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# EXOTIC PLANT SPECIES INVADE HOT SPOTS OF NATIVE PLANT DIVERSITY

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*Abstract.* Some theories and experimental studies suggest that areas of low plant species richness may be invaded more easily than areas of high plant species richness. We gathered nested-scale vegetation data on plant species richness, foliar cover, and frequency from 200 1-m² subplots (20 1000-m² modified-Whittaker plots) in the Colorado Rockies (USA), and 160 1-m² subplots (16 1000-m² plots) in the Central Grasslands in Colorado, Wyoming, South Dakota, and Minnesota (USA) to test the generality of this paradigm.

At the 1-m² scale, the paradigm was supported in four prairie types in the Central Grasslands, where exotic species richness declined with increasing plant species richness and cover. At the 1-m² scale, five forest and meadow vegetation types in the Colorado Rockies contradicted the paradigm; exotic species richness increased with native-plant species richness and foliar cover. At the 1000-m² plot scale (among vegetation types), 83% of the variance in exotic species richness in the Central Grasslands was explained by the total percentage of nitrogen in the soil and the cover of native plant species. In the Colorado Rockies, 69% of the variance in exotic species richness in 1000-m² plots was explained by the number of native plant species and the total percentage of soil carbon.

At landscape and biome scales, exotic species primarily invaded areas of high species richness in the four Central Grasslands sites and in the five Colorado Rockies vegetation types. For the nine vegetation types in both biomes, exotic species cover was positively correlated with mean foliar cover, mean soil percentage N, and the total number of exotic species. These patterns of invasibility depend on spatial scale, biome and vegetation type, spatial autocorrelation effects, availability of resources, and species-specific responses to grazing and other disturbances. We conclude that: (1) sites high in herbaceous foliar cover and soil fertility, and hot spots of plant diversity (and biodiversity), are invasible in many landscapes; and (2) this pattern may be more closely related to the degree resources are available in native plant communities, independent of species richness. Exotic plant invasions in rare habitats and distinctive plant communities pose a significant challenge to land managers and conservation biologists.

*Key words: biodiversity; Central Grasslands (USA) plant diversity patterns; exotic plant invasions; exotic species richness; native plant diversity; Rocky Mountains (USA) plant diversity patterns; spatial autocorrelation; species composition overlap; species-specific responses; vegetation sampling, multi-scale.*

## INTRODUCTION

It has been hypothesized that exotic species might more easily invade areas of low species diversity than areas of high species diversity. This pattern was first observed by Darwin (1859) and phrased as an hypothesis by Elton (1958). Areas of high species diversity should use limiting resources more completely, preventing invasion by a potentially competing species (MacArthur and Wilson 1967, Tilman 1982, 1997, McNaughton 1983, Pimm 1991). Areas of low diversity are thought to be highly invasible because, according to food-web theory (Post and Pimm 1983, Drake 1990) and coevolution theory (Pimm 1984), they have simple patterns of inter-specific interactions and use resources less completely.

Some field observations support the notion that species-rich areas are less prone to invasion. Fox and Fox (1986) report an inverse relationship between the percentage of exotic species in a flora and the number of native species in western Australia. A global review

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by Rejmánek (1996*a*) shows that at continental scales Elton's hypothesis is generally supported. Species-rich areas in the tropics contain fewer exotic species than do relatively species-poor areas in temperate latitudes in North and South America, and in Africa and Europe. However, Rejmánek also showed that the data do not strongly support the mechanism of the species-richness effect: there was no significant relationship of latitude to percentage exotic species between 50° N and 50° S latitude. Little evidence supports the idea that native species richness was directly responsible for greater resistance to invasion (Rejmánek 1996*a*). Mack (1996*a*) postulated that biotic barriers (e.g., native parasites, predators, grazers) may be partly responsible for the unsuccessful naturalization of exotic plants in the tropics and elsewhere.

Some theorists have readily accepted Elton's hypothesis. MacArthur and Wilson (1967) and Pimm (1991) concluded that fewer habitats are likely to be unexploited where more species are present. Several mathematical models suggest that areas of high species diversity should be resistant to invasion (Turelli 1981, Post and Pimm 1983, Rummel and Roughgarden 1983, Case 1990). Case (1990:9610) asked ''Why do species-rich communities repel invasion?'' His theoretical models were based on randomly constructed, stable, Lotka-Voltera competitive communities, and the models showed that the probability of invader success decreased with the size and structure of the community. The key aspect of the mathematical models was that colonization declined in the face of ''many, strongly interacting species.'' Law and Morton (1996) also presented a model supporting Elton's (1958) hypothesis.

Other theorists have argued that highly diverse communities are intrinsically unstable, with some species dropping in and out routinely (May 1973). In such a system, we might envision some native species dropping out and exotic species replacing them. Alternatively, Huston and DeAngelis (1994) demonstrate theoretically that a large number of species can coexist as a result of biogenic small-scale heterogeneity and interactions among organisms for spatially and temporally variable resources. Under this scenario, exotic plant species might invade and coexist with high numbers of native plant species as long as light, water, and nutrients were not limiting.

Some recent experimental evidence strongly supports Elton's hypothesis and the proposed effect of species richness. In a seed-addition experiment in mature oak savanna in Minnesota (USA), Tilman (1997) found that invasibility correlated negatively with plant species richness ($n = 60$ 1-m$^2$ plots). Another experiment in recently planted 3 × 3 m plots in the same vegetation type had similar results (J. Knops, *personal communication*). These plot-level results also are consistent with several studies that showed species-poor islands are particularly prone to invasions (Elton 1958, Vitousek et al. 1996). In light of this convincing evidence across multiple spatial scales, it is tempting to accept the general paradigm that exotic species tend to invade and eventually dominate areas of low diversity.

Broad acceptance of this paradigm is premature and dangerous. First, field observations and experiments have produced inconsistent results. Some field experiments in California (USA) showed that species-rich areas of annual grasslands were more easily invaded than species-poor areas (Robinson and Quinn 1988, Robinson et al. 1995). Timmins and Williams (1991) found that the number of weeds in New Zealand's forest and scrub reserves did not correlate with the number of native species. Rejmánek et al. (1996*a*) found no relationship between species richness and invasibility in a forest reserve in Uganda. Further, several fairly species-rich areas in the world (e.g., those with Mediterranean climates) have been readily invaded; perhaps invasions are facilitated by enormous and continuous seed sources via human transportation and land-use practices (Vitousek et al. 1996, Rejmánek 1996*a*). Recent studies also show that species-rich riparian zones in some areas in the northwestern United States are more prone to invasion than upland forests that are species poor (DeFerrari and Naiman 1994). These observations raise the possibility that species-rich communities that receive some level of disturbance (e.g., fire, herbivory) may have more resources available, at least temporarily, for invading species (Robinson et al. 1995).

It is humbling to note that community ecologists do not yet understand causes and patterns of native species richness. The comprehensive review by Palmer (1994; 150 citations) counted 120 plausible hypotheses attempting to explain variation in species-richness patterns. The inclusion of exotic species may further complicate this situation. Proof of Elton's paradigm that exotic species invade low-diversity areas would require consistent observations of native species richness and invasibility patterns that cross several spatial scales and a broad range of vegetation types.

A comprehensive evaluation of the relationship of native and exotic species patterns has been hampered by poor vegetation-sampling methods and a lack of standardized approaches over large areas. A recent test of commonly used rangeland sampling techniques (e.g., point-transects, Parker 1951; quadrat methods, Daubenmire 1959), revealed that small quadrats and linear techniques failed to capture about half the native and exotic plant species in tallgrass prairie, shortgrass steppe, northern mixed prairie, and mixed grasslands (Stohlgren et al. 1998).

We analyzed field data from two biomes in the central/western United States, the Rocky Mountains and the Central Grasslands, to (1) assess patterns of exotic plant invasions in nine vegetation types (two biomes) using a standardized, multi-scale vegetation sampling technique; (2) evaluate the relationship of native species richness and foliar cover to the invasion of exotic

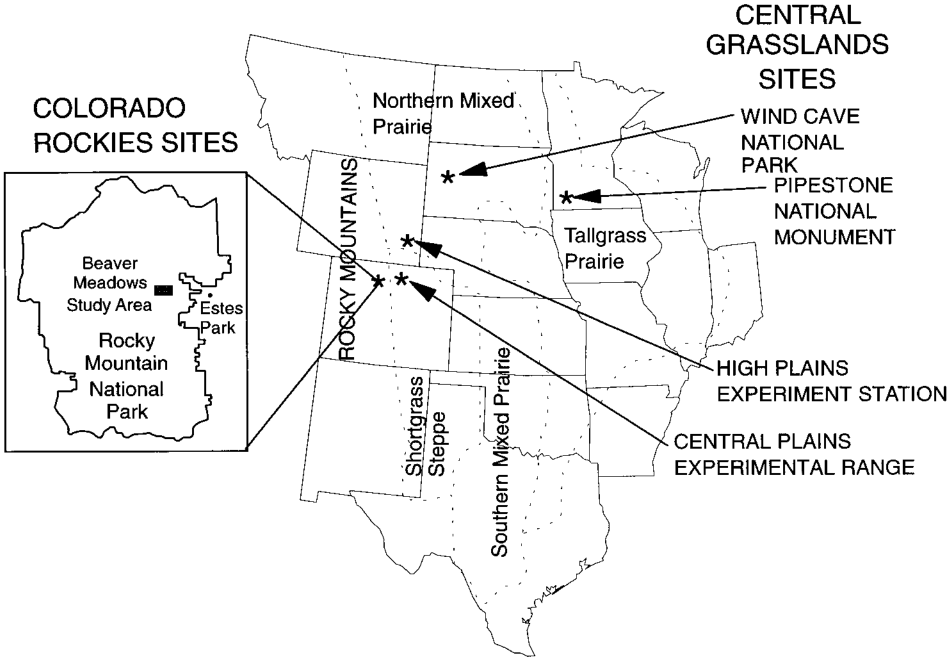


FIG. 1. Map of study sites.

plant species at multiple spatial scales (e.g., subplot, plot, vegetation-type, and biome scales); and (3) determine whether invasion patterns are a function of scale, community–environment relationships (e.g., soil texture, nitrogen, and carbon), spatial autocorrelation effects, and/or species-specific responses to grazing and other disturbances.

## STUDY AREAS AND METHODS

### *Study areas*

In the Central Grasslands (USA), we had four study locations (Fig. 1, Appendix): (1) shortgrass steppe at the Central Plains Experimental Range (Nunn, Colorado: annual mean precipitation = 354 mm, annual mean maximum temperature = 17.39°C, annual mean minimum temperature = 0.06°C); (2) mixed-grass prairie at the High Plains Experiment Station (Cheyenne, Wyoming: annual mean precipitation = 389 mm, annual mean maximum temperature 14.39°C, annual mean minimum temperature 0.61°C); (3) northern mixed prairie in Wind Cave National Park (Hot Springs, South Dakota: annual mean precipitation = 608 mm, annual mean maximum temperature 15.67°C, annual mean minimum temperature 0.78°C); and (4) tallgrass prairie in Pipestone National Monument (Pipestone, Minnesota: annual mean precipitation = 656 mm, annual mean maximum temperature 12.78°C, annual mean minimum temperature −0.39°C). Except for the tallgrass prairie location, which had no grazing, we randomly established four 20 × 50 m sample plots at each location that encompassed various grazing intensities including lightly grazed, heavily grazed, and protected habitats (Appendix). At each sampling plot we established a modified Whittaker multi-scale vegetation plot as described in *Methods,* below.

The Colorado Rockies site was a 754-ha portion of the Beaver Meadows area in Rocky Mountain National Park, Estes Park, Colorado, USA (annual mean precipitation 361 mm, annual mean maximum temperature 13.78°C, annual mean minimum temperature −1.39°C, 2500–3000 m elevation; Fig. 1). The five vegetation types included lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), ponderosa pine (*Pinus ponderosa*), wet meadow, and dry meadow. Most of the area is moderately grazed by elk and deer. About 9 ha of the ponderosa pine community was prescribed-burned (September 1994) and was excluded in this analysis. We overlaid a 48 × 32 unit grid (north to south) over the aerial photograph and randomly selected (computer random number generator) four sample points in each of the five plant communities (Appendix; see Stohlgren et al. [1997*a*] for details).

### *Methods*

The modified-Whittaker plot measured 20 × 50 m and was placed with the long axis parallel to the environmental gradient (Stohlgren et al. 1995; Fig. 2). Nested in each plot were 10 0.5 × 2 m (1-$m^2$) subplots systematically spaced along the inside border, two 2 × 5 m (10-$m^2$) subplots in alternate corners, and a 5 × 20 m (100-$m^2$) subplot in the plot center. Foliar cover for each species in the understory and percentage bare ground were estimated to the nearest percent in the 10 1-$m^2$ subplots. We were able to estimate cover to the nearest percent by carefully training to recognize a 10 × 10 cm area (i.e., 1% of the 1-$m^2$ subplot). As each

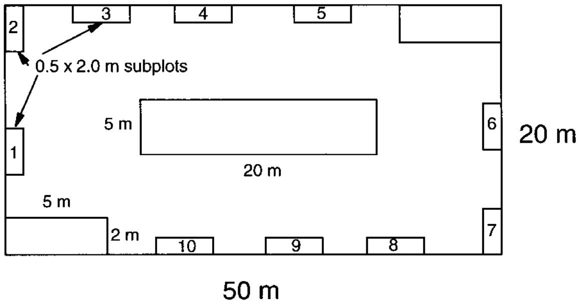


FIG. 2. Modified-Whittaker sampling design.

species was recorded, the observer mentally counted how many 10 × 10 cm areas were covered by that species. Species that occupied <1% in a subplot were recorded as 0.5% cover. Cumulative plant species were noted in the 10-m$^2$ and 100-m$^2$ subplots, and the 1000-m$^2$ plots. Ancillary data recorded for each plot included: Universal Transverse Mercator location and elevation from a global-positioning system, slope, and aspect.

Each site was sampled as close to the phenological maximum (peak biomass) as possible. Sites in the Colorado Rockies (Beaver Meadows, Rocky Mountain National Park) were sampled between 1 June and 15 July 1995. We sampled the shortgrass steppe from 1 to 3 July 1996; the mixed-grass prairie from 25 to 27 June 1996; the northern mixed prairie from 10 to 13 July 1996; and the tallgrass prairie from 24 to 27 July 1996. Plant species that could not be identified in the field were collected and identified at the Colorado State University herbarium; 156 of the 1704 plant specimens encountered (9.1% of the total specimens) could not be identified to species due to inappropriate phenological stage or missing flower parts.

In the Colorado Rockies, five soil samples were taken in each modified-Whittaker plot (in the center of subplots 1, 4, 7, and 10, and in the plot center) and pooled into one plastic bag. For the Central Grassland, five soil samples were taken at each of the four plot corners and in the center of the plot, and pooled into one plastic bag. For each sample, surface litter, if present, was removed, and the top 15 cm of soil was sampled. Samples were air-dried for 48 h, sieved with a standard number 10 (2-mm pore size) sieve, ground in a standard three-ball grinder, and then oven-dried at 55°C for 24 h. Samples were analyzed for percentage total carbon and nitrogen using a LECO-1000 CHN analyzer (LECO Corporation, Saint Joseph, Missouri, USA) (following the methods of Carter 1993), and for particle size based on the standard hydrometer method (Gee and Bauder 1986).

Soils in the Colorado Rockies also were analyzed for available nitrogen using two methods. Ion-exchange resin bags (Binkley and Hart 1989) were constructed from nylon stocking material and 14 mL of cation resins (Sybron IONAC C-251, $H^+$ form [Sybron Chemicals, Birmingham, New Jersey, USA]) and 14 mL of anion resin (IONAC ASB-1POH, $OH^-$ form). Ten resin bags were placed 20 mm below the mineral soil surface at 5-m intervals along a single diagonal transect in each 20 × 50 m plot. Resin bags were installed in early July, retrieved in early October of 1996, and then extracted with 50 mL of 2 mol KCl/L solution. Concentrations of ammonium-N and nitrate-N were determined by standard flow-injection colorimetry. Damage by animals in some plots reduced the number of resin bags retrieved.

The second index of N availability in the Colorado Rockies used on-site incubations of intact soil cores (200-mm-diameter core of 0–200 mm depth mineral soil) in plastic bags. Ten cores were collected at the same points along the transects, and then mixed, and subsampled to provide a single sample for determining initially extractable ammonium and nitrate (10 g of soil extracted with 100 mL of 2 mol KCl/L). Another 10 cores were sampled, replaced intact in plastic bags and allowed to incubate from mid-July to mid-August (30 d) in 1996. After incubation the 10 samples/plot were mixed and subsampled, and then extracted for determination of ammonium and nitrate (by flow-injection colorimetry).

### *Statistical analysis*

All statistical analyses were conducted with SYSTAT (Wilkinson 1996), and $P < 0.05$ was used to determine significance in all tests. Analysis of variance (ANOVA) was used to compare the number and foliar cover of native and exotic species in 1-m$^2$ subplots for the four vegetation types in the Central Grasslands and the five vegetation types in the Colorado Rockies. Analysis of variance is robust to violations of the assumptions of homogeneous variance and normality as long as sample sizes are nearly equal (Zar 1974). Where a significant effect of vegetation type was detected, Tukey's test was used to contrast mean values for significant differences.

Multiple regression was used to determine the relationship of the number and cover of native plant species in 1-m$^2$ subplots to the number and cover of exotic plant species, with separate analyses for the vegetation types in the two biomes. We tested the significance of each predictor with $t$ values (i.e., against the null hypothesis that the slope = 0). We repeated the analysis for the two vegetation types with the greatest species richness and cover of exotic species in each biome.

We used stepwise forward multiple regressions to assess the ability of native species richness and cover, and soil characteristics to predict exotic species richness in the two biomes. Soil characteristics included total N, total C, and percentages of sand, silt, and clay (percentage sand was not added into the model to reduce multi-collinearity). Available N replaced total N in the model for the Colorado Rockies to provide better information on resource availability. The forward lin-

TABLE 1. Results of ANOVA of number and foliar cover of native and exotic species (means, with 1 SE in parentheses) in four vegetation types in the Central Grasslands (USA). Means with different lowercase superscript letters within columns are significantly different at $P < 0.05$, Tukey's test.

| | 1-m$^2$ subplots† | | | | 1000-m$^2$ plots‡ | | | | Vegetation type | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Natives | | Exotics | | Number | | Total | | No. of natives | No. of exotics |
| | No. | Cover | No. | Cover | Native | Exotic | %N | %C | | |
| Vegetation type | | | | | | | | | | |
| Mixed-grass prairie | $10.6^{a}$<br>(0.5) | $45.9^{a}$<br>(3.3) | $0.08^{a}$<br>(0.06) | $0.04^{a}$<br>(0.03) | 35.2<br>(2.6) | $3.0^{a}$<br>(1.2) | $0.17^{a}$<br>(0.01) | $1.68^{a}$<br>(0.12) | 56 | 8 |
| Shortgrass steppe | $8.5^{b}$<br>(0.4) | $57.6^{a}$<br>(2.6) | $0.08^{a}$<br>(0.04) | $0.04^{a}$<br>(0.02) | 25.8<br>(1.7) | $1.0^{a}$<br>(0.4) | $0.04^{a}$<br>(0.01) | $0.94^{a}$<br>(0.08) | 36 | 3 |
| Northern mixed prairie | $6.5^{c}$<br>(0.5) | $31.3^{b}$<br>(3.1) | $3.05^{b}$<br>(0.14) | $28.6^{b}$<br>(3.1) | 32.0<br>(5.0) | $8.0^{b}$<br>(0.0) | $0.32^{b}$<br>(0.04) | $3.54^{b}$<br>(0.55) | 59 | 14 |
| Tallgrass prairie | $10.0^{ab}$<br>(0.7) | $57.6^{a}$<br>(4.6) | $2.2^{c}$<br>(0.16) | $20.4^{b}$<br>(3.3) | 37.8<br>(8.4) | $8.2^{b}$<br>(2.4) | $0.39^{b}$<br>(0.02) | $4.24^{b}$<br>(0.29) | 62 | 15 |
| Statistics | | | | | | | | | | |
| $F$ | 13 | 13 | 179 | 40 | 2 | 17 | 27 | 23 | | |
| $P$ | 0.001 | 0.001 | 0.001 | 0.001 | 0.157 | 0.001 | 0.001 | 0.001 | | |
| $R^2$ | 0.20 | 0.20 | 0.78 | 0.44 | 0.34 | 0.81 | 0.87 | 0.85 | | |

† $n = 40$ subplots per site.
‡ $n = 4$ plots per site.

ear regression models included only variables meeting the $P < 0.15$ criterion. Data distributions that were strongly skewed were transformed prior to analysis. $\text{Log}_{10}$ transformations were used on available N and N mineralization potential.

We assessed the relationship between total foliar cover (i.e., in the herbaceous layer) and native and exotic species richness with linear and second-order polynomial regression models. Strong nonlinear relationships depicting the ''hump-backed'' or unimodal curve of plant diversity relative to foliar cover (e.g., Grime 1973*a*, Bond 1983, Huston 1994, Huston and DeAngelis 1994) would make the interpretation of linear models problematic.

Two sample *t* tests were used to compare the foliar cover and frequency (1-m$^2$ subplots) of two exotic grasses in (1) grazed (by bison, elk, and deer) and ungrazed (fenced since 1960) areas in the northern mixed prairie and (2) two plots last burned in 1985 and 1990, respectively, in the tallgrass prairie. Linear regression was used to correlate disturbance class to the number and cover of exotic species at the plot level (1000 m$^2$) and vegetation-type level (combined data from four 1000-m$^2$ plots).

Kriging was used to assess possible spatial-autocorrelation similarities in the patterns of native and exotic species richness and foliar cover relative to soil characteristics for the 1000-m$^2$ plots in the Colorado Rockies. Kriging uses a local estimator in the vicinity of the point and the autocorrelation structure of the data to produce a contour map (Legendre and Fortin 1989). In this study we used kriging (SYSTAT version 6.0) to smooth contour maps of native and exotic plant diversity and cover and soil fertility.

Finally, we used Jaccard's coefficient ($J$) to measure the overlap between two complete species lists (Krebs 1989) as follows:

$$J = A/(A + B + C)$$

where $A$ = the number of species found in both paired sites, $B$ = species in site 1 but not in site 2, and $C$ = species in site 2 but not in site 1. A comparison of species lists for two sites resulting in a similarity coefficient of 1.0 would indicate complete overlap (i.e., identical species lists), while a value of 0.0 would indicate no overlap. The mean Jaccard's coefficient for each vegetation type was calculated from all possible pairwise comparisons between plots.

## RESULTS

### *Plant species richness and cover at the Central Grasslands and Colorado Rockies sites*

The species richness and foliar cover of native and exotic plant species varied greatly within and between the two biomes. In the Central Grasslands, exotic species richness in 1-m$^2$ subplots was significantly greater in the northern mixed and tallgrass prairie sites than in the other prairie types (Table 1). The northern mixed prairie site also had the lowest native species richness and cover. The tallgrass prairie site had the highest native species richness and cover (in 1-m$^2$ subplots) and relatively high exotic species richness and cover. Despite long-term cattle grazing at the shortgrass

TABLE 2. Results of ANOVA of number and foliar cover of native and exotic species in (means, with 1 SE in parentheses) five vegetation types in Rocky Mountain National Park, Colorado (USA). Means with different lower-case superscript letters within columns are significantly different at $P < 0.05$, Tukey's test.

| | 1-$m^2$ subplots† | | | | 1000-$m^2$ plots‡ | | | | | | Vegetation type | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Natives | | Exotics | | Number | | Total | | Resin-bag N | Soil-core N | No. of natives | No. of exotics |
| | No. | Cover | No. | cover | Native | Exotic | %N | %C | | | | |
| Vegetation type | | | | | | | | | | | | |
| Aspen | $9.7^{a}$ | $43.0^{a}$ | $1.13^{a}$ | $6.0^{a}$ | 58.2 | $5.5^{a}$ | 0.10 | 3.45 | 0.79 | 14.95 | 125 | 11 |
| | (0.9) | (5.7) | (0.3) | (1.3) | (4.8) | (1.8) | (0.01) | (0.80) | (0.35) | (9.45) | | |
| Wet meadow | $8.2^{a}$ | $83.4^{b}$ | $1.0^{a}$ | $6.7^{a}$ | 40.2 | 4.2 | 0.37 | 5.61 | 0.54 | 5.76 | 79 | 8 |
| | (0.4) | (4.3) | (0.2) | (1.9) | (8.9) | (1.0) | (0.15) | (1.86) | (0.29) | (2.59) | | |
| Dry meadow | $12.1^{b}$ | $44.5^{a}$ | $0.6^{b}$ | $0.6^{b}$ | 45.2 | 2.0 | 0.10 | 1.50 | 0.85 | 4.17 | 72 | 5 |
| | (0.6) | (1.8) | (0.1) | (0.1) | (3.2) | (0.7) | (0.02) | (0.52) | (0.20) | (1.59) | | |
| Ponderosa pine | $4.6^{c}$ | $14.7^{c}$ | $0.3^{b}$ | $0.2^{b}$ | 37.0 | 2.0 | 0.10 | 2.95 | 0.39 | 1.46 | 69 | 5 |
| | (0.5) | (2.3) | (0.1) | (0.1) | (3.2) | (0.7) | (0.04) | (0.80) | (0.10) | (0.62) | | |
| Lodgepole pine | $2.0^{c}$ | $7.6^{c}$ | $0.2^{b}$ | $0.3^{b}$ | $35.4^{b}$ | $1.4^{b}$ | 0.17 | 3.83 | 0.72 | 0.89 | 69 | 3 |
| | (0.3) | (1.9) | (0.1) | (0.2) | (3.6) | (0.2) | (0.04) | (0.59) | (0.33) | (0.29) | | |
| Statistics | | | | | | | | | | | | |
| $F$ | 48.5 | 71.9 | 9.2 | 9.7 | 3.2 | 3.1 | 2.2 | 2.3 | 0.4 | 1.8 | | |
| $P$ | 0.001 | 0.001 | 0.001 | 0.001 | 0.040 | 0.045 | 0.12 | 0.11 | 0.78 | 0.19 | | |
| $R^2$ | 0.50 | 0.60 | 0.16 | 0.17 | 0.45 | 0.44 | 0.37 | 0.38 | 0.15 | 0.34 | | |

† $n = 40$ subplots per site.
‡ $n = 4$ plots per site.

steppe and mixed prairie sites, exotic species richness and cover were significantly lower than at the other two sites. For the 1-$m^2$ subplots, the site effect (i.e., the percentage variation explained by the ANOVA model) was highly significant for all variables tested, and it was greater for exotic species richness and cover than for native species richness and cover (Table 1). At the 1000-$m^2$ plot scale, no significant differences were found in the number of native species at the four sites, but the northern mixed prairie and the tallgrass prairie had greater exotic species richness than mixed grass prairie and shortgrass steppe (Table 1).

In the Colorado Rockies, the dry-meadow type had the greatest native species richness at the 1-$m^2$ scale (Table 2). Exotic species richness and cover at the 1-$m^2$ scale was significantly greater in the wetter vegetation types (e.g., the aspen and wet-meadow types) compared to the drier, coniferous-forest types (Table 2). Again, the site effect was highly significant for all variables tested at the 1-$m^2$ scale, but it was greater for native species richness and cover than for exotic species richness and cover. The vegetation types with the highest and lowest native species richness (the dry-meadow and lodgepole pine types) did not differ significantly in the species richness and cover of exotic species at the 1-$m^2$ scale. Total herbaceous foliar cover was lowest under the dense canopy of lodgepole pine stands and highest in the open wet meadows (Table 2).

At the 1000-$m^2$ scale, the aspen type surpassed the dry-meadow type in native species richness and widened the margin in exotic species richness. The lodgepole pine type gained native plant species more rapidly than exotic plant species with increasing spatial scale compared to the other four vegetation types.

### *Effects of scale on evaluating exotic plant species invasions*

The nested plot design (Fig. 2) allowed us to evaluate the effects of plot size on the number (percentage) of exotic species in an area. In a homogeneous environment, the percentage of exotic species might be fairly constant. We found that vegetation types in both biomes had large variability in the percentage of exotic species at different spatial scales. The mixed-grass prairie type in the Central Grassland showed only 1.7% exotic species at the 1-$m^2$ scale and 12.5% exotic species (8 of 64 plant species) identified in the four 1000-$m^2$ plots (Table 1). The rate that exotic species were encountered exceeded the rate native species were added to the species pool as additional plots were established (i.e., as scale increased) due to the patchy distribution of the few exotic species. The opposite was true of the northern mixed-prairie type, which had a greater spatial mixing of exotic species throughout the study area resulting in similar percentages of exotic species at multiple spatial scales. Some exotic species (e.g., *Poa pratensis*, *Bromus japonicas*) had frequencies of >90% in the forty 1-$m^2$ subplots.

In the Colorado Rockies, the percentage of exotic species was more consistent across spatial scales (Table 2). About half the exotic species recorded for a vegetation type could be found in a 1000-$m^2$ plot. In each of the five vegetation types, the percentage of exotic species was greater at the 1-m$^2$ scale than at the 1000-m$^2$ scale. In four out of five vegetation types, however, the percentage of exotic species was less at the 1000-m$^2$ scale than at the 4000-m$^2$ scale (four plots combined). This suggests exotic species distributions vary by vegetation type and may be patchier at some scales than at others.

### *Relationships of species richness and total foliar cover*

At the 1-m$^2$ scale for the four vegetation types in the Central Grasslands, only two significant hump-backed relationships were found between native species richness and total foliar cover, and none were found for exotic species richness (Fig. 3). For native species richness in the mixed-grass and tallgrass prairie types, where the relationships were significant, only 18% and 13% of the variance, respectively, could be explained by the second-order polynomial model. The few data points with high foliar cover commonly had high leverage in the nonlinear models. For all sites combined, positive linear regressions and upsloping nonlinear regressions best described the highly variable relationship between native and exotic species richness and total foliar cover (Fig. 3).

The ''hump-back'' model (Grime 1973*a*, Bond 1983) was more evident for native and exotic species richness and total foliar cover at the 1-m$^2$ scale for vegetation types in the Colorado Rockies (Fig. 4). However, there was considerable variability in the scattergrams. The non-linear relationships were stronger for forest types than for meadow types, and stronger for native species than for exotic species. The total variance explained by non-linear models was $<$15% except for the aspen type or when all types were combined.

At the 1000-m$^2$ scale in the Central Grasslands, linear and nonlinear regressions of native or exotic species richness to total foliar cover were not significant ($n$ = 16 plots, $R^2 < 0.09$ in all cases; Fig. 5). At the 1000-m$^2$ scale in the Colorado Rockies, the nonlinear regression was weaker than at the 1-m$^2$ scale for native species richness, and linear and nonlinear regressions of exotic species richness to total foliar cover were identical and essentially linear ($n$ = 20 plots). Exotic species richness was positively linearly correlated with total cover at the 1000-m$^2$ scale in the Colorado Rockies and for both biomes combined, and weakly correlated ($r^2 = 0.38$, $P < 0.004$) in the Central Grasslands. All six graphs were at least weakly linearly correlated ($P < 0.2$; Fig. 5).

We concluded that the linear multiple regressions used in the following sections to compare biome-level responses are probably more representative than nonlinear models because: (1) very little variance was explained by nonlinear models, in particular with respect to exotic species richness (Figs. 3 and 4); (2) nonlinear models were heavily influenced by the leverage of a few high-cover data points; and (3) linear regressions best described responses for native and exotic species at larger spatial scales in both biomes for typical ranges in foliar cover (Fig. 5).

### *Predicting invasibility with data on native species richness and cover*

In both biomes, native species richness and foliar cover at the 1-m$^2$ scale was significantly correlated with species richness and foliar cover of exotic species (i.e., $P < 0.001$), but only 11–22% of the total variation was explained by these predictors (Table 3). For the four vegetation types in the Central Grasslands (combined data from the 1-m$^2$ subplots), exotic species richness was strongly, negatively correlated with both the number and cover of native plant species. The cover of exotic species in the Central Grassland sites also significantly declined with increasing numbers of native plant species. These results strongly support the paradigm that exotic species can more easily invade areas of low species diversity.

The opposite relationship was found for the five vegetation types in the Colorado Rockies: exotic species richness was strongly, positively correlated with both the number and cover of native plant species (Table 3). The cover of exotic species also was positively correlated with the number and cover of native species, although the relationship was greater between the cover of exotic and native species.

We examined the two vegetation types with the most exotic species at the 1-m$^2$ scale in both biomes to evaluate the consistency of regression results above. For the northern mixed-prairie and tallgrass prairie types, exotic-species richness strongly declined with increasing numbers of native plant species (Table 4). However, the cover of native species was a weaker predictor of exotic species richness in the tallgrass prairie type, and a nonsignificant predictor in the northern mixed-prairie type. In the aspen type in the Colorado Rockies, the number of exotic species was strongly, positively associated with the number of native plant species, but the cover of native species had a slightly negative affect on exotic species richness. The wet-meadow type showed opposite results: exotic species richness was strongly positively associated with the cover of native plant species, while the number of native species was statistically unrelated to exotic species richness (Table 4).

### *Predicting invasibility with data on native vegetation and soils*

Data on soil characteristics were pooled at the plot scale (1000-m$^2$) to better predict patterns of invasion at the landscape scale (i.e., among vegetation types and study sites). Stepwise multiple regressions showed that the percentage of total N in the soil (''soil total %N''; a measure of soil fertility; positive relationship) and the cover of native species (negative relationship) ex-

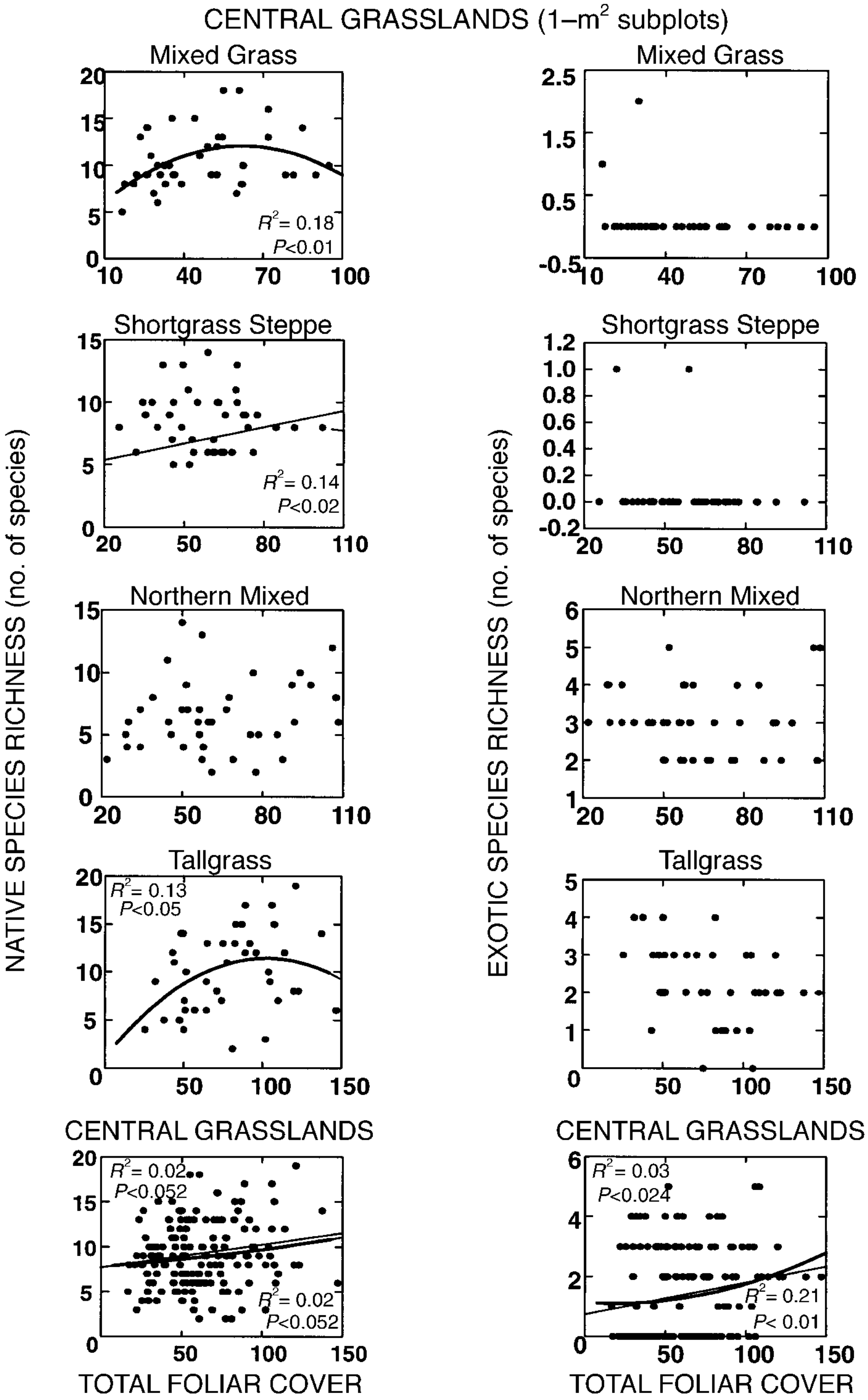


FIG. 3. Relationship (scattergram) of native and exotic species richness to total species cover for 1-$m^2$ subplots in four prairie vegetation types of the Central Grasslands (USA). Coefficients of determination and significance levels of linear and nonlinear regressions are shown where they are significant. In the top eight panels each black dot represents data from a 1-$m^2$ subplot (for a total of 40 1-$m^2$ subplots per panel); the bottom two panels include all 160 subplots from the four regional grasslands that comprise the Central Grasslands.

plained 83% of the variation in exotic-species richness among the Central Grassland sites (Table 5). For exotic species cover 73% of the variation was explained by soil %clay (positive relationship) and native species cover (negative relationship). Because the plots were clumped within study sites, and the sites themselves were widely scattered in the Central Grasslands, the regression analyses should not be used to infer similar relationships at the landscape scale.

In contrast, the plot-scale data of the five vegetation types within a 754-ha area in the Colorado Rockies was ideal for predicting invasion patterns on the landscape. Here, 69% of the variance in exotic species richness (at the 1000-$m^2$ scale) could be explained by the positive correlations with the number of native species and total soil carbon (a measure of organic matter; Table 5). For exotic species cover, 68% of the variation among vegetation types was explained by soil total %C, $\log_{10}$(available N), and the cover of native species. Total soil %C was strongly correlated with %N ($n = 35$, $r = 0.88$, $F = 118.0$, $P < 0.001$), and 47.2% of the variance in $\log_{10}$(available N) could be explained by $\log_{10}$(%clay) ($n = 20$, $t = 3.66$, $P < 0.002$) and $\log_{10}$(nitrogen mineralization potential) ($n = 20$, $t = 2.195$, $P < 0.042$). The positive interrelationships between exotic species richness/cover and soil resources is clear.

### *Species-specific responses to grazing and community responses to disturbance*

The 16 1000-$m^2$ plots in the Central Grassland sites varied in disturbance class (Appendix), but at the 1000-$m^2$ scale there were no significant relationships between disturbance and the number of exotic species ($r = 0.065$, $F = 0.060$, $P = 0.810$) or foliar cover of exotic species ($r = 0.123$, $F = 0.213$, $P = 0.651$). However, we documented many site-specific and species-specific responses to different fire and grazing regimes in the northern mixed prairie (Table 6).

Smooth brome (*Bromus inermis*), for example, averaged 9.3% cover in the tallgrass prairie area that was burned in the spring of 1986, 1987, 1988, and 1990, and it was found in 10% of the subplots (i.e., one subplot). In the area that was burned in spring of 1986, 1987, 1988, and 1989 (but not in 1990), the cover of smooth brome dropped to 3.8%, but it was found in 50% of the subplots. Quackgrass (*Agropyron repens*) was far more consistent in the two areas. Cover and frequency both doubled in the more recently burned site.

Two sample $t$ tests revealed significant species-specific responses to grazing at the northern mixed-prairie site in Wind Cave National Park, South Dakota (Table 6). The foliar cover of *B. japonicus* was >3 times greater in areas grazed by bison, elk, and deer compared to ungrazed sites. Likewise, the frequency (1-$m^2$ subplots) of *B. japonicus* (annual, seed-dispersed) was nearly twice as great in grazed vs. ungrazed sites. However, long-term cessation of grazing appeared to have little effect on the widespread distribution of a common, sod-forming, perennial exotic species, Kentucky bluegrass (*Poa pratensis*) at the same sites (Table 6).

### *Landscape-scale patterns of plant species richness and soils*

The sampling design at the Colorado Rockies site allowed for an analysis of spatial patterns of vegetation and soils in the 754-ha area (Fig. 6). Spatial interpolation (kriging maps) identified a high degree of spatial autocorrelation between the hot spots of native plant species richness and cover. Likewise, there was high spatial autocorrelation between native and exotic species richness, and between the hot spots of exotic species richness and the areas with the greatest exotic species cover. Only one sampled hot spot of native species richness (Fig. 6: $x = 28$ and $y = 20$) had not been significantly invaded (in terms of exotic species cover).

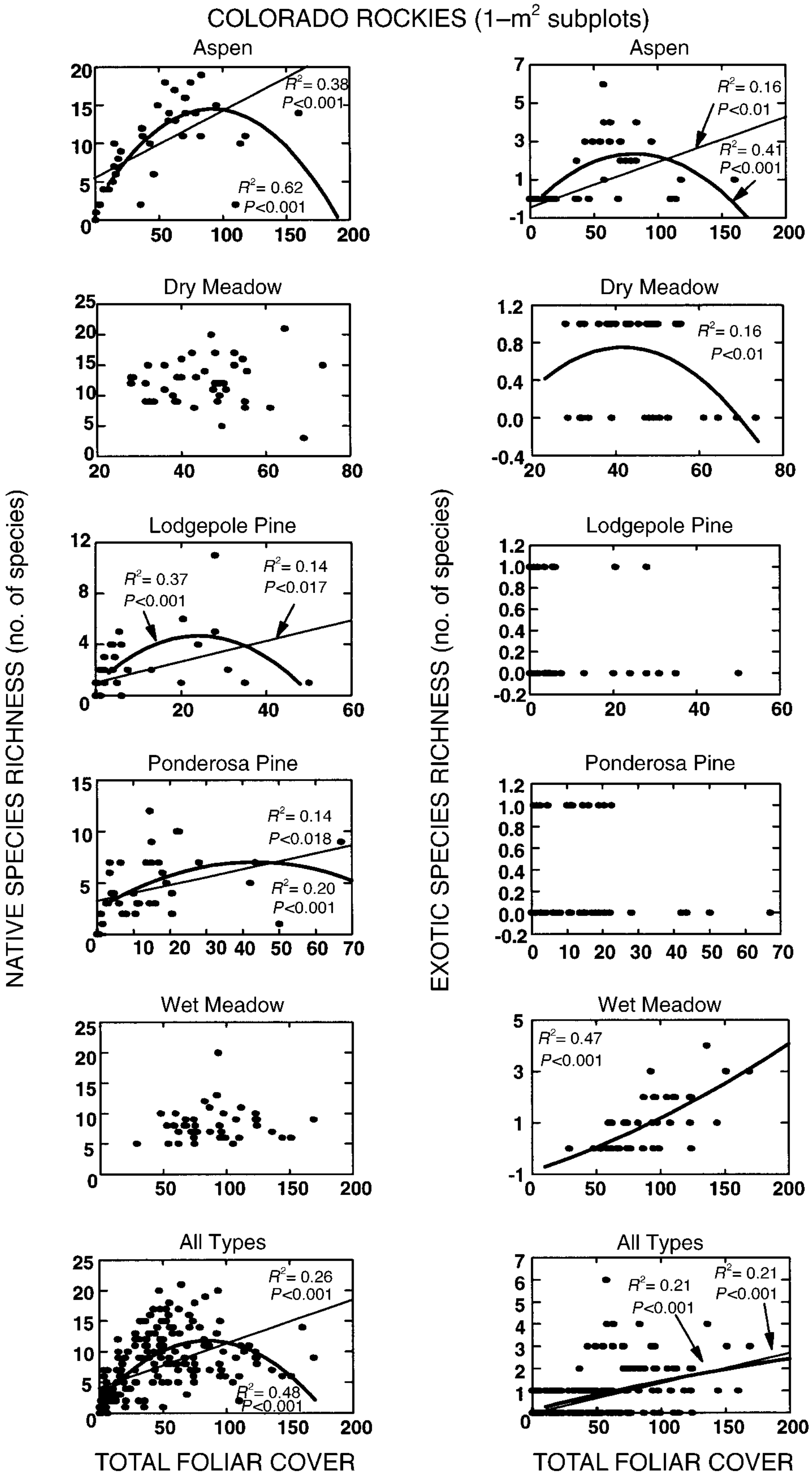
Patterns of native and exotic species richness and cover were also spatially autocorrelated with two important soil characteristics: %clay (a measure of water-holding capacity) and total %N (a measure of soil fertility). However, at least one hot spot of native and exotic species richness and cover ($x = 5$, $y = 20$–$27$) matched up poorly with %clay and even more poorly with %N. This was an area with clearings and stands of aspen in ponderosa pine forest. The clearings and aspen allowed light penetration to the forest floor, and, hence, higher understory species richness than the closed-canopy sites nearby.

Soil characteristics varied considerably among sites and vegetation types (Tables 1 and 2). In the Central Grasslands, mean values for total nitrogen in soils followed the following progression: tallgrass prairie > northern mixed prairie ≫ mixed-grass prairie > shortgrass steppe (Table 1). Mean values for %clay in soils followed the same progression: tallgrass prairie (35.3 ± 2.5%) > northern mixed prairie (32.3 ± 2.9%) ≫ mixed-grass prairie (20.9 ± 2.0%) > shortgrass steppe (14.7 ± 1.5%).

For the vegetation types in the Colorado Rockies, mean values for available nitrogen in soils followed the following progression: wet meadow ≫ aspen ≫ lodgepole pine > dry meadow > ponderosa pine, and nitrogen mineralization potential followed the progression: aspen > wet meadow > lodgepole pine > ponderosa pine ≫ dry meadow (Table 2).

### *Biome-scale patterns of native and exotic species richness and cover*

Despite differences in subplot-scale to plot-scale patterns of invasion in the Central Grasslands and Colorado Rockies, a consistent and alarming picture of exotic plant invasion emerged at the biome scale (Fig. 7). Areas of high native species richness were invaded more heavily than areas of low species richness. The tallgrass and northern mixed-prairie types in the Cen-


COLORADO ROCKIES (1–m2 subplots)
NATIVE SPECIES RICHNESS (no. of species)
EXOTIC SPECIES RICHNESS (no. of species)
Aspen
R2= 0.38
P<0.001
R2= 0.62
P<0.001
Aspen
R2= 0.16
P<0.01
R2= 0.41
P<0.001
Dry Meadow
Dry Meadow
R2= 0.16
P<0.01
Lodgepole Pine
R2= 0.37
P<0.001
R2= 0.14
P<0.017
Lodgepole Pine
Ponderosa Pine
R2= 0.14
P<0.018
R2= 0.20
P<0.001
Ponderosa Pine
Wet Meadow
Wet Meadow
R2= 0.47
P<0.001
All Types
R2= 0.26
P<0.001
R2= 0.48
P<0.001
All Types
R2= 0.21
P<0.001
R2= 0.21
P<0.001
TOTAL FOLIAR COVER
TOTAL FOLIAR COVER

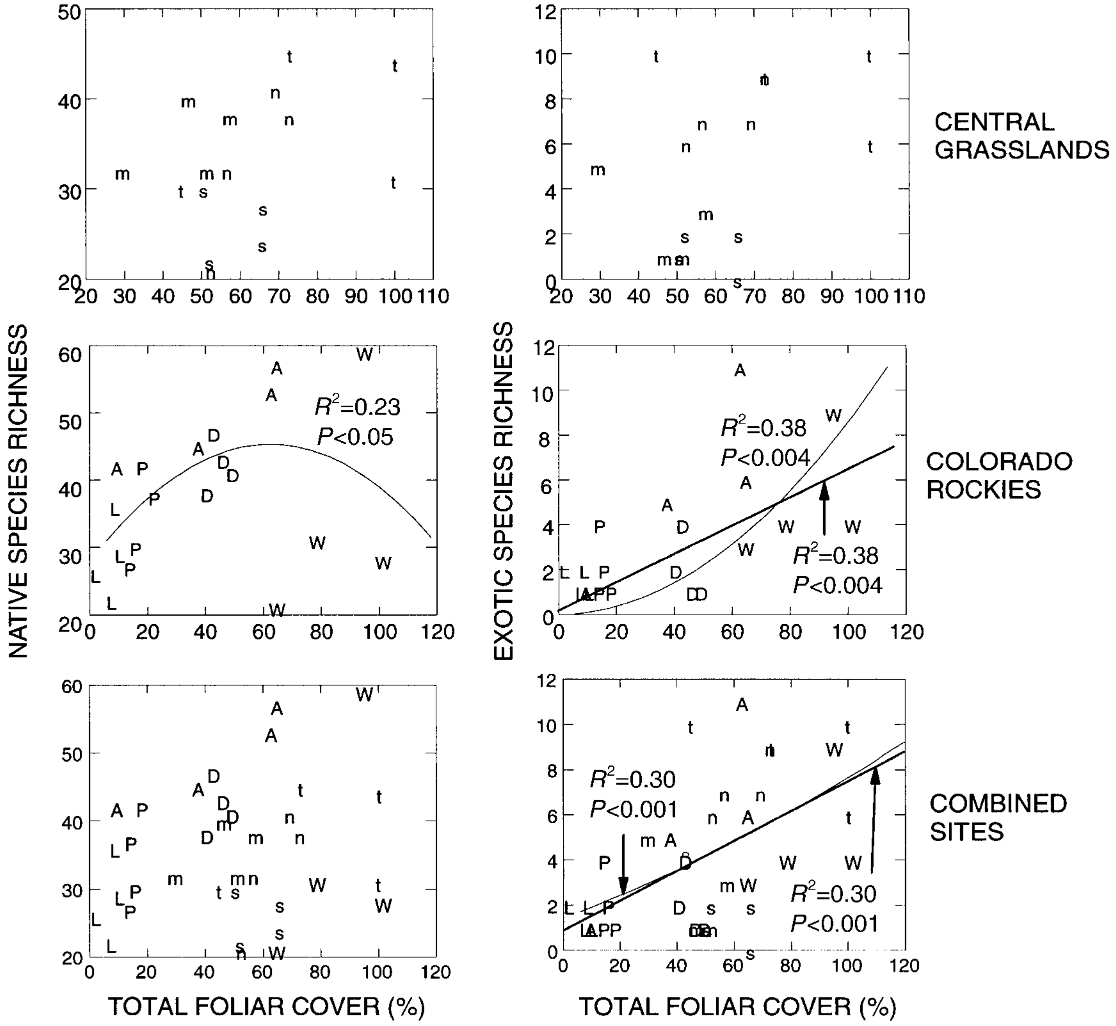


FIG. 5. Relationship of native and exotic species richness to total herbaceous cover for 1000-m² plots in the Central Grasslands, Colorado Rockies, and combined sites. Coefficients of determination and significance levels of linear and nonlinear regressions are shown where they are significant. Lowercase letters were used for the Central Grassland types (t = tallgrass prairie, n = northern mixed prairie, m = mixed-grass prairie, and s = shortgrass steppe); capital letters were used for the Colorado Rockies vegetation types (L = lodgepole pine, A = aspen, P = ponderosa pine, W = wet meadow, and D = dry meadow).

tral Grasslands also had the highest soil fertility and annual mean precipitation. The aspen and wet-meadow types, the two most invaded vegetation types in the Colorado Rockies landscape, had the greatest amounts of available nitrogen in the soils. There were strong linear relationships between the number of native species and the foliar cover of native species in the two biomes (Central Grasslands: $r = 0.47$, $F = 45.6$, $P < 0.001$; Colorado Rockies: $r = 0.50$, $F = 66.1$, $P < 0.001$), and even stronger relationships between the number of exotic species and the foliar cover of exotic species in the two biomes (Central Grasslands: $r = 0.64$, $F = 109.3$, $P < 0.001$; Colorado Rockies: $r = 0.75$, $F = 248.8$, $P < 0.001$). Nonlinear regressions described these relationships less strongly. At landscape- and biome-scales, areas of high native species richness in our study area may be heavily invaded by exotic species (Fig. 7).

To further assess patterns of invasibility within and across the two biomes, we combined the data for additional regression analysis. We found that, for the nine vegetation types in both biomes, mean foliar cover (i.e.,

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←

FIG. 4. Relationship (scattergram) of native and exotic species richness to total species cover for 1-m² subplots in five vegetation types in the Colorado Rockies (USA). Coefficients of determination and significance levels of linear and nonlinear regressions are shown where they are significant.

TABLE 3. Multiple regression of the number and foliar cover of native plant species on the number or cover of exotic species in 1-$m^2$ subplots in the Central Grasslands and Colorado Rockies study areas.

| | | Dependent variable = No. of exotic species† | | | Dependent variable = Cover exotic species‡ | | |
|---|---|---|---|---|---|---|---|
| Study areas | Independent variable | Coefficient | *t* | *P* | Coefficient | *t* | *P* |
| Central Grasslands | Constant | 3.040 | 9.927 | 0.001 | 3.589 | 15.413 | 0.000 |
| | No. native spp. | −0.126 | −3.651 | 0.001 | −0.094 | −2.755 | 0.007 |
| | Cover native spp. | −0.012 | −2.364 | 0.019 | −0.005 | −1.094 | 0.277 |
| Colorado Rockies | Constant | −0.015 | −0.128 | 0.898 | −0.589 | 0.673 | 0.502 |
| | No. native spp. | 0.069 | 4.721 | 0.001 | 0.185 | 1.683 | 0.094 |
| | Cover native spp. | 0.005 | 2.351 | 0.020 | 0.052 | 3.202 | 0.002 |

*Note:* For example, if $y$ = Central Grasslands number of exotic species, then $y = 3.04 - 0.126$ (no. native species) $-$ 0.012 (cover native species).

† For Central Grasslands: $F = 17.4$, df = 2, 157, $P < 0.001$, $R^2 = 0.182$. For Colorado Rockies: $F = 26.0$, df = 2, 197, $P < 0.001$, $R^2 = 0.209$.

‡ For Central Grasslands: $F = 11.0$, df = 2, 157, $P < 0.001$, $R^2 = 0.216$. For Colorado Rockies: $F = 12.3$, df = 2, 197, $P < 0.001$, $R^2 = 0.111$.

of the herbaceous layer, excluding tree cover) was strongly positively correlated with the total number of exotic species, mean cover of exotic species, and mean soil total %N (Fig. 8). For the nine vegetation types, mean %N in the soil was also strongly positively correlated with the total number of exotic species and the mean cover of exotic species. At this spatial scale, there was also a strong positive correlation between the total number and mean cover of exotic species (Fig. 8).

## DISCUSSION

First, we discuss our results in terms of comparisons to other studies (field observations, mathematical models, and controlled experiments). Then we discuss the application of these results to address ecological theory. Finally, we discuss the implications of this research to land managers and conservation biologists.

### *Comparisons to other studies*

At the landscape and biome scales, species-rich plant communities in our study area were particularly vulnerable to invasion by exotic species (Fig. 7), contrary to the classic paradigm. Detecting weed invasions in species-rich communities is not unprecedented. Bridgewater and Backshall (1981) reported a positive correlation between diversity and exotic plant invasions in natural communities in the South West Australian coast. Planty-Tabacchi et al. (1996) reported higher invasibility in species-rich riparian zones in southwest France and in the northwestern United States compared to upland sites: species-rich sites had greater percentages of exotic species in the flora. The authors attributed this to intermediate-disturbance regimes and habitat variability in riparian zones leading to high native and exotic species richness, while succession and canopy closure in forests reduced understory diversity over time. Exotic species invasions of species-rich riparian zones is also well documented (Fox and Fox 1986, Macdonald et al. 1986, Crawley 1987, Malanson 1993, DeFerrari and Naiman 1994). In a study of herbarium specimens for a coastal foothills landscape in California, Knops et al. (1995) found that the number

TABLE 4. Multiple regression of the number and foliar cover of native plant species on the number of exotic species in 1-$m^2$ subplots in the two most invasive sites in each study area (biome).

| | | | Dependent variable = No. of exotic species | | |
|---|---|---|---|---|---|
| Study area | Vegetation types | Independent variable | Coefficient | *t* | *P* |
| Central Grasslands | Northern mixed grass prairie† | Constant | 3.556 | 9.995 | 0.001 |
| | | No. native spp. | −0.109 | −1.956 | 0.058 |
| | | Cover native spp. | −0.007 | 0.779 | 0.441 |
| | Tallgrass prairie‡ | Constant | 3.719 | 10.751 | 0.001 |
| | | No. native spp. | −0.091 | −2.244 | 0.031 |
| | | Cover native spp. | −0.011 | −1.802 | 0.080 |
| Colorado Rockies | Aspen§ | Constant | −0.619 | −1.699 | 0.098 |
| | | No. native spp. | 0.234 | 6.341 | 0.001 |
| | | Cover native spp. | −0.008 | −1.428 | 0.162 |
| | Wet meadow‖ | Constant | −0.544 | −0.819 | 0.418 |
| | | No. native spp. | 0.004 | 0.068 | 0.946 |
| | | Cover native spp. | 0.018 | 2.929 | 0.006 |

† Wind Cave site: df = 2, 37, $P < 0.159$, $R^2 = 0.10$.

‡ Pipestone site: df = 2, 37, $P < 0.001$, $R^2 = 0.38$.

§ Rocky Mountain National Park: df = 2, 37, $P < 0.001$, $R^2 = 0.54$.

‖ Rocky Mountain National Park: df = 2, 37, $P < 0.019$, $R^2 = 0.19$.

TABLE 5. Stepwise multiple regression of native species richness and cover, and soil characteristics as predictors of exotic species richness and cover in 1000-m$^2$ plots in the Central Grasslands and Colorado Rockies.

| Study area | Dependent variable | Independent variable | Coefficient | $F$ | $P$ |
|---|---|---|---|---|---|
| Central Grasslands | No. exotic spp.† | Soil total %N | 24.10 | 57.38 | 0.001 |
| | | Cover native spp. | −0.06 | 5.74 | 0.032 |
| | Cover exotic spp.‡ | Soil % clay | 1.22 | 29.17 | 0.001 |
| | | Cover native spp. | −0.23 | 3.41 | 0.088 |
| Colorado Rockies | No. exotic spp.§ | No. native spp. | 0.147 | 31.88 | 0.001 |
| | | Soil total %C | 0.502 | 5.66 | 0.030 |
| | Cover exotic spp.‖ | Soil total %C | 1.70 | 15.89 | 0.001 |
| | | Log$_{10}$ (available N) | −3.28 | 5.73 | 0.030 |
| | | Cover native spp. | 0.20 | 26.05 | 0.001 |

*Note:* % clay is a measure of water-holding capacity; %N is a measure of soil fertility.

† $n = 16$ plots, $R^2 = 0.83$.

‡ $n = 16$ plots, $R^2 = 0.73$.

§ $n = 17$ plots, $R^2 = 0.69$.

‖ $n = 17$ plots, $R^2 = 0.68$.

of exotic species generally increased with the number of native species in a community type, except in a recently disturbed site. Here, however, the riparian type had fewer exotic species than nearby woodland and grassland types.

Only at the subplot and plot scales, and only in the Central Grasslands, did our results agree with the classic paradigm and with the experimental results of Tilman et al. (1996): species-rich areas appeared more resistant to invasion than species-poor areas. However, we found the opposite relationship (at the same 1-m$^2$ spatial scale) in the Colorado Rockies (Tables 2–4), and both study areas at the biome scale showed increased invasions with increased species richness (Fig. 7). The inconsistency of the relationship between high species richness and low invasibility at multiple spatial scales undermines the general application of Elton's hypothesis to other sites and spatial scales.

TABLE 6. Foliar cover and frequency (mean ± 1 SE) of two exotic plant species in 1-m$^2$ subplots in the Central Grasslands in (A) two burned areas in tallgrass prairie, and in (B) areas grazed by native ungulates (bison, elk, deer) and in ungrazed/exclosed areas (fenced since 1960) in northern mixed-grass prairie.

A) Tallgrass prairie site

| Parameter and species | Burned last in 1990 | Burned last in 1989 |
|---|---|---|
| Foliar cover (%) | | |
| *Bromus inermis* | 9.3 ± 2.4 | 3.8 ± 1.8 |
| *Agropyron repens* | 0.1 ± 0.1 | 0.05 ± 0.01 |
| Frequency (%) | | |
| *Bromus inermis* | 10.0$^{a}$ ± 7 | 0.05$^{b}$ ± 17 |
| *Poa pratensis* | 20.0 ± 13 | 10.0 ± 10 |

B) Northern mixed prairie

| Parameter and species | Grazed | Ungrazed |
|---|---|---|
| Foliar cover (%) | | |
| *Bromus japonicus* | 8.9$^{a}$ ± 2.3 | 2.6$^{b}$ ± 1.1 |
| *Poa pratensis* | 15.7 ± 2.0 | 18.6 ± 3.3 |
| Frequency (%) | | |
| *Bromus japonicus* | 97.5 ± 2 | 50.0 ± 12 |
| *Poa pratensis* | 92.5 ± 4 | 90.0 ± 7 |

*Note:* Means with different lowercase superscript letters within rows are significantly different, two-sample $t$ test.

Our results in the Central Grasslands showed highly varying effects of disturbance on diversity. Long-term grazing produced variable effects on native and exotic species richness and cover. The shortgrass steppe and mixed-grass prairie sites had been moderately to heavily grazed by cattle for >100 yr (and by bison before then) and were comparatively low in diversity, yet they were not invaded (Table 1, Fig. 7). These vegetation types were also comparatively low in soil fertility (%N and %C; Table 1, Fig. 8). The northern mixed-prairie sites that received moderate grazing by native ungulates were heavily invaded. Ungrazed, but recently burned sites in the tallgrass prairie were heavily invaded. These results suggest that factors other than grazing, such as soil fertility (Table 5, Fig. 8) and fire (Table 6), may facilitate invasion of exotic species in some systems. Other studies clearly demonstrate the role of disturbance in enhancing and maintaining species diversity in grasslands. McNaughton's (1983) comprehensive analysis of the Serengeti ecosystem found that grazing enhances diversity at local and landscape scales (also see McNaughton 1979). However, preliminary data from meadows in Rocky Mountain National Park showed no significant difference in the plant species richness of grazed and long-ungrazed areas (Stohlgren et al. 1997*b*). Whisenant and Uresk (1990) showed that burning in mixed-grass prairie communities could reduce *Bromus japonicus*, but that fire also negatively affected some native plant species, while positively influencing other native plant species.

At plot and landscape scales, areas of high soil fertility (total %N and %C, and available N) and water-holding capacity (%clay) were particularly invasible (Tables 1, 2, and 5). For the Colorado Rockies site, the major hot spot in the center of the kriging map for native species cover (Fig. 6) mapped neatly over the maps of total %N and %clay in this landscape. We

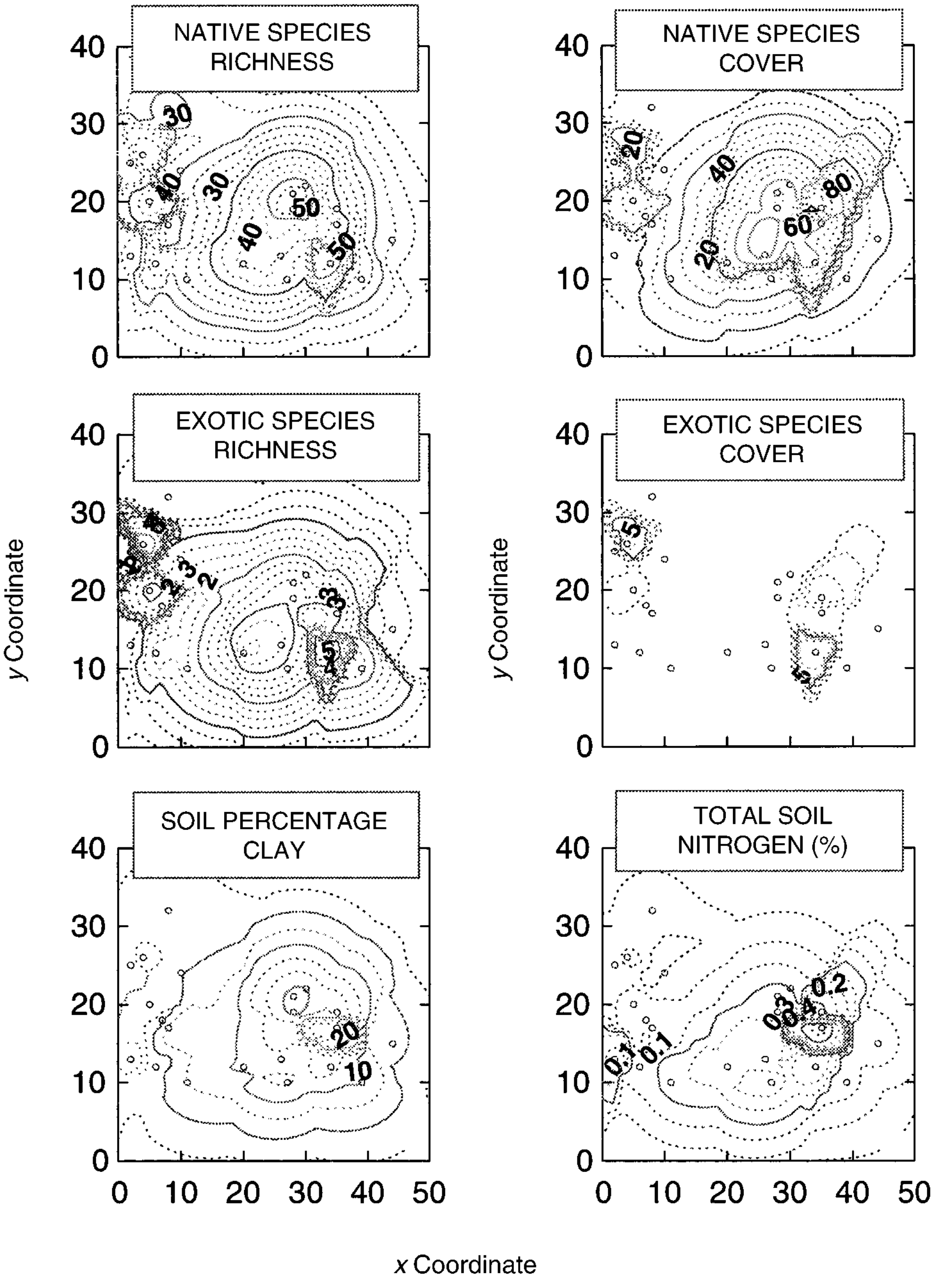

FIG. 6. Kriging maps of the number and foliar cover of native and exotic plant species, percentage clay in the top 15 cm of soil, and total soil N in the 754-ha Colorado Rockies study area.

found strong positive linear relationships between species richness and foliar cover for native and exotic plant species in both biomes. The negative relationship found in the multiple regression between available nitrogen and the cover of exotic species (Table 5) contrasts with the other soils analyses that show positive relationships between exotic species richness (and cover) and soil fertility (total %N), organic matter (total %C), and %clay. Because simple regressions were weaker between available nitrogen and the cover of exotic species at plot scales, one possible explanation is that areas high in exotic species cover may use more nitrogen than areas with similar cover of native species (i.e., the statistical analysis describes the post-invasion environment rather than the pre-invasion environment). Although we did not measure productivity directly, our results are supported by experiment results by Tilman et al. (1996) who found that more diverse communities are more productive, and contradicted by Tilman (1997) who found higher plant species richness in plots with low available nitrogen. Fox and Fox (1986) reported that in New South Wales, Australia, the inci-

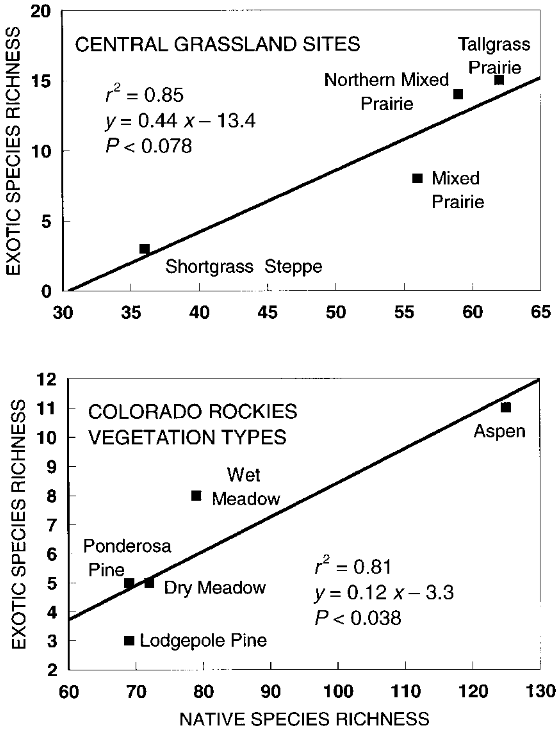

FIG. 7. Relationship of native species richness to number of exotic species at vegetation-type and biome scales (based on combined species lists from 1000-$m^2$ plots).

dence of invasion was higher in sites with higher rainfall. Our field data (Table 5, Figs. 6, 7, and 8), would lead us to conclude that fertile soils probably enhance native and exotic species richness and cover, given typical disturbance regimes (Hobbs and Huenneke 1992).

Species-specific responses to disturbance cannot be ignored, as they thwart sweeping generalizations about the effects of disturbance or grazing related to plant species richness and diversity. The examples of *Bromus japonicus* and *Poa pratensis* (Table 6) showed that exotic species cannot be viewed as a group of species with similar responses to the same level of disturbance. Moore (1959) and Pierson and Mack (1990) also found that exotic species invaded grazed and ungrazed sites in unpredictable ways. As long as species-specific responses are unpredictable (Hobbs and Huenneke 1992), generalizations about exotic species richness may be as illusive and elusive as theories about the causes of native species richness patterns (Palmer 1994).

Issues of scale also prevent many sweeping generalizations about patterns of invasibility. Small-scale experiments and field observations may produce results that are scale dependent (Tables 1 and 2). The experimental plots used by J. Knops (*personal communication*; see also Tilman et al. [1996]) identified a strong relationship between species richness and cover (productivity) and a negative relationship between species richness and the number of exotic species in small plots ($<10$ $m^2$) for one study area. Our data show that the negative relationship between species richness and the number of exotic species can be exactly the opposite at the same 1-$m^2$ scale in another biome (Tables 1–5), and even opposite in the same biome at a larger spatial scale (Fig. 7). Care must be taken not to extrapolate the results of small-scale experiments and observations to the landscape, region, and world.

Spatial autocorrelation may be an important and often overlooked component of exotic plant invasions. Our field observations and kriging maps in the Colorado Rockies suggested that sites that were close to hot spots of exotic plant species richness and cover (Fig. 6) appeared to have more seedlings of exotic species than similar sites further away from the hot spots. Many studies have shown exotic plants spreading from foci (e.g., Mack 1981, Kareiva 1990, Bergelson et al. 1993). Rejmánek (1996*a*) also showed that islands closer to continents had more exotic species than islands further away. In fact, he suggested that the distance factor was likely more important than the native species richness factor in the invasion of islands.

### *Application of results to ecological theory*

We now can reexamine the general hypothesis of Elton (1958) that species-rich communities are less easily invaded than species-poor communities. At subplot (1-$m^2$) and plot (1000-$m^2$) scales, our results in the Central Grasslands strongly support Elton's hypothesis. However, our results from the Colorado Rockies at subplot, plot, and vegetation-type scales strongly refute the hypothesis. Our biome-scale results (Fig. 7) combined with results from riparian zones (Fox and Fox 1986, Macdonald et al. 1986, Crawley 1987, Malanson 1993, DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996) suggest that many species-rich areas may be particularly invasible.

Our results more closely follow the theory of May (1973) that diverse systems are more likely to vary in time and space, which may be termed ''unstable,'' and the models of Huston and DeAngelis (1994), which showed that many species can coexist in spatially heterogeneous areas as long as nutrients and light are not limiting. May's theory suggested that high rates of species turnover may provide a mechanism for low ''stability'' (defined here as persistence of native species assemblages and resistance to invasion). Locally rare species (species with $<1\%$ cover) are a major component of species richness in grassland systems (Stohlgren et al. 1998), and they are highly spatially variable (also see McNaughton 1983, Coffin and Lauenroth 1989). Throughout the Central Grasslands and Colorado Rockies, roughly half the plant species found in each 1000-$m^2$ plot had $<1\%$ foliar cover. Furthermore, we found a higher percentage of exotic species in vegetation types with lower overlap in species composition (Fig. 9). We hypothesize that low species overlap among plots would make it difficult for species-rich communities to develop stable community–environ-

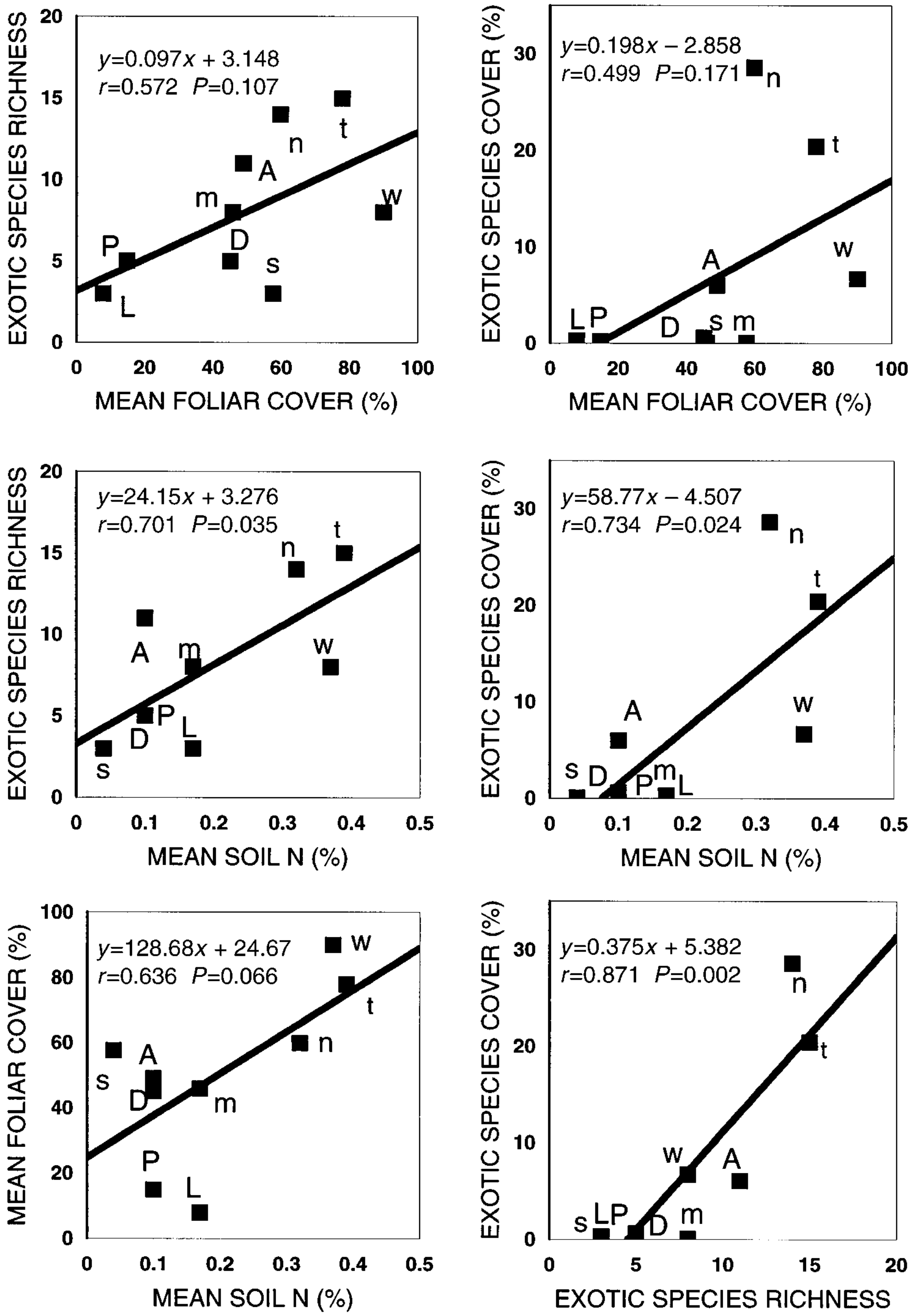

FIG. 8. Relationships of mean foliar cover (herbaceous layer only) and mean soil %N to exotic species richness and cover by vegetation type (data combined from four 1000-m$^2$ plots per vegetation type). Also shown is the relationship between exotic species richness and cover. Lowercase letters were used for the Central Grassland types (t = tallgrass prairie, n = northern mixed prairie, m = mixed-grass prairie, and s = shortgrass steppe); capital letters were used for the Colorado Rockies vegetation types (L = lodgepole pine, A = aspen, P = ponderosa pine, W = wet meadow, and D = dry meadow).

ment relationships. Even areas with similar species richness are likely to have different mixes of species and probably different levels of unused (available) resources so that ''resource shifts'' (Fox and Fox 1986) may be commonplace.

The models of Huston and DeAngelis (1994) provided an additional framework for evaluating invasions based on resource transport and supply rates, and on the distinction between local and regional effects. In contrast to transport-limited competition models that

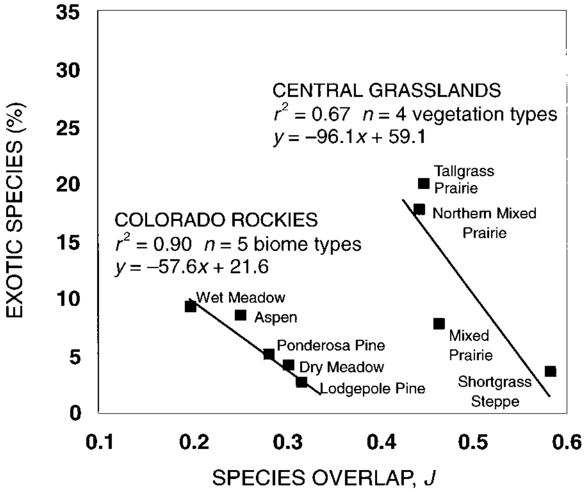

FIG. 9. Relationship of species overlap to percentage of exotic species at vegetation-type and biome scales (based on the mean similarity, *J*, of pairwise comparisons of species lists from 1000-m$^2$ plots).

assumed a complete mixing of resources and organisms (e.g., Tilman 1982), Huston and DeAngelis showed that if these assumptions were relaxed, the local coexistence of many potential competitors (i.e., native and exotic species) was likely. The low species-composition overlap within vegetation types (Fig. 9) and the variation in species richness and cover at the 1-m$^2$ scale (Figs. 1 and 2) and at multiple spatial scales (Tables 1 and 2) may create and maintain non-equilibrium conditions presumed by Huston and DeAngelis (1994: 972).

The key advancement of Huston and DeAngelis (1994) was the distinction between local and regional effects. We found that relationships at one scale, such as the relationship between native and exotic species richness, can completely reverse at a larger scale (Tables 1–3). Thus, the processes controlling local native and exotic species richness, frequency, and foliar cover (Table 5) may be different from the processes controlling regional plant diversity (Figs. 7 and 8). If diversity increases with spatial scale, such as covering more heterogeneous landscapes and environmental gradients (Fig. 6), then the growing regional pool of potential competitors (i.e., native and exotic plant species with various life-history traits) could help maintain local and regional heterogeneity (Huston 1979, Huston and Smith 1987).

Intermediate disturbances and grazing, which likely contribute to the high diversity in many ecosystems (Caswell 1978, Connell 1978, Petraitis et al. 1989), may prevent the dominance of one or a few superior competitors and further contribute to non-equilibrium conditions, high plant-species turnover (Fig. 9), and near-continuous resource shifts in time and space. Thus, it might be difficult to completely monopolize resources in fertile sites (Case 1990) to maintain stability (Tilman et al. 1996) and resist invasion (Elton 1958).

Law and Morton (1996) suggested that the key to Elton's hypothesis is that the richness of the regional pool of species dictated the complexity that lead to resistance to invasion. Instead, our field data suggest that resistance to invasion is heavily compromised by: (1) the spatial heterogeneity of locally rare species (Fig. 9; see also McNaughton 1993), and (2) the number of ''transient'' plant species in the regional species pool (Fig. 10). We defined transient species as those plant species that do not occur in all plots in a vegetation type. We propose that in non-forested areas the combination of high species richness, high spatial variability, high numbers of transient species, and high turnover rates makes it that much more difficult for a community to develop the tight interspecies–environment relationships necessary to monopolize resources. That is, the number of all possible combinations of species mixes in any site rises exponentially as new species are added to the pool (Fig. 10). Despite high plant species richness and foliar cover, soil resources may be available to invading plant species (Table 5, Fig. 8).

How do we reconcile these results with ample evidence that species-poor islands are unusually susceptible to invasion (e.g., Elton 1958, Bramwell 1979, Moulton and Pimm 1986, Loope and Mueller-Dombois

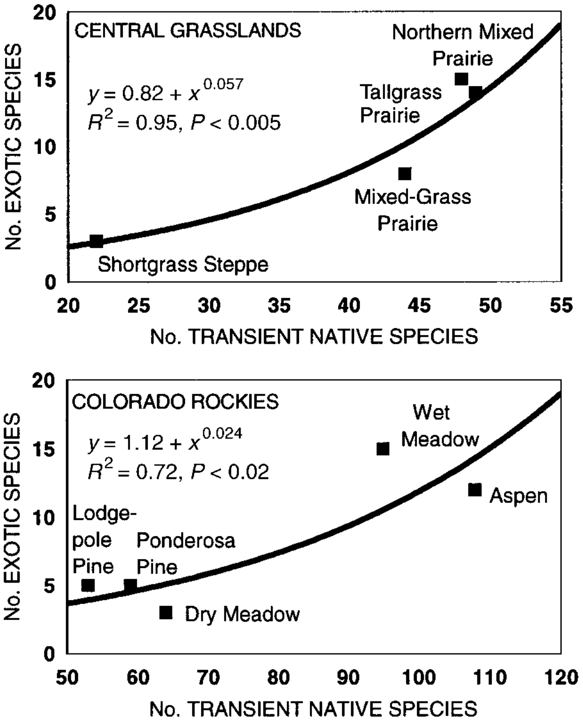

FIG. 10. Relationship of number of transient species to percentage of exotic species at vegetation-type and biome scales. Transient species are plant species that do not occur in all sample plots within a vegetation type.

1989, Vitousek 1990), and planting experiments that clearly show higher invasibility in species-poor plots (Tilman et al. 1996, Tilman 1997, J. Knops, *personal communication*)? We suggest that Elton's hypothesis is only appropriate where the species assemblage poorly monopolizes available resources and that invasibility may be independent of species richness in many systems. Invasibility may be far more dependent on resource availability. The tallgrass prairie, northern mixed prairie, and wet-meadow sites all had high levels of light, water, and nutrients. This would explain why species-poor islands and post-disturbance sites are susceptible to invasion, and why our forested sites (lodgepole pine, low light) and low soil-fertility sites (e.g., shortgrass steppe and dry meadow, low soil N) are not.

This also would help explain the results of planting experiments where species richness is manipulated (Tilman et al. 1996). In Tilman's experiments, the major effects of low species richness may have been caused by including atypically low species-richness treatments (i.e., 2–10 species per 9 $m^2$) based on random selections of species from a species pool. Even the lowest diversity grassland plots we studied rarely had $<$15 species per 10 $m^2$ (i.e., shortgrass steppe), and these areas were the least invasible of all those we investigated. Tilman's (1996:719) results appeared independent of species richness in plots where species richness was $>$5 species per 9 $m^2$. The primary difference between experimental plots and natural landscapes is that many natural landscapes are not simple random selections from a species pool (as in Case 1990, Law and Morton 1996, Tilman et al. 1996). Rather, they are nonrandom species assemblages of dominant and locally rare species with more complex spatial dynamics and inter-specific relationships that influence the availability of resources (Lack 1976) and resource transport rates (Huston and DeAngelis 1994). We suspect that many low-diversity natural systems (e.g., the shortgrass steppe, dry meadow, conifer forests; Tables 1, 2, and 5, Figs. 6 and 8) are resistant to invasion because: (1) they have low levels of total resources such as soil nutrients, light, or water available to the herbaceous layer, and (2) the native plant species in the system monopolize available resources to resist invasion.

Why does there appear to be a ''hump-back'' in the relationship between cover and diversity for the forested sites or at 1-$m^2$ scales, but a linear (or simply scattered) pattern for the non-forested sites or larger spatial scales (Figs. 3, 4, and 8)? Huston (1992) and Huston and DeAngelis (1994) speculate that the hump-backed pattern for the forests may relate to the very high cover levels leading to substantial reductions in light availability for understory plants in the forests, which may lead to reduced diversity. In grasslands, however, even the ''high'' cover end of the spectrum may have been too low for the availability of light to reduce the level of diversity that could be supported by soil resources (such as water and nutrients). Our study was not designed to address the hump-backed model of diversity and productivity (Huston 1992, Huston and DeAngelis 1994), as we did not measure productivity directly. At the 1-$m^2$ scale several vegetation types had maximum values of species richness in the moderate ranges of foliar cover (Figs. 3 and 4), which would appear to support the unimodal model. The non-forested sites we studied rarely had extremely high cover values, so data may represent the rising limb of the hump-backed model. Issues of scale were also important. The significant unimodal relationships at the 1-$m^2$ scale disappeared or were weaker at the 1000-$m^2$ scale, or weakly linear (Fig. 5 [$P < 0.2$ for all graphs] and Figs. 3, 4, and 8). Exotic species richness was positively linearly correlated with total cover at the 1000-$m^2$ scale in the Colorado Rockies and for both biomes combined, and weakly correlated ($r = 0.38$, $P = 0.14$) in the Central Grasslands (Fig. 5). At landscape and biome scales, for exotic species richness and cover we found strong positive linear relationships with total understory foliar cover and %N in the soil for the nine vegetation types studied (Fig. 8). Thus, many of the relationships we explored were strongly scale dependent, and fits to a particular model at one spatial scale my be misleading.

Contrary to the findings of Rapson et al. (1997), we found that the humped-back relationship can be strongly influenced by plot size (Figs. 3–5; also see Oksanen 1996). The largest quadrat tested by Rapson et al. (1997) was 2 × 2 m. Granted, it is difficult to measure biomass at larger scales, but we advise a multi-scale approach to such investigations. The 1-$m^2$ quadrat size endorsed by Grime (1973*a*, 1997) may not provide a realistic picture of plant species richness at larger spatial scales (Fig. 5). Our results suggest that many ecological relations are scale dependent and vegetation-type or biome specific, and that many ecological factors and interactions in addition to herbaceous foliar cover are of course important in structuring the species diversity of an ecosystem.

### *Generalizations and suggested areas of emphasis*

We cautiously offer the following generalizations and suggested areas for future research.

1) *Both native and exotic plant species respond favorably to fertile areas and available resources.* Native and exotic species richness and cover correlate positively in most vegetation types in our study areas, suggesting that both groups respond to increased available resources with increased diversity. Additional studies are needed to see if areas of low diversity are resource poor (e.g., shortgrass steppe, the dry-meadow type), and if invasibility might be limited in more stressful environments (Cale and Hobbs 1991, Hester and Hobbs 1992, Hobbs and Huenneke 1992). New studies must be designed to survey and monitor the effects of invasions across gradients of resource availability, en-

vironmental change, and disturbance (Fox and Fox 1986, Swincer 1986).

2) *The attribute of ''high species richness'' does not ensure complete use of all available resources, stability, or resistance to invasion.* Our data show that ''a few'' strongly interacting species, especially in natural communities low in resources (e.g., shortgrass steppe, mixed-grass prairies) may resist invasion, despite long-term heavy grazing. In contrast to Case (1990), and in light of Fig. 7, we challenge theorists and field ecologists to ask the question ''Why are species-rich communities so invasible?'' Why are species-rich areas of Cape South Africa, southern Australia (Rejmánek 1996*a*), California, and Florida (Vitousek et al. 1996), riparian zones (DeFerrari and Naiman 1994), and other hot spots of plant diversity so heavily invaded?

3) *Many other factors are likely far more important indicators of invasion than the attribute of species richness.* Efforts must be made to make experiments (including species addition and removal experiments) that investigate species richness as the primary causal agent more realistic (i.e., more comparable to natural systems). Models and experiments using random species mixes may mask the importance of nonrandom species assemblages and the inter-specific interactions found in natural systems (Huston 1997). Experiments in protected environments may not be representative of natural landscapes that are frequently grazed, burned, and disturbed. Integrated observational and experimental studies are needed to link levels of disturbance (Hobbs and Huenneke 1992), proximity to and abundance of seeds or reproductive tissues of exotic species (Fig. 6), interactions with other species (plants and animals; Newsome and Noble 1986, Mack 1996*b*), and resource availability (Huston and DeAngelis 1994, Wedin and Tilman 1996, Tilman 1997) at meaningful spatial scales.

4) *Species-specific responses to disturbance and habitat variation deserve far more attention than the search for sweeping generalizations.* Groves (1986), Smith (1989), Mack (1996*a, b*), Rejmánek (1996*b*) and others clearly point to the need for species-specific research, especially for naturalized exotic species, or perhaps focused on groups with similar life histories (e.g., Smith and Huston 1989). We agree with many scientists (e.g., Moulton and Pimm 1986, D'Antonio 1993, Lodge 1993) that colonist species and their target communities cannot be studied independently. Thus, integrated studies of plant demography and ecology are urgently needed where exotic species invade and dominate.

5) *Quantitative inventory and monitoring efforts should be initiated immediately to assess the status and trends of invading plants in natural areas across scales.* We must take a leadership role in developing standardized approaches to inventory and monitor invasive species and their effects on natural systems (Everitt et al. 1995, Stohlgren et al. 1997*a*, *b*, 1998). Since the factors influencing exotic species establishment (species richness; Tables 3, 4, and 5) may be different than those influencing exotic species cover (and potential dominance; Table 5, Fig. 8), we suggest that the processes of initial invasion and naturalization be studied in separate but integrated ways.

### *Implications for land managers and conservation biologists*

Parks and biological reserves are important areas to assess the invasion of exotic plant species within a region—pristine areas serve as index sites of large-scale environmental change (Vitousek et al. 1996). While the causes remain unclear, we are concerned that areas of high native plant species richness and cover (Tables 1 and 2, Fig. 7) and areas high in soil fertility (Table 5, Figs. 6 and 8) in natural landscapes may be highly invasible. Of equal concern is that these sites that are high in plant diversity are usually hot spots of biological diversity—rare habitats with distinctive plant and animal communities. The aspen and wet-meadow areas in the Colorado Rockies sites, for example, had higher diversity of vascular plants, birds (T. Stohlgren, T. Mabee, and J. Woolf, *unpublished data*), and butterflies (Simonson 1998) than the other vegetation types in the area. Tallgrass prairie systems have high endemism and biodiversity, and even higher levels of risk from land-use change, fragmentation, and fire suppression (Leach and Givnish 1996).

We are uncertain as to why many areas identified as hot spots of endangered species in the United States (Flather et al. 1994, Dobson et al. 1997) are also hot spots for invasive plant species (e.g., Hawaii, California, Florida, tallgrass prairie remnants). Exotic plant species may accelerate the rapid loss of native species in tallgrass prairie ecosystems, which have long been threatened by fragmentation and interruption of landscape-scale processes (Smith 1981, Chapman 1984, Leach and Givnish 1996).

Even if the mechanisms are poorly understood, many scientists agree that exotic plant species will eventually cause a decline in native plant species and ecosystem diversity (Bock et al. 1986, Billings 1990, D'Antonio and Vitousek 1992). Short-term effects of invasive plants include drastically altering fire cycles (D'Antonio and Vitousek 1992), nutrient cycling (Vitousek 1990), wildlife forage quality (Medina 1988, Trammell and Butler 1995), and wildlife grazing patterns (Trammell and Butler 1995). By reducing palatability and productivity, infestations of the noxious weed leafy spurge (*Euphorbia esula*), for example, can reduce the carrying capacity of pastures for livestock by 50–75% in some areas (Lym and Messersmith 1987).

Internal feedbacks and spatial-autocorrelation effects may further accelerate the spread of exotic plants (Bergelson et al. 1993). For example, *Bromus japonicus,* which we found in the northern mixed prairie site, increases litter buildup and decreases soil evaporation, which favors its germination and establishment (Whisenant 1990). Small populations of exotic species can spread quickly (Mack 1981) so their early detection is crucial (Stohlgren et al. 1998).

It may become increasingly important to maintain natural disturbance regimes. Invasion by exotic species has either already occurred or is inevitable in many systems. Maximizing the persistence of native species may depend on maintaining the natural range of disturbances. Although information is lacking for most areas, some studies suggest that reducing or exceeding the frequency, intensity, spatial patterns, or scale of disturbances will likely lead to a faster replacement of native species by exotic species (Abrams et al. 1986, Fox and Fox 1986, Milchunas et al. 1990, Hobbs and Huenneke 1992, Planty-Tabacchi et al. 1996).

Other factors could simultaneously influence native and exotic species richness. Nitrogen deposition from air pollution may further impoverish native diversity, facilitating or inhibiting the spread of exotic species (Hobbs and Huenneke 1992). Even successful control and eradication efforts do not assure that the effects of the exotic species are erased. Invasive *Acacia* species in Cape ecosystems (South Africa) can have long-term effects on soil nutrient enhancement and nutrient mineralization patterns (Stock et al. 1995). Care must be taken in applying control treatments, especially if the infested areas are hot spots of native plant diversity.

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## APPENDIX

A table giving the geographic location, vegetation, soil, and disturbance level for each 1000-m² plot in the study is available in ESA's Electronic Data Archive: *Ecological Archives* M069-002.