantified the distance dispersed from the respective release date to May 2000 (Table 1). In general, weevil populations at these study sites had not coalesced with those of other release sites and *M. quinquenervia* trees were

widely, although sometimes patchily, distributed in all 4 cardinal directions. The point of release for each site was fixed using the GPS system as described earlier. The dispersal of *O. vitiosa* from each release point was quantified by measuring the distance of the most distant individual or signs of weevil damage from the epicenter along transects radiating in the 4 cardinal directions (N, S, E, W; Caughley 1970). Foliar damage by all stages of *O. vitiosa* is diagnostic (Rayachhetry et al. 2002) and discloses the presence of the otherwise cryptic adults at very low population densities. Melaleuca trees were searched along transects for a minimum of 0.75 km beyond the last observed weevil or sign of weevil damage. We calculated the rate of spread for each site from dispersal distances measured along each transect as:

$$R = \frac{[(dN^2 + dS^2 + dE^2 + dW^2)/4]^{1/2}}{t},$$

where R is the rate of spread (km/yr) for an individual site, d is the distance (km) traveled by *O. vitiosa*, N, S, E, W represent transects in the 4 cardinal directions and t is time (years) since release (adapted from Andow et al. 1993).

To elucidate parameters that may influence the rate of spread, various characteristics of each transect were noted, including cardinal direction, melaleuca stand fragmentation, hydroperiod, predominant wind direction, maximum and mean wind speed, years since release of weevils, and number of individuals released. Melaleuca fragmentation along each transect was categorized into 3 levels: low fragmentation consisting of dense continuous stands with breaks <30m (\approx 25,000 trees/ha), moderate fragmentation with isolated stands separated by breaks of 31-100 m (\approx 12,000 trees/ha), and highly fragmented stands separated by more than 100 m (\approx 6,500 trees/ha). Hydroperiod was classified in accordance with Ewel (1990): Dry = never inundated; short = inundated < 6 months; moderate = inundated 6-9 months. It should be noted that *M. quinquenervia* also invades permanently flooded habitats but because *O. vitiosa* pupates in the soil (Purcell & Balciunas 1994) and establishment has been unsuccessful thus far in inundated sites (Center et al. 2000), these habitats were not assessed. Wind data were gathered at 1 h intervals from individual weather monitoring stations located <40 km from each study site. Wind direction was categorized into 8 components (N, NE, E, SE, S, SW, W, NW). Only wind data from 1997-2000 were used in this study. Stepwise regression was used to identify those parameters that influenced the linear distance traveled by *O. vitiosa* along each transect. The criteria for including or excluding an explanatory variable was $P < 0.05$ and ≥ 0.05 , respectively (SPSS, 1996).

Modeling the Spread of *Oxyops vitiosa*. To predict the time needed for the weevil to disperse throughout the range of melaleuca in south Florida, we modeled the dispersal of *O. vitiosa* using Matlab® R12 (The MathWorks, Inc., Natick, MA). A two dimensional matrix of 1120 x 1260 cells was created, with each cell covering 4.16 ha, and having a binary (infested/not infested) representation of the geographical extents of melaleuca in Florida. These patches of melaleuca formed the boundaries of dispersal for *O. vitiosa*. On this landscape, *O. vitiosa* was introduced according to the geographic location, month of release, and the number of weevils released at each actual release point. After release, the populations of weevils were allowed to increase and spread

according to their parameters of population increase (r ; Pratt et al. 2002), carrying capacity (K ; Pratt et al. 2003), and dispersal distance as determined by the field studies performed herein. Growth of weevil populations were simulated by Ricker's (1954) model,

$$N_{t+1} = N_t \exp[r(1 - N_t / K)]$$

where N is the population size at time interval t . Local dispersal was accomplished by a two dimensional convolution of a normal probability density function (Allen et al. 2001). The size of the dispersal kernel was set so that 95% of the dispersing weevils were within the average dispersal distance found in the field. Additionally, "long range dispersers" were modeled by having very few (0.0001%) beetles flying up to 20 km per month from parent populations that had reached a density greater than 90% of K . Reproduction, carrying capacity and dispersal parameters were input for 3 levels of fragmentation, equivalent to 25,810 (low), 12,905 (medium), and 6,452 (high) trees/ha.

New release sites. Based on the current spread of *O. vitiosa* across the melaleuca landscape, we identified 16 isolated locations where further redistribution of weevils could accelerate coverage. For each of these potential points, we simulated moving 5,000 weevils from an established population in Dade County to the new locations in September 2002. Each release point was first modeled separately, then all release points were combined.

Sensitivity analysis. Considering the various fragmentation levels of melaleuca found in south Florida, and the effect that mis-parameterization of the model may have on the results, sensitivity analysis was performed for r , K , local dispersal distance and long range dispersal distance. This was accomplished by running the model with each of the parameters at 80, 90, 100, 110, and 120% of their default values in turn, and calculating the effect the parameter change had on the time required for weevils to cover 50% of the melaleuca invaded habitats at a density of 0.5 weevils per growing tip. This weevil density was determined to significantly decrease melaleuca growth and development (Center et al. 2000; Pratt, unpub. data).

Results and Discussion

Geographic distribution of *Melaleuca quinquenervia* and *Oxyops vitiosa*.

Although widely distributed throughout the southern portions of the state, the geographic distribution of melaleuca is concentrated on the eastern and western coastal regions of southern Florida (Fig. 1). This spatial arrangement is related, in part, to early introductions (1886-1912) in the Koreshan region of Lee County on the west coast, and several independent introductions of the weed in the eastern coastal counties of West Palm, Broward and Dade (1900-1930; Dray and Bennet in press). In addition, extensive control measures have been undertaken to eradicate melaleuca on public lands occurring in central regions of the state (i.e. Lake Okeechobee, Big Cypress National Preserve and The Everglades National Park; Laroche 1999). To date, melaleuca has invaded 19 counties in south Florida (Wunderlin et al. 2000) and our spatial analysis estimates that

melaleuca occupies 295,740 ha south of the northern rim of Lake Okeechobee (Table 2; Fig. 1). As stated earlier, the method used to quantify the spatial coverage herein overestimates the actual invaded area, which was independently estimated at 202,000 ha (Wunderlin et al. 2000; Turner et al. 1998; Laroche 1999), though it accurately describes the distance *O. vitiosa* must disperse to locate distant plants.

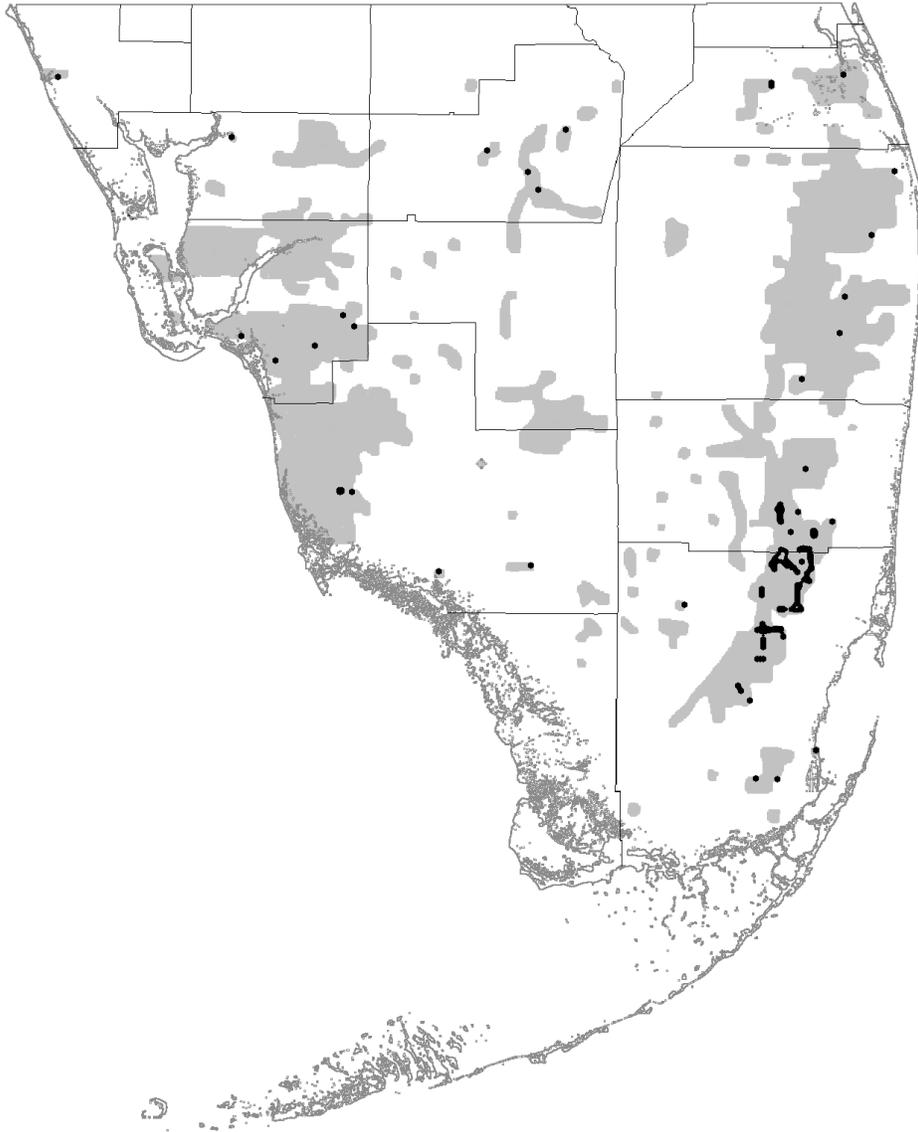


Figure 1. Geographic range of the invasive tree *M. quinquenervia* (in grey) and release points of its biological control agent *O. vitiosa* (black dots) in south Florida.

The initial geographic distribution of *O. vitiosa* is presented in Fig. 1. To date, this biological control agent has been redistributed to 135 locations and occurs in 9 south Florida counties (Table 2). The spatial orientation of these data suggests that the number of releases per county does not correlate with area infested per county (Table 2). Dade County, for instance, has the highest number of releases (81) yet possesses only 11.7% of the total melaleuca infestation. In contrast, Palm Beach County has the greatest area infested by the weed but has received only 3.7% of the total releases. The disparity between infestation levels and redistribution efforts is attributable to county level funding of redistribution efforts (for Dade County), location of lands managed by supporting agencies (Broward, Dade and Lee Counties) and logistics in relation to field-based mass rearing sites (Lee County).

Table 1. Study sites used to estimate the dispersal rates of the biological control agent *Oxyops vitiosa*

Site	Release date ^a	GPS coordinates ^b		Distance from weather station ^c	Number of individuals ^d
		North	West		
Estero	11/15/97	26.4255	-81.8103	10	4009
West Palm	5/22/97	26.7338	-80.1501	36	280
Belle Meade	10/30/98	26.10478	-81.6339	4	200
Corkscrew	11/15/97	26.46192	-81.7025	40	1051

^a Weevils were released at each site on multiple occasions within a 3-month period; therefore dates represent the median release event.

^b Global positioning system in decimal degrees.

^c Measured in kilometers.

^d Total numbers of weevils (all stages) released at each site.

Table 2. Geographic distribution and predicted population densities for *Oxyops vitiosa* in relation to that of the invasive weed *Melaleuca quinquenervia* in south Florida

County	Number of releases sites	Percent of total releases	Area infested by melaleuca (ha)	Percent of total melaleuca infestation	Estimated area occupied by <i>O. vitiosa</i> (ha)					
					Detectable ^a			Economic ^b		
					H ^c	M	L	H	M	L
Broward	30	22.22%	320	10.83%	1712	565	68	57	41	3
Charlotte	1	0.74%	115	3.88%	0	0	0	0	0	0
Collier	7	5.19%	502	16.98%	591	135	22	0	0	0
Dade	81	60.00%	346	11.69%	2083	446	50	91	0	0
Glades	4	2.96%	112	3.77%	298	5	1	0	0	0
Hendry	0	0.00%	132	4.46%	0	0	0	0	0	0
Highlands	0	0.00%	4	0.15%	0	0	0	0	0	0
Lee	4	2.96%	552	18.68%	1458	265	26	140	0	0
Martin	2	1.48%	126	4.27%	180	15	2	0	0	0
Monroe	0	0.00%	13	0.45%	0	0	0	0	0	0
Palm Beach	5	3.70%	727	24.58%	1907	326	37	347	0	0
Sarasota	1	0.74%	8	0.26%	25	0	0	0	0	0
Total	135		295740							

^a: Detectable levels of *O. vitiosa*, one individual per 1000 branch tips.

^b: Economic levels of *O. vitiosa*, 0.5 individuals per branch tip.

^c: Melaleuca fragmentation level: dense continuous stands with breaks <30m (low fragmentation), moderate fragmentation with isolated stands separated by breaks of 31-100 m, and highly fragmented stands separated by more than >100 m.

Rate of Spread and Spatial Patterns of *Oxyops vitiosa*. When averaged among all directions and sites, *O. vitiosa* spread from release points at a rate of 0.99 (± 0.28) km/yr, ranging from 0.10 to 2.78 km/yr. This preliminary rate of spread estimate for *O. vitiosa* is minimal when compared with that of other introduced weevils. The average rate of spread of the boll weevil (*Anthonomus grandis grandis* Boheman), for instance, was estimated to be 95.3 km/yr with a range of 64 to 193 km/yr (Hunter and Coad 1923, Culin et al. 1990). In Japan, the male sweetpotato weevil (*Cylas formicarius elegantulus* (Summers)) dispersed 59.4 km/yr and, in early stages of its invasion, the spread of the rice water weevil (*Lissorhoptrus oryzophilus* Kuschel) ranged from 28 to 47 km/yr (Andow et al. 1993, Miyatake et al. 1995). The disparity among these rates of spread and that of *O. vitiosa* estimated herein may be related to differences in the amount of time used to acquire the estimate. We calculated the dispersal rates of *O. vitiosa* from data collected 2-3 years after introduction in contrast to data for the boll weevil, which averaged rates of spread over approximately 20 yrs of invasion (Culin et al. 1990). When calculating estimates from larger temporal intervals, slow initial rates of spread may be masked by acceleration of an invasion front as it increases over time (Andow et al. 1993). For this reason, additional (future) studies are needed to determine if the invasion of *O. vitiosa* follows a similar accelerating trend and if the rate of spread reported herein is accurate when considering the entire invasion process.

Variation in the rate of spread by individuals through the melaleuca-dominated habitat was influenced by both ecological and human mediated parameters. Among those measured, melaleuca fragmentation ($df=1,15$; $F= 23.92$; $P=0.0002$), the number of weevils released ($df=1,15$; $F= 5.90$; $P=0.0304$) and time after release ($df=1,15$; $F= 7.75$; $P=0.0165$) significantly influenced the rate of spread of *O. vitiosa*. The predictive equation for the dispersal distance of *O. vitiosa* is best described as:

$$y = 1.813 + (5.449*f) + (0.187*t) + (0.002*n),$$

where y is the distance (km) dispersed, f is the level of weed fragmentation, t is the time (yr) after release and n is the number of *O. vitiosa* released at a given location. When pooled among all sites, dispersal distance was positively correlated with stand fragmentation levels: high= 2.04, medium= 1.07 and low= 0.30 km/yr (Fig. 2). The most intuitive explanation for this involves the increased linear dispersal required for weevils to locate widely dispersed melaleuca stands.

Center et al. (2000) determined that establishment was not influenced by the number of individuals released, with the minimum initiating density of 60 individuals establishing as readily as those in excess of a 1,000 individuals. Interestingly, these data suggest that an increase in initial release density may result in an increase in the rate of spread of the biological control agents from the release epicenter. Assuming that a high rate of spread is desired, these data indicate that increasing the number *O. vitiosa* individuals released per site in early stages of the biological control program will expedite the local (short range) movement of weevils from the release point to the surrounding infested areas.

The variation among rates of spread for *O. vitiosa* (0.10 to 2.78 km/yr) demonstrates the inaccuracy of a single value to describe the movement of biological control agents across a landscape. Rarely are habitats homogeneous and, as described herein, biological control agents may alter dispersal rates in response to habitat fragmentation, wind direction or other environmental parameters (Andow et al. 1993; Shigesada and Kawasaki 1997; Smith et al. 2001). Unfortunately, these site specific parameters can be difficult to assess over the entire range of the target weed. Therefore, modeling different scenarios may be the only option in some systems (Smith et al. 2001).

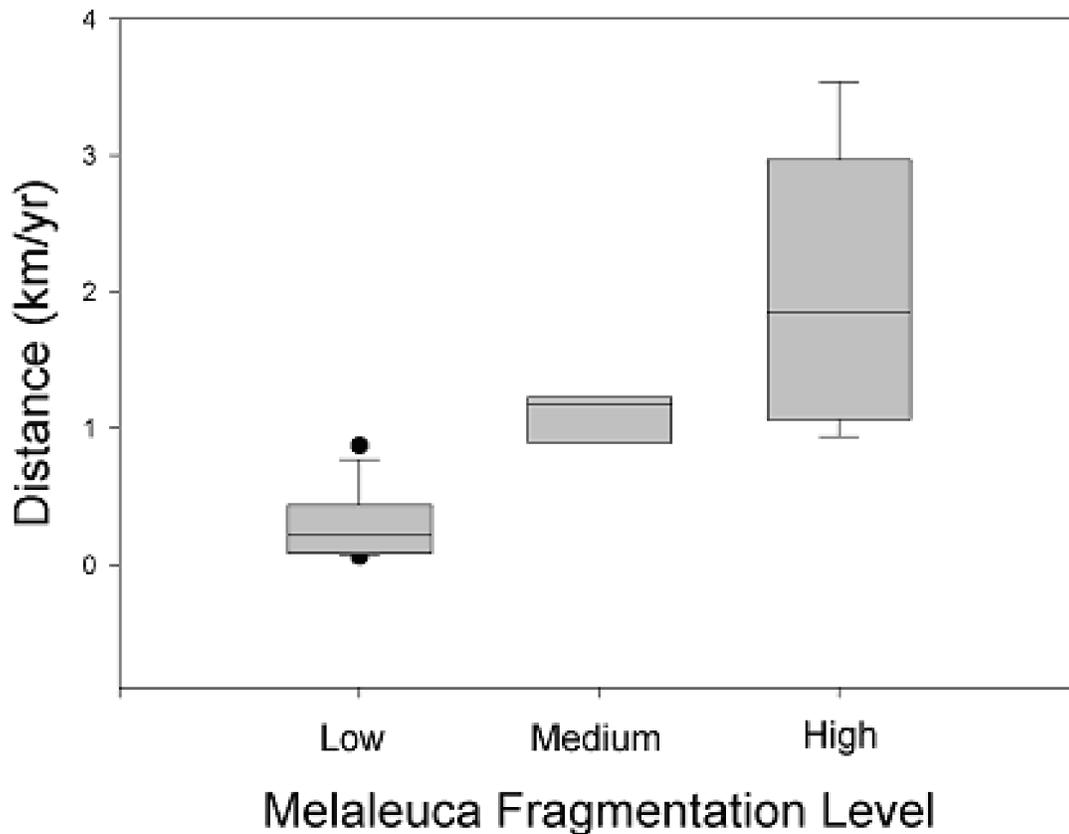


Figure 2. The rate of spread for the weed biological control agent *O. vitiosa* as related to the fragmentation of its host plant *M. quinquenervia*. Fragmentation categories were: dense continuous stands with breaks <30m (low fragmentation), moderate fragmentation with isolated stands separated by breaks of 31-100 m, and highly fragmented stands separated by more than 100 m.

Modeling the Spread of *Oxyops vitiosa*. It has now been 5 years since the initial release of *O. vitiosa* and we estimate (using a high level of fragmentation) that the weevils occupy 635 ha at an economic threshold of 0.5 weevil/branch tip, and 8418 ha at a detectable level of 1 beetle/1,000 tips (Table 2). When modeled under the highest melaleuca fragmentation level, the simulation predicts economically effective populations in Broward, Dade, Lee, and Palm Beach counties. At the medium and low fragmentation levels, only Broward County is predicted to have economic levels of weevils. All but five counties in the melaleuca-infested area are predicted to have detectable populations of *O. vitiosa* regardless of the fragmentation level (Table 2).

Based on field observations it appears that, at this stage, current regional distributions of *O. vitiosa* are best described by the model with high melaleuca fragmentation. At this fragmentation level, and assuming no additional redistribution is performed, the model predicts a total of 138 months (June 2008) until 50% of the habitat currently invaded by melaleuca is infested with an economic density of weevils. At medium and low fragmentations, the model predicts 182 (February 2012) and 191 (November 2012) months, respectively. Considering the varying densities of melaleuca found in south Florida and the constant encroachment by development into melaleuca invaded natural areas, the high fragmentation model is probably a good representation of the landscape overall.

Like many slowly dispersing biological control agents, these data suggest that redistribution efforts may greatly expedite the saturation of *O. vitiosa* throughout in the current melaleuca distribution. Examining the output from the basic model at medium fragmentation (Fig. 3), we identified 16 possible redistribution sites that may accelerate the landscape level spread of the weevil, numbered in order of effectiveness (Fig. 4). Re-running the model at a conservative, medium fragmentation level with each of the additional sites represented in turn, we found that the effect on the model was small: the time to fill 50% of the habitat was reduced by only 0 to 4 months depending on location. Redistributing 5,000 individuals each to all new release points had more of an effect: 23 months were saved, so that 50% of the habitat was infested with an economic density of weevils by 159 months (March 2010). Capturing 80,000 weevils and releasing them at the 16 sites should not require more than 100 days of effort (Pratt, unpublished data), so even at this stage in the introduction effort, the improvement in distribution for such little effort would be substantial.

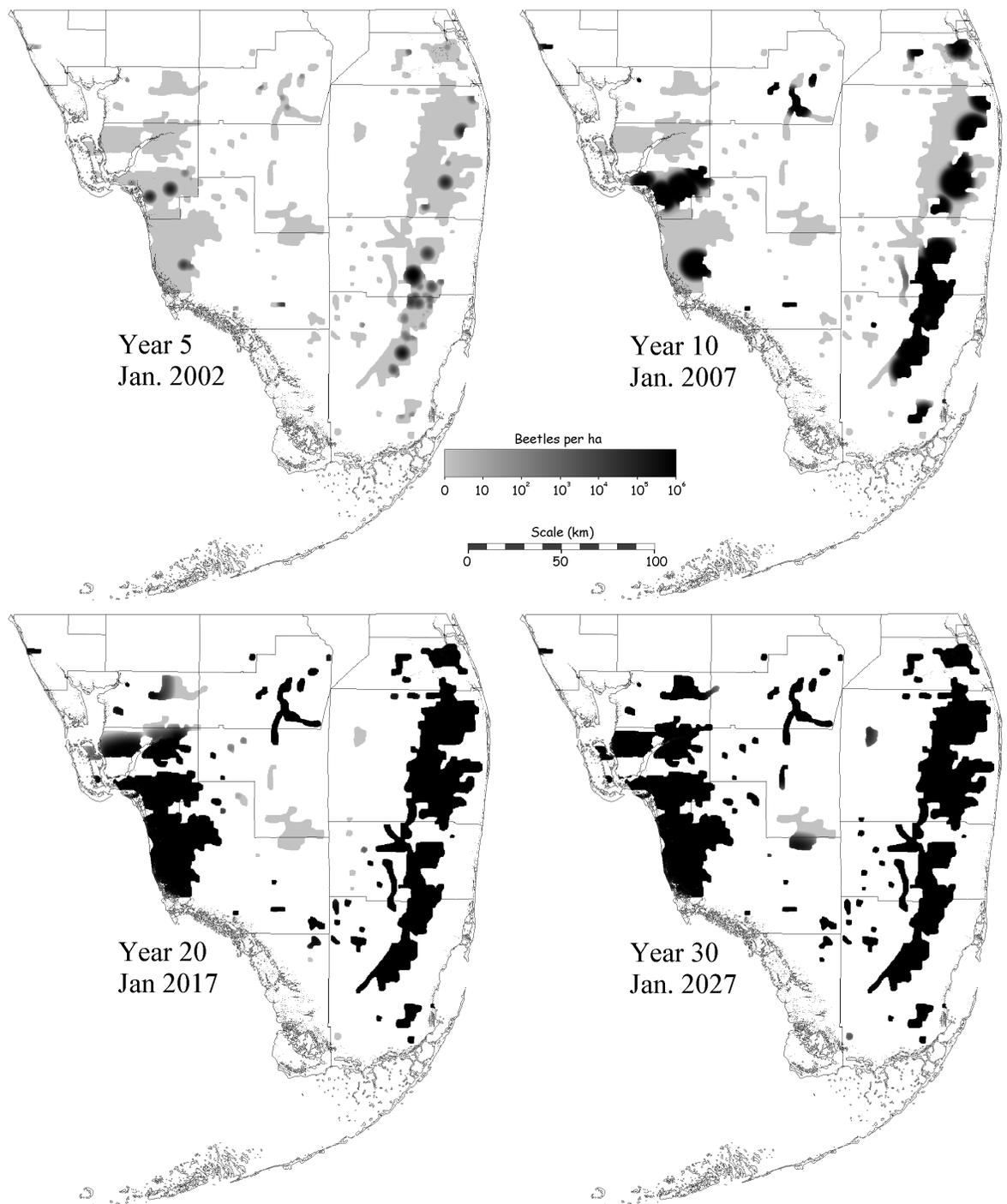


Figure 3. Predicted dispersal of *O. vitiosa* through habitats invaded by *M. quinquenervia* occurring at medium levels of fragmentation.

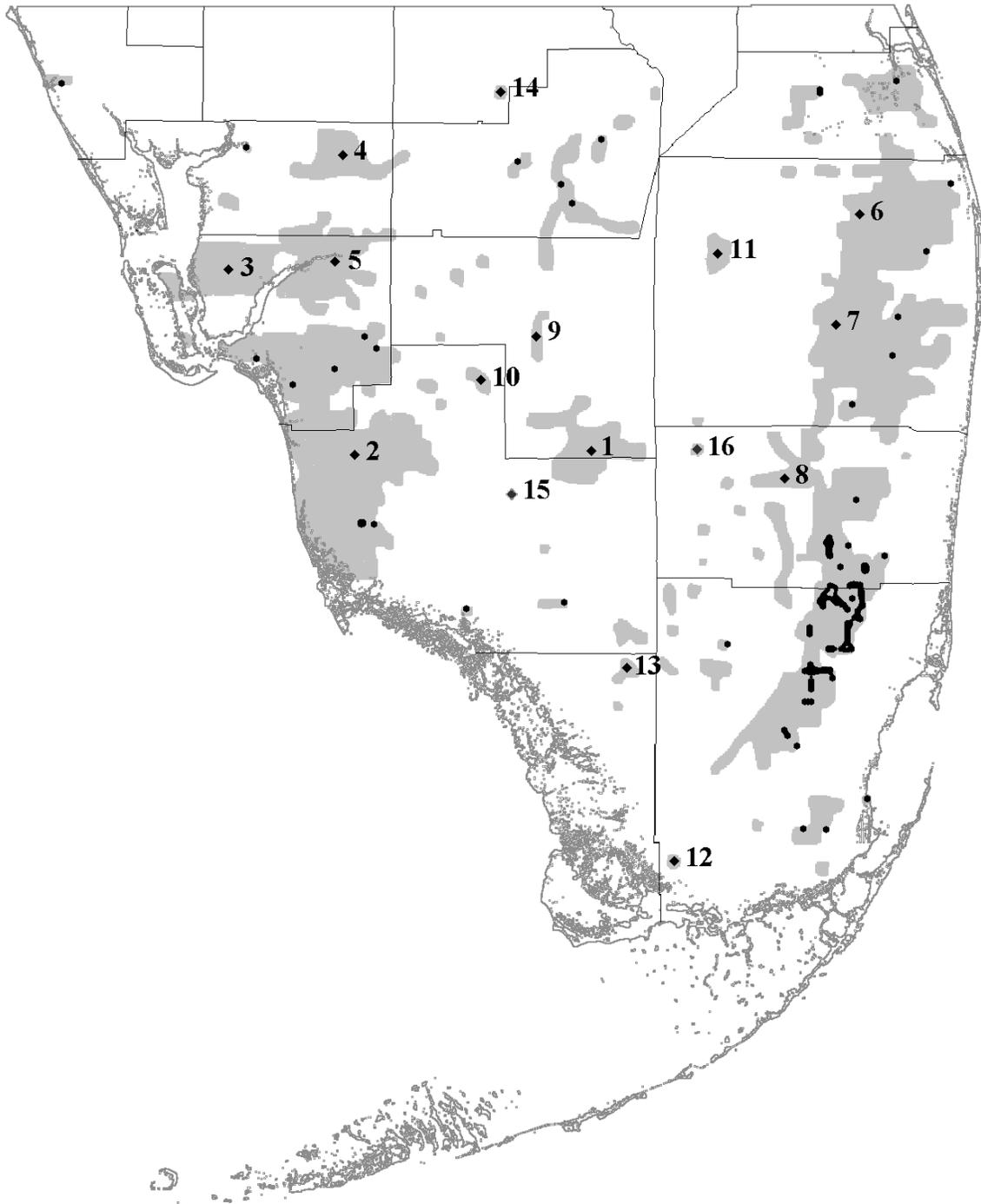


Figure 4. Existing release and redistribution sites (circles), and proposed redistribution sites (diamonds) numbered in order of their respective influence on the rate at which *O. vitiosa* occupied 50% of the melaleuca invaded habitat at an economic density (0.5 weevils per branch tip).

Results of the sensitivity analysis. Of the four variables, the *O. vitiosa* growth parameter r was found to be the most sensitive to change, with nearly a 1:1 correspondence between the parameter change and the time for the beetle to cover 50% of the melaleuca habitat at economic levels (Fig. 5). The K parameter showed moderate sensitivity when reduced and low sensitivity when increased. The two dispersal distances were not sensitive to the levels of change used in the analysis. These findings suggest that the model's precision is primarily dependent on an accurate assessment of the weevil's intrinsic rate of population increase. This parameter (r) is typically calculated from fecundity bioassays conducted under controlled environmental conditions (Carey 1993). However, the extrapolation of laboratory-based data to the field may be limited when considering the stochasticity of natural systems, which continuously vary. Therefore, a laboratory-based estimate of r may not describe the actual rates of increase in heterogeneous (realistic) environments. In contrast, the population growth estimate used in this model was quantified under field conditions (Pratt et al. 2002), thereby incorporating variation in resource quality, environmental conditions, predation, as well as other factors into the parameter estimate.

From primarily retrospective studies, an increasing body of literature supports the contention that certain life history characteristics are related to the intrinsic potential of both intended and unintended invaders to establish and impact an adventive ecosystem (Goeden 1983; Sands 1986; Crawley 1989; Waage 1990; Harris 1991; Marohasy 1997). One commonly cited characteristic of successfully introduced species (including invasive plants) is a high rate of spread or diffusion throughout the adventive range (Schooler 1998; Shigesada and Kawasaki 1997; Sakai et al. 2001). However, the successful establishment of *O. vitiosa* is not attributed to this trait and conversely, the relatively slow rate of movement by *O. vitiosa* results in a concentration of herbivory, causing high levels of localized plant damage (Center et al. 2000). Additional evidence suggests that when considering both the simplicity of collecting and redistributing field-reared populations and the potential of mass-rearing *O. vitiosa* on artificial diets (Wheeler 2001), human mediated spread may compensate (or overcompensate) for the weevil's limited dispersive abilities.

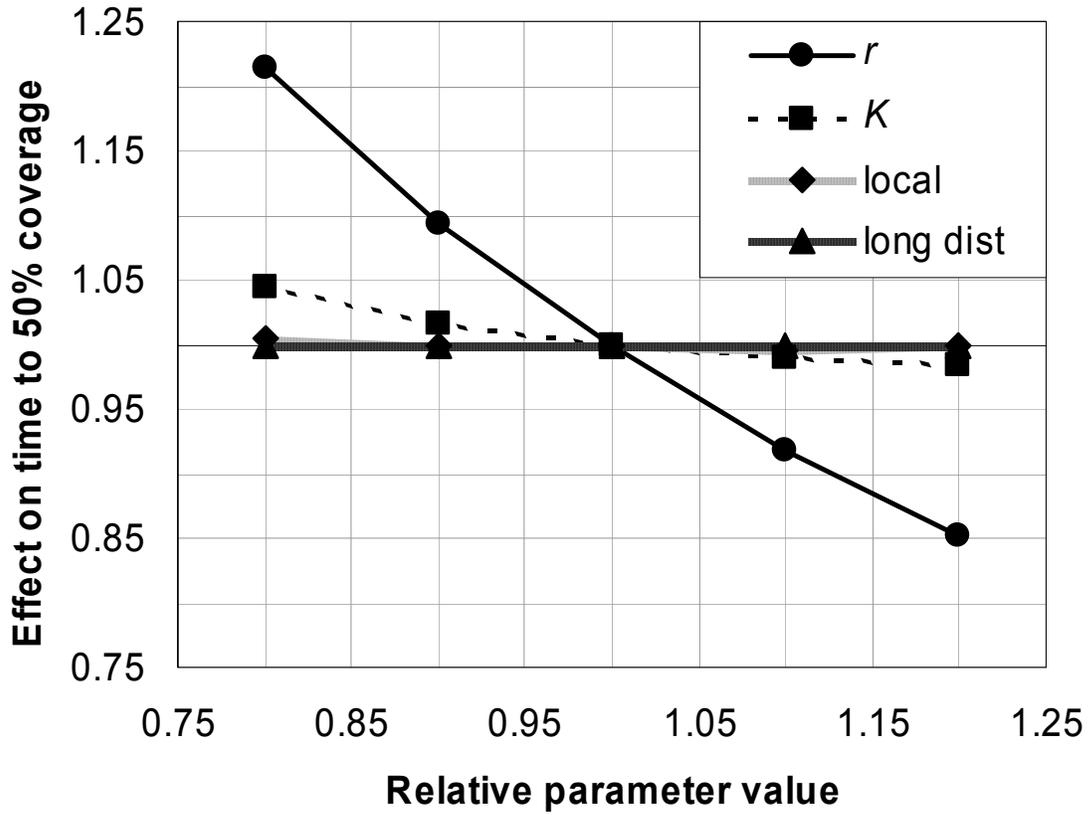


Figure 5. Results of sensitivity analysis for *r*, *K*, local dispersal distance and long range dispersal distance at various levels of model default values at a medium melaleuca fragmentation

Although classical weed biological control has been described as the most ecologically benign method of controlling invasive, exotic plants (McEvoy and Coombs 1999) the effectiveness of this tactic has rarely been quantified experimentally (McFadyen 1998). This paper is one in a series of articles in which we quantify the impacts of *O. vitiosa* as a function of the agent's geographic range, abundance per unit area and suppressive effect per individual on melaleuca in south Florida (Center et al. 2000; Pratt et al. 2002; Pratt et al. 2003). Herein we report the current distribution of *O. vitiosa* and formulate predictions for the geographic distribution of *O. vitiosa* at future points in time. In addition, the simulation model provides estimates of economic and detectable population densities at these time steps. Current studies are aimed at evaluating the influence of herbivory by *O. vitiosa* on reproduction, growth and survivorship of the target weed. The product of these three factors, geographic range, abundance per unit area, and effect per individual, will provide an overall measurement of impact by *O. vitiosa* on the invasive tree *M. quinquenervia* (Parker et al. 1999).

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