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Patterns of plant invasions: a case example in native species hotspots and rare habitats

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Abstract

Land managers require landscape-scale information on where exotic plant species have successfully established, to better guide research, control, and restoration efforts. We evaluated the vulnerability of various habitats to invasion by exotic plant species in a 100,000 ha area in the southeast corner of Grand Staircase-Escalante National Monument, Utah. For the 97 0.1-ha plots in 11 vegetation types, exotic species richness ($\log_{10}$) was strongly negatively correlated to the cover of cryptobiotic soil crusts ($r = -0.47$, $P < 0.001$), and positively correlated to native species richness ($r = 0.22$, $P < 0.03$), native species cover ($r = 0.23$, $P < 0.05$), and total nitrogen in the soil ($r = 0.40$, $P < 0.001$). Exotic species cover was strongly positively correlated to exotic species richness ($r = 0.68$, $P < 0.001$). Only 6 of 97 plots did not contain at least one exotic species. Exotic species richness was particularly high in locally rare, mesic vegetation types and nitrogen rich soils. Dry, upland plots ($n = 51$) had less than half of the exotic species richness and cover compared to plots ($n = 45$) in washes and lowland depressions that collect water intermittently. Plots dominated by trees had significantly greater native and exotic species richness compared to plots dominated by shrubs. For the 97 plots combined, 33% of the variance in exotic species richness could be explained by a positive relationship with total plant cover, and negative relationships with the cover of cryptobiotic crusts and bare ground. There are several reasons for concern: (1) Exotic plant species are invading hot spots of native plant diversity and rare/unique habitats. (2) The foliar cover of exotic species was greatest in habitats that had been invaded by several exotic species. (3) Continued disturbance of fragile cryptobiotic crusts by livestock, people, and vehicles may facilitate the further invasion of exotic plant species.

Introduction

Biological conservation efforts are increasingly moving toward an ecosystem and landscape approach, recognizing the prohibitive cost and difficulty of a species-by-species approach (Agee and Johnson 1988; Noss 1983; LaRoe 1993; Stohlgren et al. 1997a–c). A key ingredient of our approach is a careful analysis of hot spots of plant diversity and rare/unique habitats to identify critical habitats. Although rare habitats are small in total area, they often are used heavily by wildlife (McNaughton 1993; Simonson 1998). There is increasing evidence that some hot spots of native plant diversity, fertile soils, and rare habitats may be particularly vulnerable to invasion by exotic plant species (Planty-Tabacchi et al. 1996; Stohlgren et al. 1998b, 1999a).

In arid regions of the world like southeast Utah, cryptobiotic (or microbiotic) soil crusts which are filamentous webs of cyanobacteria, lichen, green algae,

mosses, and fungi, play a critical role in the sustainability of desert ecosystems. The crusts mechanically stabilize soils and increase soil fertility by fixing atmospheric N and preventing other nutrients from being leached from surface soils (Garcia-Pichel and Belnap 1996). In addition, crusts influence vascular plant seed germination and water infiltration rates (Belnap and Harper 1995; Belnap and Gillette 1998). However, the fragile organisms that make up the crusts may take hundreds of years to recover from disturbances such as trampling by livestock and people, and the use of off-road vehicles (Belnap 1995, 1998). Assessing damage to the crusts at landscape-scales is vital to land managers at the Monument, who must protect native vegetation and soils while providing opportunities for recreation, grazing, and mineral exploration.

In June 1996, the Presidential Proclamation establishing Grand Staircase-Escalante National Monument identified its important ecological values, including many endemic plant species in a floristically-rich region of the southwestern United States. The proclamation also acknowledged the abundance of unique, isolated plant communities and the extraordinary opportunity to study vegetation dynamics. The Monument is home to 50% of Utah's rare plant species, 11 of which are found nowhere else on Earth, and 84% of the state's flora (Shultz 1998). The high degree of endemism of vascular plants is exemplified by the hanging gardens (Fowler et al. 1995; May 1998). Hanging gardens are geomorphological enclaves of mesic habitats interspersed in vast areas of desert (May 1998). However, less is known about the patterns of native and exotic plant diversity in the broader landscape, and learning more will be challenging. First, the Monument is huge and floristically complex. The 691,057 ha (1.7 M acre) Monument ranges in elevation from 1372 m (4500 ft) to 2530 m (8300 ft), from low desert shrub, steppe, sage (*Artemesia* spp.), and pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) woodlands to forests of ponderosa pine (*Pinus ponderosa*) (Welsh and Atwood 1998). Second, land use practices such as grazing, recreation, mining, and oil and gas exploration and extraction threaten the native plants, cryptobiotic crusts, and soils in the Monument. Third, in Grand Staircase-Escalante National Monument, riparian zones and small wetlands are expected to be hot spots of biodiversity. It is important to know if these hot spots of native plant diversity and rare habitats are vulnerable to invasion by exotic plant species (D'Antonio and Vitousek 1992).

Our understanding of the role of the Monument's cryptobiotic crusts in maintaining and stabilizing soils and protecting native plant diversity can be greatly improved with systematic surveys combined with controlled experiments (Belnap and Harper 1995; Belnap and Gillette 1998). Cryptobiotic crusts are more prevalent in some areas of the Monument than in others. Crusts have different resistance and resilience to disturbance. Crusts on coarse-textured soils are much less able to handle disturbance and recover much more slowly than crusts on fine-textured soils. Also, some areas receive more trampling by livestock and people, off-road vehicle use, and other disturbances. We know of no previous landscape-scale studies investigating crust cover, level of crust development, soil characteristics, and invasion by exotic plant species.

Our objectives were to: (1) quantify patterns of native and exotic plant species, cryptobiotic crust habitats, rare/unique habitats, and soil characteristics at landscape scales; and (2) determine which habitats in the southeast portion of the Monument were more invaded by exotic plant species to better guide research, control, and restoration efforts. Thus, we surveyed patterns in native and exotic plant diversity, crust cover and development, and soil characteristics to evaluate *where* exotic plant species have successfully invaded, not *why* they have invaded specific habitats.

Materials and methods

A 100,000 ha in the southeast corner of the Grand Staircase-Escalante National Monument was selected for the intensive survey (Figure 1). The area contains both a high plateau (up to 2530 m) and low canyon-land (1372 m) geography, but little in between, and hosts a variety of habitat types. We used a simple random study design with unbiased site selection for 85 sites, complemented by survey data of rare habitat type for 12 sites. The randomly-generated points were located on a topographic map, then located in the field using global positioning system (GPS). The other 12 sites (three wet meadow, five aspen, two ponderosa pine, and two lowland riparian sites) were located in more moist areas to better assess the invasion of rare habitats typically missed with random sampling (Stohlgren et al. 1997a, b, 1998c). The 97 sites total were later classified into eleven vegetation types (identified by dominant species) including aspen (Populus tremuloides), blackbrush (Coleogyne ramossissima), desert mixed

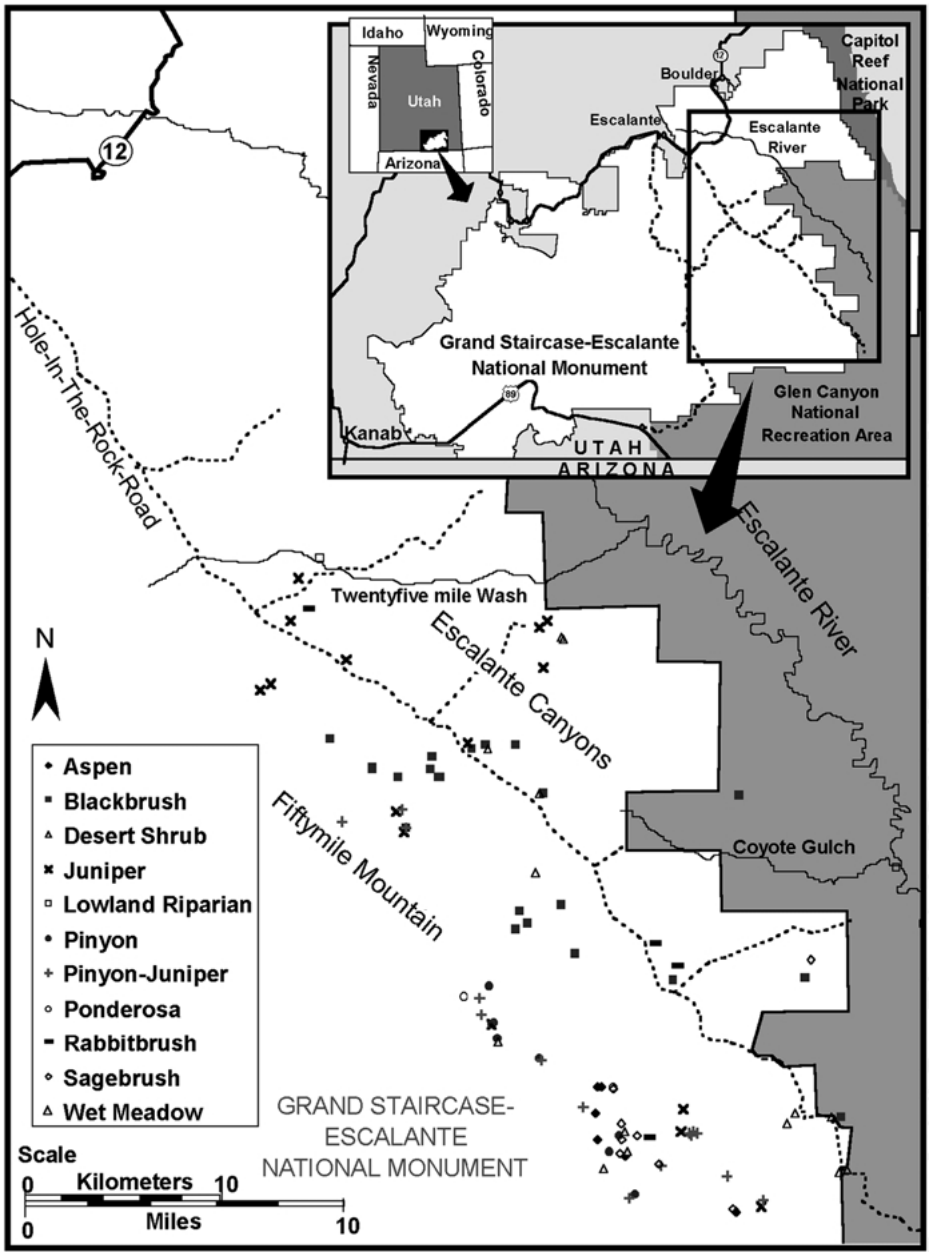

Figure 1. Map of the study sites in Grand Staircase-Escalante National Monument, Utah.

shrub (*Gutierrezia sarothrae* and many others), juniper (*Juniperus osteosperma*), lowland riparian (*Salix* spp., *Tamari*x spp.), Pinyon (*Pinus edulis*), pinyon-juniper (*P. edulis-Juniperus* spp.), ponderosa pine (*Pinus ponderosa*), rabbitbrush (*Chrysothamnus* spp.), sagebrush (*Artemisia tridentata*, *A. bigelovii*), and wet meadow (*Agrostis stolonifera*, *Juncus arcticus*).

At each sample site, a multi-scale plot was established for vegetation, cryptobiotic crust, and soil sampling. The Modified-Whittaker plot included ten 1-m^2 subplots, two 10-m^2 subplots, and a 100-m^2 subplot nested within a 20 × 50 m plot (Stohlgren et al. 1995; Stohlgren et al. 1998a). In the 1-m^2 subplots, we recorded the foliar cover by species, and the cover

of bare ground (no plants or crusts), cryptobiotic crust (by level of development; see below), rock, litter, duff, water, and dung. Cumulative species (species not found in the ten 1-m^2 subplots) were recorded successively in the two 10-m^2 subplots, the 100-m^2 subplot, and the remaining unsampled areas of the 20 × 50 m plot. The developmental stage of cryptobiotic crusts was recorded in the ten 1-m^2 subplots in eight classes from 1 (weakly developed) to 20 (fully developed; see Belnap 1995, 1996). Ancillary data recorded for each plot included: UTM location and elevation from a GPS, and general comments about the site.

Each site was sampled as close to the vegetative phenological maximum (peak biomass) as possible. Plant species that could not be identified in the field were collected and later identified at Brigham Young University, Utah (by Drs Stanley Welsh and Duane Atwood), Southern Utah State University (by Dr Jim Bowns), or at the herberia at the Colorado State University or University of Wyoming, Laramie. About 10% of the total specimens collected could not be identified to species due to inappropriate phenological stage or missing flower parts. These were ignored in statistical analyses.

Five soil samples (maximum depth = 15 cm) were taken throughout each Modified-Whittaker plot and pooled into one plastic bag. Surface litter, if present, was removed before coring. Samples were air-dried for at least 48 h and sieved with a standard #10 (2 mm pore size) sieve and analyzed for particle size based on the standard hydrometer method (Gee and Bauder 1986). Soil samples were also ground in a standard ball mill grinder, and analyzed for total percentage of N and C using a LECO-1000 CHN Analyzer (following the methods of Carter 1993).

Statistical analysis

All statistical analyses were conducted with SYSTAT (version 7.0, SPSS, Inc.), and $P < 0.05$ was used to determine significance in all tests. Data distributions that were strongly skewed were transformed prior to analysis. Log_{10} transformations were used on the C : N ratio, and exotic species richness and cover.

Analysis of variance (ANOVA) was used to compare native and exotic species richness and cover among various vegetation classes. Tukey's means comparison test was used where the ANOVA model was significant. *T*-tests were used to compare vegetation and soil characteristics between washes (and lowland depressions) that collect intermittent flooding and more xeric upland plots, and between shrub-dominated plots and tree-dominated plots.

Linear regressions were used to determine the relationship of native and exotic species richness and cover to each other, and to soil and crust characteristics. We used stepwise forward multiple regressions to predict native and exotic species richness and cover from crust characteristics, topographic variables, and soil characteristics. Soil characteristics included total percentages of N, C, and sand, silt and clay (percentage of silt was not added into the model to reduce multi-collinearity). The forward linear regression models included only variables meeting the $P < 0.15$ criterion. We used path analysis (Dewey and Lu 1959) to display multiple regression results where 'direct effects' between the independent variables and the dependent variables were shown with standardized partial regression coefficients, and 'indirect effects' were shown as simple regression coefficients between independent variables (i.e., indirectly affecting the dependent variable).

Finally, we used kriging models (see Legendre and Fortin 1989; SYSTAT 8.0) to create contour maps of native and exotic species richness, and soil percentage of N and C in relation to plot location. We mapped exotic species richness and crust cover in the same way.

Results

Native and exotic plant diversity and soil crusts

For the 97 0.1-ha plots combined, we encountered 350 native species, 38 exotic species, and 63 specimens identified to genus. Plots, on average, contained 25.0 (±0.7; 1 SE) native plant species, and 2.3 (±0.2) exotic plant species, and four plant species that could not be identified due to phenological stage, desiccation, or missing parts from herbivory. Only 6 of 97 plots contained no exotic plant species, while 28 plots had three or more exotic plant species per plot (Figure 2). The cover of native plant species averaged 29.1% (±1.6%) per plot, while exotic plant species cover averaged 5.0% (±0.8%) per plot. The dominant exotic plant species was *Bromus tectorum*, which averaged 3.4% (±0.5%) cover, or about 68% of the exotic species cover in the landscape. Total bare ground (i.e., rock, bare soil, dung, etc.) averaged 68.4% (±1.8%), while the cover of cryptobiotic

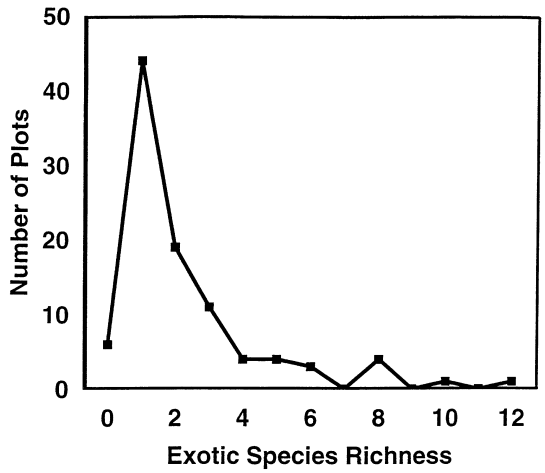

Figure 2. Frequency of exotic species in the 97 plots.

crusts averaged 19.7% (±1.9%) cover. Only 3 plots had no cover of cryptobiotic crusts, 25 plots had <5% cover, and 31 plots had >25% cover of cryptobiotic crusts.

Plant diversity, crust cover, and soils by vegetation type

Native and exotic plant species richness and cover varied considerably by vegetation type (Table 1). Mean native species richness ranged from 32.3 (±3.1) species per 0.1-ha plot in the relatively mesic, high-elevation aspen type to 19.8 (±1.2) species per plot in the xeric, lowland blackbrush type. The maximum number of native species was also found in an aspen plot (45 species), while the most species-poor plot was in the blackbrush type (11 species). The relatively rare ponderosa pine and wet meadow types were also high in native species richness (Table 1).

Exotic species richness generally increased with native species richness in many vegetation types (Table 1). One aspen plot had 12 exotic species, while the wet meadow type averaged 8.0 exotic species/plot. The lowland riparian type was also rich in exotic species. Drier vegetation types such as the blackbrush, desert shrub, sagebrush, and pinyon-juniper types averaged fewer than two exotic species per plot (Table 1). Exotic species cover was highest in the wet meadow type (27.9% ± 5.4% cover) and lowest in the desert shrub type (1.6% ± 0.8% cover). The maximum cover of exotic species was 34% in a wet meadow plot.

Table 1. Mean native species richness and cover, and the number of species with <1% foliar cover for various vegetation types in Grand Staircase-Escalante National Monument (Standard error in parentheses).

Vegetation type	No. of plots	Species richness			Average % cover	
		Native	Exotic	Plants w/<1% cover	Native	Exotic
Aspen	6	32.3 (3.1)	5.2 (1.4)	15.2 (1.5)	42.2 (11.5)	11.2 (3.7)
Blackbrush	22	19.8 (1.2)	1.2 (0.1)	9.8 (0.6)	29.2 (2.3)	2.8 (1.0)
Desert shrub	11	25.4 (2.0)	1.8 (0.3)	11.8 (1.9)	24.0 (3.5)	1.6 (0.8)
Juniper	15	26.9 (1.6)	1.7 (0.5)	12.9 (1.3)	23.8 (3.3)	4.2 (1.9)
Lowland riparian	2	23.5 (0.5)	5.0 (1.0)	7.5 (3.5)	41.4 (23.9)	15.5 (5.6)
Pinyon	8	29.5 (1.6)	4.0 (0.8)	17.1 (2.3)	31.2 (7.6)	3.8 (1.3)
Pinyon-juniper	16	24.2 (1.0)	1.4 (0.2)	12.4 (1.0)	24.1 (3.0)	1.8 (0.8)
Ponderosa	2	31.5 (3.5)	1.0 (0.0)	21.5 (0.5)	47.4 (16.5)	2.9 (1.5)
Rabbitbrush	4	25.8 (1.4)	4.2 (1.4)	14.0 (1.9)	28.7 (11.5)	11.6 (6.7)
Sagebrush	8	22.8 (1.9)	1.6 (0.4)	12.6 (1.4)	35.7 (4.9)	6.3 (2.3)
Wet meadow	3	30.3 (4.9)	8.0 (1.2)	16.0 (6.0)	31.5 (12.2)	27.9 (5.4)
All types	97	25.0 (0.7)	2.3 (0.2)	12.7 (0.5)	29.1 (1.6)	5.0 (0.8)

Mean crust cover and mean maximum crust development also varied considerably by vegetation type (Table 2). The xeric blackbrush type had the highest mean crust cover (39.9% ± 3.8% cover), while the wet meadow type averaged only 0.1% ± 0.1% crust cover. The most xeric vegetation types (e.g., rabbitbrush, desert shrub, blackbrush type) had the highest mean maximum crust development scores (>10; well developed crusts).

Soil characteristics also varied by vegetation type (Table 2). The two plots in the ponderosa pine type, for example, averaged 93% sand and virtually no silt in the surface soil. The 16 plots in pinyon-junper averaged only 70.7% sand, the lowest sand content of all types, and 19.4% clay, the highest of all types. Mean percent C and N in the surface soil were relatively high in the mesic aspen type (1.89% ± 0.21% C; 0.13% ± 0.02% N) and wet meadow type (1.40% ± 0.44% C; 0.09% ± 0.03% N). However, the xeric, pinyon-juniper

Table 2. Mean cryptobiotic crust cover, maximum crust class, percent bare ground, sand, silt, clay, carbon and nitrogen for the various vegetation types in Table 1 (standard error in parentheses).

Vegetation type	No. of plots	Crust cover (%)	Max. class	Bare ground (%)	Sand (%)	Silt (%)	Clay (%)	C (%)	N (%)
Aspen	6	1.3 (0.5)	5.8 (2.9)	61.6 (4.0)	80.1 (2.2)	6.6 (1.9)	13.4 (1.1)	1.89 (0.21)	0.13 (0.02)
Blackbrush	22	39.9 (3.8)	11.5 (1.2)	75.0 (2.1)	85.1 (2.0)	4.3 (0.9)	10.6 (1.2)	0.80 (0.13)	0.02 (0.00)
Desert shrub	11	25.1 (5.0)	12.6 (1.6)	66.2 (4.2)	89.5 (2.0)	2.8 (1.0)	7.7 (1.1)	0.53 (0.10)	0.02 (0.00)
Juniper	15	17.0 (3.8)	9.7 (1.6)	68.2 (7.2)	80.6 (3.6)	6.3 (1.6)	13.1 (2.0)	1.09 (0.22)	0.04 (0.01)
Lowland riparian	2	2.8 (0.9)	8.5 (6.5)	77.9 (3.2)	83.3 (8.9)	6.8 (6.3)	9.9 (2.6)	0.97 (0.30)	0.02 (0.01)
Pinyon	8	9.5 (2.9)	9.8 (2.6)	63.8 (5.4)	82.1 (3.3)	6.4 (2.1)	11.5 (1.6)	1.08 (0.25)	0.05 (0.02)
Pinyon-juniper	16	14.0 (3.1)	10.1 (1.7)	77.4 (1.4)	70.7 (3.4)	9.8 (1.2)	19.4 (2.6)	1.77 (0.24)	0.08 (0.01)
Ponderosa	2	5.3 (2.3)	1.5 (0.5)	64.0 (13.4)	93.0 (1.9)	0.0	7.5 (0.8)	0.46 (0.14)	0.03 (0.02)
Rabbitbrush	4	23.1 (10.1)	14.0 (4.5)	64.6 (11.4)	89.2 (1.6)	2.5 (1.7)	8.3 (0.9)	0.55 (0.09)	0.03 (0.02)
Sagebrush	8	10.1 (3.4)	5.9 (2.6)	60.9 (6.2)	85.4 (2.9)	6.1 (2.2)	8.5 (1.2)	0.58 (0.12)	0.05 (0.01)
Wet meadow	3	0.1 (0.1)	0.3 (0.3)	29.8 (15.9)	83.5 (0.1)	6.8 (0.9)	9.7 (1.0)	1.40 (0.44)	0.09 (0.03)
All types	97	19.7 (1.9)	9.7 (0.7)	68.4 (1.8)	82.2 (1.1)	5.8 (0.5)	12.0 (0.7)	1.06 (0.08)	0.05 (0.00)

type was also high in percentage of C and N, while most other xeric vegetation types (e.g., desert shrub, rabbitbrush, and sagebrush) were low in them (Table 2).

Plant diversity, crust cover, and soils by topographic position

Native plant species richness, percent bare ground, and soil characteristics did not vary by topographic position (i.e., plots entirely in washes and lowland depressions versus drier, upslope areas; Table 3). However, mean exotic species richness was significantly greater in washes (3.2 ± 0.4 species/plot) than in upland sites (1.5 ± 0.1 species/plot). Likewise, the cover of exotic species was significantly greater in washes ($7.3\% \pm 1.4\%$) compared to upland sites ($3.1\% \pm 0.7\%$). Meanwhile, the cover of cryptobiotic crusts was significantly greater on the upland sites ($23.8\% \pm 2.7\%$) compared to washes ($15.2\% \pm 2.5\%$). The striking similarity between upland and wash sites in soil texture, percentages of N, C, and C : N was unexpected, given the differences in exotic species richness and cover (Table 3).

Plant diversity, crust cover, and soils by vegetation structure

Native and exotic plant species richness, crust cover, and all soil characteristics tested varied considerably by vegetation structure (shrublands versus forest; Table 4). Shrublands, on average, contained significantly fewer native and exotic species, and nearly three times the cover of cryptobiotic crusts as compared to forests. Shrublands, on average, had about half the percentage of N and C, and half the silt + clay fraction in the surface soil compared to plots with trees (Table 4). There were no significant differences in total bare ground, native species cover, or exotic species cover between shrublands and forests, although exotic species cover was consistently higher on plots with trees compared to plots dominated by shrubs (Table 4).

Table 3. Comparison of upland (dry) plots ($n = 51$) and plots in washes ($n = 45$) (Mean values shown with standard errors in parentheses).

Characteristic	Upland ($n = 51$)	Wash ($n = 45$)	$P <$
Total species	29.2 (1.1)	33.9 (1.6)	0.017
Native species	24.3 (0.9)	25.9 (1.0)	NS
Exotic species	1.5 (0.1)	3.2 (0.4)	0.001
Spp. <1% cover	13.0 (0.7)	12.4 (0.8)	NS
Native spp. cover	27.0 (1.7)	31.7 (2.9)	0.16
Exotic spp. cover	3.1 (0.7)	7.3 (1.4)	0.01
Bare ground cover	68.9 (2.7)	67.6 (2.5)	NS
Crypto cover	23.8 (2.7)	15.2 (2.5)	0.02
Max. crypto cover	9.8 (0.9)	9.3 (1.0)	NS
C (%)	0.97 (0.11)	1.13 (0.11)	NS
N (%)	0.05 (0.01)	0.05 (0.01)	NS
Sand	83.4 (1.5)	81.3 (1.7)	NS
Silt	5.4 (0.7)	6.1 (0.8)	NS
Clay	11.2 (1.0)	12.6 (1.1)	NS
C/N	31.1 (6.4)	35.2 (5.8)	NS

Table 4. Comparison of plots with a vegetation structure of shrubs ($n = 45$) or trees ($n = 49$) (Mean values shown with standard errors in parentheses).

Characteristic	Shrubs	Trees	$P <$
Total species	26.8 (1.1)	34.4 (1.3)	0.001
Native species	22.2 (0.9)	27.2 (0.8)	0.001
Exotic species	1.7 (0.2)	2.5 (0.3)	0.042
Spp. <1% cover	11.2 (0.6)	13.8 (0.7)	0.008
Native spp. cover	29.0 (1.9)	29.0 (2.6)	NS
Exotic spp. cover	3.9 (0.9)	4.6 (1.0)	NS
Bare ground cover	69.4 (2.1)	69.9 (2.6)	NS
Crust cover	29.5 (2.9)	11.8 (1.8)	0.001
Max. crypto cover	11.0 (1.0)	9.0 (0.9)	0.14
C (%)	0.68 (0.07)	1.17 (0.12)	0.001
N (%)	0.03 (0.00)	0.06 (0.01)	0.001
Sand	86.6 (1.2)	78.3 (1.8)	0.001
Silt	4.1 (0.7)	7.2 (0.8)	0.005
Clay	9.3 (0.7)	14.5 (1.2)	0.001
C/N	41.3 (8.8)	26.3 (2.6)	0.110

Relationships of plant species richness and cover to crust cover and soil percentage of N

Several significant linear relationships emerged between plant diversity characteristics and soil characteristics. For the 97 plots combined, native species richness was significantly positively correlated to elevation ($r = 0.28$, $P < 0.005$), and significantly negatively correlated to crust cover ($r = -0.22$, $P < 0.029$), soil percentage of clay ($r = -0.25$, $P < 0.015$), and $\log_{10}$ C : N ($r = -0.19$, $P < 0.07$). Exotic species richness was significantly, positively correlated to both native species richness ($r = 0.21$, $P < 0.039$) and native species cover ($r = 0.23$, $P < 0.025$). Exotic species richness was more strongly negatively correlated to the cover of cryptobiotic crusts ($r = -0.47$, $P < 0.001$). The cover of exotic plant species was also strongly negatively correlated to the cover of cryptobiotic crusts ($r = -0.39$, $P < 0.001$). Total percentage of N was strongly positively correlated with exotic species richness ($r = 0.40$, $P < 0.001$) and the cover of exotic plant species ($r = 0.37$, $P < 0.001$).

Predicting native and exotic species richness and cover

Multiple regression and path coefficient diagrams showed that native species richness and cover were difficult to predict from the suite of environmental variables analyzed (Figure 3A,B). Elevation and percent bare ground had 'direct' (Dewey and Lu 1959), positive effects on native species richness (i.e., positive standardized partial regression coefficients), while soil percentage of clay had a direct, negative affect (Figure 3A).

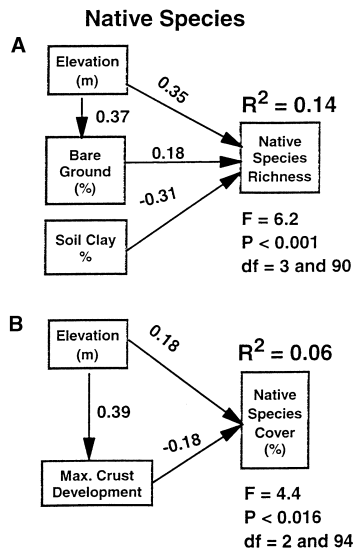

Figure 3. Path analysis of native species richness and cover. Direct arrows to native species richness (A) or cover (B) from prediction variables include standardized partial regression coefficient values, while arrows between prediction variables are simple regression coefficients.

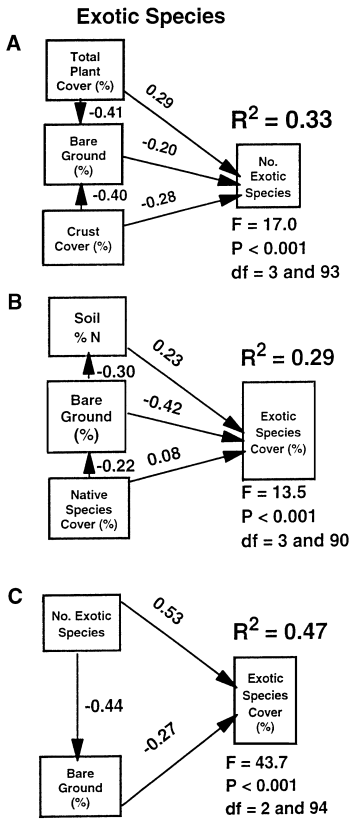

Figure 4. Path analysis of exotic species richness and cover. Direct arrows to exotic species richness (A) or cover (B and C) from prediction variables include standardized partial regression coefficient values, while arrows between prediction variables are simple regression coefficients.

There was also an 'indirect effect' of elevation on native species richness by the positive correlation of elevation to percent bare ground. Still, only 14% of the variance in native species richness was explained by these three variables, and this was partly due to the extremely low variance in native species richness for all the plots (Table 1).

There were weaker predictions for the cover of native plant species, with only 6% of the variance explained (Figure 3B). Elevation had a direct, positive effect, and maximum crust development had a direct, negative effect. Elevation was positively correlated to maximum crust development, which, in turn, was negatively correlated to native species cover.

Exotic species richness was far more predictable than native species richness and cover, with 33% of the variance explained by the model (Figure 4A). The total plant cover was a strong positive contributor to exotic species richness, while crust cover and percent bare ground had negative direct effects on exotic species richness. Both total plant cover and crust cover had negative effects on percent bare ground as would be expected. High total plant cover may indicate favorable habitats for plant productivity, and high crust cover may indicate habitats that are less disturbed by grazing, trampling, or flooding.

Exotic species cover was also far more predictable than native species richness and cover, with 29% of the variance explained by the model (Figure 4B). Here, soil percentage of N and native species cover were positively correlated with exotic species cover, while percent bare ground had a strong negative correlation. There was also a negative correlation between percent bare ground and soil percentage of N, and the more obvious negative correlation between native species cover and percent bare ground.

With information on the number of exotic species in a plot (i.e., the success of exotic species establishment), the cover of exotic plant species can be more accurately predicted (Figure 4C). About 47% of the variance in exotic species cover can be explained by the number of exotic species present and the cover of bare ground. This relationship is driven by the very strong positive

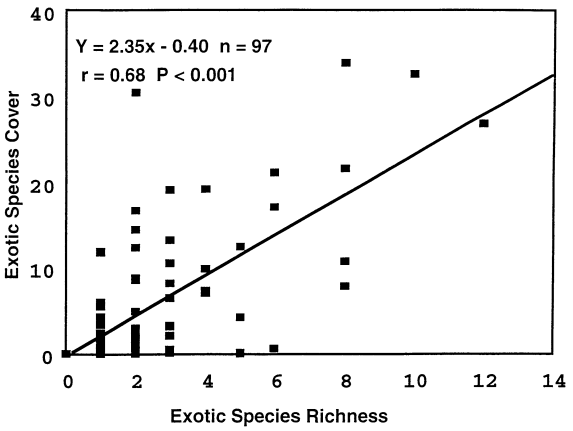

Figure 5. Relationship of exotic species richness and cover in 97 plots.

relationship between exotic species richness and cover ($r = 0.68$, $P < 0.001$; Figure 5).

Spatial coincidence of plant diversity and soil quality

There were obvious topologically coinciding gradients of plant diversity and soil quality in the study area (Figure 6). Thus, hot spots for exotic plant richness generally overlapped hot spots of native species richness, and both generally overlapped with patterns of high soil percentages of N and C. Equally obvious is the negative spatial relationship between exotic species richness and the cover of cryptobiotic crusts (Figure 7). The hot spots for exotic species richness are neatly offset from the hot spots of crust cover.

Discussion

Patterns of native plant diversity

In our recent studies in the Central Plains and Rocky Mountains, native species richness has proven to be an important predictor of exotic species richness and cover (Stohlgren et al. 1998b, 1999a,b). In addition to identifying hot spots of native plant diversity (Figure 6), there may be some urgency in locating areas of high native species richness to quickly detect, monitor, and potentially control exotic plant species in the Grand Staircase-Escalante National Monument.

There are several generalizations that can be made about the patterns of native plant diversity in this area of the Monument. Areas high in native species richness tended to be higher in elevation, and lower in crust cover, soil percentage of clay, and C : N relative to species-poor areas (Tables 1 and 2). For example, aspen, wet meadow, and ponderosa pine stands tended to be higher elevation sites than were species-rich areas low in crust cover and low in C : N (ca. 14–15). Note that we found native species richness was significantly negatively correlated to crust cover ($r = -0.22$, $P < 0.029$), while Jeffries (1989) and Kleiner and Harper (1977b) reported that vascular plant species richness and cover were positively correlated with crusted soils, and Anderson et al. (1982a,b) found no significant correlation between crusts and vascular plant cover. Our findings may have profound implications, particularly for species-rich habitat types. For example, the aspen, wet meadow, and ponderosa pine habitats tended to be relatively rare on the landscape, they are more mesic than most species-poor vegetation types, and except for ponderosa pine, the species-rich types tended to have higher soil percentage of N. Meanwhile, species-poor vegetation types such as blackbrush, sagebrush, and rabbitbrush tended to be more xeric, more common on the landscape, and lower in soil percentage of N and C : N (Tables 1 and 2). This general pattern has been found in the Rocky Mountains and Central Grasslands in the US (Stohlgren et al. 1999a, b). Aspen stands and wet meadows in Rocky Mountain National Park, Colorado, were species rich, mesic sites, and high in percentage of N relative to species-poor sites (Stohlgren et al. 1997a). As with riparian zones in the Central Grasslands (Stohlgren et al. 1998b) and northwest US (Planty-Tabacci et al. 1996), these species-rich, productive habitats were highly vulnerable to invasion by exotic plant species (Table 1).

Vulnerability of habitats to invasion

We can also make broad generalizations about the vulnerability of certain habitats to invasion in the study area, but there were notable local exceptions. Most of the heavily invaded sites were mesic, relatively rare habitat types that were rich in native species and cover, high in soil percentages of N and C, and low in crust cover, crust development, and bare ground. For example, the wet meadow vegetation type was the most heavily invaded habitat in the study area

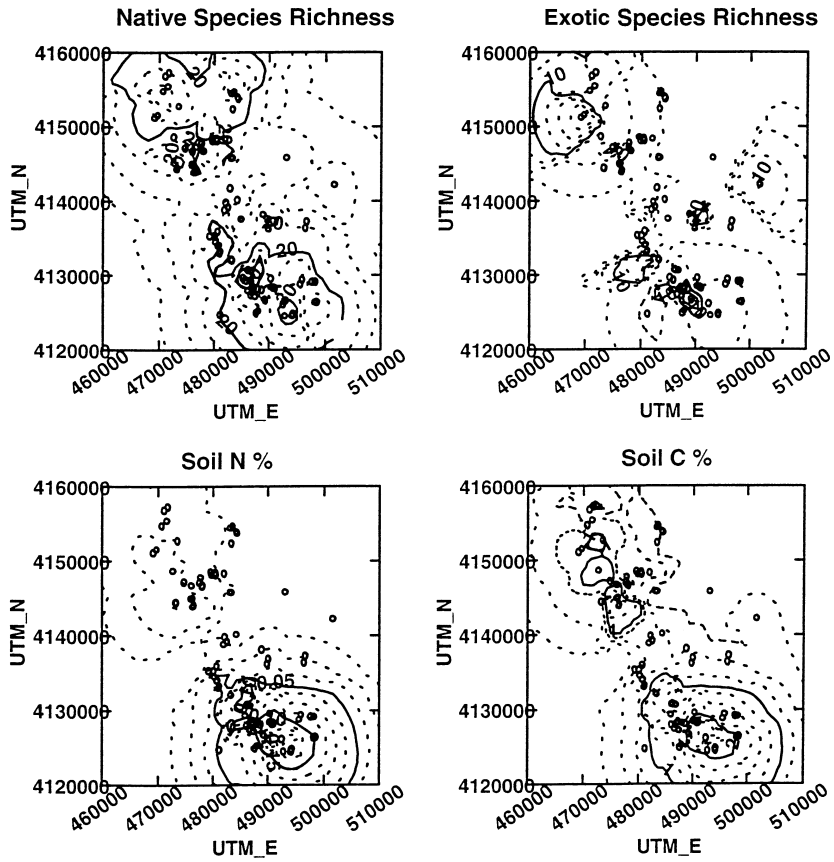

Figure 6. Kriging diagrams of native and exotic species richness, soil percentages of C and N over the study area. UTM coordinates are on the x- and y-axis.

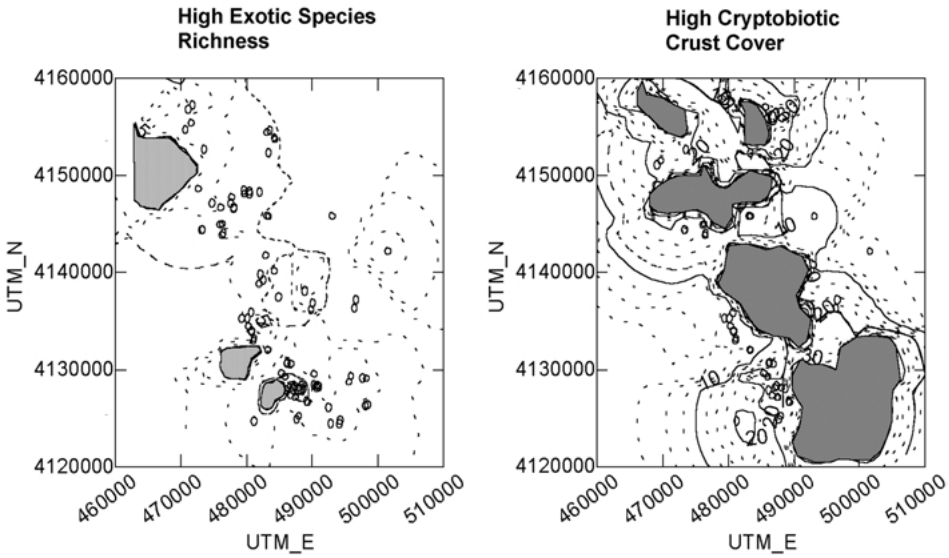

Figure 7. Kriging diagrams of areas of high exotic species richness (>2 species/plot) and the high cover of cryptobiotic crusts (>20%/plot) in the study region. UTM coordinates are on the x- and y-axis.

with an average of 8.0 exotic species per plot and 27.9% cover of exotic species (Table 1). Plots in the wet meadow type ranked third in native species richness, second in soil percentage of N, third in soil percentage of C, and lowest in crust cover, crust development, and bare ground (Table 2). The aspen type had the second greatest mean exotic species richness and third highest exotic species cover. The aspen type had the highest native species richness, ranked second in native species cover, ranked first in mean soil percentages of N and C, and had the second lowest crust cover and third lowest cover of bare ground. Meanwhile, the drier blackbrush, desert shrub, and sagebrush types were relatively poorly invaded by exotic species, contained fewer native species, and generally had higher crust cover, more bare ground, and lower soil percentages of C and N (Tables 1 and 2). There are now many studies suggesting that many species-rich areas may be particularly invasible (Fox and Fox 1986; Malanson 1993; DeFerrari and Naiman 1994; Robinson et al. 1995; Planty-Tabacchi et al. 1996; Stohlgren et al. 1997a, 1998b, 1999a; Levine 2000).

There were local exceptions to the general patterns of invasion in the Monument. The lowland riparian type had the second highest exotic species cover and third highest exotic species richness. This vegetation type had the third highest cover of native species and had the third lowest crust cover, but unlike the other heavily invaded vegetation types, the lowland riparian plots had the highest bare ground, were lowest in soil percentage of N, and were the second lowest in native species richness. This may be due to intermittent flooding that may reduce native species richness and total percentage of N in the soil, or to the increasing spread of the exotic salt cedar (*Tamarix* spp.) throughout the riparian zone, which may reduce limiting resources (e.g., light, nutrients, water). Plots in the ponderosa pine type were high in native species richness and cover, hence we would have anticipated high exotic species richness. However, few exotic species were found in these plots. We suspect that native species richness was high due to a mix of habitat-specific plant species in ponderosa pine stands (including shade-tolerant species), with habitat generalists from the surrounding vegetation types in more xeric micro-habitats. High percentage of sand in the upper soil layers (low soil moisture holding capacity), combined with low soil nitrogen (Table 2) and low light under the canopy may provide only marginal habitat for many invasive species in the ponderosa pine habitat.

Consistent patterns and possible mechanisms of invasion

There are many other possible causes for the patterns of invasion reported here. Propagule pressure may be disproportionately higher in certain areas, but it is difficult and impractical to measure, monitor, regulate, or manage propagule pressure at landscape scales, especially for seeds that are ubiquitously distributed by wind, large and small mammals, and insects. Historical factors such as species origin, autecology, and genetic variation may also be important (Mack et al. 2000). That is, exotic species in this species pool may favor fertile sites or more disturbed habitats. Likewise, escape from natural enemies may aid exotic species (Mack et al. 2000). Habitat characteristics are unquestionably important predictors of successful invasions (Tables 1–4; Figures 3, 4, 6, and 7), and they are relatively easier and inexpensive to measure and monitor. Isolating the causes of the patterns reported here are beyond the scope of this observational study. Instead, we draw the land manager's attention to the locations, habitats, and physical factors associated with the current patterns of successful invasion to aid in future research, control, and restoration efforts.

Several recent landscape-scale studies are reporting an alarming and consistent pattern in the Central Grasslands (Stohlgren et al. 1998b), Rocky Mountains (Stohlgren et al. 1997a, 1999a), and in portions of the Grand Staircase-Escalante National Monument (this study). Where resources are plentiful for native plant species (high light, soil percentage of N, and water), exotic plant species are also plentiful. We found strong positive relationships between total percentage of N and exotic species richness and cover, and mesic sites were generally more invaded than xeric sites (Tables 2–4, Figures 4 and 6). The easiest explanation is that native and exotic plant species take advantage of the same types of resources (Stohlgren et al. 1998b, 1999b) at the same time or at different times. Resources for invading species must be available, even in species-rich areas.

In arid environments like the Grand Staircase-Escalante National Monument, intact soil crusts may add available resources to a site by fixing nitrogen. Up to 70% of the nitrogen fixed by cyanobacteria and cyanolichens is released immediately into the surrounding soil environment, and is available to associated organisms including native and exotic plants, and native mosses, fungi, and other microbes

(Mayland et al. 1966). Studies have reported that the presence of soil crusts increase surrounding soil N by up to 200% (Jeffries 1989; DeFalco 1995). In addition, stable isotopes show soil crusts can be the dominant source of N for desert soils and plants (Evans and Ehleringer 1993; Evans and Belnap 1999). Though areas of intact crust are less invaded, resources may often be available for the establishment of invasive plant species in undisturbed habitats.

There could be many non-mutually exclusive mechanisms involved in invasibility. We propose that turnover (plant mortality and replacement, and subtle changes in species composition) may be one important mechanism in invasibility in predominantly undisturbed areas. In most of the habitats in the central US that we have surveyed, about half of the plant species averaged <1% foliar cover (Table 1; Stohlgren et al. 1999b). Low frequency and low cover may indicate high turnover in space and time, creating many opportunities for both native and exotic plants. There was a significant positive relationship between exotic species richness and the number of species with <1% cover ($r = 0.20$, $P < 0.045$). There was an even stronger significant positive relationship between total native species richness and the number of species with <1% cover ($r = 0.72$, $P < 0.001$). This may indicate that high species richness and high turnover may go hand in hand, but we are still investigating this relationship. This generally follows the theory of May (1973), who postulated that diverse systems would be particularly susceptible to high turnover. Likewise, Huston and DeAngelis (1994) showed that many species can coexist in spatially heterogeneous areas as long as nutrients and light are not limiting. Seed sources for exotic plant species are often readily available in the soil seed bank or via the matrix of riparian zones and roads that are corridors for invasion (Stohlgren et al. 1998b), and from other ubiquitous dispersers of invasive species (e.g., wildlife, wind, and livestock). Still, plant turnover in undisturbed areas may result in only moderate frequency and relatively low cover of invasive plant species (Stohlgren et al. 1999b), so seed availability (Tilman 1997) and plant turnover in harsh environments may be only part of the story.

The second general mechanism is that disturbance of soil crusts greatly accelerates the invasion process (DeFalco 1995; Larsen 1995; Howell 1998). Intact soil crusts often present a physical barrier to invasive species establishment and growth by preempting space. We found that exotic species richness was strongly negatively correlated to the cover of cryptobiotic soil crusts ($r = -0.47$, $P < 0.001$). Larsen (1995) and Howell (1998) showed that germination of native *Stipa* was not affected by soil crust cover, while germination of *Bromus tectorum* was inhibited by intact crusts. *Bromus* germination was stimulated when crusts were broken but left in place. Once the crusts are disturbed by grazing, trampling, or vehicle use, resources, particularly nitrogen, becomes temporarily available for the establishment of native or exotic plant species (Belnap 1995, 1996).

The moderate frequency and relatively low cover of invasive species resulting from plant turnover may predispose the greater landscape to disturbance-enhanced invasion. Plant turnover throughout a landscape may provide widely dispersed seed sources and seed reserves in soils. Subsequent trampling by livestock or recreationists can produce moderately high cover of exotic species richness and cover (Table 2 and 3) such that previously rare disturbances such as fire could become more commonplace, further enhancing the invasion. Increased invasion of exotic species could lead to extirpation of native plant species. In contrast to previous theories about invasion, this study and our other studies (Stohlgren et al. 1998b, 1999a) suggest that it might be difficult for the plants and crusts in species-rich areas to completely monopolize resources in fertile sites (Case 1990) to maintain stability (Tilman et al. 1996), and to resist invasion (Elton 1958). The invasion is taking place in disturbed and undisturbed habitats throughout many continental landscapes (Stohlgren et al. 1999a,b).

Management implications

Exotic plant species have successfully invaded Grand Staircase-Escalante National Monument. Over this broad landscape, 94% of the plots in the study area have been invaded by at least one exotic plant species. There are several reasons for concern. First, exotic plant species are invading hot spots of native plant diversity and rare/unique habitats. These habitats often contain our most treasured botanical resources (i.e., rare species). Second, although the mechanisms are poorly understood at this time, it is clear that habitats that were vulnerable to invasion by several exotic plant species had higher cover of exotic species (Figure 5). Assuming some upper limit of resource availability, increased cover by exotic species may put some native

species at a disadvantage as exotic species sequester resources. This sets the stage for the local replacement of native species by exotic species. Third, continued disturbance of fragile cryptobiotic crusts by livestock and recreationists may facilitate the further invasion of exotic plant species. The long recovery times of damaged crust may provide ample opportunity for invasive exotic plants to gain a foothold on the landscape.

Given current patterns of invasion, endemic and other native plant species, pollinators, and soil organisms and crusts for which the National Monument was established, will be particularly difficult to preserve. We recognize that trampling by ecologists also negatively impact crusts and we will rely more heavily on species-area relationships and predictive models to reduce trampling of the most fragile habitats and we have reduced our sampling of crusts.

Control efforts for exotic plant species need to be focused on heavily invaded areas and newly invaded areas. Care must be taken in the use of control agents targeted at exotic species within areas of high native species richness.

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