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Soil characteristics and plant exotic species invasions in the Grand Staircase—Escalante National Monument, Utah, USA

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Abstract

The Grand Staircase—Escalante National Monument (GSENM) contains a rich diversity of native plant communities. However, many exotic plant species have become established, potentially threatening native plant diversity. We sought to quantify patterns of native and exotic plant species and cryptobiotic crusts (mats of lichens, algae, and mosses on the soil surface), and to examine soil characteristics that may indicate or predict exotic species establishment and success. We established 97 modified-Whittaker vegetation plots in 11 vegetation types over a 29,000 ha area in the Monument. Canonical correspondence analysis (CCA) and multiple linear regressions were used to quantify relationships between soil characteristics and associated native and exotic plant species richness and cover. CCA showed that exotic species richness was significantly ($P < 0.05$) associated with soil P ($r = 0.84$), percentage bare ground ($r = 0.71$), and elevation ($r = 0.67$). Soil characteristics alone were able to predict 41 and 46% of the variation in exotic species richness and cover, respectively. In general, exotic species invasions tend to occur in fertile soils relatively high in C, N and P. These areas are represented by rare mesic high-elevation habitats that are rich in native plant diversity. This suggests that management should focus on the protection of the rare but important vegetation types with fertile soils.
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Keywords: Native plant diversity; Cryptobiotic crusts; Modified-Whittaker plots

1. Introduction

The proclamation and establishment of the Grand Staircase—Escalante National Monument (GSENM) acknowledges the area's important ecological values. The Monument includes many endemic plant species and an abundance of unique isolated plant communities. The Monument is home to 50% of Utah's rare plant species, 11 of which are endemic, and 84% of the state's flora (Shultz, 1998). However, exotic plant species comprise one of the most significant threats to the ecological integrity of the Monument (Davidson and Belnap, 1997). Exotic plants species can be toxic to livestock and wildlife and can replace native plant species (Harper et al., 1996). Recent studies have shown that exotic plant species have successfully invaded areas rich in native plant diversity, such as the tallgrass prairie, wet meadows and

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aspen vegetation types in the Rocky Mountains and central grasslands (Stohlgren et al., 1999, 2001). In some of the areas of the Monument, exotic species are widely dispersed and in many areas may become locally dominant. Stohlgren et al. (2001) reported that exotic species were found in 94% of sample plots ($n = 97$) in the Fifty Mile Mountain area, and suggested that given current patterns of invasion, it may be challenging to preserve native plant species and soil crusts for which the National Monument was established. In particular, cheatgrass (*Bromus tectorum*) can rapidly establish in disturbed areas after fire, causing increased fuel loads and a decrease in the fire return interval in a positive feedback cycle (Davidson and Belnap, 1997).

The Monument's managers face numerous challenges including, protecting native plants while providing for recreation, grazing, mineral exploration and natural fire regimes on the landscape. Our interest was whether exotic species invasion were correlated with particular soil characteristics. We use survey data on vegetation, soils and crusts, and a correlative approach to examine specific soil characteristics under which exotic plants have successfully established in the Monument.

Our objectives were to: (1) quantify patterns of native and exotic plant species and cryptobiotic crusts; and (2) determine the relationships of soil characteristics, at the landscape scale, to successful invasions by exotic plant species in the study area.

2. Materials and methods

2.1. Study areas

As part of the Colorado Plateau, GSENM ranges in elevation from 1372 to 2530 m and encompasses over 772,000 ha. The Monument's rugged configurations of canyons, monolithic cliffs, arid climate and extreme temperatures allow a unique array of biological diversity. A 29,000 ha area in the southeast corner of the Grand Staircase—Escalante National Monument was selected for intensive study (Fig. 1). Random plot locations were selected in 11 vegetation types recognized on the Monument's vegetation map (Table 1). Additional sites were randomly located in rare habitat types (e.g. wetlands, relict plant habitats; Stohlgren et al., 1995, 1998); as they were encountered in the field.

Table 1
Major vegetation types within the Monument study area

Vegetation type	Scientific name of dominant(s)
Aspen	*Populus tremuloides*
Blackbrush	*Coleogyne ramossissima*
Desert shrub	*Gutierrezia sarothrae*
Juniper	*Juniperus* spp.
Lowland riparian	*Salix* spp.
Pinyon	*Pinus edulis*
Pinyon/juniper	*P. edulis*/*Juniperus* spp.
Ponderosa pine	*Pinus ponderosa*
Rabbitbrush	*Chrysothomnus* spp.
Sagebrush	*Artemisia tridentata*
Wet meadow	*Agrostis stolonifera*

2.2. Multi-scale vegetation plots and soil analyses

Each modified-Whittaker plot measured 20 m × 50 m and was placed with the long axis parallel to the environmental gradient (Stohlgren et al., 1995; Fig. 2). Multi-scale plots provide far more detailed information on plant diversity than single-scale plots by capturing more locally rare native and exotic plant species (Stohlgren et al., 1998, 1999). Nested in each plot were ten 0.5 m × 2 m (1 m^2) subplots systematically spaced along the inside border, two 2 m × 5 m (10 m^2) subplots in alternate corners, and a 5 m × 20 m (100 m^2) subplot in the plot center. Foliar cover for each species, and cover of cryptobiotic crust (by class; see below), bare ground, rock, litter (detached dead plant material), duff (attached dead plant material), water and dung were estimated to the nearest percent in the ten 1 m^2 subplots. Species that occupied <1% in a subplot were recorded as 0.5% cover. Additional plant species (not found in the ten 1 m^2 subplots) were noted in the 10 and 100 m^2 subplots, and in the entire 1000 m^2 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; Belnap, 1995, 1996). Ancillary data recorded for each plot included slope, aspect, UTM location and elevation from a Global Positioning System.

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 herbaria at the Colorado State

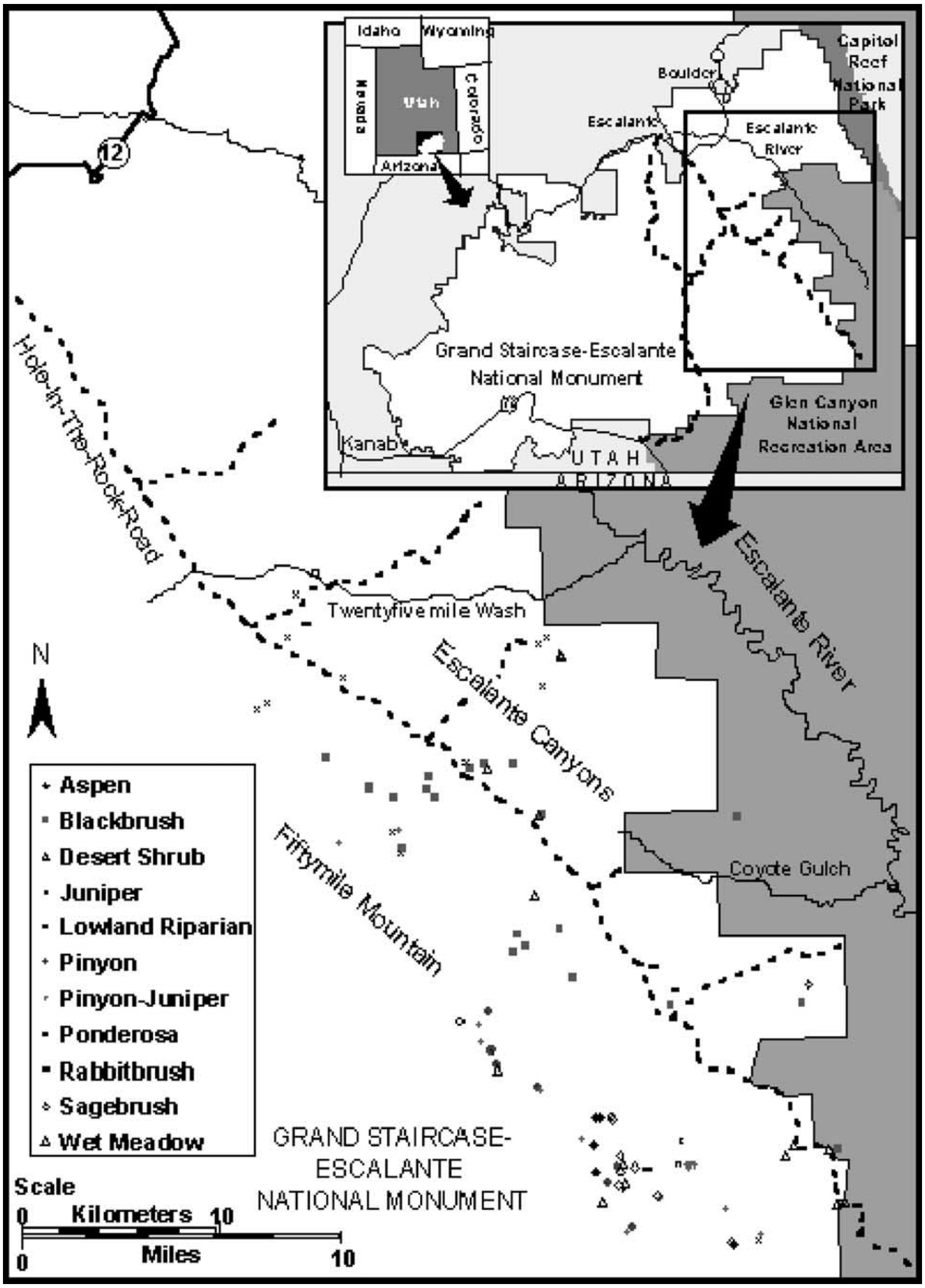

Fig. 1. Map of the study sites.

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. Unidentified species were not used in analyses. Species were classified as native or exotic according to the Natural Resource Conservation Service PLANTS database (USDA, 1999).

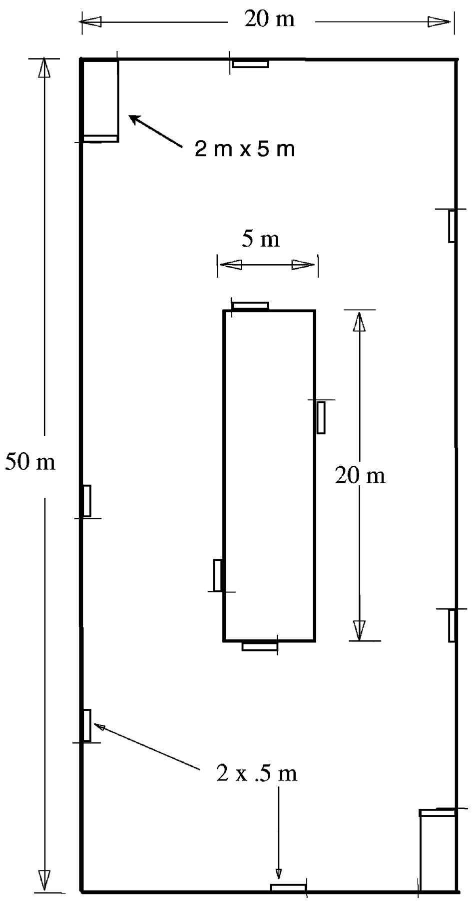

Fig. 2. Diagram of modified-Whittaker plot.

Five soils samples, one in each corner and the center, were taken with 2.5 cm diameter core to a depth of 15 cm in each modified-Whittaker plot and pooled into one composite sample. Samples were air-dried for at least 48 h and sieved to 2 mm (number 10 standard sieve). Particle size was determined using the standard hydrometer method (Gee and Bauder, 1986). To determine Ca, K, Na and Mg, 25 ml of ammonium acetate was added to 5 g of soil and buffered to pH 8.5. The soil + solution was shaken for 5 min, centrifuged, and the supernatant was decanted off. This process was repeated three more times for a total of 100 ml of extract (Sumner and Miller, 1996). Cations were determined from the filtered extract by inductively coupled plasma emission spectrometry.

For soil C, N and P, soils were ground to a fine powder in a three-ball grinder. Samples were then oven-dried at 55 °C for 48 h prior to analyses. Samples were analyzed for percentage of total carbon and nitrogen using a LECO-1000 CHN analyzer (LECO Corporation, Saint Joseph, MO, USA). Inorganic carbon from carbonates was determined using a volumetric method (Wagner et al., 1998). Organic carbon was calculated by difference between total and inorganic C. Soil P was determined colorimetrically from a sodium bicarbonate extraction (Kou, 1996).

2.3. Statistical analysis

Data distributions were skewed and transformed prior to analyses with either $\log_{10}$ or square root to improve normality. We used canonical correspondence analysis (CCA; PC-ORD, version 3.0; ter Braak, 1986, 1987) to characterize the relationships between species composition (cover and richness) and the environmental measurements (e.g. soil characteristics, elevation). CCA is a direct gradient analysis technique that constrains the extracted pattern to linear combinations of the measured environmental variables (ter Braak, 1986, 1987), and is proven a robust method for describing species–environment relationships (Palmer, 1993; Reed et al., 1993). We first ran detrended correspondence analysis to test for linear, unimodal responses of key variables and we were reasonably assured that CCA would provide reasonable results (also see Palmer, 1993). We ran CCA on two separate data sets. The first contained species richness for dominant (>1% cover) and subdominant (<1% cover) native and exotic species and cryptobiotic class. The second data set consisted of cover data for native and exotic species, *B. tectorum* and cryptobiotic crust. The species richness and cover data sets were evaluated against the same 11 environmental variables: soil C (total carbon), Ci (inorganic carbon), N, P, K, Na, K, Mg, clay, elevation and bare ground. We assessed all environmental variables for multicollinearity problems and none were found. Monte Carlo permutation tests were performed to test the significance of the first axis, a randomization of the plots with 99 permutations (ter Braak, 1991). Finally, environmental variables used in CCA were used as independent variables in stepwise forward multiple regressions (SPSS, 2000) to predict native and exotic species cover and richness, *B. tectorum* cover, and cryptobiotic cover and class.

3. Results

3.1. Native and exotic species richness and cryptobiotic crusts

The plots averaged 28.0 ± 0.8 native plant species, and 2.3±0.2 exotic plant species ($n = 97$). Ninety-one of 97 plots contained at least one exotic species, and of those 28 plots had more than three exotic plant species per 0.1 ha plot. On average native species cover was 30.6 ± 1.8%, and exotic species cover was 4.8 ± 0.8% per plot (Table 2). *B. tectorum* was the dominant exotic species, accounting for 68% of total exotic species cover. Cryptobiotic crusts averaged 19.6±1.9% cover, and bare ground averaged 68.4 ± 1.8%. Cryptobiotic crusts were present in 94 of the 97 plots, 25 plots had <5% cover, and 31 plots had >25% crust cover.

3.2. Species richness and cover, crust cover, and soils by vegetation type

Plant species richness and cover varied greatly among vegetation types (Table 2). In the high-elevation aspen type native species richness averaged 35.6±3.3 species per 0.1 ha plot, while the low-elevation blackbrush type averaged only 21.3 ± 1.3 species per plot. Likewise, an aspen plot contained the greatest number of native species (45 species), in comparison to blackbrush, which contained the fewest native species (11 species). The ponderosa pine and wet meadow types were also high in native species richness: 39.5 ± 6.5 and 37.3 ± 4.9, respectively.

In general, exotic species richness increased with native species richness (Table 2). The wet meadow type averaged 6.3 ± 1.2, the aspen averaged 4.5 ± 0.9, and the lowland riparian type averaged 4.5 ± 0.5 exotic species. In comparison, the xeric lowland vegetation types like blackbrush, desert shrub, sagebrush and pinyon/juniper contained less than two exotic species per plot (Table 2). The exception to this trend was the species-rich ponderosa pine type (39.5 ± 6.5 native species per plot), which averaged only one exotic species per plot. Exotic species cover was highest in the wet meadow type (24.0 ± 8.8% cover) and lowest in the desert shrub type (1.4 ± 0.8% cover).

Cryptobiotic crust cover and maximum crust development also varied between vegetation types (Table 2). The wet meadow types averaged 0.1 ± 0.1% crust cover, while the blackbrush type had the highest average crust cover (39.9 ± 3.8% cover). The drier vegetation types (e.g. rabbitbrush, desert shrub, blackbrush type) contained the highest mean maximum crust development classes (>10; well-developed crusts).

3.3. Canonical correspondence analysis of native and exotic species richness

Canonical correspondence analysis found that the centroids of native and exotic species richness

Table 2
Summary statistics for 11 vegetation types in the Monument study area

Vegetation type	Number of plots	Number of native species	Number of exotic species	Native cover (%)	Exotic cover (%)	*Bromus* cover (%)	Cryptobiotic cover (%)
Juniper	15	28.9 ± 1.9	1.7 ± 0.5	25.7 ± 3.9	4.2 ± 1.9	3.6 ± 1.61	17.7 ± 3.8
Pinyon/juniper	16	26.9 ± 1.4	1.4 ± 0.2	25.1 ± 3.5	1.8 ± 0.8	1.6 ± 0.83	13.9 ± 3.1
Sagebrush	8	27.2 ± 2.8	1.7 ± 0.4	37.3 ± 5.0	6.3 ± 2.3	6.2 ± 2.31	10.1 ± 3.4
Rabbitbrush	4	28.2 ± 1.1	4.2 ± 1.4	32.3 ± 12.0	11.1 ± 6.7	8.8 ± 7.31	23.1 ± 10.1
Blackbrush	22	21.3 ± 1.3	1.3 ± 0.1	29.6 ± 2.3	2.8 ± 1.0	2.8 ± 0.96	39.9 ± 3.8
Low riparian	2	26.0 ± 1.0	4.5 ± 0.5	40.2 ± 22.0	15.5 ± 5.6	9.5 ± 0.42	2.8 ± 0.9
Aspen	6	35.6 ± 3.3	4.5 ± 0.9	47.0 ± 9.7	8.6 ± 2.5	7.4 ± 2.15	1.3 ± 0.5
Desert shrub	11	27.5 ± 2.0	1.7 ± 0.3	26.4 ± 3.6	1.4 ± 0.8	1.4 ± 0.76	25.0 ± 4.9
Ponderosa	2	39.5 ± 6.5	1.0 ± 0.0	49.2 ± 17.0	2.9 ± 1.5	2.9 ± 1.52	5.3 ± 2.3
Pinyon	8	33.7 ± 2.3	3.2 ± 0.4	34.4 ± 7.9	3.4 ± 1.6	3.1 ± 1.15	9.5 ± 2.8
Wet meadow	3	37.3 ± 4.9	6.3 ± 1.2	35.7 ± 14.0	24.0 ± 8.8	1.9 ± 1.06	0.1 ± 0.1
All vegetation types	97	28.1 ± 0.8	2.3 ± 0.2	30.6 ± 1.8	4.8 ± 0.2	4.2 ± 0.6	19.6 ± 1.9

The values are given as mean ± S.E.

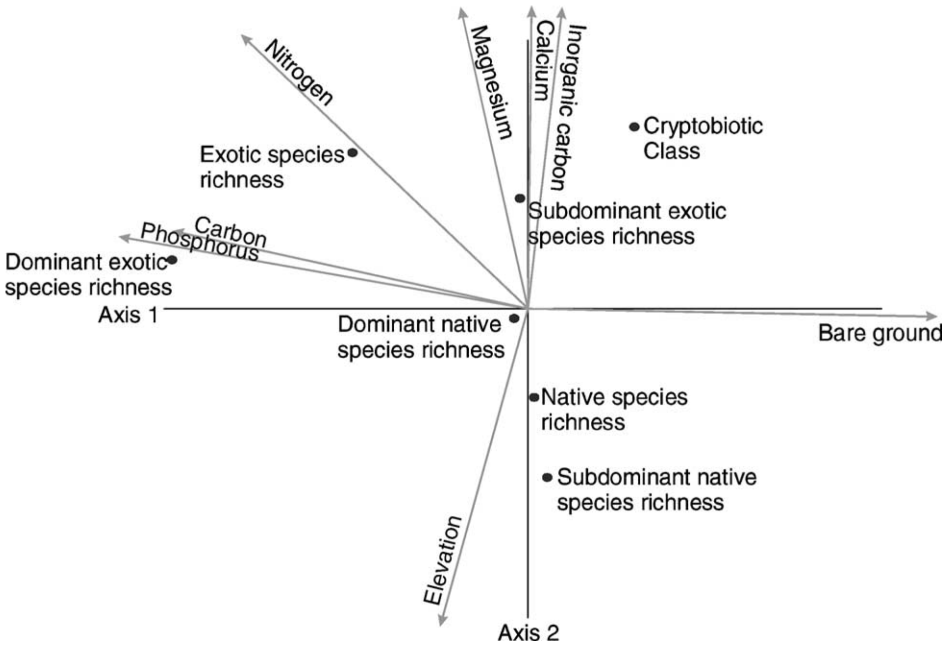

Fig. 3. Canonical correspondence analysis ordination for native and exotic species richness and cryptobiotic class. The "dominant" designation refers to the number of species with >1% cover. The "subdominant" designation refers to the number of species with <1% cover. Total richness is the total number of species regardless of cover.

were separated by many soil characteristics (Fig. 3). The centroid for native species richness was located closer to the center of the diagram, corresponding to low-elevation and less-fertile soils. The centroid for exotic species richness was located in higher soil nutrient areas lying directly on the soil N gradient. The centroid for dominant exotic species richness (the number of exotic species with cover >1%) also was linked to a soil nutrient gradient most closely associated with increasing soil C and P.

The first two canonical axes explained 36.9% of the cumulative variance for species richness. The top three environmental factors that correlated significantly ($P < 0.05$) with canonical axis 1 included: soil P ($r = -0.84$), bare ground ($r = 0.71$) and elevation ($r = -0.67$). The top three environmental factors that correlated significantly ($P < 0.05$) with canonical axis 2 included: soil Mg ($r = 0.54$), soil inorganic carbon ($r = 0.54$), and elevation ($r = -0.44$). Monte Carlo permutations tests showed that first canonical axis was significant (eigenvalue $= 0.029$; $P < 0.01$).

3.4. Canonical correspondence analysis of native and exotic species cover

The centroid of native species cover corresponded to higher elevation areas with moderately high soil nutrients (Fig. 4). The exotic species cover centroid corresponded to areas high in soil P and other nutrients. The centroid for cryptobiotic cover corresponded to areas of high bare ground and lower soil nutrients. The centroid for *B. tectorum* cover, located between axes 1 and 2, is positively correlated with soil P and negatively correlated with bare ground. The first two canonical axes explained 41.6% of the cumulative variance for native, exotic, cryptobiotic and *B. tectorum* cover. The top three environmental factors that correlated significantly ($P < 0.05$) with canonical axis 1 included: soil P ($r = -0.81$), bare ground ($r = 0.77$) and elevation ($r = -0.65$). Environmental factors that correlated significantly ($P < 0.05$) with canonical axis 2 included: soil in organic carbon ($r = 0.42$), soil C ($r = -0.42$) and elevation ($r = -0.44$). Monte Carlo permutations tests showed that first

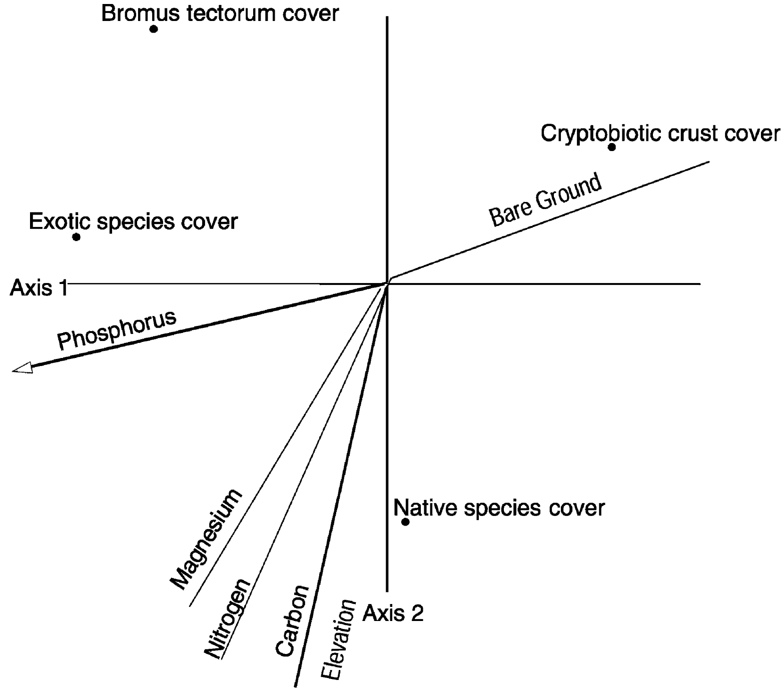

Fig. 4. Canonical correspondence analysis ordination for native and exotic species, cryptobiotic crust and *B. tectorum* cover.

canonical axis was significant (eigenvalue = 0.098; $P < 0.001$).

3.5. Predictors of native, exotic and cryptobiotic richness and cover

Multiple regression analysis showed that only a subset of the abiotic variables measured were significant predictors of native and exotic species richness and cover, and cryptobiotic class and cover (Table 3). Elevation and bare ground were the most common and significant of the variables measured. Soil P was also a significant predictor for exotic species cover ($P < 0.001$) and richness ($P < 0.001$). The percent variance explained by the environmental variables ranged from a low of 13% for native cover to a high of 53% for exotic species richness.

When biotic variables (e.g. native species richness and cover, cryptobiotic cover), were added to the multiple regression, the coefficients of determination (R^2) for two out of the seven dependent variables increased by more than 5%. Twelve percent more variation in the exotic species richness was explained by the addition of cryptobiotic cover and native species richness. Six percent more variation was explained by the addition of exotic species richness. The remaining variables changed by $<\pm2\%$.

4. Discussion

4.1. Patterns of native and exotic species richness and cover

As expected native plant species establish and succeed in a broad array of environments. The canonical correspondence analysis showed that the centroids for dominant and total native species richness appear near the origin, suggesting equal preference for all habitats (Figs. 3 and 4). A variety of native species have adapted to various environments from xeric lowlands (e.g. blackbrush), to rare mesic habitats (e.g. aspen, wet meadows). Meanwhile native cryptobiotic crusts appear to fill in soil habitats typically lower in soil

Table 3
Stepwise forward multiple regressions for species composition (richness and cover), *Bromus* and cryptobiotic cover

Dependent variable/predictor	Coefficient	t	P	Model F, R^2, P
Number of native species				
Constant	3.016	17.488	<0.001	$F = 16.2$, $R^2 = 0.25$, $P < 0.001$
Elevation	<0.001	5.595	<0.001	
Mg	−0.247	−3.161	0.001	
Native species cover				
Constant	4.247	16.691	<0.001	$F = 7.9$, $R^2 = 0.13$, $P = 0.001$
Bare ground	−0.010	−2.664	0.009	
Cryptobiotic class	−0.116	−1.617	0.110	
Cryptobiotic cover				
Constant	2.817	4.222	<0.001	$F = 17.5$, $R^2 = 0.44$, $P < 0.001$
Ca	<0.001	3.290	0.002	
C	−1.659	−5.165	<0.001	
Bare ground	0.012	1.722	0.089	
Number of exotic species	−0.542	−2.173	0.033	
Cryptobiotic class				
Constant	2.469	3.325	0.001	$F = 13.7$, $R^2 = 0.22$, $P \leq 0.001$
Elevation	−0.001	−2.979	0.004	
Bare ground	0.015	2.627	0.010	
Number of exotic species				
Constant	0.119	0.200	0.842	$F = 16.2$, $R^2 = 0.53$, $P < 0.001$
Elevation	−0.001	−4.161	<0.001	
Mg	0.344	2.601	0.011	
P	0.275	3.813	<0.001	
Bare ground	−0.008	−3.005	0.004	
Cryptobiotic cover	−0.093	−2.464	0.016	
Number of native species	0.528	3.654	<0.001	
Exotic species cover				
Constant	2.671	3.556	0.001	$F = 23.1$, $R^2 = 0.43$, $P < 0.001$
Elevation	−0.001	−1.465	0.147	
P	0.622	4.204	<0.001	
Bare ground	−0.026	−4.505	<0.001	
Bromus cover				
Constant	3.086	3.768	<0.001	$F = 10.3$, $R^2 = 0.33$, $P < 0.001$
Elevation	−0.001	−1.906	0.061	
Na	−0.003	−1.610	0.112	
P	0.569	3.491	0.001	
Bare ground	−0.022	−3.523	0.001	

nutrients. The interpretation of the cryptobiotic data is preliminary and disturbance history needs to be considered (Belnap, 1995). The distribution of cryptobiotic crusts and their complex interactions with exotic plant species is beyond the scope of this paper and requires further study.

In pre-European America, native plant species and cryptobiotic crusts shared the soil resources without many large grazing animals and invading plant species from Europe, Asia, Africa and elsewhere. Trampling from grazing animals and tourists can reduce crust cover and increase the germination of *B. tectorum* (Larsen, 1995; Howell, 1998). When crusts are disturbed soil nitrogen availability temporarily increases and can facilitate the germination of exotic or native plant species.

4.2. The role of soils in exotic plant invasions

The Grand Staircase—Escalante National Monument is a complex landscape and our current ability to predict exotic species richness and cover is better than our ability to predict native species richness and cover. Soil characteristics explained 24 and 14% of native species richness and cover, respectively. In contrast, soil characteristics explained 41 and 46% of exotic species richness and cover, respectively. Certain patterns are evident. First, exotic species establish and succeed better in resource-rich areas. For example, the wet meadow and aspen types have the most fertile soils (highest in C, N and P) and receive more precipitation because they are located at high elevations, or located near natural springs. These habitats are also among the highest for exotic cover and richness (Table 2). The CCA biplots for species richness shows the centroid for exotic species richness is closely associated with increasing soil N, and the centroid for dominant exotic species (exotic species richness where cover >1%) is closely associated with increasing soil C and P (high resource environments; Fig. 3). Likewise, the centroid for exotic species cover is associated with soil P (Fig. 4). The reverse is also true. Exotic species tend to have lower establishment and success in low resource environments. For example, blackbrush and desert shrub vegetation types are the lowest in exotic species richness and cover (Table 2).

The distribution of exotic species on this landscape is troubling for several reasons. Exotic species do not grow well in all habitats, thus we are gaining a moderate ability to predict current distributions based on soils habitat data. Soil P may prove to be a powerful indicator of exotic species establishment and success.

In this study, we used linear models to assess relationships between species composition and soil characteristics. However, the relationships we aim to describe may be non-linear (Fig. 5). There could be threshold effects in which above a certain

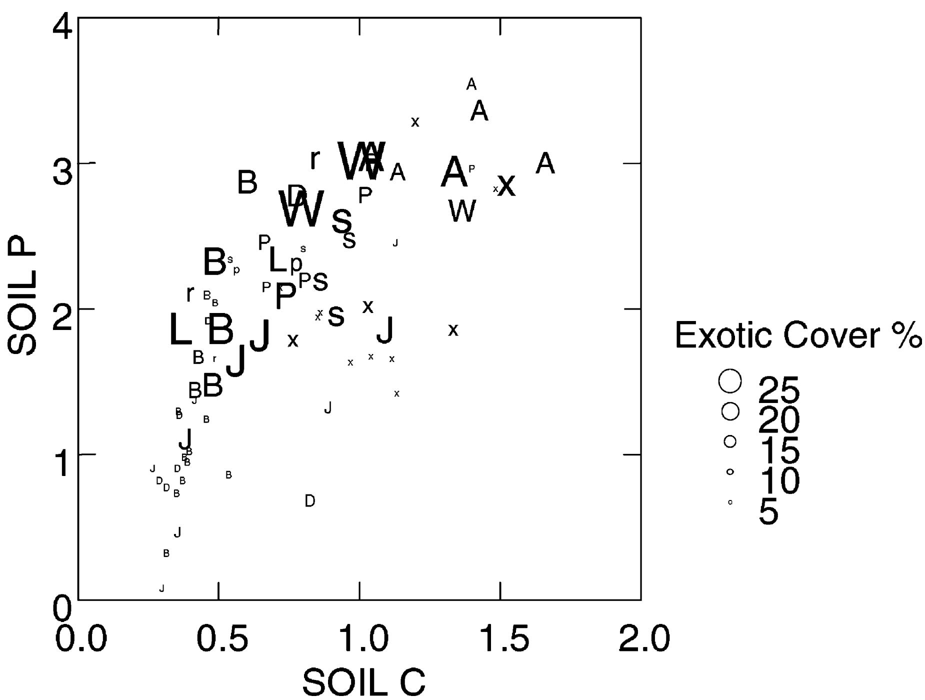

Fig. 5. Relationship between soil $P_{\log 10}$ and soil $C_{\text{square root}}$ and exotic species cover$_{\log}$ by vegetation types within the study area. The size of the symbol represents the approximate percent exotic cover in the modified-Whittaker plot. A, Aspen; B, blackbrush; D, desert shrub; J, juniper; S, sagebrush; L, lowland riparian; r, rabbitbrush; w, wet meadow; P, pinyon; p, ponderosa; x, pinyon/juniper.

concentration of soil P, exotics may establish and succeed. Defining these threshold levels requires further research.

4.3. Management implications

Habitats containing fertile soils appear more vulnerable than those with less-fertile soils. Thus, a shift in soil conditions brought about by air pollution (N deposition) or manure fertilizer could shift the balance for native and exotic species locally. Rare habitat types appear more vulnerable than common vegetation types. Aspen, wet meadow and riparian types, which are the most biologically diverse, are the most heavily invaded. This suggests management should focus on the protection of these rare habitats types within the Monument. Heavily disturbed areas, such as roadsides, burned areas and trampled sites appear vulnerable to invasions. Where soil fertility is high, disturbance may greatly enhance the invasion process. Ultimately, management actions may dictate the success or failure of exotic species in the Monument.

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