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Craig R. Allen
U.S. Geological Survey

Ahjond S. Garmestani
South Carolina Cooperative Fish and Wildlife Research Unit

Jill A. LaBram
South Carolina Cooperative Fish and Wildlife Research Unit

Amanda E. Peck
South Carolina Cooperative Fish and Wildlife Research Unit

Luanna B. Prevost
Clemson University

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Allen, Craig R.; Garmestani, Ahjond S.; LaBram, Jill A.; Peck, Amanda E.; and Prevost, Luanna B., "When landscaping goes bad: the incipient invasion of *Mahonia bealei* in the southeastern United States" (2006). *Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications.* Paper 18.
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Biological Invasions (2006) 8: 169–176
DOI 10.1007/s10530-004-2896-4

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When landscaping goes bad: the incipient invasion of *Mahonia bealei* in the southeastern United States

Craig R. Allen[1,*], Ahjond S. Garmestani[2], Jill A. LaBram[2], Amanda E. Peck[2] & Luanna B. Prevost[3]
[1]*USGS – South Carolina Cooperative Fish and Wildlife Research Unit;* [2]*South Carolina Cooperative Fish and Wildlife Research Unit;* [3]*Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA;* [*]*Author for correspondence (e-mail: allencr@clemson.edu; fax: +1-864-656-1034)*

Received 8 July 2004; accepted in revised form 3 September 2004

Key words: horticulture, landscaping, *Mahonia bealei*, non-indigenous species, ornamentals, woodlots

Abstract

Woodlots are forest islands embedded within an urban matrix, and often represent the only natural areas remaining in suburban areas. Woodlots represent critical conservation areas for native plants, and are important habitat for wildlife in urban areas. Invasion by non-indigenous (NIS) plants can alter ecological structure and function, and may be especially severe in remnant forests where NIS propagule pressure is high. Woody shrubs in the Family Berberidaceae have been well documented as invaders of the forest–urban matrix in North America. *Mahonia bealei* (Berberidaceae) is a clonal shrub native to China, and is a popular ornamental in the Southeastern United States. *Mahoni bealei* is listed as "present" on some local and state floras, but almost nothing is known regarding its invasion potential in the United States. We sampled 15 woodlots in Clemson, South Carolina, to assess the invasion of *M. bealei* and other woody non-indigenous species (NIS). *M. bealei* invaded 87% of the woodlots surveyed and species richness of NIS on these woodlots varied from 5 to 14. Stepwise-multiple regression indicated that less canopy cover and older *M. bealei* predicted greater abundance of *M. bealei*, and that not all subdivisions were equally invaded ($P < 0.0001$; $r^2 = 0.88$). The impact of *M. bealei* on native flora and fauna may be considerable, and it is likely to continue to spread in the Southeastern United States. *M. bealei* should be recognized as an aggressive invader in the Southeastern United States, with the potential for negative impacts on native flora and fauna.

Introduction

Invasion by non-indigenous (NIS) plants can alter ecological structure and function, and is one of the primary threats to rare and endangered species (Gordon 1998). The majority of woody invasive plants in the United States were introduced for horticultural purposes, including landscaping (Reichard and White 2001). Many NIS plants were introduced into the United States as ornamentals (e.g., Chinese privet, *Ligustrum sinense*; Japanese honeysuckle, *Lonicera japonica*; Nandina, *Nandina domestica*). *L. sinense* has been characterized as an aggressive invader in the southeastern USA, with the ability to reduce growth of native species (Merriam and Feil 2002). *Lonicera japonica* is tolerant of shade and can overwhelm forest edges once established (Robertson et al. 1994).

The southern Piedmont region of the United States, 161,430 km^2 between the Appalachian Mountains and the Coastal Plain, extends from

Virginia in the northeast to east-central Alabama in the southwest. Regional population growth has contributed to the conversion of rural, forested or agricultural land-uses and land-covers to urban and suburban uses in many areas. The southern Piedmont is expected to experience a greater loss of forested land than other regions of the south (Wear and Greis 2001). High rates of forest fragmentation are expected to increase, as human population growth accelerates in urban, suburban and rural communities (Wear and Greis 2001). As human population growth and developmental sprawl continue in this region, concomitant changes in ecosystem integrity and the production of ecological goods and services can be expected, including losses in water availability and quality, loss of native habitats, loss of biological diversity, and conversion of forest land to non-natural states. As the southern Piedmont further fragments and suburbanizes, remnant woodlots may become increasingly important in maintaining the integrity and resilience of the linked human-ecological system.

Woodlots are characterized as forest islands within an urban matrix, and often represent the only semi-natural areas remaining in suburban areas (Levenson 1981; Boutin and Jobin 1998). Forest "islands" and fragments may be more easily invaded than continuous forests (Fine 2002). However, empirical evidence for island invasibility is mixed (Lonsdale 1999). Woodlots can have twice as many native plant species as old fields, wooded fencerows, ditches, and hay fields (Freemark et al. 2002). A small patch of forest (4 ha) may be sufficient to sustain native, forest-interior plants (Usher 1987). Therefore, woodlots represent critical conservation areas for native plants (Boutin and Jobin 1998). Additionally, woodlots represent important habitat for wildlife in urban areas (Matthiae and Stearns 1981). Understanding the role of NIS plants in woodlots is especially important, as they may have a greater impact on remnant woodlots in urbanized areas (Miller and Hobbs 2002) than in more extensive patches.

Woody shrubs in the Family Berberidaceae (Barberry family) have been well documented as invaders of the forest–urban matrix in North America (Ehrenfeld 1997, 1999; Silander and Klepeis 1999). Invasion by woody shrubs may create a shift in forest under- and mid-story composition, which in turn may alter primary production, nutrient cycling, and carbon storage (Jackson et al. 2002). *Mahonia bealei* (Berberidaceae) is a clonal shrub native to China. It is a popular ornamental because of its bright yellow, slightly fragrant flowers that appear in late winter or spring and its dark blue berries that remain through the summer. *M. bealei* can grow to 4 m tall (Basinger 2001). The leaves are pinnately compound with 9–15 spiny leaflets, giving the plant a width of approximately 1–2.5 m. *M. bealei* is recommended as a wildlife attractant by several resource management agencies in the southeastern United States, yet the Southeast Exotic Pest Plant Council (www.se-eppc.org) lists it as a rank 2 (significant threat) NIS plant. Plants of this rank possess characteristics of an invasive species but are not currently considered to spread easily into native plant communities. *M. bealei* is listed as present on several local or state floras (Basinger 2001; Bowen et al. 2002; Leidolf et al. 2002) and is readily available at nurseries, but almost nothing is known regarding its invasion potential in the United States. A closely related congener, *Mahonia aquifolium*, is recognized as an aggressive invader in central Europe (Auge and Brandl 1997).

Here we: (1) document the presence of *M. bealei* and NIS, (2) assess the abundance and structure of invasive *M. bealei* populations, and (3) determine predictors of *M. bealei* abundance and overall NIS richness in southern Piedmont woodlots.

Materials and methods

We randomly selected five woodlots in each of three suburban subdivisions in the city limits of Clemson, South Carolina, USA. Between January and April, 2003, we collected information on the invasion of *M. bealei* and other woody NIS on these 15 replicates. For each replicate we recorded the adjacent land use (house, road, or undeveloped) surrounding the lot in the four cardinal directions, the age of the oldest and newest adjacent houses, size of the woodlot (ha), slope, aspect, species richness of NIS, and percent cover of *M. bealei* and English ivy (*Hedera helix*). Lot

size was determined from GIS coverage of ownership parcels, and land use was determined by observation. Adjacent land use was quantified categorically, by assigning a house or road a value of one and native woodlands a 0, and values were totaled for each site, with the highest land use value equal to four. We also documented the number and age (by counting internodes) of genets of all *M. bealei*, as well as presence or absence of flowers, by noting persistent rachides of the inflorescence. Counting internodes clearly assessed age for plants <7 years of age and for recent growth (up to 7 years) on older plants, based on the observation of growth of specimens over several years and the frequent persistence of rachides of not only the current year but also previous years. Estimates of age for plants >7 years of age were less certain, and our age estimates are conservative for older specimens.

Within each replicate we established two 78.5-m^2 circular plots at the end of two 15-m transects diagonally opposite from each other at opposite corners of a lot. In each plot, all native and NIS woody species were identified, and percent coverage of dominant native and NIS species was documented in the ground (<1.5 m height), midstory (1.5–6 m) and canopy (>6 m) strata in five categories (0–20, 21–40, 41–60, 61–80, and 81–100%). For vertical structure, we used a 2.5-m vertical structure board to record the percent of the five sections of the board covered (same 5 categories) at 0.5 m intervals, observed at a distance of 15 m from the cardinal directions (Nudds 1977). Percent canopy cover was determined using a densiometer. Structure and cover at the two plots were averaged to get a total for each site.

We used PROC REG to develop two separate stepwise multiple regression models in SAS (SAS Institute 2000) to determine if any of the habitat characteristics predicted *M. bealei* abundance and NIS richness. The independent variables used to predict abundance of *M. bealei* were size of woodlot, oldest adjacent house, subdivision, slope, NIS richness, canopy cover, vertical structure, non-native ground cover, percent *H. helix* cover, and age of oldest *M. bealei*. The independent variables used in the model to predict NIS richness were size of woodlot, oldest adjacent house, slope, abundance of *M. bealei*, canopy cover, vertical structure, percent *H. helix* cover, and age of oldest *M. bealei*. Assumptions of equal variance and normality were tested with a Levene median test and a Kolmogorov–Smirnov distance equation, respectively. *Mahonia* abundance was not normally distributed, and we used a square root transformation to normalize the data.

Results

Our 15 sites, and the subdivisions in which they were embedded, were typical of older subdivisions in the southern Piedmont. Tree cover was high, even outside remnant woodlots. Woodlots varied in area from 0.05 to 0.36 ha (Table 1). All woodlots were invaded to some degree by NIS. *L. sinense* occurred on all sites. *H. helix* and *L. japonica* occurred on 14 sites, while *N. domestica* and *M. bealei* occurred on 13 sites (Table 2). Species richness of NIS varied from 5 to 14.

The *M. bealei* abundance at a site ranged from 0 (2 sites) to 291, with a mean of 47 and a median of 14. The oldest individual was at least 15 years of age. In one subdivision, *M. bealei* was present in all 5 woodlots and abundance ranged from 43 to 291. These sites had more *M. bealei* than 9 of the 10 remaining sites. Conversely, in another subdivision, only 3 of the sites contained *M. bealei* and the abundance was much lower (≤8; Table 1). *M. bealei* individuals were not restricted to the edge of woodlots, and were found up to 61 m from an edge. The independent variables "oldest adjacent house" and "percent *H. helix*" were removed to reduce multi-collinearity. A significant three variable model was determined ($P < 0.0001$; $r^2 = 0.88$). Significant predictor variables were "subdivision C" ($P = 0.0094$) "age of oldest *M. bealei*" ($P = 0.0007$; Figure 1) and "canopy cover" ($P = 0.0179$; Figure 2) on a particular woodlot. Less canopy cover and older *M. bealei* predicted greater abundance, with a greater number of *M. bealei* in the younger age classes (Table 3).

The earliest evidence of flowering in *M. bealei* occurred at age two (2%). By age five 60% of individuals flowered (Figure 3). The population structure on our sites suggests rapid population

Table 1. Results from 15 replicate suburban woodlots sampled between January and April, 2003 in Clemson, South Carolina.

Plot	Sub-division	Size of woodlot (hectares)	*M. bealei* abundance (# of genets)	Age of oldest *M. bealei* (years)	# NIS	% cover ivy	canopy cover (%)	Age of oldest adjacent house	Age of newest adjacent house	Slope (°)
1	A	0.219	23	10	13	55	96	52	11	15
2	A	0.129	14	10	13	70	94	55	35	3
3	A	0.357	4	10	12	3	95	50	24	23
4	A	0.244	54	15	12	65	96	50	24	12
5	A	0.076	6	9	10	90	95	39	26	20
6	B	0.166	8	9	5	0	95	28	21	5
7	B	0.184	0	0	10	7	92	53	43	7
8	B	0.114	4	8	7	30	93	33	27	15
9	B	0.155	2	5	7	3	87	23	14	1
10	B	0.170	0	0	8	2	85	24	17	3
11	C	0.180	64	12	10	20	92	36	17	15
12	C	0.125	291	12	9	100	85	34	13	5
13	C	0.047	43	7	10	30	91	36	4	10
14	C	0.125	84	12	14	60	94	34	21	8
15	C	0.125	108	10	11	20	91	34	21	10

On these sites information was collected on the invasion of *Mahonia bealei* and other woody non-indigenous species (NIS).

growth. An exponential growth model fit the data better ($r^2 = 0.97$) than a simple linear model ($r^2 = 0.78$).

In the model of NIS richness we removed the variable "age of the oldest *M. bealei*" to reduce multi-collinearity among variables. Overall NIS richness was best predicted by a single variable model (age of the oldest adjacent house) ($P = 0.005$; $r^2 = 0.47$) (Table 4 and Figure 4):

Table 2. Non-indigenous species present in suburban woodlots sampled in Clemson, South Carolina between January and April, 2003.

Common name	Scientific name	Number of sites present
Chinese privet	*Ligustrum sinense*	15
English ivy	*Hedera helix*	14
Japanese honeysuckle	*Lonicera japonica*	14
Mondo grass	*Ophiopogon planiscapus*	14
Leatherleaf mahonia	*Mahonia bealei*	13
Nandina	*Nandina domestica*	13
Thorny olive	*Elaeagnus pungens*	12
Japanese holly	*Ilex crenata*	11
Vinca minor	*Vinca minor*	10
Multi-flora rose	*Rosa multiflora*	9
Super dwarf mondo grass	*Ophiopogon japonicus*	8
Japanese privet	*Ligustrum japonicum*	7
Red top Photinia	*Photinia glabra*	5
Vinca major	*Vinca major*	2
Japanese acuba	*Acuba japonica*	2
Chinese holly	*Ilex cornuta*	1
Japanese pachysandra	*Pachysandra terminalis*	1

Discussion

Mahonia bealei has invaded 87% of the suburban woodlots we surveyed in the Clemson, South Carolina area. The abundance of *M. bealei* was predicted by the age of the *M. bealei* on a woodlot and canopy cover, and also varied by subdivision. All our sites are best considered closed-canopy forest (cover range 85–96%), and it appears that *M. bealei* can exploit very small light gaps and does well in very low light conditions. This suggests that *M. bealei* is not only a threat to remnant woodlots in the piedmont, but

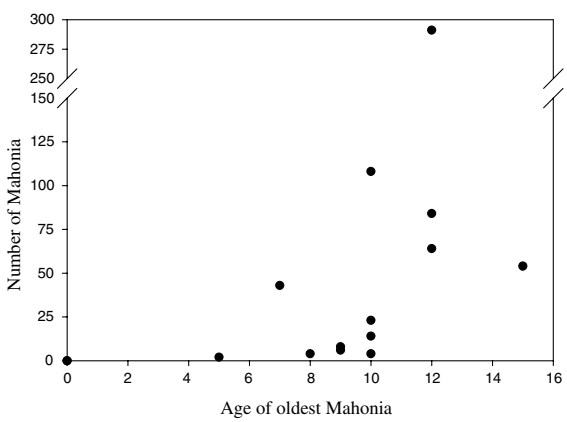

Figure 1. Relationship between the abundance of *Mahonia bealei* and age of oldest *M. bealei* on 15 remnant woodlots in the southern Piedmont of the United States.

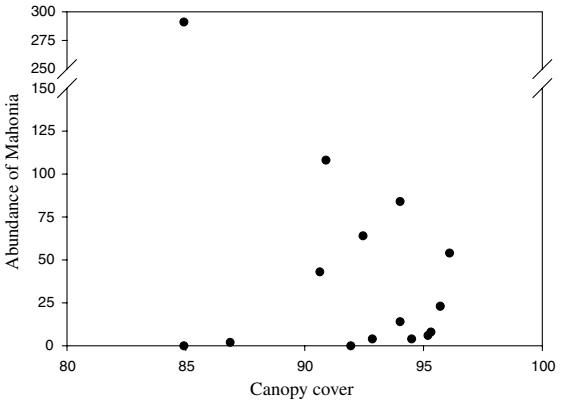

Figure 2. Relationship between the abundance of *Mahonia bealei* and canopy cover on 15 remnant woodlots in the southern Piedmont of the United States.

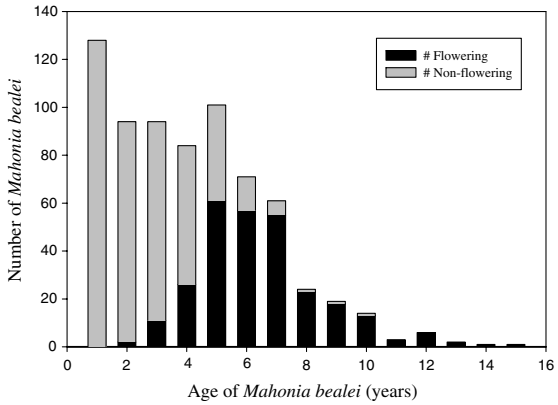

Figure 3. Population structure of *Mahonia bealei* on 15 remnant woodlots in the southern Piedmont of the United States.

to more extensive forests as well. The population structure we documented suggests that these sites have been recently invaded, and that rapid population growth of *M. bealei* can be expected.

A closely related congener of *M. bealei* is the Oregon grape (*M. aquifolium*), native to the western USA *Mahonia aquifolium* has been documented as an aggressive invader in Germany and other areas in central Europe (Auge and Brandl 1997). It is used as a host plant by herbivores and pathogens native to its new habitat (Auge et al. 1997). *M. aquifolium* has several characteristics proposed as indicators of increased success of invasion for plants: high seed production and a lack of specialist herbivores in its new habitat (Soldaat and Auge 1998), and small seed mass (Rejmanek 1996). Additionally, it has been suggested that cultivated *Mahonia* have higher reproductive potential than their wild relatives, because of the likelihood that the plants have been bred for more flowers and fruit (Soldaat and Auge 1998). The success of *M. aquifolium* in Germany suggests that *M. bealei* may become a successful, aggressive invader in North America.

Japanese barberry (*Berberis thunbergii*), a woody, clonal shrub in the same Family (Berberidaceae) as *M. bealei*, also utilizes multiple forms of vegetative and seed-based population growth (Ehrenfeld 1999). It has been characterized as one of the most widely known and planted non-indigenous shrubs in the United States (Silander and Klepeis 1999) and has been highly successful at spreading into the forest matrix and producing dense, persistent populations (Ehrenfeld 1997). As *M. bealei* plants become older, reproduction by seed and clonal ramets increases leading to increased plant density. Most *M. bealei* on our sites were at least 4 years old before reaching sexual maturity. A similar period to maturity was observed with amur honeysuckle (*Lonicera maackii*), an invasive shrub in the eastern United States and Canada (Deering and Vankat 1999).

Disturbance along with continued and widespread planting for ornamental purposes may lead to greater *M. bealei* invasion of woodlots via propagule pressure (Fine 2002). Propagule pressure can be important in determining the success of establishment and spread of invasive species (Williamson and Fitter 1996). Edge effects in

Table 3. Stepwise-multiple regression model of predictors of *Mahonia bealei* abundance.

Variable	Parameter estimate	Standard error	*F*-value	*P*-value	Partial r^2	Overall r^2
Intercept	42.822	15.785	7.36	0.0202		0.875
Subdivision C	4.096	1.304	9.87	0.0094	0.634	
Oldest *M. bealei*	0.778	0.168	21.37	0.0007	0.155	
Canopy cover	−0.496	0.178	7.72	0.0179	0.087	

Table 4. Stepwise-multiple regression model of predictors of non-indigenous species (NIS) richness.

Variable	Parameter estimate	Standard error	*F*-value	*P*-value	r^2
Intercept	3.689	1.925	3.67	0.078	0.475
Age of oldest house	0.165	0.048	11.76	0.005	

a woodlot, manifested in changes in light, temperature, and litter moisture can be detected up to 50 m into woodlots (Matlack 1993). *Mahonia repens* are known to exhibit a dramatic decrease in photosynthetic capacity in partially shaded conditions (Logan et al. 1998). However, survival of *B. thunbergii* was found to drop significantly only at very low light levels (Silander and Klepeis 1999). Our data suggest *M. bealei* can tolerate low light conditions.

We observed honeybees and ants (*Prenolepsis imparins*) visiting the flowers of *M. bealei*, with the majority of bees coated with pollen. Pollination and dispersal have been documented in related species. The pollination of the flowers of *B. thunbergii* is effected by small and large bees, Adrenids and *Bombus* spp., respectively (Martin et al. 1951; Lebuhn and Anderson 1994). Bumblebees (*Bombus* spp.) have also been documented visiting *Mahonia* spp. in the United Kingdom (Fussell and Corbet 1992). The flowers of *M. japonica*, another close relative of *M. bealei*, are utilized by blackcaps (*Sylvia atricapilla*) and blue tits (*Parus caeruleus*) in the United Kingdom (Harrup 1998).

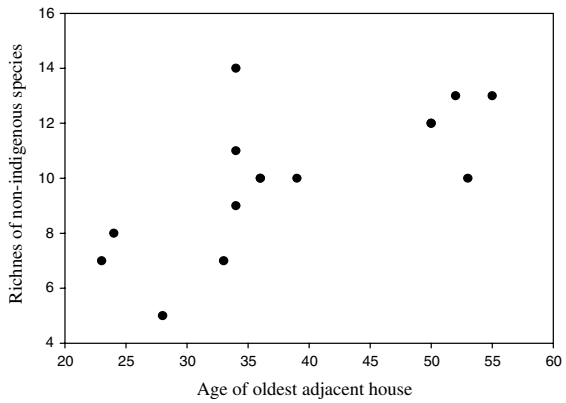

Figure 4. Relationship between species richness of woody non-indigenous species on 15 remnant woodlots in the southern Piedmont of the United States and age of the oldest adjacent home.

For *M. aquifolium*, dispersal by vertebrates has been identified as a necessity for the colonization of new sites, and to buffer against the mortality of seedlings beneath the canopy of adults (Soldaat and Auge 1998). A congener of *M. bealei, M. repens,* is spread by black bears (*Ursus americanus*) in the western USA (Auger et al. 2002). Bears can transport huge numbers of seeds for dispersal, and one male is known to have defecated approximately 60,000 *M. repens* seeds within 24 h (Auger et al. 2002). It is estimated that those seeds accounted for 10,000 individual *M. repens* fruits. Bears also may be effective long distance dispersers of *Mahonia*, and their digestive tracts may have a role in accelerating germination times (Auger et al. 2002). The berries of *B. thunbergii* are eaten infrequently by most songbirds (Martin et al. 1951; Lebuhn and Anderson 1994). Other western *Berberis* species are dispersed by white-tailed and mule deer (Martin et al. 1951). Wild turkeys and grouse are also known to utilize the berries (Ehrenfeld 1997). Although we have no direct evidence, we assume that warblers and many other passerines in the eastern United States could pollinate *M. bealei* and disperse the fruits produced by the shrubs. Dispersal by vertebrates with their potential for long distance movements increases the probability of invasion by *M. bealei* into native forests.

Little is known about the effects of urbanization on ecosystems, communities, species, and populations (Cairns 1988). Woodlots can be areas of high plant diversity (Freemark et al. 2002) and supply habitat for birds in urban areas (Savard et al. 2000). With increases in the wildland–urban interface and forest fragmentation, "forest island" suburban woodlots may serve as refuges for native plants (Honnay et al. 1999) and animals in urbanized areas. When NIS invade these areas, ecological structure and function may be modified. The spread of *M. bealei* may shade areas beneath the plant, and prevent the growth of native mid-story species, such as flowering dogwood (*Cornus florida*). This growth habit is common to other members of the barberry family such as *B. thunbergii* and *M. aquifolium*. We documented invasion by a

variety of species on woodlots, but the interactions among these species are not clear (Simberloff and Von Holle 1999).

The spread of *M. bealei* should be studied at the regional as well as local scale to document its current distribution and potential for spread. We have observed *M. bealei* in more extensive woodlands outside of suburban areas in western South Carolina. It is important to understand the population dynamics of this plant while in the early stages of invasion. Invasive species often undergo a lag phase during which spread is often localized (Hobbs and Humphries 1995). With the reproductive pattern of *M. bealei*, once maturity is reached by colonizers and their progeny, the growth of each population and potential for spread increases exponentially (Auge and Brandl 1997).

Additional collaborative efforts are needed to reduce horticulture as a pathway of invasive plant introduction and spread. Gardening is a top hobby in the United States and the public needs to be educated about the impact of invasive species (Reichard and White 2001). *M. bealei* are readily available from nurseries and other retail establishments in the Clemson, South Carolina area. Further, the shrub is presented to the public as an excellent species for attracting birds to suburban yards in the winter by horticulturalists (Ellis 1995; Miller 2002; Pfeiffer 2002), and by state agencies (Black 1999; Gilman 1999). The impact on native flora and fauna could be considerable with the continued spread of *M. bealei* in the southeastern United States. *M. bealei* should be recognized as an aggressive invader with the potential to negatively impact native flora and fauna in the southeastern United States.

Acknowledgements

The South Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement among the United States Geological Survey/Biological Resources Division, South Carolina Department of Natural Resources, Clemson University, and the Wildlife Management Institute. We would like to thank J. Walker and H. Auge for helpful suggestions, P. McMillan for plant identification, J. Zettler for ant identification, private landowners for access to woodlots, and the Clemson Land Planning office for maps and GIS coverage of the area. This manuscript was improved by helpful comments from K. Manry and three anonymous reviewers.

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