

## Research Article

## Effects of removing exotic invasive species from the ecotones of two granite rock outcrops in the southeastern Piedmont of the United States

Melissa Caspary<sup>1\*</sup> and James Affolter<sup>2</sup>

<sup>1</sup> School of Science and Technology, Georgia Gwinnett College, 1000 University Center Lane, Lawrenceville, GA 30043, USA

<sup>2</sup> Department of Horticulture, University of Georgia and the State Botanical Garden of Georgia, 2450 S. Milledge Avenue, Athens, Georgia 30605, USA

E-mail: [mcaspary@ggc.edu](mailto:mcaspary@ggc.edu) (MC), [affolter@uga.edu](mailto:affolter@uga.edu) (JA)

\*Corresponding author

Received: 8 May 2013 / Accepted: 17 September 2013 / Published online: 25 September 2013

Handling editor: Vadim Panov

### Abstract

Piedmont granite rock outcrops in the southeastern United States support a plant community rich in endemic and rare plant species. The ecotones of the granite outcrop and Piedmont oak hickory forest communities are under increasing pressure from exotic invasion and the potential impacts of this invasion on the native plants in these communities are unclear. We conducted an experimental removal of invasive plant species at the ecotone of two granite rock outcrops and monitored species richness and plant occurrence along random belt transects in invaded, uninvaded, and removal plots for three years. These transects captured a representative sample of the plant community from the rock edge 20 m into the forest interior. Hemispherical photographs and soil samples were used to monitor changes in light availability and soil nutrients. Vegetation classes demonstrated spatial distribution patterns related to proximity to rock edge and depth of soil, but removal of invasive species had no apparent effect on percent cover or native plant richness. Sodium, calcium, and magnesium were all found to be significant predictors of invasive species occurrence and sodium and calcium were correlated with soil depth. This research effort suggests that the occurrence of invasive species are not significantly impacting overall species richness in the ecotone of outcrop plant communities, however changes to the species richness of this plant community in response to invasive species removal may take longer to detect.

**Key words:** ecotone; endemic species; invasive species; invasion; granite outcrop; management; species richness

### Introduction

In the southeastern United States, outcrops of bare rock exist in the midst of oak-hickory forests. The insular nature of these exposures encourages allopatric speciation, which has contributed to endemism and rarity in the outcrop flora and resulted in a unique assemblage of plant species (Wyatt and Allison 2000). Most of this granite rock outcrop habitat lies in the Piedmont of Georgia, with the majority of outcrops occurring just outside the Atlanta metropolitan area. The predominant threat to these exposures has been quarrying, but they are also impacted by exotic species invasion, cattle grazing and eutrophication, dumping, quarry dust deposition, fire, vandalism, foot traffic, and off-road vehicles. Growth of the Atlanta metropolitan area is increasing anthro-

pogenic disturbance on these rock exposures and creating new opportunities for invasion of surrounding habitats by exotic species.

This research was undertaken to better understand the extent to which invasive species have altered plant community structure on rock outcrop ecotones of the southeastern Piedmont and how species richness has been affected. Here, all references to “invasive species” or “exotic invasion” etc. are specific to invasive plant species. The insular nature of the rock outcrop habitat coupled with a relatively high proportion of narrow endemic species makes this community vulnerable to rapid colonization by invasive opportunists, which could ultimately lead to extirpation of native species. In Western Australia, weeds threaten the diversity of granite outcrop communities (Pigott 2000). Wyatt (1997)

predicted that the open nature and low competition in outcrop habitats present an opportunity for invasion by weedy species. Harrison et al. (2006) explored invasion on serpentine barrens, systems with soils derived from ultramafic rock that have low calcium to magnesium ratios and are generally understood to be nutrient poor and high in heavy metals. These systems are particularly rich in endemic plant species but they found that invaded areas had a low occurrence of endemic and rare forbs.

The frequency and impact of colonization by invasive species in the edge communities of many southeastern U.S. rock exposures is extensive. In a survey of 52 outcrops from Alabama through Georgia and into South Carolina, Caspary and Rickard (2007) reported that 39 were impacted by invasive species. *Ligustrum sinense* Lour. and *Lonicera japonica* Thunb. appear to be the most dominant colonizers of rock outcrop margins and are known to crowd out native understory plants (Oosting and Livingstone 1964; Wharton 1978; Wyatt and Allison 2000). A number of studies in southeastern Piedmont forests have documented that the presence of *Ligustrum sinense* resulted in decreased species richness and abundance (Kittell 2001; Wilcox and Beck 2007). Baskin and Baskin (1988) determined that granite outcrop endemics are not shade tolerant, so a change in canopy cover could trigger a change in species community composition. In Australian outcrops, invasion results in resource competition, prevention of recruitment of endemic species, and altered fire regimes (Csurhes and Edwards 1998), and can also reduce the amount of light reaching the forest floor. Moreover, competition from invading species for resources can transform the spatial distributions of individual species in the ecotone (Connell 1972; Vilà and Ibanez 2011).

Interspecific competition is believed to play a major role in structuring communities (Connell 1983; Blank 2010; Mangla et al. 2011). Research documenting interspecific competition on rock outcrops has identified soil depth, soil moisture, and biotic competition as significant factors influencing the population dynamics of endemics (Houlé 1990; Sharitz and McCormick 1973). Competition and shading have been identified in previous studies as the main limiting factors in southeastern United States outcrop vegetation (Baskin and Baskin 1988). Here we hypothesize that if the species composition of the ecotone community changes, those alterations will carry through to the rest of the rock outcrop community. Baskin and Baskin (1988) urged study of the

interaction between aggressive weeds and rock outcrop endemics. While invasive species have been inventoried as part of a number of outcrop surveys and studies (Oosting and Livingstone 1964; Wharton 1978; Wyatt and Allison 2000), no research to date has focused specifically on the problem of invasion in Southeastern granite rock outcrops by invasive species.

Disturbance can promote the establishment of invasive species (Mack and D'Antonio 1998; Mawson 2000; Grime 2001). It can initiate a change in resource availability by exposing bare soil and freeing bound nutrients, which creates an opportunity for invasive species to enter a system (Davis et al. 2000; Hobbs 1989). Williamson and Harrison (2002) found disturbance and seed supply to be equally important in promoting the spread of invasion in the serpentine soils of California. Invasive species have been known to alter disturbance regimes (Hobbs and Huenneke 1992). Outcrops in Western Australia have become vulnerable to opportunistic invasions as a result of fertilizer drift and disturbance from fire and recreational activities (Porembski 2000). From previous studies, we know that invasion of the ecotone can affect the structure and composition of the bordering communities (Hoffman et al. 2004; Yager et al. 2011). In the case of rock outcrops in the Southeast USA, increasing anthropogenic disturbance appears to be impacting habitat through physical disturbance of quarrying, horse, cattle, all-terrain vehicle and foot traffic, increased nutrient inputs from waste and runoff, and introduction of exotic invasive species (Patrick 1997). This physical and chemical disturbance is both negatively impacting native species and facilitating invasion (Caspary and Rickard 2007).

Rock outcrop communities are ideal habitats in which to study edge effects and spatial trends because the transition from the forest edge to the rock surface is so abrupt. It is not clear whether ecotone habitats moderate or facilitate disturbance. To address this question, we surveyed the vegetation along the ecotone of rock outcrop habitats where active invasion is occurring by *Ligustrum sinense*, *Lonicera japonica*, *Elaeagnus umbellata* Thunb., *Microstegium vimineum* (Trin.) A. Camus, *Lespedeza cuneata* (Dum. Cours.) G. Don, *Nandina domestica* Thunb., *Rosa multiflora* Thunb., and *Lonicera maackii* (Rupr.) Herder. We studied the effects of removing invasive flora on species richness and percent cover of native vascular and non-vascular flora, and site openness, by comparing invaded, uninvaded, and removal treatments in the ecotones of two

granite outcrops. We expected that the removal treatment would lead to increased species richness for forbs/ferns/fern allies, grasses, and woody plants. We analyzed soil nutrients in the soil to see if we could detect any spatial trends between cation levels and vegetation class occurrence or species richness. We predicted that removing the invasive layer would free resources for native flora, resulting in increased occurrence of outcrop vegetation classes composed of native species.

## Methods

### Study sites

Panola Mountain, a 370-hectare Georgia Department of Natural Resources State Conservation Park, is located in Rockdale County, Georgia (33°14'32" N, 85°08'49"W, ca. 10.5 km from Lithonia, Georgia). Panola Mountain is a monadnock that rises 55 m above the surrounding landscape. The vegetation surveys were performed in an adjacent area of rolling flatrocks with a much less pronounced slope. The park is underlain by Panola Granite, a non-porphyrritic igneous rock (USGS 2000). Ashlar sandy loam, Pacolet sandy loam, and Ashlar-Pacolet-Wedowee complex soils characterize the forest community surrounding the rock (USDA 2006a). Mean daily maximum and minimum temperatures were 23.8°C and 10.9°C for 2006, 24.1°C and 11.1°C for 2007, and 23°C and 10.4°C for 2008 at the Jonesboro Weather Station (located ca. 17 km southwest of Panola Mountain). Total rainfall measurements for 2006, 2007, and 2008 were 1.100 m, 0.770 m, and 0.980 m, respectively.

Rock and Shoals, jointly owned by the Georgia Department of Natural Resources and Athens-Clarke County, is located in Clarke County, Georgia (33°32'35" N, 82°15'13" W, ca. 8 km from Athens, Georgia). Rock and Shoals is a glade flatrock, with *Ligustrum sinense*, *Elaeagnus umbellata*, and *Lonicera japonica* invasion documented at the site by Nourse and Nourse (2004). The rock is a combination of biotite gneiss and feldspathic biotite gneiss (Georgia Geological Survey 1999). Pacolet sandy clay loams with slopes varying from 0–15 % and Madison Louisa complex soils surround the rock exposure (USDA 2006b). Weather data recorded by the Watkinsville RAWS Weather Station (located ca. 3.2 km southwest of Rock and Shoals) measured mean daily maximum and minimum temperatures at 23.6°C and 10.5°C for 2006, 23.9°C and 10.9°C for 2007, and 22.6°C and 10.2°C for 2008. Total rainfall for 2006, 2007,

and 2008 was measured at 1.130 m, 0.782 m, and 0.960 m, respectively.

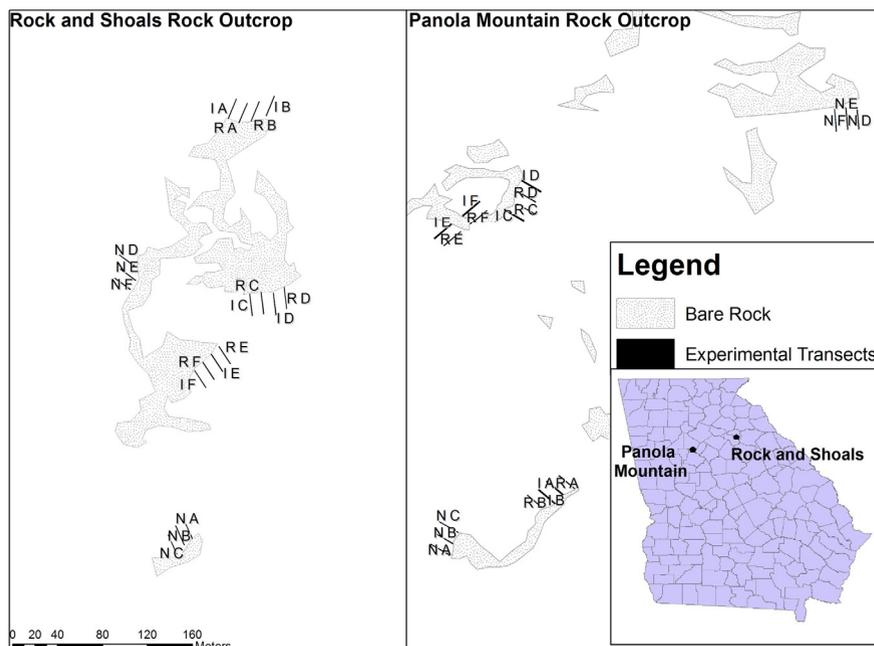
### Botanical survey

At each site, 18 random belt transects, 1 m wide by 20 m long, were surveyed in the fall of 2006 and spring of 2007 (study-year 0), the fall of 2007 and spring of 2008 (study-year 1) and fall of 2008 and spring of 2009 (study-year 2) (Figure 1). The position of the first transect was chosen at random and subsequent transects were placed at 10 m intervals along that same line perpendicular to the rock edge. These transects extended from the edge of the rock exposure into the surrounding forest. Six of the belt transects served as control transects and were located in relatively uninvaded ecotonal areas. The remaining 12 transects were located in a heavily invaded ecotone, and six of these were chosen at random to be cleared of invasive species.

When invasive species were encountered in the “uninvaded transects” these occurrences were recorded as part of the survey data. The Georgia Exotic Pest Plant Council maintains a ranked list of invasive plants and only invasive species with the highest designations (Category One and Category Two) were removed from transects (GA-EPPC 2011). The species removed include *Ligustrum sinense*, *Lonicera japonica*, *Elaeagnus umbellata*, *Microstegium vimineum*, *Lespedeza cuneata*, *Nandina domestica*, *Rosa multiflora* Thunb. and *Lonicera maackii*. Approximately 90% of the invasive cover removed was *Ligustrum sinense*, while *Lonicera japonica* comprised the majority of the remaining invasive cover.

Removal was conducted by hand pulling and cutting and painting stems with Glyphosate. Effort was made to minimize the physical disturbance caused by the removal process. Each removal transect was cleared 2 m beyond the existing transect in all directions and invasive species were regularly cleared throughout the study period. Drought and high summer temperatures kill many plants, so surveys were performed in the spring and fall of the research period. Total species richness and woody species richness were measured for plots 1, 10, and 20 of each transect during each survey session, which are 1 m, 10 m, and 20 m from the rock edge, respectively. Vegetation was classified as grasses, forbs, ferns and fern allies, invasive species, lichens, mosses, vines, and woody plants, and the occurrence of these vegetation classes was recorded in plots 1, 10, and 20. This means that vegetation was

**Figure 1.** Transect locations at Rock and Shoals Outcrop and Panola Mountain Rock Outcrop, where NA-NF represent survey areas of little invasion, IA-IF represent heavily invaded transects that were not cleared, and RA-RF represent areas of heavy invasion that were cleared and surveyed.



classified according to vascular type and habit, with the exception of the invasive species category, which were lumped all together irrespective of type and habit.

#### *Soil nutrients and depth*

Soil samples were taken at the beginning of the experimental treatments and again at the end. These samples were taken at a depth of 0–5 cm in the O horizon of plots 1, 10, and 20 of each transect at each site. In this study, we chose to focus on the cations of calcium, magnesium, potassium, and sodium because it is believed that uptake capacity is important for the acquisition of critical nutrients in nutrient poor soils (Jackson et al. 1990; Aerts 1999). Soils were analyzed for pH and for calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na) using atomic absorption. During data analysis, soil nutrient data were log transformed to help normalize data distributions. Soil depth was taken using a metal probe and averaged from three independent measurements recorded for plots 1, 6, 10, 16, and 20 in each transect at each site, which correlate with distances of 0–1 m, 5–6 m, 9–10 m, 15–16 m, and 19–20 m from the rock edge, respectively.

#### *Canopy light*

Hemispherical photography, an indirect optical technique, was used to characterize canopy openness. Hemispherical photographs were taken in plots 1, 6, 10, 16, and 20 in each transect at each site using a Nikon F 35 mm digital camera and a Nikkor 8 mm f2.9 fisheye lens. The resulting image had a 183 degree view. Site canopy typically started with a shrub layer at a distance of 2–6 m from the rock edge and progressed into full oak-hickory tree canopy at a distance of 8–12 m from the rock edge. This canopy ranged from 3–18 m and averaged 10 m at both sites. Photographs were taken at ground level with the top of the image oriented north in fall of 2006 before the removal treatment and in fall of 2008 after the removal treatment.

#### *Data analysis*

Soil depths were not normally distributed and were transformed by taking the square root of the three independent observations for each plot, and then averaging over those observations to create the variable “sqdepthav”. A t-test was used to determine soil depth similarity between the two sites, and an Analysis of Variance (ANOVA)

was used to determine differences between treatment types and soil depths. A linear model was used to analyze differences in soil nutrients at different distances along the transects. This model was created in SAS v. 9.2 and uses the variables of fixed effect of the site (Panola Mountain or Rock and Shoals), treatment (Uninvaded, Invaded, or Removed), fixed effect of transect (A–R), plot-distance (1, 10, or 20), and the effect of the continuous soil depth measurement (sqdepthav) in each plot. Soil nutrient variables Na and Ca were transformed using the natural log because they demonstrated extremely right-skewed distributions.

Gap Light Analyzer (GLA) software was used to compute the parameter “percent site openness” (Frazer et al. 1999). Percent site openness is percentage of total sky area that is found in overlapping gaps in the canopy.

A linear mixed model with a natural log-transformed response was used to analyze percent cover for the classes of grasses; forbs, ferns, and fern allies; invasive species; vines; and woody plants. This model uses the variables of effect of the site (PM or RS), treatment (Uninvaded, Invaded, or Removed), transect (A–R), study-season (Fall 0, Spr 0, Fall 2, Spr 2), plot-distance (1, 10, or 20), and the interaction of study-season  $\times$  treatment. A logistic regression was used to analyze percent cover in the lichen class and a two-step analysis using a logistic regression and a linear mixed model was used to perform an analysis on percent cover for the moss and invasion classes, due to a large number of plots with no occurrence for these vegetation classes. The invasive class variable for the invasive linear mixed model was square root transformed to help normalize data distributions.

A Poisson regression was performed to determine the relative influence of soil depth, canopy openness, Ca, Mg, Na, and K on forbs, ferns, and fern allies species richness, grass species richness, woody species richness, and total species richness. Tukey-Kramer adjustments to p-values were used to allow for multiple comparisons with an  $\alpha$  value  $< 0.05$ .

## Results

### *Soil depth, soil nutrients, and light*

Average soil depths did not vary significantly between sites or among transects at each site (Table 1). Plots at distance 1 had significantly less soil depth than those at distances 6, 10, 16,

and 20; plots at distance 6 had significantly less soil depth than 10, 16, and 20; plots at distance 10 had significantly less soil depth than plots at distance 20 but were similar to 16. Plots at distance 16 and 20 are not statistically different. The general trend is a pattern of increased depth with increased distance from the rock edge.

Table 2 shows the percent available soil nutrients, pH, and percent site openness for control, invaded, and removal transects at each site. Linear mixed models demonstrated a positive significant correlation between soil depth and pH (p-value = 0.05). Plot distance was shown to be a significant predictor of K, Ca, and Na (p-value = 0.03 for K, p-value = 0.02 for Ca, and p-value  $< 0.0001$  for Na). Plots at distance of 1 m have significantly lower K and Ca, on average, than at a distance of 10 m, and a significantly lower Na at 1 m than at a distance of 20 m, but all other comparisons between nutrient values in plots are not statistically different. Analysis of the hemispherical photographs through linear regression indicates that site openness does not show any significant correlation with soil depth. Study-year 0 was significantly more open than study-year 2 (p-value  $< 0.0001$ ) but no interaction between study-year and treatment could be found, so the change in canopy openness cannot be attributed to the invasive removal treatment.

### *Vegetation class*

Vegetation percent cover was recorded for the classes: grasses, forbs, ferns and fern allies, invasive flora, lichens, mosses, vines, and woody plants. Vegetation class percent cover was not significantly impacted by the removal treatment. Sodium, calcium, and magnesium were all found to be significant predictors of invasive occurrence (p-value  $< 0.002$  for lnNa, p-value  $< 0.0003$  for lnCa, p-value = 0.0103 for Mg) (Table 3). In most cases, plot was the most significant variable in vegetation class occurrence (p-value  $< 0.0001$  for grasses, mosses, invasive species, vines, p-value = 0.03 for lichens, p-value = 0.09 for woody plants).

Most vegetation classes demonstrate a significant correlation with plot-distance from the rock. Plot 1 in a given transect typically displays a very different plant community than expected from random chance when compared to plot 20. Grasses, forbs and ferns, and vines demonstrate a positive relationship with magnesium and calcium (p-value  $< 0.0001$  for Ca in grasses, p-value = 0.0026 for Mg and p-value  $< 0.0001$

**Table 1.** Average Soil Depth by Plot and Soil Depth ANOVA. Plot number indicates meters along the transect moving outward from the rock outcrop.

Site	Function	Plot 1	Plot 6	Plot 10	Plot 16	Plot 20	Overall Mean
<b>Panola Mountain</b>		(cm)	(cm)	(cm)	(cm)	(cm)	
	Mean	6.0	28.2	46.7	67.7	64.9	42.7
	S.D.	3.8	11.3	16.1	29.3	32.5	31.6
	Max	16.0	51.0	89.0	100.0	100.0	100.0
	Min	0.0	4.0	18.0	12.0	2.0	0.0
<b>Rock and Shoals</b>							
	Mean	7.0	22.9	30.6	32.5	41.7	35.4
	S.D.	10.2	23.7	24.1	20.2	25.2	25.3
	Max	51.0	100.0	100.0	89.0	100.0	100.0
	Min	0.0	1.0	2.0	4.0	11.0	1.0
ANOVA soil depth and site, P-Value							0.2
ANOVA soil depth and transects, P-Value							0.5
ANOVA soil depth and plot, P-Value							<.0001

**Table 2.** Soil Nutrients, pH, and Percent Site Openness.

Site	Transect Type/ Function	% Ca	% Mg	% K	% Na	pH	% Site Openness Year 0	Year 2
Panola Mountain	Uninvaded Plot							
	Mean	0.0275	0.0020	0.0307	0.0046	5.15	47.59	41.09
	S.D.	0.0828	0.0005	0.0047	0.0021	0.46	6.97	7.11
Panola Mountain	Invaded Plot							
	Mean	0.0026	0.0019	0.0289	0.0037	5.33	47.44	41.39
	S.D.	0.0049	0.0004	0.0060	0.0014	0.53	7.25	7.17
Panola Mountain	Removal Plot							
	Mean	0.0011	0.0022	0.0285	0.0036	5.10	48.41	42.58
	S.D.	0.0019	0.0005	0.0047	0.0010	0.47	6.85	6.25
Rock and Shoals	Uninvaded Plot							
	Mean	0.1200	0.0010	0.0296	0.0024	5.62	40.24	35.52
	S.D.	0.1548	0.0005	0.0046	0.0006	0.63	8.94	5.91
Rock and Shoals	Invaded Plot							
	Mean	0.0335	0.0011	0.0261	0.0025	5.47	39.65	36.00
	S.D.	0.0634	0.0003	0.0068	0.0011	0.50	6.44	7.72
Rock and Shoals	Removal Plot							
	Mean	0.0808	0.0010	0.0268	0.0026	5.78	42.03	36.76
	S.D.	0.1545	0.0003	0.0081	0.0009	0.57	8.91	6.45

for Ca in forbs and ferns,  $p$ -value = 0.0097 for Mg and  $p$ -value = 0.0002 for Ca in vines). Vines also correlate positively with pH ( $p$ -value = 0.0038). Mosses display a negative correlation with calcium ( $p$ -value < 0.0001). Woody plants appear to have a positive relationship with available magnesium ( $p$ -value = 0.0279) and a negative relationship with sodium ( $p$ -value = 0.0063) in the soil. For the invasive cover class, the control treatments had significantly less invasive occurrences than the invaded transects ( $p$ -value = 0.0001) and invasive species did demonstrate a spatial distribution, in which they were more likely to occur at a greater distance from the rock edge ( $p$ -value < 0.0001). Vines showed a significant

difference between the treatments of Control and Invasive and Control and Removal ( $p$ -value = 0.0012), but not a significant difference between Removal and Invasive, so these differences cannot be attributed to the Removal treatment.

#### *Species richness*

A total of 136 species of vascular and non-vascular plants were identified in the surveys at Panola Mountain, and 10 of these or 7.4% are rock outcrop endemics as defined by Wyatt and Allison (2000). The survey performed at Rock and Shoals documented a total of 165 species with 13 of these (7.4%) identified as rock outcrop

**Table 3.** Vegetation Class Model Results.

Effect	Treatment or Season	Plot Comparisons	Estimate	Standard Error	F-Value	P-Value
<b>G Class (Linear Mixed Model (ln trans.)) with Tukey Kramer Adjustment</b>						
Intercept			-5.1182	1.7115	.	0.2054
Plot		1/10	0.9492	0.2	14.55	<.0001
Plot		1/20	1.2183	0.2265	.	<.0001
Plot		10/20	0.269	0.1239	.	0.0774
sqdepthav			0.1509	0.03647	17.13	<.0001
lnCa			-0.1211	0.02621	21.33	<.0001
K			66.7349	13.9912	22.75	<.0001
lnNa			-0.4859	0.1956	6.17	<b>0.0134</b>
<b>H Class (Linear Mixed Model (ln transformed))</b>						
Intercept			1.0789	0.5978	.	0.3221
lnCa			0.1088	0.0245	19.71	<.0001
Mg			430.71	142.07	9.19	<b>0.0026</b>
<b>L Class (Logistic Regression) with Tukey Kramer Adjustment</b>						
Intercept			-0.3653	0.9639	.	0.7694
Plot		1/10	1.4917	0.5783	4.59	<b>0.0276</b>
Plot		1/20	1.9606	0.6491	.	<b>0.0076</b>
Plot		10/20	0.4688	0.3851	.	0.4435
sqdepthav			-0.3348	0.126	7.06	<b>0.0082</b>
<b>M Class (Linear Mixed model)</b>						
Intercept			25.0936	6.2561	.	<b>0.1555</b>
Plot		1/10	4.6411	0.6376	30.96	<.0001
Plot		1/20	2.6973	0.4487	.	<.0001
Plot		10/20	0	.	.	.
K			-240.36	63.0554	14.53	<b>0.0002</b>
lnNa			2.7636	0.8246	11.23	<b>0.0009</b>
Mg			-1583.35	597.07	7.03	<b>0.0083</b>
<b>I Class (Logistic Model for comparing Control to Invaded transects)</b>						
Intercept			5.054	0.9477	.	0.118
Treatment	C		-5.051	1.0935	21.34	<b>0.0001</b>
Treatment	I		0	.	.	.
Plot		1/10	-3.7909	0.6664	21.64	<.0001
Plot		10/20	0.7664	0.5143	.	0.1374
Plot		1/20	0	.	.	.
<b>I Class (Lin. Mixed Model for Invaded trans.) with Tukey Kramer Adjustment</b>						
Intercept			10.5813	2.0774	.	0.1234
Plot		1/10	-2.4479	0.2318	64.16	<.0001
Plot		1/20	-2.4689	0.2646	.	<.0001
Plot		10/20	-0.021	0.2339	.	0.9956
lnNa			1.0474	0.3321	9.95	<b>0.002</b>
lnCa			0.2523	0.06721	14.09	<b>0.0003</b>
Mg			854.08	327.97	6.78	<b>0.0103</b>
<b>V Class (Linear Mixed Model (ln transformed))</b>						
Intercept			2.5711	0.7368	.	0.1777
Treatment	C		-0.6298	0.1765	8.52	<b>0.0012</b>
Treatment	I		-0.00106	0.175	.	0.9952
Treatment	R		0	.	.	.
Plot		1/10	-0.7313	0.1869	9.14	<b>0.0001</b>
Plot		10/20	-0.03477	0.1061	.	0.7432
Plot		1/20	0	.	.	.
Season	Fall_0		-0.2687	0.1188	3.38	<b>0.0242</b>
Season	Spr_0		0.08172	0.1188	.	0.4919
Season	Fall_2		0.0132	0.1188	.	0.9116
Season	Spr_2		0	.	.	.
sqdepthav			0.1294	0.03076	17.69	<.0001
lnCa			0.09863	0.02594	14.46	<b>0.0002</b>
pH			-0.2955	0.1015	8.48	<b>0.0038</b>
Mg			370.51	142.61	6.75	<b>0.0097</b>

**Table 3 (continued).** Vegetation Class Model Results.

Effect	Treatment or Season	Plot Comparisons	Estimate	Standard Error	F-Value	P-Value
<b>W Class (Linear Mixed Model (ln trans.)) with Tukey Kramer Adjustment</b>						
Intercept			-2.5374	1.0066	.	0.2404
Plot		1/10	-0.364	0.1723	3.2	<b>0.0887</b>
Plot		1/20	-0.1827	0.1993	.	0.6301
Plot		10/20	0.1813	0.1156	.	0.2608
lnNa			-0.4215	0.1535	7.54	<b>0.0063</b>
Sqdepthav			0.1814	0.0335	29.34	<b>&lt;.0001</b>
Mg			249.31	112.93	4.87	<b>0.0279</b>

**Table 4.** Species Richness Model Results.

Effect	Treatment or Season	Plot Comparisons	Estimate	Standard Error	F-Value	P-Value
<b>G Species Richness (Poisson regression)</b>						
Intercept			0.3953	0.4106	.	0.5121
lnCa			-0.0363	0.01486	5.97	0.015
<b>HF Species Richness (Poisson regression) with Tukey Kramer Adjustment</b>						
Intercept			0.9608	0.5241	.	0.3179
Season	Fall_0 vs. Spr_0		-0.4146	0.08728	21.2	<.0001
Season	Fall_0 vs. Fall_2		0.09119	0.09804	.	0.7887
Season	Fall_0 vs. Spr_2		-0.4763	0.08623	.	<.0001
Season	Spr_0 vs. Spr_2		0.5058	0.08975	.	<.0001
Season	Spr_0 vs. Fall_2		-0.06169	0.07668	.	0.8523
Season	Spr_2 vs. Fall_2		-0.5675	0.08874	.	<.0001
<b>W Species Richness (Poisson regression) with Tukey Kramer Adjustment</b>						
Intercept			0.4109	0.2454	.	0.3427
Plot		1/10	-0.4415	0.1456	6.12	0.0073
Plot		1/20	-0.3188	0.1668	.	0.1368
lnCa			0.08954	0.02172	17	<.0001
sqdepthav			0.09644	0.02616	13.58	0.0003
Mg			217.45	109.01	3.98	0.0468
<b>Total Species Richness (Poisson regression) with Tukey Kramer Adjustment</b>						
Intercept			2.2267	0.1705	.	0.0486
Plot		1/10	-0.06917	0.0559	4.48	0.4318
Plot		1/20	0.03122	0.06454	.	0.8791
Plot		10/20	0.1004	0.03589	.	0.0149
sqdepthav			0.03404	0.01131	9.05	0.0028
Season	Fall_0 vs. Spr_2		-0.1526	0.04059	9.06	0.0011
Season	Spr_0 vs. Spr_2		0.145	0.04101	.	0.0026
Season	Spr_0 vs. Fall_2		-0.02465	0.03926	.	0.923
Season	Spr_2 vs. Fall_2		-0.1696	0.04078	.	0.0002

endemic species. Panola Mountain had documented occurrences of *Lonicera japonica*, *Ligustrum sinense*, *Rosa multiflora* and *Elaeagnus umbellata*. Rock and Shoals also has a higher species richness of invading species in the sampled transects, with *Microstegium vimineum*, *Lonicera japonica*, *Ligustrum sinense*, *Lespedeza cuneata*, *Nandina domestica*, *Lonicera maackii*

and *Elaeagnus umbellata* all in abundance. For the majority of individual plants, removal was only necessary at the beginning of the study, however a small percentage (approximately 10%) needed to be removed again in the first year of the study.

Table 4 summarizes the regression model results for species richness and Figure 2 illustrates

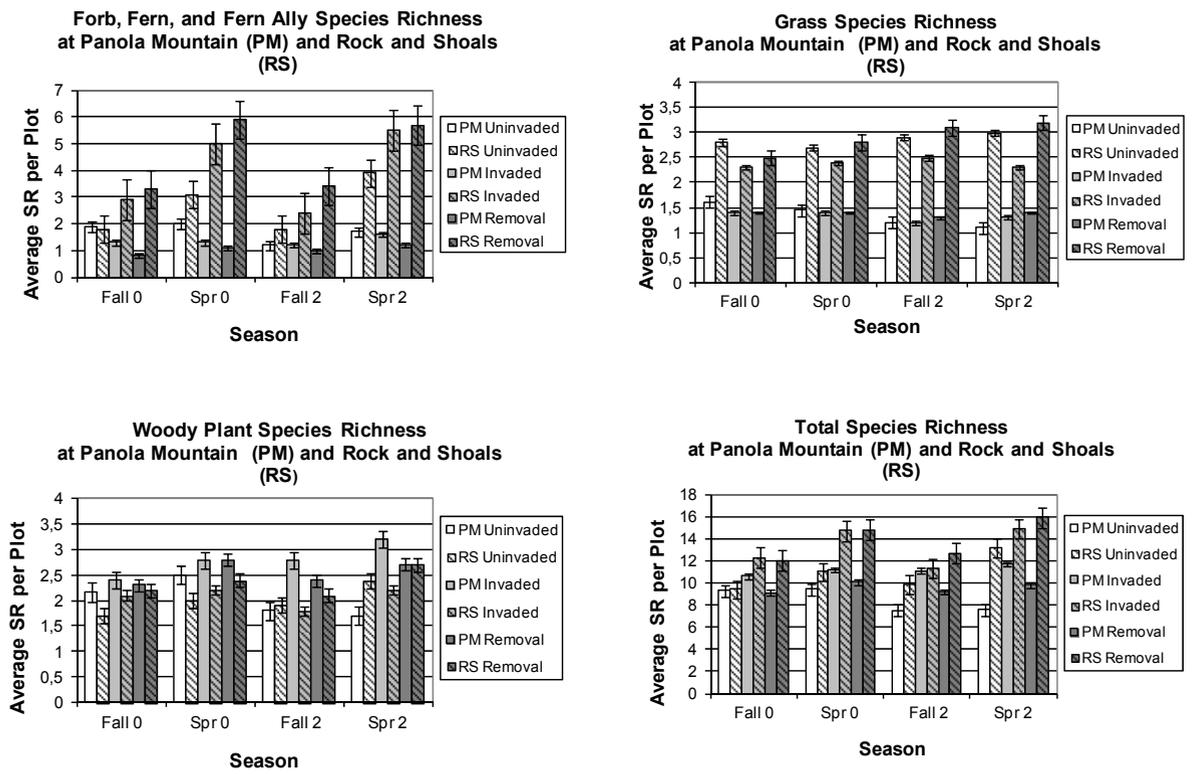


Figure 2. Species richness by vegetation class. Note that the y-axis scale differs among the graphs.

how the richness of grass, forb/fern/fern allies, woody plant, and total species richness changed over the study period. The removal treatment did not significantly affect species richness. Grass species richness was negatively correlated with calcium. Survey season was the only significant predictor of forb/fern/fern ally species richness ( $p$ -value  $< 0.0001$ ), likely because many of the forbs encountered at rock outcrops are annual plants that reproduce in the spring. Woody species richness is positively correlated with calcium and magnesium in the soil ( $p$ -value  $< 0.0001$  for Ca and  $p$ -value = 0.05 for Mg). Plot distance and soil depth are significant predictors of both woody plant species richness and total species richness ( $p$ -values  $< 0.0001$  for plot distance in both woody plant richness and total richness,  $p$ -value = 0.0003 for soil depth in woody plant richness,  $p$ -value = 0.0028 for total species richness). Survey-season is a significant predictor of overall species richness ( $p$ -value  $< 0.0001$ ).

## Discussion

In this study, removing invasive species from experimental transects at the margins of granite outcrops did not significantly alter species richness or vegetation class cover or distribution. This was a surprising result, given the sensitivity of many native plant communities to exotic invasion. Hemispherical photographs revealed a significant difference in canopy openness over the duration of the study, but these changes occurred evenly across the different transects and could not be attributed to treatment. While endemic species were not categorized as a separate vegetation class in this analysis, the majority of rock outcrop endemics are herbaceous plants and followed the same trends in terms of percent cover and species richness reflected by the forb/fern/fern ally vegetation class. Removal did not appear to increase cover or richness of endemics within the outcrop habitat.

Similar experiments revealed that removal of invasive species alone did not increase species richness or cover (MacDougall and Turkington 2005; Hahn and Dornbush 2012; Dornbush and Hahn 2013), however these studies did find that active enhancement and restoration with native species did increase native cover and native species richness. Hester and Hobbs (1992) applied an invasive removal treatment after prescribed burning on southwestern Australian outcrops and were able to document increased plant vigor and seed-set. An increase in plant vigor was noted through qualitative observations after the removal treatment was applied in our study, but this did not result in a long-term quantitative significant difference in percent cover of vegetation classes or species richness for these altered plots.

Extreme variation in precipitation during the study period may have influenced the outcome of the removal treatment. The state of Georgia experienced a severe drought from May to December of 2007. Nearby weather stations reported total annual precipitation levels of 770 mm for Panola Mountain (330 mm less than 2006 annual precipitation totals) in 2007 and 782 mm for Rock and Shoals (348 mm less than 2006 levels) in 2007. Soil moisture in the ecotone can vary, as site topography encourages run-off from the rock to channel through some areas but not others. Therefore, a patchy response to low moisture is expected in the ecotone. Study observations confirm that heavier mortality was experienced in some areas of the ecotone due to shallower soils and lack of rain (pers. obs.). Rock outcrop plant communities experience periodic fluctuations in moisture and temperature. Thus, it is possible that the environmental extremes in the course of the study period did little to alter long-term trends in the plant community structure of the outcrop ecotone. It is also possible that time or area scales were too small to capture a community response to the treatment.

Soil depth has been found to be a predictor of vegetation class (Burbanck and Platt 1964; Dornbush and Wilsey 2010). In this study, soil depth correlated with distance from the rock edge, and soil depth predicted vegetation class distributions as well (Table 1). The rock outcrop ecotone habitat at both study sites is glade-like, with shallow soils separating islands of bare rock. Some species of grasses, mosses, forbs and ferns typically occur in the first couple of meters from the rock edge, but this suite of plants was found at a greater distance from the rock edge because of a continued trend in shallow soils.

Soil nutrients in rock outcrop communities are known to be limited, and cation availability in the soil appears to be a predictor of plant occurrence (Harrison 1999). The resource availability hypothesis suggests that invasive species will be positively correlated with available nutrients (Davis et al. 2000). In serpentine communities, low Ca has been an important restrictive factor for many invasive and native plant species (Kruckeberg 1984; Harrison 1999; Safford and Harrison 2004). Harrison (1999) found that herbaceous species richness (grasses were included in this species class designation) on serpentine outcrops showed significant negative correlations with soil calcium levels. In this study, higher calcium levels were predictive of grass, forb/fern/fern ally, and vine vegetation class occurrence. Invasive plant occurrence was tied to calcium, magnesium, and sodium. Woody vegetation class and woody species richness also showed a spatial correlation with magnesium. Forb/fern/fern ally species richness, however, did not correlate with calcium levels, only with study season.

A number of studies have suggested that abiotically harsh and unproductive environments tend to be less invaded than more productive ones (Zartman et al. 1964; Crawley 1987; Hobbs 1989; Mack 1989; Maron and Marler 2007). The results of this study fit with that pattern, with greater invasion documented at greater distances from the rock edge and corresponding greater soil depth. Studies have shown that in serpentine barrens, limitations in soil nutrients combined with plant competition have made these environments more resistant to invasion (Williamson and Harrison 2002; Daehler 2003; Going et al. 2009). Huenneke et al. (1990) suggested that this lack of nutrient availability may be more important than physical disturbance in determining community invasibility. These findings suggest that, whereas the ecotone environment may be affected, the soil islands on the rock surface may remain more intact.

*Ligustrum sinense*, *Lonicera japonica*, *Microstegium vimineum*, *Lespedeza cuneata*, *Rosa multiflora* Thunb., *Nandina domestica*, *Lonicera maackii*, and *Elaeagnus umbellata* are the Category One and Category Two (GA EPPC 2011) invasive species encountered in the surveys. *Ligustrum sinense* is by far the greatest in abundance and does the most to visibly modify a rock outcrop community by closing the mid-story canopy. *Ligustrum* spp. are known for their abundant production of highly dispersible fruits, wide range of adaptability, and limited

natural predators (Batcher 2000). Invasive Category One and Category Two species were removed throughout the study period. After the initial clearing, removal transects were cleared again the following year, but this effort involved removing seedlings. New establishment of invasive species was dominated by seedlings of *Ligustrum sinense*. In a study by Webb et al. (2001), removal experiments applied to invasive *Acer platanoides* revealed that other invasive species spread where tree removals opened the canopy. In this experiment, *Ligustrum sinense* appeared to seed back into plots from the overhanging canopy, and is expected to take over removal plots again. However, based on the speed of recolonization throughout the study, reestablishment of invasive species is expected to be slower than previously thought.

Even with the high mortality of invasive species caused by extreme environmental conditions in rock outcrop habitats, an established buffer of parent plants provides a means of quick replacement. In a study performed by Bartuszevige and colleagues (2006), edge habitat was identified as critical for invasion success, and this was attributed to propagule pressure from the invading species. If invasive species alter the ecotone of the rock outcrop system into a more closed canopy, wind-dispersed seed flow from one island-like rock to another will be affected. Cadenasso and Pickett (2001) have demonstrated how the structure of the forest edge can regulate seed dispersal. Local dynamics among populations will invariably determine the processes of migration, extinction, and colonization (Husband and Barrett 1996). More work is required to understand better how long-distance dispersal events take place with rock outcrop endemics. Performing a study to explore how density of native and invasive species may be affecting immigration success is warranted. Undertaking a study that allows for the review of longer time-scales and larger removal areas could help to better illustrate the relationship between invasive species and native endemics in rock outcrop habitats. Until we have a better understanding of this dynamic, it is critical that we act to protect the remaining population reserves of rock outcrop endemic species through site management and conservation. The results of this study suggest that the use of limited management resources may be better allocated toward minimizing physical site disturbance and enhancing native species through active restoration rather than focusing on invasive species eradication.

## Acknowledgements

We would like to thank the State Botanical Garden of Georgia for financial and logistical support. This research has been supported by the Center for Plant Conservation's Catherine Beattie Fellowship, and the generosity of the Georgia Botanical Society and the Georgia Native Plant Society. We would like to thank the Georgia Plant Conservation Alliance for serving as a network of professionals always willing to provide logistic support and expertise. We are also grateful to the staff at Panola Mountain State Park and to Chis Canalos, Elaine Nash, Hugh and Carol Nourse, Jack Lingard, and Albie and Paul Smith for their volunteer support. We are grateful to two anonymous reviewers for their suggestions and comments on the manuscript.

## References

- Aerts R (1999) Interspecific competition in natural plant communities: Mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany* 50: 29–37
- Bartuszevige AM, Gorchov DL, Raab L (2006) The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. *Ecography* 29: 213–222, <http://dx.doi.org/10.1111/j.2006.0906-7590.04359.x>
- Baskin JM, Baskin CC (1988) Endemism in rock outcrop plant communities of unglaciated eastern United States: An evaluation of the roles of the edaphic, genetic and light factors. *Journal of Biogeography* 15: 829–840, <http://dx.doi.org/10.2307/2845343>
- Batcher MS (2000) Elemental stewardship abstract for *Ligustrum* spp., Privet. The Nature Conservancy, Arlington, VA, USA, 10 pp
- Blank RR (2010) Intraspecific and interspecific pair-wise seedling competition between exotic annual grasses and native perennials: plant-soil relationship. *Plant Soil* 326: 331–343, <http://dx.doi.org/10.1007/s11104-009-0012-3>
- Burbank MP, Platt RB (1964) Granite outcrop communities of the Piedmont Plateau in Georgia. *Ecology* 45: 292–306, <http://dx.doi.org/10.2307/1933842>
- Cadenasso ML, Pickett STA (2001) Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* 15: 91–97
- Casparly M, Rickard J (2007) A survey of *Amphianthus pusillus*, *Isoetes tegetiformans*, and *I. melanospora*. U.S. Fish and Wildlife Service, Athens, GA
- Connell JH (1972) Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* 3: 169–192, <http://dx.doi.org/10.1146/annurev.es.03.110172.001125>
- Connell JH (1983) On the prevalence and relative importance of interspecific competition—evidence from field experiments. *American Naturalist* 122: 661–696, <http://dx.doi.org/10.1086/284165>
- Crawley MJ (1987) What makes a community invulnerable? In: Gray AJ, Crawley MJ, Edwards PJ (eds), *Colonization, succession, and stability*. Blackwell, Oxford, UK, pp 429–453
- Csurhes S, Edwards R (1998) Potential environmental weeds in Australia: Candidate species for preventative control. Environment Australia, Canberra, Australia, 202 pp
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics* 34: 183–211, <http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132403>
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: A general theory of invasibility. *The*

- Journal of Ecology* 88: 528–534, <http://dx.doi.org/10.1046/j.1365-2745.2000.00473.x>
- Dornbush ME, Wilsey BJ (2010) Experimental manipulation of soil depth alters species richness and co-occurrence in restored tallgrass prairie. *Journal of Ecology* 98: 117–125, <http://dx.doi.org/10.1111/j.1365-2745.2009.01605.x>
- Dornbush ME, Hahn PG (2013) Consumers and establishment limitations contribute more than competitive interactions in sustaining dominance of the exotic herb garlic mustard in a Wisconsin, USA forest. *Biological Invasions*, <http://dx.doi.org/10.1007/s10530-013-0484-1>
- Frazer GW, Canham CD, KP Lertzman (1999) Gap Light Analyzer (GLA) Imaging software to extract canopy structure and gap light transmission indices from true color fish-eye photograph, users manual and program documentation. Simon Fraser University, Burnaby, BC
- GA EPPC (2011) Georgia Exotic Pest Plant Council Category One and Category Two Invasive Species Lists. <http://www.gaepcc.org/list.cfm> (Accessed on 10 January 2011)
- Georgia Geological Survey (1999) Digital Geology Map of Georgia (Version 2). Digital Geologic Map of Georgia, Georgia Geologic Survey, Atlanta, Georgia, USA
- Going BM, Hillerislambers J, Levine JM (2009) Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia* 159: 839–847, <http://dx.doi.org/10.1007/s00442-008-1264-y>
- Grime JP (2001) Plant Strategies, Vegetation Processes, and Ecosystem Properties, 2nd edn. John Wiley & Sons, Chichester
- Hahn PG, Dornbush ME (2012) Exotic consumers interact with exotic plants to mediate native plant survival in a Midwestern forest herb layer. *Biological Invasions* 14: 449–460, <http://dx.doi.org/10.1007/s10530-011-0089-5>
- Harrison S (1999) Local and regional diversity in a patchy landscape: Native, alien, and endemic herbs on Serpentine. *Ecology* 80: 70–80, [http://dx.doi.org/10.1890/0012-9658\(1999\)080\[0070:LARDIA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1999)080[0070:LARDIA]2.0.CO;2)
- Harrison S, Grace JB, Davies KF, Safford HD, Viers JH (2006) Invasion in a diversity hotspot: Exotic cover and native richness in the Californian Serpentine flora. *Ecology* 87: 695–703, <http://dx.doi.org/10.1890/05-0778>
- Hester AJ, Hobbs RJ (1992) Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science* 3: 101–108, <http://dx.doi.org/10.2307/3236003>
- Hobbs RJ (1989) The nature and effects of disturbance relative to invasions. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds), *Biological invasions: A global perspective*. John Wiley, Chichester, UK, pp 389–405
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* 6: 324–337, <http://dx.doi.org/10.1046/j.1523-1739.1992.06030324.x>
- Hoffmann WA, Lucatelli VC, Silva FJ, Azevedo IC, Marinho MS, Albuquerque A, Moreira SP (2004) Impact of the invasive alien grass *Melinis minutiflora* at the savanna-forest ecotone in the Brazilian Cerrado. *Diversity and Distributions* 10: 99–103, <http://dx.doi.org/10.1111/j.1366-9516.2004.00063.x>
- Houlé G (1990) Species-area relationship during primary succession in granite outcrop plant communities. *American Journal of Botany* 77: 1433–1439, <http://dx.doi.org/10.2307/2444753>
- Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian Serpentine grassland. *Ecology* 71: 478–491, <http://dx.doi.org/10.2307/1940302>
- Husband BC, Barrett SCH (1996) A metapopulation perspective in plant population biology. *Journal of Ecology* 84: 461–469, <http://dx.doi.org/10.2307/2261207>
- Jackson RB, Manwaring JH, Caldwell MM (1990) Rapid physiological adjustment of roots to localized soil enrichment. *Nature* 334: 58–60, <http://dx.doi.org/10.1038/344058a0>
- Kittell MM (2001) Relationships among invasive Chinese privet, diversity, and small mammal captures in southeastern deciduous forests. MS Thesis. Clemson University, Clemson, SC, USA, 35 pp
- Kruckeberg AR (1984) California serpentine: Flora, vegetation, geology, soils, and management problems, University of California Press, Berkeley, CA, USA
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA, 203 pp
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55, <http://dx.doi.org/10.1890/04-0669>
- Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13: 195–198, [http://dx.doi.org/10.1016/S0169-5347\(97\)01286-X](http://dx.doi.org/10.1016/S0169-5347(97)01286-X)
- Mack RN (1989) Temperate grasslands vulnerable to plant invasions: Characteristics and consequences. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M (eds), *Biological Invasions: A Global Perspective*, John Wiley and Sons, New York, USA, 155–179 pp
- Mangla S, Sheley R, James J, Radosevich S (2011) Intra and interspecific competition among invasive and native species during early stages of plant growth. *Plant Ecology* 212: 531–542, <http://dx.doi.org/10.1007/s11258-011-9909-z>
- Maron JL, Marler M (2007) Native plant diversity resists invasion at both low and high resource levels. *Ecology* 88: 2651–2661, <http://dx.doi.org/10.1890/06-1993.1>
- Mawson PR (2000) Conservation of native fauna inhabiting granite outcrops: How do you manage it? *Journal of the Royal Society of Western Australia* 83: 163–167
- Nourse H, Nourse C (2004) Flora of Rock and Shoals Outcrop Natural Area. *Tipularia* 19: 19–25
- Oosting HJ, Livingstone RB (1964) A resurvey of a loblolly pine community twenty-nine years after ground and crown fire. *Bulletin of the Torrey Botanical Club* 91: 387–395, <http://dx.doi.org/10.2307/2483431>
- Patrick TS (1997) Rare Plant Checklist No. 2: Piedmont Granite Outcrops. In: Program GNH (ed), Social Circle, GA
- Pigott JP (2000) Environmental weeds and granite outcrops: Possible solutions in the "too hard basket"? *Journal of the Royal Society of Western Australia* 83: 135–137
- Porembski S (2000) The invasibility of tropical granite rock outcrops ('inselbergs') by exotic weeds. *Journal of the Royal Society of Western Australia* 83: 131–134
- Safford HD, Harrison S (2004) Fire effects on plant diversity in serpentine vs. sandstone chaparral. *Ecology* 85: 539–548, <http://dx.doi.org/10.1890/03-0039>
- Sharitz RR, McCormick JF (1973) Population dynamics of two competing annual plant species. *Ecology* 54: 723–740, <http://dx.doi.org/10.2307/1935669>
- USDA (2006a) Soil Survey Geographic (SSURGO) database for Clarke and Oconee Counties, Georgia. U.S. Department of Agriculture, Natural Resources Conservation Service, Fort Worth, TX, USA
- USDA (2006b) Soil Survey Geographic (SSURGO) database for Newton and Rockdale Counties, Georgia. U.S. Department of Agriculture, Natural Resources Conservation Service, Fort Worth, TX, USA
- USGS (2000) Panola Mountain, Georgia, A Water, Energy, and Biogeochemical Budgets Program Site. U.S. Department of the Interior, USGS, Atlanta, Georgia, USA

- Vilà M, Ibáñez I (2011) Plant invasions in the landscape. *Landscape Ecology* 26: 461–472, <http://dx.doi.org/10.1007/s10980-011-9585-3>
- Webb SL, Pendergast TH, Dwyer ME (2001) Response of native and exotic maple seedling banks to removal of the exotic, invasive Norway maple (*Acer platanoides*). *Journal of the Torrey Botanical Society* 128: 141–149, <http://dx.doi.org/10.2307/3088736>
- Wharton CH (1978) The Natural Environments of Georgia. Office of Planning and Research, Georgia Department of Natural Resources, Atlanta, GA, USA, 227 pp
- Wilcox J, Beck CW (2007) Effects of *Ligustrum sinense* Lour. (Chinese privet) on abundance and diversity of songbirds and native plants in a southeastern nature preserve. *Southeastern Naturalist* 6: 535–550, [http://dx.doi.org/10.1656/1528-7092\(2007\)6\[535:EOLSLC\]2.0.CO;2](http://dx.doi.org/10.1656/1528-7092(2007)6[535:EOLSLC]2.0.CO;2)
- Williamson J, Harrison, S (2002) Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications* 12: 40–51, [http://dx.doi.org/10.1890/1051-0761\(2002\)012\[0040:BAALTT\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(2002)012[0040:BAALTT]2.0.CO;2)
- Wyatt R (1997) Reproductive ecology of granite outcrop plants from the southeastern United States. *Journal of the Royal Society of Western Australia* 80: 123–129
- Wyatt R, Allison JR (2000) Flora and vegetation of granite outcrops in the southeastern United States. *Ecological Studies* 146:409–433, [http://dx.doi.org/10.1007/978-3-642-59773-2\\_19](http://dx.doi.org/10.1007/978-3-642-59773-2_19)
- Yager LY, Miller DL, Jones J (2011) Woody shrubs as a barrier to invasion by cogongrass (*Imperata cylindrica*). *Invasive Plant Science and Management* 4: 207–211, <http://dx.doi.org/10.1614/IPSM-D-10-00052.1>
- Zartman RE, Norton JJ, Stern TW (1964) Ancient granite gneiss in the Black Hills, South Dakota. *Science* 145: 479–481, <http://dx.doi.org/10.1126/science.145.3631.479>