

PATTERNS OF PLANT SPECIES RICHNESS, RARITY, ENDEMISM, AND UNIQUENESS IN AN ARID LANDSCAPE

THOMAS J. STOHLGREN,^{1,3} DEBRA A. GUENTHER,² PAUL H. EVANGELISTA,² AND NATHANIEL ALLEY²

¹Fort Collins Science Center, U.S. Geological Survey, 2050 Centre Street, Building C, Fort Collins, Colorado 80526 USA

²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA

Abstract. Most current conservation literature focuses on the preservation of hotspots of species diversity and endemism, as if the two were geographically synonymous. At landscape scales this may not be the case. We collected data from 367 1000-m² plots in the Grand Staircase–Escalante National Monument, Utah, USA, to show that: (1) the vast majority of plant species are locally rare; (2) species-rich areas are generally in rare, mesic, or high-elevation habitats such as aspen stands or riparian zones high in soil N and P; (3) endemic species (to the Colorado Plateau and the Monument) were generally found in relatively species-rich, but low-elevation, xeric vegetation type areas low in soil P; (4) unique species assemblages were found in areas moderately high in endemism and species richness; and (5) nonnative plant species were widely distributed, but more prevalent in species-rich, mesic sites high in soil fertility or disturbed sites, and significantly less prevalent in plots with endemic species. We show that primary hotspots of species richness, high endemism, and unique species assemblages are not co-located on the landscape. Hence, conservation strategies may have to consider a much broader concept of “hotspots” to adequately preserve native plant species and the processes that foster persistence.

Key words: conservation strategies; Grand Staircase–Escalante National Monument, Utah, USA; hotspots; nonnative species; plant species diversity; species–environment relationships.

INTRODUCTION

When Myers et al. (2000) reported that 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 1.4% of the globe, there was only a mild uproar from the scientific community on the species that would be disregarded (e.g., Smith et al. 2001, Kareiva and Marvier 2003). Preserving “hotspots” of endemism and diversity is appealing for many reasons. Only small areas of land need be protected to preserve many species, so this is cost-efficient. This, in turn, could leave more land for consumptive uses. More importantly, safeguard measures could be put in place to reduce threats to biodiversity in the highest priority areas. Recently, it was shown that for 121 areas worldwide, species richness and endemism were strongly positively correlated (Hobohm 2003); thus, ranking hotspots of both would be relatively straightforward. Alternative strategies for conservation might concentrate on rare species patterns (Prendergast et al. 1993, Dobson et al. 1997), highly threatened ecosystems (Sisk et al. 1994), and even “biodiversity coldspots” (e.g., the Greater Yellowstone Ecosystem, polar bear habitat, and wetlands; Kareiva and Marvier 2003). While these philosophical debates

continue, we find surprisingly few attempts to accurately quantify large-scale patterns of various attributes of diversity (e.g., Williams et al. 1996, Kier and Barthlott 2001).

Whether any of these “silver bullet” approaches might work at smaller spatial scales, such as a national park or wildlife refuge, has yet to be tested. The concept of hotspots may apply at local, regional, and global scales. For example, in Rocky Mountain National Park, Colorado, over 70% of the bird species utilize stands of aspen (*Populus tremuloides*), which comprise <8% of forest cover (DeByle 1985, Kaye et al. 2004). Narrow riparian zones dissecting large tracts of desert and arid ecosystems throughout the world serve as major hotspots of plants, mammals, amphibians, fish, butterflies, and other groups (Malanson 1993). Designation as a national monument does not infer complete protection of biodiversity from invasive species, livestock grazing, air pollution, climate change, recreation, altered disturbance regimes, resource extraction, or other internal or external threats. With limited operating funds, it may be possible for land managers to concentrate conservation efforts on a subset of habitats in large natural areas.

There are reasons to be suspicious of simple solutions to the complexities of biodiversity conservation. Smith et al. (2001) reasoned that external processes may be responsible for the persistence of species that frequently reside inside hotspots, but temporarily in other areas, and that ecological processes in the en-

Manuscript received 31 October 2003; revised 18 May 2004; accepted 27 July 2004; final version received 20 August 2004.
Corresponding Editor: T. D. Sisk.

³ Present address: Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA. E-mail: toms@NREL.Colostate.edu

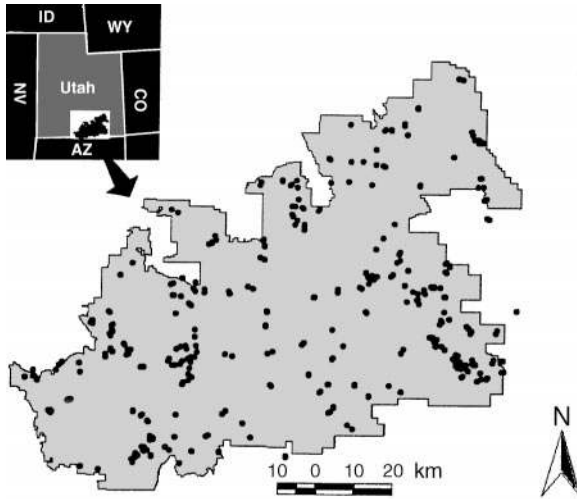


FIG. 1. Map of the 367 modified-Whittaker plot locations surveyed on the Grand Staircase-Escalante National Monument, Utah, USA, from 1998 to 2002.

Environmental transition zones may generate and maintain the hotspots. Kareiva and Marvier (2003) argued that large carnivores require large tracts of land, and that some species-poor areas (e.g., salt marshes) provide ample ecological services in terms of wastewater treatment and fish production. Emphasis placed on protecting hotspots of diversity or endemism may ignore the contribution of species-poor or moderately rich areas for species preservation. These same cautionary notes may apply from global down to local scales. Many national parks, wildlife refuges, and national forests have legal mandates to protect native biodiversity in total, including threatened and rare species and unique species assemblages, whether they are confined to hotspots or not. Clearly, large-scale inventories of native diversity and habitat characteristics are needed to guide conservation strategies in complex environments.

Our objectives were to document plant species rarity, patterns of high and low species richness and endemism, and to identify areas of unique species assemblages in the Grand Staircase-Escalante National Monument, Utah. The 850 000-ha Monument was established in 1996 (Presidential Proclamation 6920), in part, to preserve the unique plant diversity in an arid, southwestern U.S. ecosystem. The Monument serves as a typical case study to show the value of multi-scale resource assessments in developing conservation strategies for complex landscapes.

STUDY AREA AND METHODS

The study area included the entire Grand Staircase-Escalante National Monument, Utah, USA (Fig. 1), which is a portion of the Colorado Plateau. The tablelands of the Colorado Plateau include arid grasslands and shrublands, sparse to closed woodlands, and large

and small patches of forests (Comstock and Ehleringer 1992). Utah is ranked in the top five states in the United States for endemic species (Shultz 1993), and 174 plant species are locally or regionally endemic to the Colorado Plateau or the Monument (Fertig et al. 2002). This concentration of endemic species is attributed to arid, stressful environments, multiple exposed soil and bedrock types, and adjoining phylogeographic elements (Comstock and Ehleringer 1992, Shultz 1993). McLaughlin (1986) concluded that many plant species in the Southwest are of recent postglacial origin (neo-endemic) that have not migrated very far, making them extremely valuable for conservation. The Monument has 43 plant species that are considered globally rare (ranked G1–G3 by the Nature Conservancy) and ~83 plant species are considered rare within the state (ranked S1–S3 by the Nature Conservancy; Fertig et al. 2002), and 11 plant species are found nowhere else in the world (Shultz 1993, Fertig et al. 2002).

Like many areas in the western United States, southern Utah is also plagued by nonnative plant species. Cheatgrass (*Bromus tectorum*) is widespread and can dominate in disturbed areas, while tamarisk (*Tamarix* spp.) can dominate riparian zones (Stohlgren et al. 2001, Waters 2003). Nonnative plant species in the American West can have direct and indirect negative effects on rare plant species (Rosentreter 1994).

During peak phenology from 1998 to 2002, 367 modified-Whittaker multi-scale plots (Stohlgren et al. 1995, 1998) were established across the Monument in 19 different vegetation types (Fig. 1). We used a stratified-random design in which 280 of the plot locations were randomly pre-selected based on a coarse-scale vegetation-type map. To reduce travel costs and capture less common, poorly mapped mesic vegetation types, 63 “second plot” locations were randomly located in such types as they were encountered traveling to the pre-selected points. In addition to the randomly located plots established in 2001 and 2002, we located 24 plots in under-represented types (riparian zones, springs, and burned areas). The plots still missed extremely rare features such as hanging gardens, but we feel the plots provide a near-complete, and widespread representation of the Monument’s typical vegetation types.

The nested plot was 20 × 50 m and contained one 100-m² subplot in the center, two 10-m² subplots in opposite corners, and 10 1-m² subplots systematically arranged around the edge of the 1000-m² and 100-m² plots. Foliar cover and average height by plant species was recorded in the 10 1-m² subplots, along with the nearest percent cover of soil, cryptobiotic crusts by development stage (eight classes from weakly developed to fully developed; modified from USDI 1995), litter (detached dead plant material), duff (attached or standing dead plant material), woody debris, water, dung, bare soil, and rock. Plant species were recorded as 0.5% cover if they occupied <1% in a 1-m² subplot. Cumulative plant species presence was recorded in the

10-m², 100-m², and 1000-m² plots. Ancillary data included the slope and aspect of the plot, and elevation derived from a Digital Elevation Model. Prior to field sampling, we developed a simple “moisture index” by ranking the individual vegetation types and then groups of vegetation types from the most xeric types (from desert shrub, 1, to rabbitbrush, 15) to the most mesic types (from aspen, 16, to perennial riparian, 19), based on basic plant ecology (e.g., Comstock and Ehleringer 1992, Shultz 1993) and on local knowledge.

Soil samples were taken with a 2.5-cm diameter core to a depth of 15 cm in the center and in the corners of the 1000-m² plot, and combined to represent the plot. The samples were air dried for at least 48 h and sieved to 2-mm particles (number 10 standard sieve). The standard hydrometer method (Gee and Bauder 1986) was used to determine soil particle size. Remaining samples were ground to a fine powder in a three-ball grinder and then oven-dried at 55°C for 48 h for soil C, N, and P analysis. A LECO-1000 CHN analyzer (LECO corporation, Saint Joseph, Missouri, USA) was used to analyze the samples for the percentage of total carbon and nitrogen. A volumetric method (Wagner et al. 1998) was used to distinguish inorganic carbon from carbonates. The difference between total and inorganic carbon was calculated as the organic carbon. Soil P was determined colorimetrically from a sodium-bicarbonate extraction (Kou 1996). To calculate 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 plus solution was shaken for 5 min, centrifuged, and the supernatant was decanted off. The process was repeated for three more times for a total of 100 mL of extract (Sumner and Miller 1996). Inductively coupled plasma emission spectrometry (model IRIS Advantage spectrometer, Thermo Jarrell Ash Corporation, Franklin, Massachusetts, USA) was used to determine cations from the filtered extract.

All plant species were identified and classified as native or nonnative based on Welsh et al. (1993). Specimens we were unable to identify in the field were collected and sent to S. L. Welsh and N. D. Atwood at Brigham Young University, Provo, Utah, USA. Approximately 8% of the collected plant specimens were unidentifiable due to grazing or pre-mature phenology stage. Unidentified species were not used in analyses.

We created a “uniqueness value” for each 1000-m² modified-Whittaker plot based on the average relative frequencies for the plant species recorded in the study. Thus, a plot that contained many common, ubiquitous species would have a lower uniqueness value than a plot that contained many locally rare, infrequently occurring species. Relative frequencies ranged from 0.8 for *Gutierrezia sarothrae* (293 of 367 plots; 80%) to 0.003 (0.3%) for species that occurred in only one plot. We calculated each plot’s uniqueness value based on the average frequency values for all plant species within a plot, divided by plot species richness as follows:

Uniqueness

$$= 1 - \frac{\sum \text{species proportional frequencies on a plot}}{\text{plot species richness}}.$$

Thus, the uniqueness values reflected the relative rarity of species in the sample plots and were corrected for plot species richness. Plot uniqueness values ranged from 0.54 for a plot in the sagebrush type (14 total species, many of them common generalists) to a high of 0.97 for a perennial riparian plot with 38 plant species with most of the species found on very few plots.

Species-accumulation curves were developed using Estimate-S software (Colwell 1997). The program randomizes the plots to create generalized curves for various species groups (e.g., native or nonnative species, endemic species) or for various vegetation types. Forward stepwise discriminant analysis (SYSTAT version 10.0; SPSS 2000) was used to compare plot characteristics in xeric vs. mesic vegetation types, and to identify the vegetation, soils, and cryptobiotic crust characteristics that differentiated plots that contained endemic species from those plots without endemic species present. Multiple forward stepwise regression was used to determine what biotic and environmental factors were important in predicting native and nonnative species richness, number of endemic species, and uniqueness at the 0.1-ha plot scale. In the discriminant and multiple regression analyses, we reduced the effects of multicollinearity in two important ways. First, we excluded complementary variables (e.g., percentage of soil sand and percentage of clay were included, but silt was removed; young and well-developed crust cover were included, but intermediate crust classes were excluded) from the models. Second, all variables used in the regressions were screened for high cross-correlation (i.e., tolerance values >0.9), and would have been removed from further models, but none were found. We recognize the over-reliance of multiple regression models (Neter et al. 1990), but we used them here to compare the predictability of native and nonnative species richness, uniqueness, and endemism of the same group of plots in a consistent manner. In addition, only variables that met the $P < 0.15$ criterion were included in the models. These regression models may not always result in the “best” regression model for all comparisons (see Neter et al. 1990: 452–453), but the reported relationships agreed with field observations.

Finally, we used inverse-distance weighting and kriging algorithms (with 10 nearest neighbors) to develop trend surface maps of hotspots of native and nonnative species richness, endemism, and uniqueness (ArcGIS, Version 8.2 with standard software defaults; ESRI 2004). The inverse-distance weighting method predicts values for all unmeasured locations (i.e., only plot data were used), assuming that each measured point has a local influence on unmeasured locations

(i.e., predicted values) that diminishes with distance (Alley et al. 2004). Kriging is a simple way to interpolate findings from points (i.e., the 367 plots) to the broader landscape, and to group, map, and display similar neighboring points (see Chong et al. 2001, Alley et al. 2004). The default grouping mapped “smart quantiles,” which is an appropriate technique for our specific data set and others like it. Smart quantiles delineate “classes based on natural groupings of data values” where “breakpoints are identified by looking for groupings and patterns inherent in the data” (ArcGIS, version 8.2; ESRI 2004). Thus, the resulting classes delineated big jumps in the data values, where groups of plots with similar values were placed in the same class. Five “smart quantile” classes were displayed for each response variable above. The highest quantiles were considered “primary” hotspots, the second quantiles were “secondary” hotspots, etc. Areas of the hotspots were calculated individually and collectively for primary and secondary sites.

RESULTS

In this section, we report on species commonness and rarity, the completeness of sampling, and the contribution of vegetation types to patterns of richness, endemism, and uniqueness. Only after examining these issues can we evaluate factors associated with the spatial patterns of richness, endemism, and uniqueness in the Monument.

Species commonness and rarity

We found that only a few species are common and that most plant species in the Monument are rare and patchily distributed. Common native species included *Gutierrezia sarothrae* (broom snakeweed; 304 plots), *Stipa hymenoides* (Indian ricegrass; 283 plots), *Juniperus osteosperma*, (Utah juniper; 250 plots), *Artemisia tridentata* (big sagebrush; 233 plots), and *Elymus elymoides* (bottlebrush squirreltail; 215 plots). However, only eight species occurred in 50% of the plots. Only 59 plant species found occurred on 10% or more of the plots, and about one-third of the species captured were only encountered in one or two of the 367 plots sampled, creating a sharp inverse-J-shaped frequency distribution.

Most nonnative species also were rare and patchily distributed with the exception of *Bromus tectorum* (cheatgrass), a nonnative annual grass found on 252 plots. The second most-frequent nonnative plant species was redstem stork's bill (*Erodium cicutarium*), which was found on 53 plots, while Russian thistle (*Salsola iberica*) was found on 44 plots. Very few plant species appear to be generalists.

Two endemic species, *Shepherdia rotundifolia* and *Cymopterus purpureus* var. *purpureus*, had a wide regional range, occurring on 19 and 15 bedrock types, respectively, of the 45 primary bedrock types that are found in the Monument. Thirty-five other endemic spe-

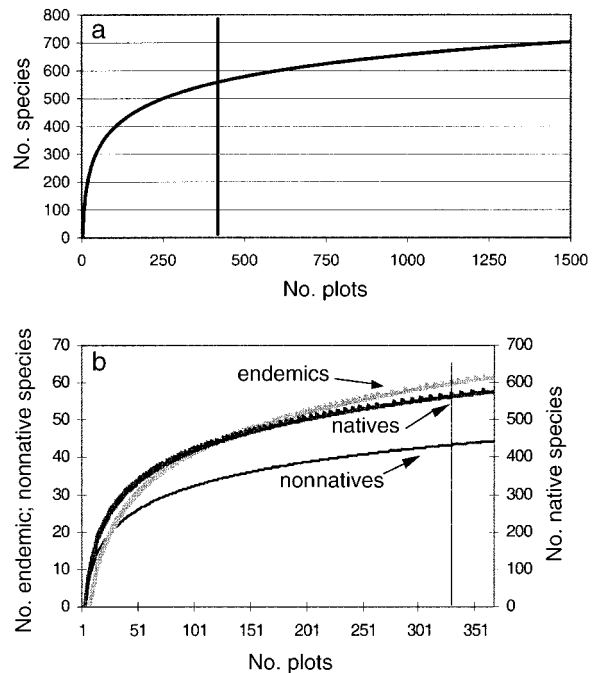


FIG. 2. (a) Extrapolated species accumulation curves for all species (vertical line indicates 367 plots) and (b) species accumulation curves for native, nonnative, and endemic plant species (vertical line indicates 332 plots) in the Grand Staircase–Escalante National Monument. Disturbed, seeded plots were excluded in panel (b).

cies were found on only one or two bedrock types in the sample.

Completeness of sampling

The 367 0.1-ha plots sampled translated to 36.7 ha of the 850 000-ha Monument, which represents a sampling intensity of 0.004% of the study area. Remarkably, we captured 550 of the 940 plant species known to occur in the Monument, including 63 of the 174 endemic species. The endemic species consisted of 15 annual forb, 44 perennial forb, and four shrub species. Species accumulation curves for all plant species (Fig. 2a), and for native and nonnative plant species and endemic plant species specifically (Fig. 2b), began to level off, suggesting a fairly complete and balanced sampling of the groups for our purposes. We estimated that it would take ~20 300 randomly selected, 0.1-ha plots to capture all plant species in the Monument. This would represent a sampling intensity of 0.23% of the Monument, which sounds modest, but would have been cost prohibitive. However, it is instructive that native, nonnative, and endemic species were captured at fairly similar rates in the sample so that broad patterns of each group can be evenly evaluated (Fig. 2b).

Contribution of different vegetation types to richness, endemism, and uniqueness

Native species richness per 0.1-ha plot was greatest in more mesic habitats, which are uncommon on the

TABLE 1. Mean (± 1 SE in parentheses) plant species richness, frequency of endemic species (number of plots with endemic species divided by number of plots in that type), and uniqueness values (lower values indicate more unique sites) per modified-Whittaker plot by vegetation type on the Grand Staircase–Escalante National Monument, Utah, USA, surveyed from 1998 to 2002.

Moisture index and vegetation type	No. plots	Species richness		Percent cover		Frequency of endemics (%)	Uniqueness
		Native	Nonnative	Native	Nonnative		
1) Desert shrub	29	22.4 (1.4)	1.9 (0.2)	16.2 (2.0)	2.0 (0.6)	55	0.79 (0.01)
2) Blackbrush	27	21.2 (1.1)	1.2 (0.2)	29.2 (2.0)	2.4 (0.9)	44	0.76 (0.01)
3) DS/grassland	16	26.8 (1.8)	1.6 (0.3)	21.5 (4.3)	2.2 (0.6)	75	0.77 (0.02)
4) Sagebrush	31	20.6 (1.7)	1.7 (0.2)	24.6 (1.9)	3.1 (0.8)	35	0.72 (0.02)
5) Juniper/sage	17	20.1 (1.5)	2.5 (0.4)	24.7 (3.1)	7.4 (2.0)	35	0.72 (0.01)
6) Juniper	22	28.5 (1.8)	1.3 (0.2)	16.5 (1.9)	0.4 (0.2)	54	0.76 (0.01)
7) PJ/sage	21	22.8 (1.3)	1.2 (0.2)	31.2 (2.4)	0.9 (0.3)	38	0.70 (0.01)
8) Disturbed PJ	35	17.9 (1.3)	3.9 (0.4)	15.2 (2.4)	11.9 (1.7)	46	0.74 (0.01)
9) PJ	81	25.6 (0.8)	0.8 (0.1)	25.1 (1.5)	0.7 (0.4)	73	0.75 (0.01)
10) PJ/Manz.	6	35.8 (1.9)	0.3 (0.2)	35.8 (6.2)	0.1 (0.04)	83	0.80 (0.01)
11) PJ/oak	18	32.3 (2.1)	1.2 (0.4)	42.6 (4.4)	0.5 (0.3)	67	0.79 (0.01)
12) Pinyon pine	4	26.0 (4.6)	1.2 (0.5)	35.3 (10.6)	1.3 (0.8)	75	0.80 (0.01)
13) Ponderosa/Manz.	7	27.6 (2.1)	0.6 (0.2)	38.8 (7.3)	0.8 (0.6)	28	0.78 (0.01)
14) Mountain shrub	11	30.4 (2.2)	1.2 (0.3)	34.6 (4.8)	1.9 (1.1)	82	0.78 (0.01)
15) Rabbitbrush	9	24.9 (1.5)	3.1 (0.7)	29.7 (5.1)	5.5 (3.3)	44	0.80 (0.01)
16) Aspen	6	33.3 (3.1)	4.7 (1.0)	57.6 (6.0)	8.7 (2.5)	50	0.87 (0.01)
17) Wet meadow	3	33.7 (5.0)	6.7 (0.9)	37.0 (9.5)	27.5 (5.3)	33	0.88 (0.01)
18) Spring	2	39.5 (3.5)	6.5 (2.5)	29.8 (6.7)	5.4 (4.7)	100	0.83 (0.01)
19) Perennial riparian	22	26.3 (2.2)	5.8 (0.4)	35.3 (4.7)	12.3 (2.2)	32	0.86 (0.01)
1–15) Xeric types combined	333	24.2 (0.5)	1.6 (0.1)	25.2 (0.8)	2.9 (0.3)	56.0 (2.7)	0.75 (0.01)
16–19) Mesic types combined	33	29.1 (1.8)	5.7 (0.4)	39.2 (3.7)	12.6 (1.8)	39.4 (8.6)	0.86 (0.03)

Notes: Abbreviations are: PJ, pinyon-juniper; DS, desert shrub; and Manz., Manzanita. Vegetation types are ordered by a moisture index; values >15 indicate mesic types. The stepwise discriminant analysis model included only the richness and cover of native and nonnative species and could correctly classify 92% of the xeric vs. mesic plots ($P < 0.0001$, Wilks' lambda = 0.60).

landscape of the Monument (Table 1). Xeric vegetation types (desert shrub to sagebrush) with low moisture index values averaged about five fewer native species and five fewer nonnative species per plot than mesic types (aspen to perennial riparian zone types). Native and nonnative species cover also were greater in the same mesic habitats. However, nonnative species richness and cover were also high in disturbed pinyon-juniper stands. Because many of these disturbed sites were seeded with some nonnative species in restoration efforts, they were excluded from the regression and mapping results that follow later.

Endemic species occurred in 146 of 332 plots (post-fire and seeded plots excluded). The frequency of endemic species was generally greatest in the more common xeric plant communities in the Monument (Table 1). Xeric vegetation types (types 1–15) averaged 0.98 ± 0.06 endemic species per plot, while mesic types averaged 0.48 ± 0.12 endemic species per plot (t test $P = 0.014$). Field observations indicated that plots in pinyon pine associations had consistently higher frequencies of endemism. The two plots by springs contained endemic species, but they were located in the drier portions of the large 20×50 m plots.

Uniqueness tended to increase with the moisture index (Table 1). Mean uniqueness was significantly lower for the xeric vegetation types (0.75 ± 0.01 ; mean ± 1 SE) compared to the mesic vegetation types (0.86 ± 0.03 ; $P < 0.05$). Our data suggest that plots in xeric

vegetation types generally contain fewer total species per plot, a higher frequency of endemic species, and a few more generalist, common species than mesic plots, which have high richness of native and nonnative plant species and more unique species assemblages (Table 1).

Species accumulation curves for native species were similar among vegetation types (Fig. 3). That is, species richness accumulated almost as quickly in common vegetation types (e.g., desert shrub) as in rare vegetation types (e.g., perennial riparian). However, species accumulation curves for nonnative species or endemic species could be very different among vegetation types. For example, mesic vegetation types, such as the perennial riparian type, quickly accumulated nonnative species, while xeric types slowly accumulated nonnative species (Fig. 3). In contrast, it was the xeric vegetation types, such as desert shrub, that quickly accumulated endemic species, while mesic types accumulated endemic species more slowly with additional sampling. The steeply increasing species accumulation curve for endemic species in the common desert shrub vegetation type suggests that many more endemic species would be recorded with additional sampling (Fig. 3).

Factors associated with endemism, richness, and uniqueness

Plots that contained endemic species often differed significantly in biotic and abiotic characteristics. Analysis showed that five factors discriminated plots that

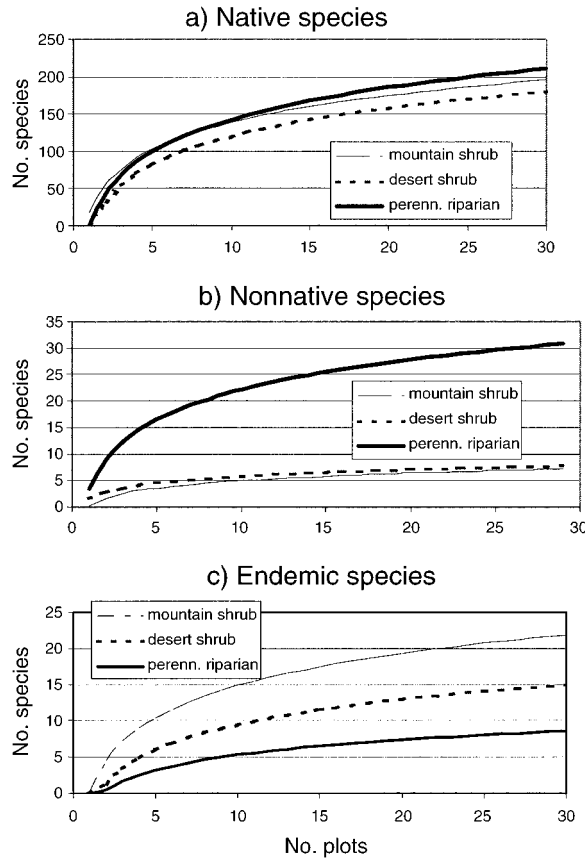


FIG. 3. Example vegetation-type contributions to (a) native species richness, (b) nonnative species richness, and (c) endemic species richness as calculated by species accumulation curves. Data are from 332 plots in the Grand Staircase–Escalante National Monument.

contained endemic species, including higher native species richness but slightly lower native species cover, lower cover of *Bromus tectorum*, and high clay content in the soil but lower soil N (Table 2). Plots with or without endemic species were correctly classified 67% of the time. In addition, plots with endemic species consistently had more unique species assemblages, greater cover of intermediate and well-developed soil crusts, lower nonnative species richness and cover, and lower soil P compared to plots without endemic species, but these were not singled out by the discriminant analysis.

There were significant positive correlations between native species richness per plot and the \log_{10} number of endemic species per plot ($r = 0.36$, $P < 0.0001$), the \log_{10} number of nonnative species per plot ($r = 0.12$, $P < 0.03$), and plot uniqueness ($r = 0.52$, $P < 0.0001$). Uniqueness also was positively correlated with the \log_{10} number of endemic species per plot ($r = 0.25$, $P < 0.001$). Meanwhile, the \log_{10} number of nonnative species per plot was negatively associated with the \log_{10} number of endemic species per plot (r

$= -0.16$, $P = 0.004$), but positively associated with the plot uniqueness ($r = 0.37$, $P = 0.0001$).

Native species richness varied little across the Monument, with a standard error of only 0.5 species/plot for the mean of 25.4 species per plot ($n = 332$ plots). Multiple linear regressions showed that native species richness per plot was strongly positively correlated to the percentage of sand and clay in the soils, elevation, and the moisture index (i.e., more mesic vegetation types; Table 3). Only 15% of the variation in native species richness was explained by the six independent variables.

The primary predictor variables for endemic species richness included strong positive correlations with native species richness and the percentage of soil clay, and strong negative correlations with total foliar cover and the percentage of soil P (Table 3). Note that native species richness was significantly positively correlated with total foliar cover ($r = 0.20$, $P < 0.001$), which is generally associated with increased productivity. Therefore, endemic species were found in the native species-rich, but lower productivity sites. Almost 28% of the variation in endemic species richness was explained by the seven independent variables.

Native species richness was the primary determinant of uniqueness (Table 3). However, while native species richness and endemic species richness increased with elevation, uniqueness was significantly negatively correlated with elevation. Forty-six percent of the variation in plot uniqueness was explained by the seven independent variables.

Over 79% of the plots contained at least one nonnative plant species, and the foliar cover of nonnative species was significantly positively correlated to native species richness ($r = 0.66$, $P < 0.0001$). The primary predictors of nonnative species richness included a negative correlation with elevation, and positive correlations with soil P, moisture, and total foliar cover (Table 3). Forty percent of the variation in nonnative species richness was explained by the 10 factors.

TABLE 2. Variables selected in stepwise forward discriminant analysis differentiating plots (mean ± 1 SE in parentheses) with endemic species ($n = 199$) or without endemic species ($n = 168$) in the Grand Staircase–Escalante National Monument from 1998 to 2002.

Variable	Plots with endemic species	Plots without endemic species
Native species cover (%)	26.3 (1.1)	26.6 (1.4)
Native species richness (%)	27.3 (0.6)	21.5 (0.6)
<i>Bromus tectorum</i> cover (%)	1.3 (0.2)	3.1 (0.5)
Soil clay (%)	17.5 (0.9)	15.0 (0.6)
Soil N (%)	0.14 (0.02)	0.22 (0.04)

Note: The stepwise forward discriminant analysis model was significant at $P < 0.0001$, with Wilks' lambda = 0.83, and with 67% plots correctly classified as plots with or without endemic species.

TABLE 3. Summary of multiple regression results for the dependent variables of native species richness, endemic species richness, uniqueness, and nonnative species richness per 1000-m² plot.

Variables and habitat characteristics	Coefficient	Standardized coefficient	P
Native species richness ($N = 318$, $F_{6,312} = 10.6$, $R^2 = 0.15$, $P < 0.001$, $SE = 7.8$)			
Constant	-3.955	0.000	0.549
Moisture index	0.234	0.137	0.015
Bare ground (%)	-0.042	-0.101	0.061
Sand (%)	0.205	0.434	0.000
Clay (%)	0.242	0.311	0.007
Soil K	-0.009	-0.107	0.072
Elevation	0.006	0.202	0.000
No. endemic species (\log_{10}) ($N = 316$, $F_{7,309} = 18.5$, $R^2 = 0.28$, $P < 0.001$, $SE = 0.2$)			
Constant	-0.135	0.000	0.075
Clay (%)	0.006	0.274	0.000
Total cover (%)	-0.002	-0.202	0.000
Soil P	-0.007	-0.182	0.001
Soil Mg	-0.000	-0.123	0.037
Soil Ca	0.000	0.075	0.144
Elevation	0.000	0.096	0.080
Native species richness	0.011	0.398	0.000
Uniqueness ($N = 328$, $F_{7,321} = 40.8$, $R^2 = 0.46$, $P < 0.001$, $SE = 0.05$)			
Constant	0.627	0.000	0.000
Moisture index	0.004	0.266	0.000
Crust cover	-0.001	-0.234	0.000
Sand (%)	0.001	0.319	0.001
Clay (%)	0.003	0.424	0.000
Soil N	0.010	0.048	0.267
Elevation	-0.000	-0.248	0.000
Native species richness	0.004	0.501	0.000
Nonnative species richness (\log_{10}) ($N = 312$, $F_{10,302} = 21.5$, $R^2 = 0.40$, $P < 0.001$, $SE = 0.2$)			
Constant	0.747	0.000	0.000
Moisture index	0.013	0.256	0.000
Bare ground (%)	0.001	0.071	0.135
Highly developed crust	-0.009	-0.108	0.020
Total cover (%)	0.003	0.234	0.000
Inorganic C	-0.036	-0.112	0.025
Soil P	0.012	0.276	0.000
Soil Mg	0.000	0.149	0.002
Elevation	-0.000	-0.502	0.000
Native species richness	0.005	0.172	0.001
No. endemic species	-0.089	-0.077	0.131

Landscape patterns of richness, endemism, and uniqueness

Primary hotspots of native species richness, endemism, and uniqueness overlapped little on the landscape (Fig. 4, Table 4). Primary hotspots of native species richness were patchily distributed and represented a little over 1% of the landscape. Several primary hotspots for endemic species coincided with larger secondary hotspots of native species richness (Fig. 4). Primary hotspots of unique species assemblages included some native-rich areas (secondary hotspots) and some primary and secondary endemic hotspots, but different areas also had unique assemblages. Nonnative species hotspots commonly overlapped hotspots of native species richness and unique species assemblages,

but they were not common in areas of high endemism (Fig. 4).

DISCUSSION

The commonness of species rarity

This case study provided a clear example that most plant species are locally rare and patchily distributed. Our vegetation plots covered just 0.0043% of the landscape and captured 550 plant species, but missed ~390 plant species in the Monument. However, the rapidly declining rates of increase on the species accumulation curves (Fig. 2a, b), combined with the rapidly declining species frequency histogram, suggests that the remaining 390 species would likely be very rare and patchily distributed on the landscape. Thus, the 189 plant species that occurred in only one or two plots, plus the 390 species that were so rare they were missed, comprise almost 62% of the flora. Despite our modest sampling effort, we captured 35% of the endemic species reported to occur in the Monument by random sampling with large 0.1-ha plots. We didn't observe the listed threatened *Cycladenia humilis* var. *jonesii* or endangered species *Lesquerella tumulosa*, which occur on sandy and shale soil types, respectively, in the Monument. Nor did we capture plant species restricted to very rare habitats including "hanging gardens" (seeps) that were not sampled by our crews. Still, the overall pattern of plant frequencies and distributions are clear and statistically robust. The frequency distribution of a few common species and a plethora of rare species may be one of the most universal patterns in the biological sciences (Rosenzweig 1995), whether in the Grand Staircase–National Monument in Utah (as we found in this study), Central U.S. grasslands (Stohlgren et al. 1999), Panama (Hubbell 2001), or the tropical forests of Peru (Mistry et al. 1999). Preserving plant diversity in complex landscapes requires conservation strategies designed to specifically address the commonness of plant species rarity.

The rarity of hotspots

Concentrated hotspots of native species diversity have been reported at local (Stohlgren et al. 1997a, b), regional (Itow 1988, Williams et al. 1996, Dobson et al. 1997), and global scales (Myers et al. 2000). Interestingly, Myers et al. (2000) found ~12% of the Earth's land mass supported primary areas of endemism, similar to our reported 16% of the Monument that supported the highest concentrations of endemic species (Table 4). This might be because: (1) at most spatial scales, the concentrated hotspots are associated with site-specific evolutionary patterns and processes and unique environments (Davis et al. 1994, 1995, 1997); and (2) there is often a strong positive correlation between endemic species richness and total native species richness (Hobohm 2003). In our study, we did find concentrated hotspots of native species richness (~1%

of the landscape) and endemic species (16% of the landscape), and a significant positive correlation between native species richness per plot and the log₁₀ number of endemic species per plot ($r = 0.36$, $P < 0.0001$). But this is only a part of the story.

The most surprising result of our study was how little overlap there was among the various types of hotspots on the landscape (Fig. 4, Table 4). There was virtually no overlap in the primary hotspots of native species richness, endemism, and uniqueness. And, there was only ~11% overlap in the primary plus secondary hotspots for native species richness, endemism, and uniqueness, which in total covered 74% of the Monument. Corresponding analysis of the different biotic and abiotic variables correlated with patterns of richness, endemism, and uniqueness (Table 4) further suggests that different evolutionary and ecological mechanisms may be maintaining these patterns.

Invasions and other threats to plant diversity

Considering threats to plant diversity must be done in concert with developing strategies for preserving various hotspots and species from extinction (Sisk et al. 1994). In the Grand Staircase–Escalante National Monument, we found that ~80% of the plots contained at least one nonnative plant species, and that, on average, nonnative plant species comprise 7.5% of the species and 12.4% of the total cover on a given 0.1-ha plot. Like ecosystems in the Rocky Mountains of Colorado and Central Grasslands of the United States (Stohlgren et al. 1999), we found that nonnative plant invasions had been most successful in mesic habitats high in native species richness and soil nutrients (Table 1, Fig. 3; also see Bashkin et al. 2003). It may become increasingly difficult to protect native species hotspots if nonnative species continue to successfully establish and gain foliar cover in these rare landscape features. Those fairly rare native species more restricted to mesic habitats (e.g., *Populus* spp., *Salix* spp.) may be particularly vulnerable to replacement by nonnative species such as *Tamarix* spp. because surrounding arid habitats may offer little refuge.

Nonnative species also pose a threat to broad areas of unique species assemblages (Fig. 4, Table 4). The significant positive correlations between uniqueness and nonnative species richness ($r = 0.37$, $P < 0.0001$) and cover ($r = 0.21$, $P < 0.0001$) demonstrate successful invasions where native plant species have very low frequencies of occurrence (and probably small population sizes). While primary unique hotspots occur over a much larger area than native species hotspots (16% vs. 1%; Table 4), very small populations of native species may be at greater risk of local extirpation (White 1996).

In this study region, endemic species seem to proliferate in the arid habitats that are low in soil nutrients and foliar cover (i.e., low productivity sites, but moderately high in native species richness). The same pat-

tern was observed in serpentine outcrops in California (Harrison 1999). In these and other locations, the primary hotspots for endemic species (Fig. 4) may be able to serve as refugia for endemic and other native species, by virtue of the sites being too stressful for many nonnative species (Fig. 3b, c).

MANAGEMENT APPLICATIONS

It may become increasingly difficult to preserve native plant species in the Grand Staircase–Escalante National Monument and in many ecosystems. Most species are very rare, and limited species-rich habitats and unique species assemblages are threatened and fragmented by land-use practices and successfully invaded by nonnative species (Stohlgren et al. 1999). In this Monument, common vegetation types (e.g., pinyon, juniper, and desert-shrub types) had high frequencies of endemic species, so conservation efforts cannot concentrate solely on rare habitat types. In fact, the hotspots of endemism, which are commonly the primary targets of conservation (Myers et al. 2000), were less threatened by invasive plant species than native species hotspots and unique species assemblages. Conserving native plant diversity and rarity may require actively protecting and restoring species-rich habitats and areas with high uniqueness.

Protecting only hotspots of endemism in this Monument may not be a “silver bullet!” Rare hanging gardens and important riparian zones contain few endemic species, but they serve an extremely valuable role for many native birds, mammals, and invertebrates in the Monument. Preservation of the more xeric habitats that support many endemic species represent between 16% (primary hotspots) and 27% (secondary hotspots) of the Monument would simply miss many of these mesic habitats.

The hotspots of endemism may not be permanently protected from invasive plant species. Even modest increases in the cover of the invasive annual grass *Bromus tectorum* may support wildfires that further promote *Bromus* invasions. Wildfires may have been rare in the absence of *Bromus*, which creates more continuous fuels between shrubs and trees. Fires then decrease competition from shrubs and crusts, increase available nitrogen and phosphorus, and promote continued invasions (Melgoza et al. 1990, D’Antonio and Vitousek 1992, Belnap 1998, Evangelista et al. 2004). With the high frequency of *Bromus tectorum* (in 69% of the plots), a seed source is available over much of the Monument. Grazing by cattle, common throughout the landscape, may further damage soil crusts, releasing nutrients, and facilitating future invasions (Belnap 1998).

Other potential threats to native plant species include oil and gas development and associated road building and disturbance of biological crusts (Belnap 1998). These threats could be minimized by carefully avoiding hotspots of richness, endemism, and uniqueness (Fig.

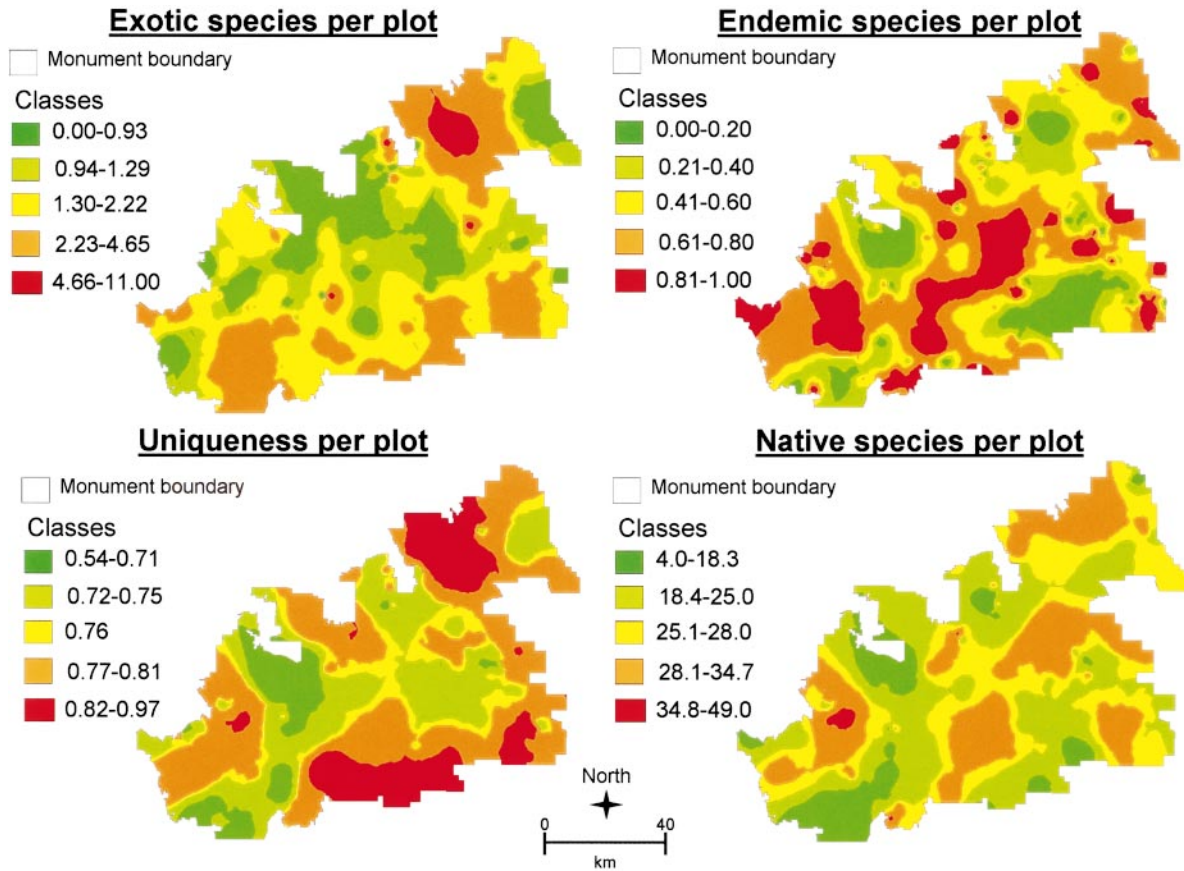


FIG. 4. Modeled locations of five “smart quantiles” (see *Methods*) of plot values for nonnative plant species richness, endemic species richness, uniqueness, and native species richness, in the Grand Staircase–Escalante National Monument.

4). Additional threats include new or accelerated invasions by nonnative plants, animals, and diseases, which may further target habitats high in native species richness and unique habitats.

It may be risky to protect only “primary” hotspots of richness, endemism, and uniqueness in the Monument (i.e., 32% of the Monument; Table 4, Fig. 4) or at regional and global scales since the hotspots are patchily distributed (Kareiva and Marvier 2003). This may preserve too few populations of the many infrequent species. Preserving primary and secondary hot-

spots of richness, endemism, and uniqueness, with greater effective population sizes of more species and greater connectedness among them, would require actively protecting 74% or more of the Monument, and possibly adjacent lands.

The plant diversity patterns observed here are not atypical. In tropical forests in Peru, Mistry et al. (1999) recorded almost 500 taxa in 10 scattered 0.1-ha plots, with half the species represented by a single individual. Likewise, most plant species in the Central Grasslands and Rocky Mountains are locally rare (Stohlgren et al. 1998, 1999). Because most species are patchily distributed, care must be taken to buffer these small populations from extirpation and extinction by preserving large enough areas to maintain effective pollination, establishment, and persistence. Targeting only one form of diversity (such as endemism) or protecting too small a hotspot (e.g., Myers et al. 2000) may provide the illusion of preserving diversity, while actually protecting too few individuals and populations of vulnerable species (Sisk et al. 1994, Kareiva and Marvier 2003).

ACKNOWLEDGMENTS

The authors would like to thank Walt Fertig, Thom O'Dell, and the Grand Staircase–Escalante National Monument staff

TABLE 4. Percentage of the 850 000-ha Grand Staircase–Escalante National Monument occupied by primary (top smart quartile) and secondary (second top smart quartile) hotspots of native species, endemic species, and unique species assemblages.

Hotspot type	Hotspot area	
	Primary (%)	Primary plus secondary (%)
Native species	1	16
Endemic species	16	29
Uniqueness	16	37
Cumulative	32	74

for financial support and project coordination. The U.S. Geological Survey (Fort Collins Science Center) and the Natural Resource Ecology Laboratory at Colorado State University assisted in logistical support. Rick Shory provided database and data analysis assistance. Many thanks to the dedicated and hard working field crews from 1998 to 2002. Tom Sisk and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. To all we are grateful.

LITERATURE CITED

- Alley, N., T. J. Stohlgren, P. Evangelista, and D. Guenther. 2004. Iterative model development for natural resource managers: a case example in Utah's Grand Staircase-Escalante National Monument. *Geographic Information Sciences* **10**:1-9.
- Bashkin, M., T. J. Stohlgren, Y. Otsuki, M. Lee, P. Evangelista, and J. Belnap. 2003. Soil characteristics and exotic species invasions in the Grand Staircase-Escalante National Monument, Utah. *Applied Soil Ecology* **22**:67-77.
- Belnap, J. 1998. Impacts of trampling soils in southeast Utah ecosystems. Pages 231-244 in L. M. Hill and J. J. Kosalek, editors. *Learning from the land. Grand Staircase-Escalante National Monument Science Symposium Proceedings*, Southern Utah University, 4-5 November 1997. Bureau of Land Management, Salt Lake City, Utah, USA.
- Chong, G. W., R. M. Reich, M. A. Kalkhan, and T. J. Stohlgren. 2001. New approaches for sampling and modeling native and exotic plant species richness. *Western North American Naturalist* **61**:328-335.
- Colwell, R. K. 1997. Estimate-S: statistical estimation of species richness and shared species from samples. Version 5.0.1. Available at: (<http://viceroy.eeb.uconn.edu/estimates/>). Last updated 16 September 2002.
- Comstock, J. P., and J. R. Ehleringer. 1992. Plant adaptation in the Great Basin and Colorado Plateau. *Great Basin Naturalist* **52**:195-215.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**: 63-87.
- Davis, S. D., V. H. Haywood, and A. C. Hamilton, editors. 1994. *Centres of plant diversity. Volume 1. Europe, Africa, South West Asia and the Middle East*. IUCN (World Conservation Union) Publications Unit, Gland, Switzerland.
- Davis, S. D., V. H. Haywood, and A. C. Hamilton, editors. 1995. *Centres of plant diversity. Volume 2. Asia, Australia and the Pacific*. IUCN (World Conservation Union) Publications Unit, Gland, Switzerland.
- Davis, S. D., V. H. Haywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, editors. 1997. *Centres of plant diversity. Volume 3. The Americas*. IUCN (World Conservation Union) Publications Unit, Gland, Switzerland.
- DeByle, N. V. 1985. Wildlife. Pages 135-152 in *Aspen: ecology and management in the western United States*. USDA Forest Service General Technical Report RM-119. Fort Collins, Colorado, USA.
- Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. *Science* **275**:550-553.
- ESRI. 2004. ArcGIS version 8.2. ESRI, Redlands, California, USA.
- Evangelista, P. H., T. J. Stohlgren, D. A. Guenther, and S. Stewart. 2004. Vegetation response to fire and post-burn seeding treatments in juniper woodlands of the Grand Staircase-Escalante National Monument, Utah. *Western North American Naturalist* **64**:293-305.
- Fertig, W., L. Fertig, H. Beck, S. Bartlett, and L. Pfennifer. 2002. Annotated checklist of the flora of Grand Staircase-Escalante National Monument. Bureau of Land Management, Kanab, Utah, USA.
- Gee, G. W., and J. Bauder. 1986. Particle size analysis. Pages 383-411 in A. Klute, editor. *Methods of soil analysis. Part 1: physical and mineralogical methods*. ASA, Madison, Wisconsin, USA.
- Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. *Ecology* **80**:70-80.
- Hobohm, C. 2003. Characterization and ranking of biodiversity hotspots: centres of species richness and endemism. *Biodiversity and Conservation* **12**:279-287.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Itow, S. 1988. Species diversity of mainland and island forests in the Pacific area. *Vegetatio* **77**:193-200.
- Kareiva, P., and M. Marvier. 2003. Conserving biodiversity coldspots. *American Scientist* **91**:344-351.
- Kaye, M., D. Binkley, and T. Stohlgren. 2004. Estimating populations of aspen (*Populus tremuloides*) in Rocky Mountain National Park, Colorado. *Landscape Ecology*, in press.
- Kier, G., and W. Barthlott. 2001. Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. *Biodiversity and Conservation* **10**:1513-1529.
- Kou, S. 1996. Phosphorous. Pages 869-920 in D. L. Sparks, editor. *Methods of soil analysis. Part 3: chemical methods*. Soil Science Society of America, Madison, Wisconsin, USA.
- Malanson, G. P. 1993. *Riparian landscapes*. Cambridge University Press, New York, New York, USA.
- McLaughlin, S. P. 1986. Floristic analysis of the Southwestern United States. *Great Basin Naturalist* **46**:46-65.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**: 7-13.
- Mistry, S., J. Comiskey, and T. J. Stohlgren. 1999. Pages 114-123 in A. Alonso and F. Dallmeier, editors. *Biodiversity assessment and monitoring of the Urumbaba Region, Peru*. Smithsonian Institution Monitoring and Assessment of Biodiversity Program, SI/MAB Series 3, Washington, D.C., USA.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853-858.
- Neter, J., W. Wasserman, and M. H. Kutner. 1990. *Applied linear statistical models: regression, analysis of variance, and experimental designs*. Third edition. Irwin, Homewood, Illinois, USA.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Everham, and D. W. Gibbons. 1993. Rare species: the coincidence of diversity hotspots and conservation strategies. *Nature* **365**:335-337.
- Rosentreter, R. 1994. Displacement of rare plants by exotic grasses. Pages 170-174 in S. B. Monsen and S. G. Kitchen, editors. *Proceedings, ecology and management of annual rangelands; 1994 September*. General Technical Report INT-GTR-313. USDA Forest Service, Intermountain Research Station.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Shultz, L. 1993. Patterns of endemism in the Utah flora. Pages 249-263 in R. Sivinski and K. Lightfoot, editors. *Southwestern rare and endangered plants: conference proceedings*. Miscellaneous Publication Number 22, New Mexico Department of Energy, Minerals, and Natural Resources, Division of Forestry and Resource Conservation, Albuquerque, New Mexico, USA.

- Sisk, T. D., A. E. Launer, K. R. Switky, and P. R. Ehrlich. 1994. Identifying extinction threats. *Bioscience* **44**:592–604.
- Smith, T. B., S. Kark, C. J. Schneider, R. K. Wayne, and C. Moritz. 2001. Biodiversity hotspots: the need for preserving environmental transitions. *Trends in Ecology and Evolution* **16**:431.
- SPSS. 2000. SYSTAT 10.0. SPSS, Chicago, Illinois, USA.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *Journal of Range Management* **51**:164–172.
- Stohlgren, T. J., G. W. Chong, M. A. Kalkhan, and L. D. Schell. 1997a. Rapid assessment of plant diversity patterns: a methodology for landscapes. *Environmental Monitoring and Assessment* **48**:25–43.
- Stohlgren, T. J., M. B. Coughenour, G. W. Chong, D. Binkley, M. A. Kalkhan, L. D. Schell, D. J. Buckley, and J. K. Berry. 1997b. Landscape analysis of plant diversity. *Landscape Ecology* **12**:155–170.
- Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified Whittaker nested vegetation sampling method. *Vegetatio* **117**:113–121.
- Stohlgren, T. J., Y. Otsuki, C. A. Villa, M. Lee, and J. Belnap. 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. *Biological Invasions* **3**:37–50.
- Sumner, M. E., and W. P. Miller. 1996. Cation exchange capacity and exchange coefficients. Pages 1201–1229 in D. L. Sparks, editor. *Methods of soil analysis. Part 3: chemical methods*. Soil Science Society of America, Madison, Wisconsin, USA.
- USDI [U.S. Department of the Interior]. 1995. Visitor experience and resource protection implementation plan. NPS D-70. National Park Service, Denver, Colorado, USA.
- Wagner, S. W., J. D. Hanson, A. Olness, and W. B. Voorhees. 1998. A volumetric inorganic carbon analysis system. *Soil Science Society of America Journal* **62**:690–693.
- Waters, M. A. 2003. The need for a multivariate approach to understand patterns of species richness and invasion: a case study in Grand Staircase–Escalante National Monument, Utah. Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Welsh, S. L., N. D. Atwood, S. Goodrich, and L. C. Higgins. 1993. *A Utah flora*. Second edition. Jones Endowment Fund, Provo, Utah, USA.
- White, P. S. 1996. Spatial and biological scales in reintroduction. Pages 49–86 in D. A. Falk, C. I. Millar, and M. Olwell, editors. *Restoring diversity: strategies for reintroduction of endangered plants*. Island Press, Washington D.C., USA.
- Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humphries, and R. Pressey. 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology* **10**:155–174.