

Scale and plant invasions: a theory of biotic acceptance

Měřitko studia a rostlinné invaze: teorie biotické akceptance

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Dedicated to Marcel Rejmánek

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We examined the relationship between native and alien plant species richness, cover, and estimated biomass at multiple spatial scales. The large dataset included 7051 1-m² subplots, 1443 10-m² subplots, and 727 100-m² subplots, nested in 727 1000-m² plots in 37 natural vegetation types in seven states in the central United States. We found that native and alien species richness (averaged across the vegetation types) increased significantly with plot area. Furthermore, the relationship between native and alien species richness became increasingly positive and significant from the plant neighbourhood scale (1-m²) to the 10-m², 100-m², and the 1000-m² scale where over 80% of the vegetation types had positive slopes between native and alien species richness. Both native and alien plant species may be responding to increased resource availability and/or habitat heterogeneity with increased area. We found significant positive relationships between the coefficient of variation of native cover in 1-m² subplots in a vegetation type (i.e. a measure of habitat heterogeneity), and both the relative cover and relative biomass of alien plant species. At the 1000-m² scale, we did find weak negative relationships between native species richness and the cover, biomass, and relative cover of alien plant species. However, we found very strong positive relationships between alien species richness and the cover, relative cover, and relative biomass of alien species at regional scales. These results, along with many other field studies in natural ecosystems, show that the dominant general pattern in invasion ecology at multiple spatial scales is one of “biotic acceptance” where natural ecosystems tend to accommodate the establishment and coexistence of introduced species despite the presence and abundance of native species.

Key words: alien species dominance, biotic acceptance, diversity and invasibility, exotic plant species, multi-scale sampling.

Introduction

Observational studies, controlled experiments, and theoretical models have been used to investigate the role of diversity in inhibiting invasions. The prevailing paradigm was based largely on observations that low diversity islands were easily invaded (i.e. with greatly reduced environmental gradients and levels of habitat heterogeneity, Elton 1958), and reinforced by the immensely successful invasions of alien plants and animals on Guam and the Hawaiian Islands (Mack et al. 2000). However, different environmental characteristics of islands produced different levels of plant invasions, with tropical islands being more heavily invaded than islands in temperate zones (Rejmánek 1996). Because islands also

varied in distances from the mainlands, area, and habitat heterogeneity, generalizations were slow to emerge, especially for largely ignored continental areas (Rejmánek 1996, Chytrý et al. 2005, Stohlgren et al. 2005b, Richardson & Pyšek 2006).

Contradictory field observations at different spatial scales (i.e. scales of observations, plot size) have contributed to the confusion. For example, Stohlgren et al. (1999) reported that four grassland vegetation types in the central grasslands biome in the US showed negative relationships between native and alien species richness at 1-m² and 1000-m² scales, while five vegetation types in a montane biome of Colorado showed positive relationships at the same two spatial scales. These findings and other contradictory site-specific studies underscore the dire need for additional multi-scale studies of native and alien plant species patterns (Fridley et al. 2006).

Small-scale, controlled experiments of artificially constructed “communities” (Knops et al. 1997, Tilman 1997, Kennedy et al. 2002) generally supported the “biotic resistance” paradigm whereby species-rich habitats would be less prone to invasion than species-poor habitats, presumably due to competitive exclusion (Grime 1973) and by usurping available resources (Tilman 1997). Likewise, small-scale experiments supporting biotic resistance have been corroborated by some theoretical studies (Case 1990). Shea & Chesson (2002) presumed negative relationships between native and alien species within species-poor habitats and species-rich habitats at small spatial scales, where extrinsic factors do not vary, but a positive relationship across habitats, where extrinsic factors do vary. One of many implicit assumptions of small-scale studies is that the patterns and processes observed in small plots are directly scalable to larger areas (Fridley et al. 2006). For example, after a series of small-scale experiments Kennedy et al. (2002) proclaimed that “diverse communities will probably require minimal maintenance and monitoring because they are generally effective at excluding undesirable invaders.” Fridley et al. (2004) used null models and multi-scale plot data in one area to show that the relationship between native and alien species richness may be positive at small and large scales, but it was more positive at larger spatial scales (also see Brown & Peet 2003). Unfortunately, the null models of Fridley et al. assumed “uniform random selection of species” (i.e. random community assembly) in a small species pool of 20 to 100 species, a constant proportion of species by origin (75% native, 15% exotic, and 10% “blank” species or open spaces), a constant plant density, equilibrium abundance (*sensu* Hubbell 2001), and equal-sized individuals regardless of species and age; conditions that are rarely if ever found in nature. Thus, direct comparisons of observational studies to these types of null models are problematic (also see Huston 1997).

Issues of scale have been embraced by observational ecologists as a means of documenting patterns of invasion at local, regional, and national scales (Stohlgren et al. 1999, 2003, 2005b, Sax 2002, Brown & Peet 2003, Fridley et al. 2006). As a result, some consistent patterns are emerging. At sub-continental scales, for example, there is convincing evidence of strong positive relationships between native and alien plant species richness (Stohlgren et al. 2003), and for plant, bird and fish species in the conterminous United States (Stohlgren et al. 2005a, 2006). These results complement landscape-scale observational studies (e.g., Stohlgren et al. 1999, Brown & Peet 2003, Keeley et al. 2003), but they do not provide a mechanism for the observed patterns across scales (Levine et al. 2003, 2004). Still, there have been no studies to examine the continuum of relationships between native and alien species from the scale of meters to regions and across many vegetation

types and biomes. Questions remain about how typical positive or negative relationships between native and alien species are at small spatial scales, and about how the relationships change with increasing scale and within and across vegetation types.

Having gathered consistent, multi-scale data in many areas in the central US, we had a unique opportunity to quantify the relationship between native and alien species at six spatial scales from 1-, 10-, 100-, and 1000-m² scales, at landscape scales, and for the region. Our objective was to quantify the relationship between native and alien species richness, cover, and biomass at multiple spatial scales and for many vegetation types. Increases in native and alien richness across scales may suggest that similar mechanisms affect both native and alien plant species.

Study areas

This is the first regional synthesis of our past landscape-scale studies and those of other investigators that used the modified-Whittaker multi-scale sampling design (described below). Primary study sites included Rocky Mountain National Park, Colorado, and the Grand Staircase-Escalante National Monument, Utah (Fig. 1, Appendix 1), with secondary sites scattered across the central United States.

The 108,000 ha Rocky Mountain National Park is characterized by mountainous geography spanning elevations from 2500–4345 m with diverse vegetation including meadows, montane pine and fir forests, subalpine forests and alpine tundra (Fig. 1, Lee 2001). The Park contained 181 vegetation plots sampled between 1993 and 2001 (Chong 2002).

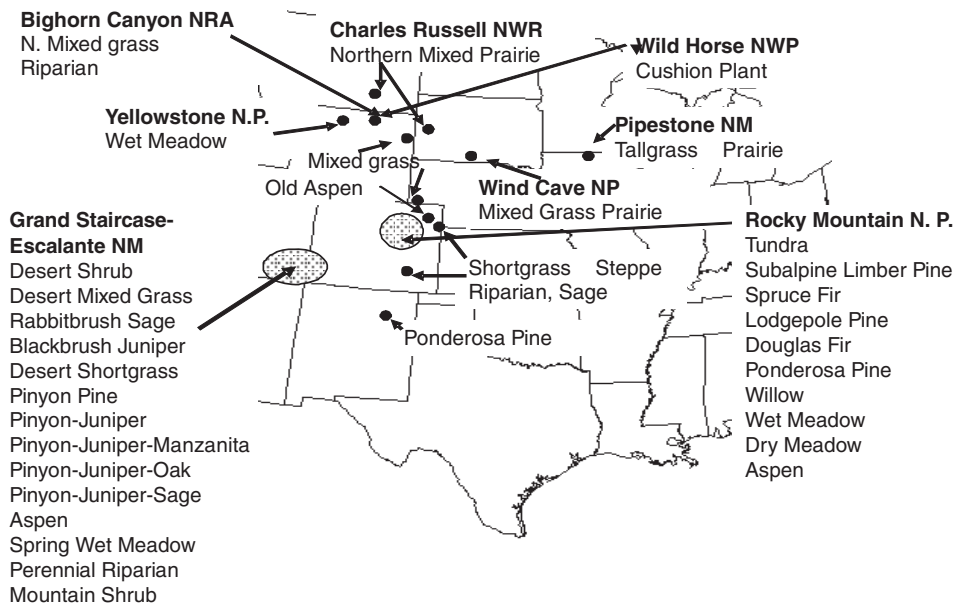


Fig. 1. – General map of the vegetation types surveyed between 1993–2004 (see also Appendix 1).

The 850,000-ha Grand Staircase-Escalante National Monument, Utah includes tablelands of the Colorado Plateau, arid grasslands and shrublands, sparse to closed woodlands, and large and small patches of forests (Comstock & Elhleringer 1992). The area contains a wide array of desert shrub, pinyon-juniper, and riparian vegetation types (Fig. 1, Appendix 1), endemic species, hot spots of native plant diversity amid arid, stressful environments, and multiple exposed soil and geology types (Comstock & Elhleringer 1992, Shultz 1998, Stohlgren et al. 2005b). Field sampling occurred between 1998 and 2002 (see Stohlgren et al. 2005b for details).

Another 159 plots were established at secondary study sites in various states, biomes, and vegetation types using the same field methods (i.e. modified-Whittaker plot) in each vegetation type. Plots were located from tallgrass prairie in Minnesota, to mixed grasslands and forests in Montana, Wyoming, South Dakota, and Colorado. These other sites ranged in elevation from 500 m to over 3000 m, in a wide range of geologic and soil types (Appendix 1).

Methods

In each study location, and during peak phenology, modified-Whittaker multi-scale plots (Stohlgren et al. 1995, 1998a) were established initially in 48 different vegetation associations. The nested plot was 20 m × 50 m containing one 100-m² subplot (5 m × 20 m) in the center, two 10-m² subplots (2 m × 5 m) in opposite corners, and ten 1-m² subplots (0.5 m × 2 m) systematically arranged around the inside edges of the 100-m² plot and the outside edges of the 10-m² subplot. Foliar cover (nearest percent) and average height by plant species were recorded in the ten 1-m² subplots, along with the percent cover of soil, litter, bare soil, and rock. Plant species were recorded as 0.5% cover if they occupied less than 1% in a 1-m² subplot. For more details see Stohlgren et al. (1995, 1998a). The dominance of aliens in a plot was expressed as the relative cover (percent of total cover) or the relative biomass (percent of total biomass) of alien species. Cumulative plant species presence was recorded in the 10-, 100- and 1000-m² plots. Ancillary data included the slope and aspect of the plot, GPS location and elevation derived from a digital elevation model.

Statistical approach

We used detailed information on foliar cover and height by species on 7042 1-m² subplots to create an index of aboveground biomass by multiplying foliar cover times mean plant height for native and alien species. Previous research relating cover and height to plant biomass for *Bromus tectorum* showed that foliar cover, predicted biomass (cover × height), and actual biomass (clipped, dried, and weighed samples) were highly positively related ($R^2 > 0.80$, Waters 2003). We lacked actual biomass information for other species, but we concluded that biomass estimates were a better measure of dominance than foliar cover or height measurements alone when comparing wildly different vegetation types (tundra to tallgrass prairie, thick conifer forests to desert grasslands).

Linear and non-linear regression analyses (SYSTAT version 11.0) were used to relate native and alien plant species richness at the 1-, 10-, 100- and 1000-m² scales, and when plots were combined within vegetation types. In all analyses described below, data were

log-transformed ($\log_{10} x+1$) prior to analyses to improve normality. Due to small sample sizes or high species overlap among types, the 48 original vegetation associations surveyed were collapsed into 37 vegetation “types” for all analyses (Fig. 1, Appendix 1). Still, the study encompassed a wide range of environments across seven states (Appendix 1 and 2). Because the number of 1000-m² plots varied greatly by vegetation type, we summarized the data as mean values of vegetation characteristics by vegetation type (Appendix 2). This minimized the effect of unequal sampling in different vegetation types and more accurately represented regional patterns. We did not have the aerial coverage of vegetation types across the region to aerially weight the results. Still, this approach provides direct comparisons to the primary studies cited in the Introduction (e.g., Brown & Peet 2003, Keeley et al. 2003, Bruno et al. 2004). We evaluated whether high native species richness would be positively associated with alien species richness, cover, and biomass at multiple spatial scales.

We further evaluated whether the cover, estimated biomass, relative cover, and relative biomass of alien plant species would be positively related to alien species richness for the vegetation types surveyed. Based on preliminary results (Stohlgren et al. 1999, 2001), we suspected that habitats vulnerable to the establishment of several alien plant species would eventually be invaded by a high-biomass producing alien species (Huston 1997).

We evaluated the relationship of native to alien species richness at the vegetation type scale using the cumulative native and alien species in each type. We assumed this to be a simple index of the proportional diversity of native and alien species in a type regardless of sample size. For example, aspen plots in Colorado contained 377 native species and 35 alien species in 45 plots, while the pinyon-juniper type in Utah contained 252 native species and 16 alien species in 114 plots.

Lastly, we used the coefficient of variation in the foliar cover of native species in all 1-m² subplots in each vegetation type as a measure of habitat heterogeneity at the plot and vegetation-type scales. We suspected that a high coefficient of variation in foliar cover of native species, as an index of habitat heterogeneity, would be positively associated with the level of establishment and dominance of alien plant species in a vegetation type, as indicated by high richness, relative cover, and estimated biomass of alien species in a vegetation type.

Results

Multi-scale plot results

Mean native species richness varied greatly among vegetation types ranging from 1.9 to 13.9 species in 1-m² subplots in spring-desert vegetation in Utah and high-elevation tundra in Colorado, respectively. These same two vegetation types each had about 38 species per 1000-m² plot (Appendix 2). Mean alien species richness among vegetation types ranged from zero alien species in 1-m² subplots in four vegetation types to a mean of 10 alien species per 1000-m² plot in the irrigated shortgrass steppe type in southern Colorado.

The mean understory foliar cover of native and alien plant species also varied considerably among vegetation types (Appendix 2). Mean foliar cover per plot for native plant species ranged from 89% cover in aspen stands in Colorado to just 13% cover for the desert shrub type in Utah. For alien plant species, mean foliar cover was near zero for tundra plots

(with a very occasional *Taraxacum officinale*) to 32%, again for the irrigated shortgrass steppe in Colorado (Appendix 2).

The multi-scale plot design allowed for a cursory comparison of the slopes of the relationship between native and alien plant species richness at various scales within vegetation types. While the slopes (and significance of slopes) varied widely by scale (i.e. 1-m², 10-m², 100-m², and 1000-m² scales) and vegetation type, we found that 60% of the vegetation types had positive relationships between native and alien species richness at the 1-m² scale, and 15 vegetation types had positive slopes at all four spatial scales. Only two vegetation types, the sagebrush type in Colorado and the recently burned pinyon-juniper sage type, had negative slopes at all four spatial scales. When we looked across vegetation types, we found a consistent, progressive pattern whereby the percentage of vegetation types with positive relationships between native and alien species richness increased with increasing spatial scale. At the 1000-m² scale, about 19% of the vegetation types had negative relationships, while 81% of the vegetation types surveyed had positive relationships.

We found that both the slope and intercept of the relationship between native species cover and richness consistently increased across the four spatial scales (Table 1). All the relationships were highly significant and the correlation coefficients increased with spatial scale. However, the relationship between alien species richness and native species cover was trending negative at the four spatial scales, but it was only statistically significant at the 1-m² scale. There was a consistent increase in the intercept, combined with the consistent decline in the correlation coefficient (and significance level) with increasing spatial scale (Table 1).

When we evaluated the mean slope of the relationship between native and alien species richness, averaged across the 37 vegetation types, we found a significantly increasing positive slope with increasing spatial scale (Fig. 2). The polynomial model was a better fit than a linear model. In addition, the coefficients of variation on the slope steadily decreased for the 1-m², 10-m², 100-m², and 1000-m² scales, respectively. The mean slope for the vegetation types was negative (−0.002), but near zero for the 1-m² scale, and was significantly different from zero at the 100-m² and 1000-m² scales. The proximate reasons for the increasing positive slope in Fig. 2 were: (1) native species richness (averaged across the vegetation types) increased significantly and quickly with plot area (x) where native species richness = $2.4x^2 + 0.63x + 5.57$ ($R^2 = 0.75$; $n = 37$; $P < 0.0001$ vegetation types for four plot sizes); (2) alien species richness increased significantly, but slowly, with plot area (x) where alien species richness = $0.27x^2 - 0.08x + 0.61$ ($R^2 = 0.26$; $P < 0.0001$); and (3) while species-area relationships were positive for both native and alien species, the non-linear species-area relationship was much stronger and more predictable for native plant species. In addition, we found a significant positive relationship between the mean gain in native plant species from 100-m² to 1000-m² in the plots, to the mean gain in alien plant species over the same spatial scales. Thus, alien species may be responding to similar factors responsible for native species increases with area (e.g. habitat heterogeneity, disturbance, water availability; Fig.3). Again, the polynomial model was a better fit than a linear model.

Regional-scale results

We found a positive relationship between cumulative native and alien species (in a given vegetation type) across the 37 vegetation types in the survey (Fig. 4). Once more, the poly-

Table 1. – Correlations of mean native species cover per plot (averaged from all 1-m² subplots in each vegetation type) and the richness of native and alien plant species at various spatial scales; n = 35 vegetation types with at least four 1000-m² plots in each type (see Appendix 1).

Native species cover to:	Slope	Intercept	R	P
1-m ² (native species richness)	0.086	2.057	0.595	0.0001
10-m ² (native species richness)	0.149	3.914	0.657	0.0001
100-m ² (native species richness)	0.229	7.137	0.711	0.0001
1000-m ² (native species richness)	0.349	16.539	0.719	0.0001
1-m ² (alien species richness)	-0.015	1.137	-0.379	0.017
10-m ² (alien species richness)	-0.016	1.460	-0.270	0.096 (ns)
100-m ² (alien species richness)	-0.020	2.221	-0.241	0.139 (ns)
1000-m ² (alien species richness)	-0.012	3.262	-0.085	0.608 (ns)

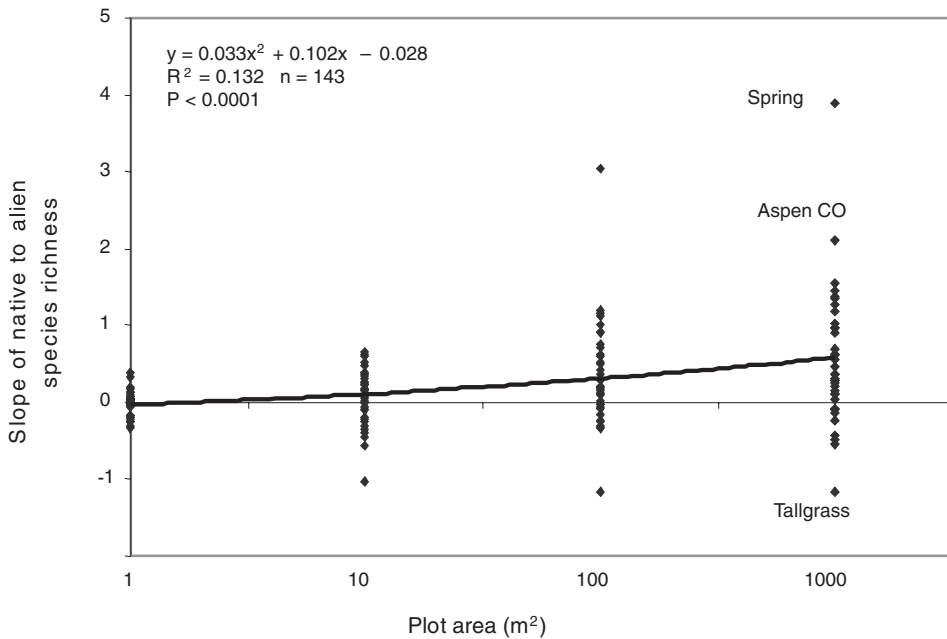


Fig. 2. – Relationship between the slope of correlations of native to alien species richness, averaged for each of the 37 vegetation types at 1-m², 10-m², 100-m², and 1000-m² scales. The coefficients of variation on the slope were 1390%, 94%, 34%, and 25% for the 1-m², 10-m², 100-m², and 1000-m² scales, respectively.

nomial model was a better fit than a linear model. Rare vegetation types such as aspen stands in Colorado and perennial riparian types in Utah, and the northern mixed grass prairie type in Montana exemplified native and alien species-rich habitats. Vegetation types with low cumulative native species (e.g. tundra and pinyon-juniper) with increased sampling effort, usually had high species composition overlap among plots, and thus lower beta-diversity in native and alien species. Measured in this way, native beta-diversity in a vegetation type explained 33% of the variation in the beta-diversity of alien plant species (Fig. 4).

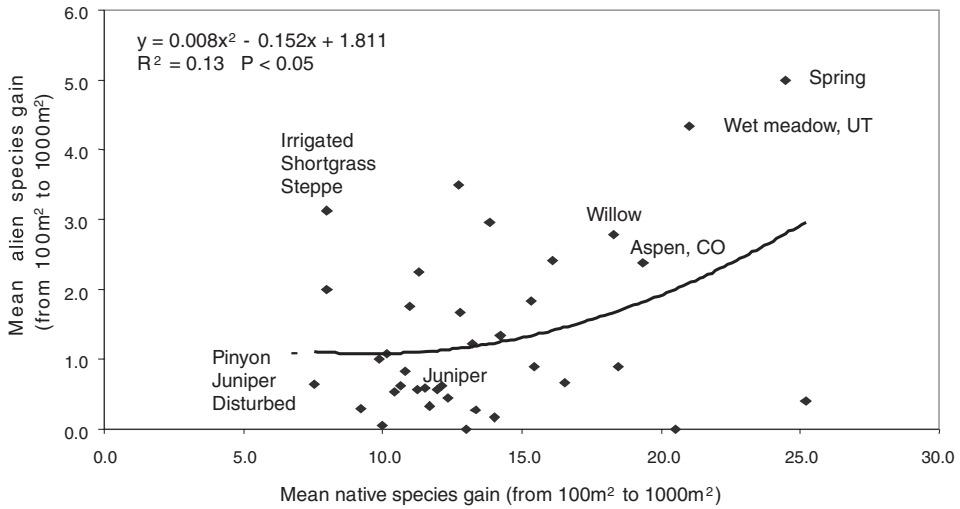


Fig. 3. – Gain in native versus alien plant species from 100-m² plots to 1000-m² plots in 37 vegetation types in the central United States, averaged by vegetation type.

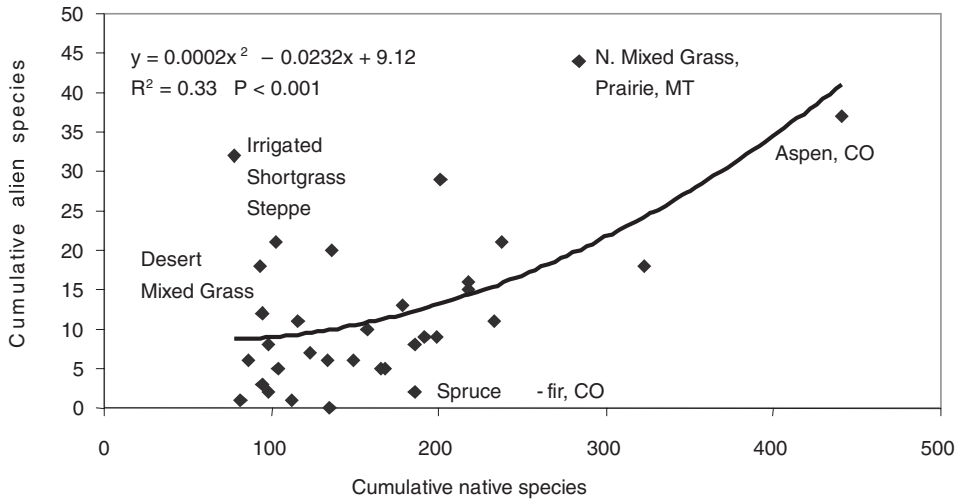


Fig. 4. – The relationship of cumulative native and alien species by vegetation type (i.e. an estimate of native and alien beta-diversity for a vegetation type) for the 37 vegetation types.

In support of biotic resistance arguments, we generally found significant negative relationships between native species richness (or biomass) and the cover, biomass, relative cover, and relative biomass of alien plant species (Fig. 5). For example, 26% of the variation in the relative cover of alien species in a vegetation type could be explained by a negative relationship with native species richness (Fig. 5d). Likewise, about 16% of the variation in the cover of alien species per plot in a vegetation type could be explained by a nega-

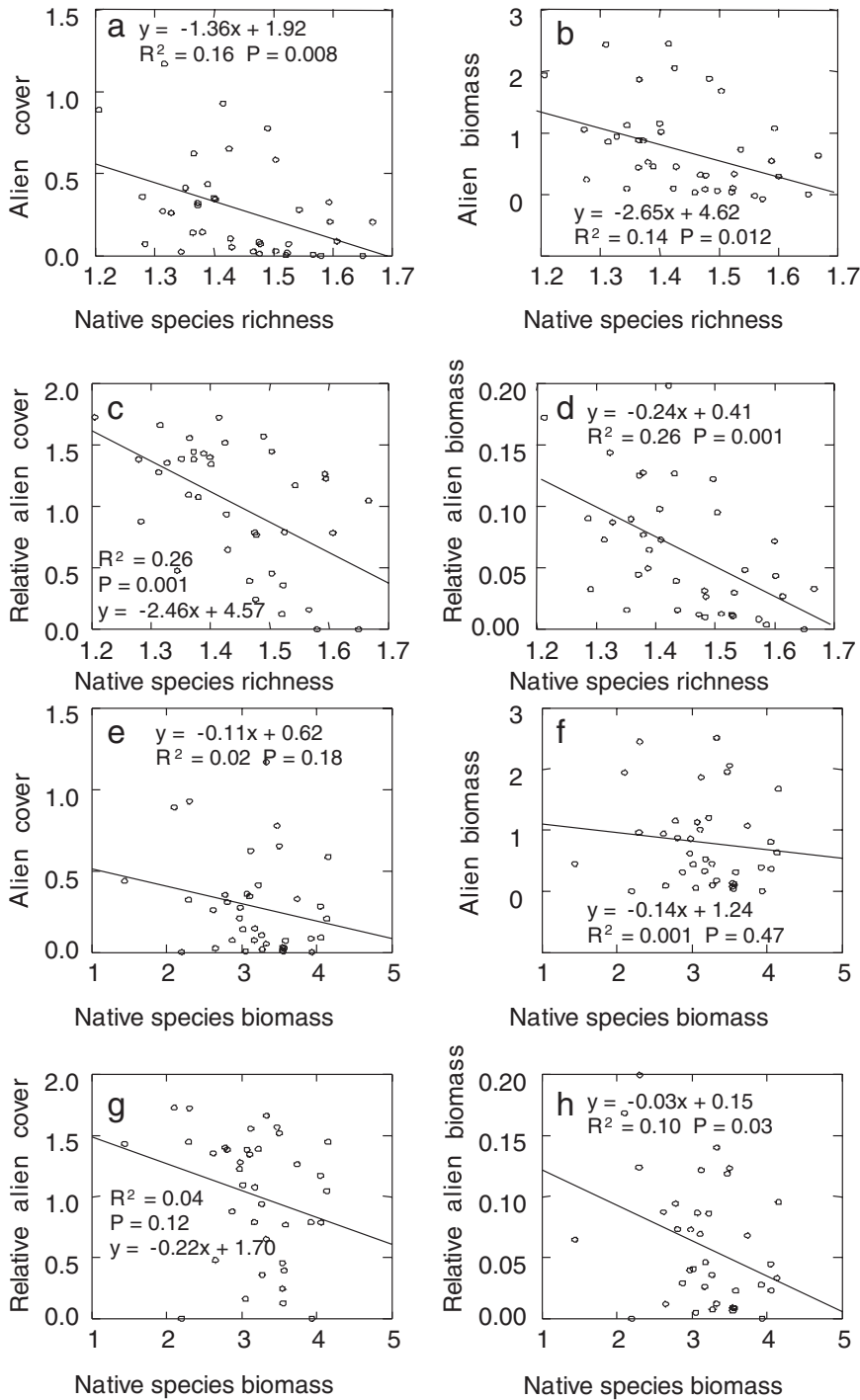


Fig. 5. – The relationships between native plant species richness (a–d) and biomass (e–h) to alien species cover, biomass, relative cover, and relative biomass for 37 vegetation types. Data were log-transformed.

Table 2. – The mean coefficient of variation of native and alien species richness and cover in 1-m² subplots (averaged by vegetation type). The minimum and maximum of the mean coefficient of variation among vegetation types are also presented.

	Mean	C.V.	Min.	Max.
Native species richness	5.3	0.52	0.3	0.8
Native species cover	38.1	0.85	0.4	1.4
Alien species richness	0.6	1.97	0.0	7.0
Alien species cover	3.9	3.36	0.0	12.1

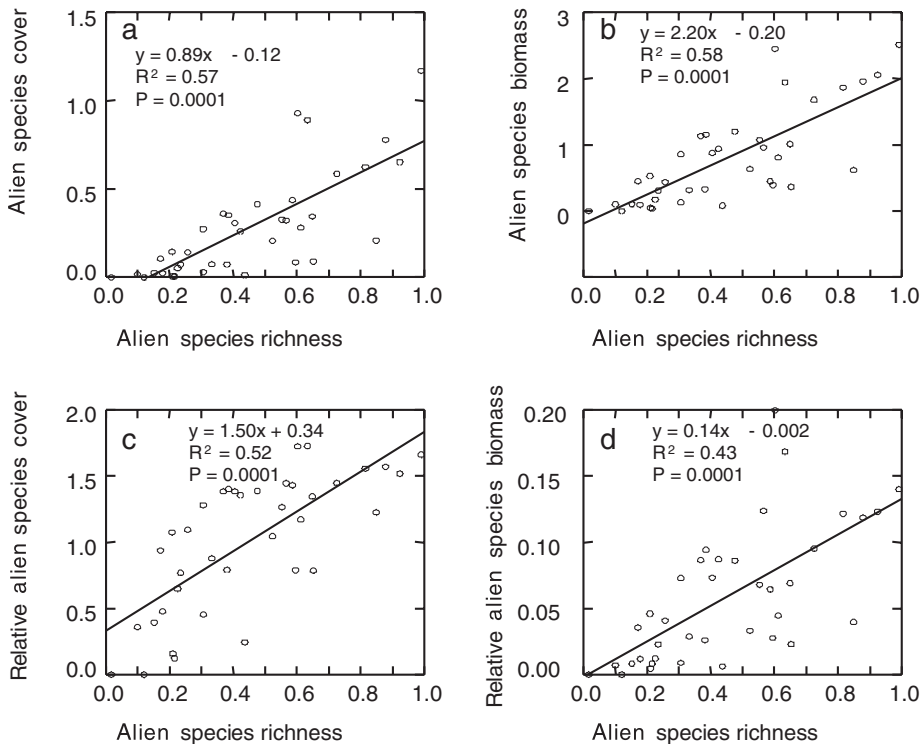


Fig. 6. –The relationship of alien plant species richness to alien species cover, biomass, relative cover, and relative biomass for 37 vegetation types. Data were log-transformed.

tive relationship with native species richness (Fig. 5a). The relationships of alien species cover, biomass, relative cover, and relative biomass for the 37 vegetation types were weaker for native biomass (as we calculated it; Fig. 5e-h) compared to native species richness (Fig. 5a-d). There was considerable natural variation evident in all the graphs, and three of the eight relationships were not significant (Fig. 5).

The cover, biomass, relative cover, and relative biomass of alien plant species were strongly positively related to alien species richness per plot for the 37 vegetation types (Fig. 6). These relationships were far stronger and more predictable than the relationships to na-

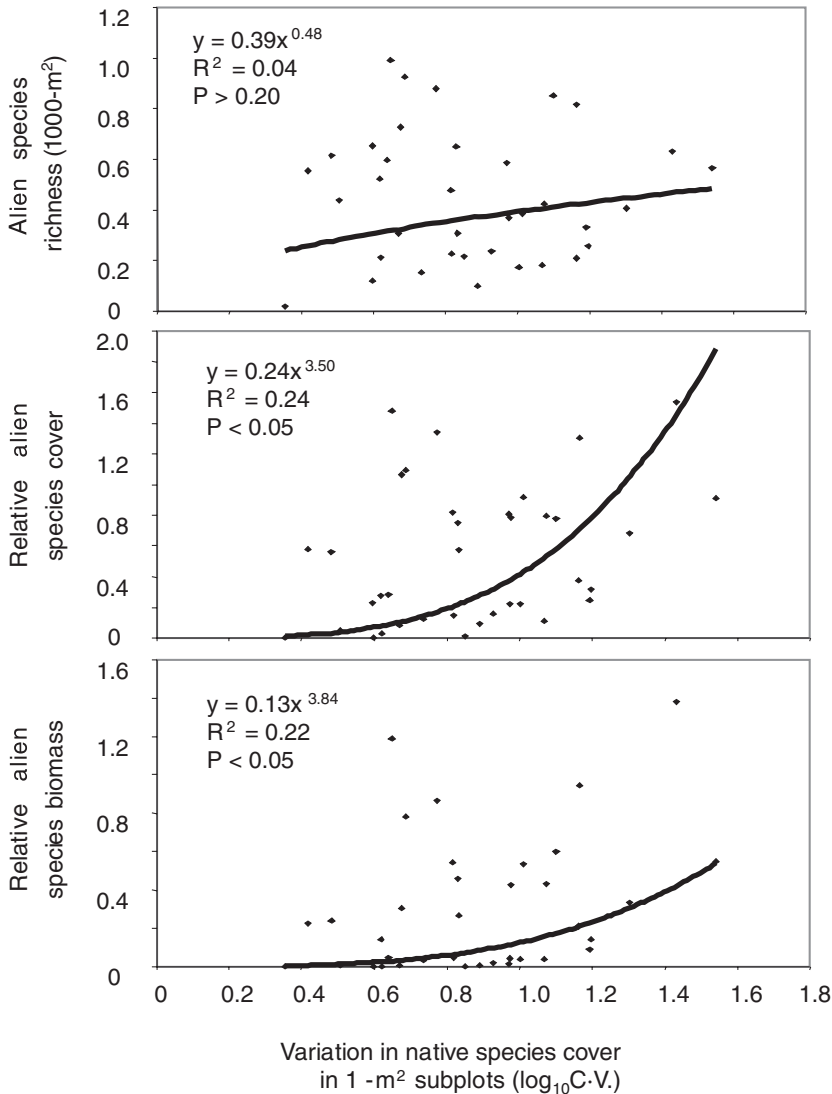


Fig. 7. –The relationship between the coefficient of variation of the foliar cover of native plants in 1-m² subplots in each vegetation type and alien species richness, relative cover, and relative biomass. Data were log-transformed.

tive species richness per plot for the vegetation types (Fig. 5a–d). For example, 58% of the variation in alien species biomass could be explained by a positive relationship with mean alien species richness for a vegetation type (Fig. 6b). Likewise, 57% of the variation in alien species cover could be explained by a positive relationship with alien species richness.

Habitat heterogeneity (i.e. the coefficient of variation in the richness or foliar cover of native or alien plant species in 1-m² subplots) varied greatly for native and alien species (Table 2). For example, native species cover in 1-m² subplots, with a coefficient of variation of 85% of the mean was considerably more variable than native species richness per

1-m² (52%) in the same vegetation type. Meanwhile, the cover of alien species in 1-m² subplots was about four times more variable than native species cover because only about 60% of the subplots contained alien species, and because that foliar cover was very patchily distributed in some types (maximum CV over 1200%; Table 2).

We assessed whether the variation in native species cover in a plot might allow spatial refugia for the establishment and dominance of alien plant species. We found no relationship between alien plant species richness in 1000-m² plots and variation of native foliar cover. However, we found significant positive relationships between the coefficient of variation of native cover and both the relative cover and relative biomass of alien plant species for the 37 vegetation types (Fig. 7). Power models fit the data better than linear, exponential, and polynomial models. The results suggested that the growth of alien plant species was significantly greater in vegetation types with higher spatial variability in native species cover (Fig. 7).

Discussion

We demonstrate how the scale of observation influences our understanding of the patterns of invasion in many natural vegetation types. However, there are several caveats to observational studies, and this study is no exception. We display statistical relationships between native and alien species richness, cover, estimated biomass, and relative dominance recognizing that cause and effect relationships cannot be determined by observational studies. We also recognize that the sites used in this study were only measured once, and they may not be representative of the regional vegetation types in space or time (Hamilton et al. 2005, Pyšek & Hulme 2005, Pauchard & Shea 2006). The studies employed stratified random sampling within major study areas (e.g. Rocky Mountain National Park, Grand Staircase-Escalante National Monument, riparian and upland sites, etc.), but this was not a stratified-random selection of plots or study sites throughout the region. Still, the data represent a broad range of environmental conditions in the region ranging from desert shrublands in Utah to tallgrass prairie in Minnesota, and from low-elevation grasslands to forests and high-elevation tundra (Fig. 1, Appendix 1 and 2). When these regional data are augmented with site-specific study results for natural vegetation types in California (Sax 2002, Keeley et al. 2003), Rhode Island (Bruno et al. 2004), and the southeast US (Brown & Peet 2003), a more complete and consistent evaluation of scale and invasion emerges, where invasion of alien plant species and coexistence with native plant species likely increase with spatial scale (Stohlgren et al. 1999, Knight & Reich 2005).

We emphasized comparisons of native to alien species relationships across scales from 1 m² to 1000 m² (within plots). And, within a vegetation type, native species richness and cover could vary considerably (Table 1, Appendix 2). On average across vegetation types, alien species represent only 10% of the total foliar cover, and only 9% of the total species richness per plot in a vegetation type. Only five vegetation types had > 10% cover of alien species (irrigated shortgrass steppe, the wet meadow type in Utah, disturbed pinyon-juniper-sage, the perennial riparian type, and the desert mixed-grass type; Appendix 2). Thus, observed patterns may not represent other vegetation types or associations, or extremely disturbed or highly invaded habitats, but they are corroborated in burned areas in California (Keeley et al. 2003) and Utah (Evangelista et al. 2004).

We do not presume to distinguish among the many possible causes for the patterns we observed. Evaluating the complex processes of escape from pathogens and predators, niche sharing and overlap, quantifying seed dispersal (and longevity and viability in the soil), life-history characteristics and many other potential causal factors are beyond the scope of this investigation (Hamilton et al. 2005). We assume that the patterns we observed follow well-established observations about natural ecosystems: (1) both native and alien species richness generally increase with the area surveyed (Arrhenius 1921, Stohlgren et al. 1999); and (2) environmental heterogeneity also increases with spatial scale (Palmer 1994, Jiang & Morin 2004, Davies et al. 2005), and this likely influences establishment and growth of alien species where propagules are available (Table 1, Figs 2–4 and 7). Thus, it is likely that the rates of immigration of native plant species and the invasion of alien species are heavily influenced by a multitude of factors that co-vary with spatial and temporal scales such as climate and weather, vegetation structure, micro- and macro-disturbances, resource availability, species pools and propagule pressure, and associated ecosystem processes (e.g. herbivory, competition, disease, hybridization, adaptation).

Effects of scale on the establishment of alien species

We were surprised to find that: (1) at the 1-m² scale, about 60% of the vegetation types had positive relationships between native and alien species richness; (2) only two vegetation types maintained negative relationships between native and alien species richness as scales increased to 1000 m²; and (3) the mean slope of the relationship between native and alien species increased significantly from the 1- to 1000-m² scale (Fig. 2). However, these findings provide possible mechanisms for previously reported patterns (Stohlgren et al. 1999, 2003) and perhaps observational studies in other vegetation types in California (Levine 2000, Keeley et al. 2003), Rhode Island (Bruno et al. 2004), and North Carolina (Brown & Peet 2003, Fridley et al. 2004): positive relationships strengthen between native and alien species richness at scales > 1-m². A statistical caveat is that at very small spatial scales, the relationship between native and alien species may be affected by the sizes of individuals (Fridley et al. 2004). So we tend to emphasize the more significant and positive relationships between native and alien species richness at scales >100-m².

In the individual plant's extended neighbourhood (from 100 m² to 1000 m² in the same habitat), it was clear that the average slope of the relationship between native and alien species richness increased in a significant, non-linear pattern (Fig. 2), and that native and alien species accumulation were positively associated (Fig. 3). It is well established that species richness increases with area (Arrhenius 1921, Palmer 1994). In our study areas, native plant species richness increased faster than alien plant species richness with plot area. We propose that similar factors associated with native species increases with area, such as habitat heterogeneity, extensions of environmental gradients, and increased probabilities of encountering disturbed habitats or micro habitats, also are responsible for increasing establishment of alien plant species as the spatial scale of observation is increased (Stohlgren et al. 1999, 2001, 2002, 2003). Fewer species in the local and regional species pools, time since invasion, and many other factors may have contributed to the less-steep species-area relationship for alien plant species in the study areas.

It was intriguing to measure a weakening relationship between alien species richness and native species foliar cover with increasing area, despite an increase in native species

richness with area and an increasing positive relationship between native species richness and foliar cover per plot across vegetation types (Table 1). It must be that despite the increasing number of native species in the extended plant neighbourhood, opportunities still exist in many vegetation types for the increasing establishment of alien species. We suspect that even modest changes in the spatial extent of the study (e.g. 1 m² to 10 m², or 10 m² to 100 m², etc.) may add considerably to local heterogeneity, niche availability, small-scale disturbances, or resource availability related to plant mortality, herbivory, or loss of competition prowess as a result of age, pathogens, climate, or many other factors that favour co-existence (Table 2; also see Huston 2004, Levine et al. 2004).

A Theory of “Biotic Acceptance”

We speculate that early in the invasion of any area greater than 1 m² (Figs. 2, 3), native species greatly outnumbered newly arriving invaders, but that biotic resistance (Fig. 5) becomes overwhelmed by “biotic acceptance” (Figs 2–4 and 6), where co-existence (Levine et al. 2003, 2004) is a stronger force than competitive exclusion (Grime 1973, Corbin & D’Antonio 2004), resulting in the broad-scale establishment of many alien species. The theory of biotic acceptance would suggest that natural ecosystems tend to accommodate the establishment and coexistence of introduced species despite the presence and abundance of native species (Table 3). This is in sharp contrast to the previous framework of biotic resistance, where competitive exclusion is the dominant mechanism determining the structure and composition of communities. Our data strongly supported this theory of biotic resistance across scales from meters to regions. Disturbance and increasing habitat suitability for invasive species, along with a positive feedback cycle due to increased propagule pressure (from growing “source” populations of invasive species) may further facilitate the invasion process (Hobbs & Huenneke 1992, D’Antonio et al. 1999, Levine et al. 2004, Pyšek & Hulme 2005).

What can we say about the potential of biotic acceptance in the establishment phase of the invasion process? Based on these landscape- to regional-scale datasets, we would predict that across the United States, the introduction and establishment of alien plant species (i.e. biotic acceptance) would be greatest in areas high in native species richness and with optimal conditions for plant growth. This is exactly the pattern observed at county, state, region, and national scales (Brown & Peet 2003, Stohlgren et al. 2003, 2005a, 2006, Crozier & Stohlgren 2004, Dark 2004). Strikingly similar results have been reported for South Africa (Richardson et al. 2005).

These very broad-scale patterns might be predicted by a variety of conceptual models (Shea & Chesson 2002, Huston 2004, Tilman 2004). However, only Huston’s (2004) dynamic equilibrium model fits our observations at the scales of plant neighbourhoods, plots, vegetation types, regions, and the nation. The dynamic equilibrium model allows for extrinsic factors and species diversity to increase across all spatial scales, productivity gradients, and disturbance regimes within vegetation types or across regions.

Effects of scale on alien species dominance

For an alien plant species to attain dominance amongst well-established native plant species remains a difficult task. The establishing alien species must compete in environments where native species richness and cover are significantly positively related at 1-m² scales

Table 3. – General comparison of the theories of biotic resistance and biotic acceptance.

	Biotic Resistance	Biotic Acceptance
Definition	“Forces of nature”, natural processes or ecosystem properties that contribute to a reduction in the rate of establishment and spread of introduced species. [paraphrasing Elton 1958 by D’Antonio & Thomsen 2004]	Where natural ecosystems tend to accommodate the establishment and coexistence of introduced species despite the presence and abundance of native species. [This paper]
Proposed mechanisms	Competitive exclusion, predation, herbivory, pathogens, among others.	Individual and species turnover in space and time, habitat heterogeneity, disturbance, open niches, and dispersal, among others.
Primary assumptions	Assumes neighbourhood interactions scale directly to large areas and determine community structure and composition.	Assumes environmental heterogeneity, environmental gradients, disturbance and turnover increase with spatial scale.

($R^2 = 0.35$; $P < 0.0001$), and where native species richness and estimated biomass are significantly positively related at 1000-m² scales across all vegetation types ($R^2 = 0.14$; $P < 0.0001$). So, it was not surprising to see some local (plot-scale) evidence of biotic resistance. However, many of the relationships between native and alien species richness, cover, and biomass are weak (i.e. R^2 values ranging from 0.001 to 0.36) with an average of only 12% of the variation explained at the 1000-m² scale (Fig. 5). Many other factors must be important in determining invasion success in space and time (Stohlgren et al. 1999, Bashkin et al. 2003, Huston 2004).

Availability of light, water, and nutrients may be important in invasion success (i.e. the relative cover of alien plant species). While only five of the 37 vegetation types studied had >10% relative cover of alien plant species, four of those vegetation types had higher water availability relative to surrounding vegetation types: irrigated shortgrass steppe (alien relative cover = 40%), wet meadow in Utah (35%) perennial riparian areas in Utah (17%), and freshwater springs in Utah (16%). Likewise, the burned pinyon-juniper-sage type in Utah had 15% relative cover of alien species perhaps reflecting greater light, water, and nitrogen/phosphorus availability combined with decreased competition from native shrubs and trees, which were consumed by the fire (Evangelista et al. 2004). Desert mixed grass plots with 21% relative alien species cover typically have higher native species richness, soil fertility, plant production, and corresponding higher levels of grazing than adjacent, more xeric plant associations (e.g. blackbrush, desert shrub types; Bashkin et al. 2003, Appendix 1). Within the scale of a few hectares, we often have observed small nutrient-rich sites serving as focal points of invasion (Stohlgren et al. 1997, 1998b, 1999, 2001).

There are several ways in which an alien species might become locally dominant in natural landscapes. Local, infrequent disturbances such as fire (Fox & Fox 1986, Keeley et al. 2003) and flooding (DeFerrari & Naiman 1994) often have been proposed as prerequisites for invasion success, but we believe more gradual and wide-spread invasions may be more typical at landscape scales (Stohlgren et al. 1997, 1999), regional scales (Stohlgren et al. 2002), and national scales as alien species establish and reproduce in favourable climates,

on fertile soils, and in conjunction with other factors that also contribute to high native species diversity (Stohlgren et al. 2003, 2005a, b, 2006).

The strong relationships between alien species richness and alien cover or biomass may be cause for concern (Fig. 6). These field data (Figs 4 and 6), and continental-scale findings (Stohlgren et al. 2003, 2005a, 2006) strongly suggest that the continued establishment of alien plants may be directly linked to the factors responsible for growth, cover, and biomass of other alien plants in the wide range of vegetation types studied (Fig. 6). Within-plot habitat heterogeneity (Fig. 7, Davies et al. 2005) combined with high resource availability (e.g. energy/water/nutrients; Bashkin et al. 2003, Stohlgren et al. 2005b) and disturbance (Fox & Fox 1986) may promote the coexistence of native and alien species (Fig. 4). However, we are also learning that habitat heterogeneity around plots (~240 m diameter) may also contribute to coexistence (Kumar et al. 2006). It is too early to tell if there will be widespread dominance of alien species as is evident in the lowlands in Hawaii (Mack et al. 2000), the foothills of California (Keeley et al. 2003), and some riparian zones in the United States (DeFerrari & Naiman 1994, Stohlgren et al. 1998b).

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Souhrn

V práci je analyzován vztah mezi druhovou bohatostí, pokryvností a odhadnutou biomasou původních a nepůvodních druhů v různém prostorovém měřítku. Datový soubor zahrnoval 7051 ploch velikosti 1 m², 1443 velikosti 10 m² a 727 velikosti 100 m², vřazených do 727 1000 m² velkých ploch, rozmístěných v 37 typech přirozené vegetace sedmi států centrální části USA. Druhová bohatost původních a nepůvodních druhů (vyjádřená jako průměr pro všechny vegetační typy) průkazně rostla s velikostí plochy. Se zvětšujícím se měřítkem byl vztah mezi oběma proměnnými průkaznějším a vzrůstala četnost pozitivních vztahů (u ploch velikosti 1000 m² byl nalezen pozitivní vztah v 80 % případů). Jak původní, tak nepůvodní druhy pravděpodobně reagují na dostupnost zdrojů, jež narůstá s měřítkem studia, a stanovištní heterogenitu, jež se zvětšuje se stoupající velikostí plochy. Byl nalezen průkazný pozitivní vztah mezi stanovištní heterogenitou vegetačního typu, vyjádřenou jako hodnota variačního koeficientu pokryvnosti původních druhů v 1 m² plochách, a relativní pokryvností a relativní biomasou nepůvodních druhů. Pro měřítko 1000 m² byl zjištěn slabý negativní vztah mezi bohatostí původních druhů a bohatostí, pokryvností, biomasou a relativní pokryvností nepůvodních druhů, ale velmi silný pozitivní vztah mezi bohatostí nepůvodních druhů a jejich pokryvností, relativní pokryvností a relativní biomasou. Tyto výsledky, podpořené mnoha dalšími studiiemi u přirozené vegetaci, podporují teorii „biotické akceptance“, podle níž do přirozených ekosystémů pronikají nepůvodní druhy bez ohledu na přítomnost původních druhů a jejich abundanci.

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Appendix 1. – Vegetation types and codes (i.e. short names) identified in this and previous studies (Stohlgren et al. 1998b, 1999, 2001, 2002), site descriptions, locations, and number of 1000 m² sample plots (n).

Vegetation type code	Description and location	n
Aspen	<i>Populus tremuloides</i> stands in Grand Staircase-Escalante National Monument, UT	6
AspenCO	<i>Populus tremuloides</i> stands in the Colorado Rocky Mountains	45
AspenOldCO	Decadent <i>Populus tremuloides</i> stands in Arapaho-Roosevelt National Forest, CO	5
Blackbrush	<i>Coleogyne ramosissima</i> dominated stands in Grand Staircase-Escalante National Monument, UT	27
CushMG	Cushion plant communities and mixed grass prairie dominated areas in Northern WY	8
Desert Shrub	<i>Ephedra</i> spp., <i>Gutierrezia sarothrae</i> , <i>Atriplex confertifolia</i> , <i>Ceratoides lanata</i> and <i>Chrysothamnus</i> spp. dominated stands in Grand Staircase-Escalante National Monument, UT	29
DesertMG	Desert Mixed Grass prairie of Badlands National Park, SD	8
DesertShGr	Desert shrub species mixed with <i>Stipa</i> spp., <i>Hilaria jamesii</i> , <i>Agropyron smithii</i> , <i>Bouteloua gracilis</i> , and <i>Bromus tectorum</i> in Grand Staircase-Escalante National Monument, UT	16
Douglas fir	<i>Pseudotsuga menziesii</i> stands in Northern CO Rocky Mountains	10
Dry meadow	<i>Carex helianthus</i> and <i>Artemisia tridentata</i> dominated meadows in Rocky Mountain National Park, CO	9
Juniper	<i>Juniperus osteosperma</i> stands in Grand Staircase-Escalante National Monument, UT	37
Lodgepole	<i>Pinus contorta</i> stands in Rocky Mountain National Park, CO	23
MixGrPrWyo	Mixed grass prairie of <i>Bouteloua gracilis</i> , <i>Koeleria pyramidata</i> , <i>Stipa comata</i> , and <i>Artemisia frigida</i> in Southeastern WY	4

NMixGrPrMT	Northern mixed grass prairie dominated by <i>Poa pratensis</i> , <i>Stipa comata</i> , <i>Bromus japonicus</i> , and <i>Agropyron smithii</i> in north-eastern WY, eastern MT, and western SD	57
PerenRipUT	<i>Populus fremontii</i> , <i>Tamarix</i> spp., <i>Salix</i> spp., and <i>Elaeagnus angustifolia</i> stands in Grand Staircase-Escalante National Monument, UT	22
Pinyon Pine	<i>Pinus edulis</i> stands in Grand Staircase-Escalante National Monument, UT	6
Pinyon-Junip	<i>P. edulis</i> / <i>Juniperus osteosperma</i> mixed stands in Grand Staircase-Escalante National Monument, UT	114
PJManz	<i>P. edulis</i> / <i>J. osteosperma</i> / <i>Arctostaphylos patula</i> mixed stands in Grand Staircase-Escalante National Monument, UT	6
PJOak	<i>P. edulis</i> / <i>J. osteosperma</i> / <i>Quercus</i> spp. mixed stands in Grand Staircase-Escalante National Monument, UT	18
PJSageDist	Post-fire of <i>P. edulis</i> / <i>J. osteosperma</i> / <i>Artemisia tridentata</i> stands in Grand Staircase-Escalante National Monument, UT, samples a few years after burning.	28
PondPineCO	<i>Pinus ponderosa</i> stands in Northern CO Rocky Mountains	32
PondPineUT	<i>Pinus ponderosa</i> stands in Grand Staircase-Escalante National Monument, UT	7
Rabbitbrush	<i>Chrysothamnus nauseosus</i> dominated stands in Grand Staircase-Escalante National Monument, UT	9
SageBrCO	<i>Artemisia tridentata</i> dominated areas in western CO and southwestern WY	33
SageBrUT	<i>A. tridentata</i> stands in Grand Staircase-Escalante National Monument, UT	37
MntShrubUT	<i>Cercocarpus montanus</i> , <i>Purshia mexicana</i> , <i>Amelanchier</i> spp., and <i>Symphoricarpos</i> spp. dominated overstory in Grand Staircase-Escalante National Monument, UT	12
ShoGRStCUp	<i>Bouteloua gracilis</i> and <i>Opuntia</i> spp. dominated Short grass steppe in Eastern CO	8
ShortGRStlrr	<i>Bromus inermis</i> , <i>Juncus balticus</i> , <i>Mulenbergia asperifolia</i> , and <i>Hordeum jubatum</i> dominated area in the San Luis Valley, CO	8
Spring	<i>Scirpus</i> and <i>Juncus</i> spp. dominated stands in Grand Staircase-Escalante National Monument, UT	2
Spruce Fir	<i>Picea engelmannii</i> / <i>Abies lasiocarpa</i> stands in Rocky Mountain National Park, CO	11
Subalpine	<i>Pinus flexilis</i> and <i>A. lasiocarpa</i> stands in Rocky Mountain National Park, CO	17
tallgrass pr	<i>Bromus inermis</i> , <i>Aster oblongifolia</i> , and <i>Symphoricarpos occidentalis</i> dominated tallgrass prairie at Pipestone National Monument, Minnesota	4
Tundra	High elevation alpine tundra in Rocky Mountain National Park, CO	36
WetMeadCO	<i>Poa palustris</i> , <i>P. interior</i> and <i>Deschampsia caespitosa</i> dominated meadows in Rocky Mountain National Park, CO	12
WetMeadUT	<i>Juncus</i> , <i>Carex</i> and <i>Poa</i> spp. mixed meadows in Grand Staircase-Escalante National Monument, UT	3
wetMeadYELL	<i>Festuca idahoensis</i> and <i>Artemisia tridentata</i> dominated wet meadows in Yellowstone National Park, WY	9
Willow	<i>Salix</i> spp. dominated stands in Rocky Mountain National Park, CO	9

Appendix 2. – Mean native (nat) and alien (ali) plant species richness (rich) and cover (cov) at the 1-m² scale, and mean native and alien plant species richness at the 10-m², 100-m², and 1000-m² scale, respectively, by vegetation type. Standard errors (SE) on second row of each vegetation type.

	n	nat rich	ali rich	nat cov	ali cov	nat rich	ali rich	nat rich	ali rich	nat rich	ali rich
		1 m ²	1 m ²	%	%	10 m ²	10 m ²	100 m ²	100 m ²	1000 m ²	1000 m ²
Aspen	60	4.4	0.9	52.8	8.0	7.7	1.1	16.3	2.8	31.7	4.7
	SE	0.2	0.1	4.6	2.1	0.6	0.1	1.4	0.7	3.2	1.0
AspenCO	448	9.2	0.4	88.6	2.5	16.5	0.8	27.4	1.4	46.7	3.7
	SE	0.2	0.0	2.6	0.3	0.6	0.2	1.1	0.3	1.7	0.6
AspenOldCO	50	7.0	0.0	71.6	0.0	15.1	0.0	19.4	0.0	44.6	0.4
	SE	0.6	0.0	6.1	0.0	3.2	0.0	4.1	0.0	4.4	0.2
Blackbrush	253	3.8	0.6	26.7	2.6	6.3	0.7	11.2	0.9	20.4	1.2
	SE	0.1	0.0	1.4	0.4	0.3	0.1	0.9	0.2	1.1	0.2
CushMG	80	4.6	0.9	26.2	7.1	8.5	1.3	14.9	3.5	24.8	4.5
	SE	0.2	0.1	2.9	1.6	1.0	0.4	1.2	1.2	3.1	1.6
Desert Shrub	270	3.9	0.7	13.0	1.8	7.5	0.9	11.2	1.3	21.6	1.9
	SE	0.1	0.0	0.9	0.3	0.5	0.1	1.0	0.2	1.5	0.2
DesertMG	80	5.4	1.9	29.4	10.9	8.6	2.6	13.9	4.1	26.6	7.6
	SE	0.2	0.2	2.3	2.3	1.0	0.4	1.9	0.8	2.8	0.8
DesertShGr	157	5.1	0.8	20.0	2.3	8.9	1.1	12.8	1.1	25.2	1.6
	SE	0.2	0.1	1.6	0.3	0.5	0.1	1.2	0.2	1.7	0.2
Douglas fir	100	5.7	0.0	49.9	0.0	10.3	0.2	18.9	0.1	37.4	1.0
	SE	0.5	0.0	4.3	0.0	1.7	0.1	3.0	0.1	6.2	0.4
Dry meadow	90	9.0	0.7	38.6	2.2	15.8	0.9	25.2	1.6	39.4	2.9
	SE	0.4	0.1	1.7	0.4	1.2	0.2	2.9	0.3	3.4	0.6
Juniper	350	3.9	0.6	18.2	3.5	7.1	0.8	11.9	1.2	24.0	1.8
	SE	0.1	0.0	1.3	0.5	0.4	0.1	0.9	0.2	1.4	0.2
Lodgepole	195	2.9	0.1	29.1	0.4	6.3	0.1	11.7	0.2	22.9	0.8
	SE	0.1	0.0	2.2	0.4	0.5	0.0	1.2	0.1	1.9	0.2
MixGrPrWyo	40	9.3	0.1	40.9	0.0	14.5	0.5	21.3	0.5	29.3	2.5
	SE	0.4	0.1	3.3	0.0	2.0	0.4	3.1	0.3	2.5	1.3
NMixGrPrMT	481	5.7	0.8	26.7	4.0	9.5	1.2	15.8	2.2	27.1	4.4
	SE	0.2	0.1	1.0	0.4	0.6	0.1	1.0	0.3	1.4	0.4
PerenRipUT	193	3.0	1.1	32.6	12.3	5.7	2.0	10.6	2.9	24.5	5.8
	SE	0.1	0.1	2.6	1.6	0.5	0.2	1.1	0.3	2.1	0.4
Pinyon Pine	59	3.2	0.3	31.2	0.9	5.5	0.3	12.0	0.5	23.7	0.8
	SE	0.2	0.1	4.7	0.3	0.8	0.1	1.1	0.3	2.6	0.4
Pinyon-Junip	1064	3.3	0.3	25.6	1.4	6.2	0.4	11.2	0.6	23.2	1.1
	SE	0.1	0.0	0.9	0.2	0.2	0.0	0.4	0.1	0.7	0.1
PJManz	60	4.8	0.1	33.3	0.1	7.3	0.1	18.7	0.2	32.7	0.3
	SE	0.3	0.0	3.8	0.0	1.1	0.1	1.6	0.2	2.0	0.2
PJOak	175	4.1	0.2	41.6	0.4	8.4	0.3	14.7	0.3	30.2	1.2
	SE	0.2	0.0	2.9	0.1	0.7	0.1	1.1	0.1	1.9	0.4
PJSageDist	280	2.8	1.8	12.8	12.6	5.2	2.4	9.2	3.2	16.7	3.8
	SE	0.1	0.1	1.1	0.9	0.5	0.2	0.9	0.3	1.4	0.4
PondPineCO	296	5.5	0.2	37.0	0.5	12.5	0.5	21.0	0.7	34.3	1.9
	SE	0.2	0.0	2.1	0.1	1.1	0.1	1.4	0.2	1.9	0.3
PondPineUT	68	3.5	0.2	37.6	0.9	6.9	0.3	13.3	0.6	26.3	0.6
	SE	0.3	0.1	4.6	0.5	0.8	0.1	1.7	0.2	2.3	0.2
Rabbitbrush	89	2.4	0.6	17.5	4.7	5.3	0.7	10.2	1.3	23.0	3.0
	SE	0.2	0.1	2.9	1.6	0.7	0.2	1.3	0.3	1.5	0.6
SageBrCO	327	5.3	0.7	29.9	3.4	10.2	1.0	14.7	1.5	25.5	2.4
	SE	0.2	0.0	1.3	0.3	0.7	0.1	1.3	0.2	2.4	0.3
SageBrUT	368	3.7	0.6	25.4	3.2	6.2	0.8	9.4	1.0	20.0	1.6
	SE	0.1	0.0	1.3	0.4	0.4	0.1	0.9	0.2	1.4	0.2
MntShrubUT	112	2.8	0.2	20.3	0.6	5.1	0.2	8.8	0.5	18.9	1.6

	n	nat rich 1 m ²	ali rich 1 m ²	nat cov %	ali cov %	nat rich 10 m ²	ali rich 10 m ²	nat rich 100 m ²	ali rich 100 m ²	nat rich 1000 m ²	ali rich 1000 m ²
	SE	0.2	0.0	2.3	0.3	0.4	0.1	1.2	0.2	1.4	0.5
ShoGRStCUp	80	5.8	0.0	34.8	0.0	10.4	0.1	17.4	0.9	37.9	0.9
	SE	0.3	0.0	2.4	0.0	0.7	0.1	2.4	0.5	5.1	0.4
ShortGRStIrr	80	4.3	2.9	34.1	32.2	7.4	5.2	12.0	6.9	20.0	10.0
	SE	0.2	0.3	2.5	3.6	0.7	0.9	1.5	1.5	1.3	2.0
Spring	18	1.8	0.2	31.4	5.5	5.0	0.3	14.0	1.5	38.5	6.5
	SE	0.3	0.1	8.1	3.8	0.6	0.3	1.0	0.5	3.5	2.5
Spruce Fir	101	6.2	0.1	65.8	0.1	11.1	0.2	20.2	0.3	33.5	0.5
	SE	0.4	0.0	4.8	0.1	1.4	0.1	3.4	0.2	5.9	0.2
Subalpine	163	4.0	0.1	48.8	0.6	10.7	0.2	16.4	0.4	27.9	0.9
	SE	0.2	0.0	3.1	0.3	1.2	0.1	2.1	0.2	2.6	0.3
Tallgrass pr	40	7.7	0.2	47.0	0.6	11.6	0.8	18.3	1.5	29.3	3.3
	SE	0.5	0.1	4.8	0.4	1.9	0.4	3.0	0.6	2.8	0.9
Tundra	359	13.9	0.0	54.4	0.0	20.6	0.0	28.3	0.0	38.3	0.1
	SE	0.2	0.0	1.0	0.0	0.6	0.0	1.1	0.0	1.6	0.0
WetMeadCO	120	7.3	0.4	66.4	4.2	11.8	0.7	19.5	1.4	35.6	3.8
	SE	0.3	0.1	2.9	1.0	0.9	0.2	1.4	0.4	3.3	0.8
WetMeadUT	30	4.6	1.1	34.1	13.0	7.7	1.0	10.0	2.3	31.0	6.7
	SE	0.4	0.2	4.8	3.7	2.2	0.3	2.5	0.9	5.6	0.9
WetMeadYELL	88	7.6	0.1	43.8	0.1	13.6	0.3	15.1	0.7	31.7	1.3
	SE	0.3	0.0	3.1	0.1	0.5	0.1	1.3	0.3	2.4	0.4
Willow	90	7.3	0.3	58.4	0.6	12.0	0.6	23.0	1.4	41.3	4.2
	SE	0.3	0.1	3.7	0.3	1.1	0.3	1.8	0.7	4.6	1.0