

Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach

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Abstract: Invading species often are close relatives, and therefore share many characteristics as a consequence of their common ancestry. This tends to confound studies of invasions, since many irrelevant characteristics are likely to be correlated with a species' geographic origin (alien or native). We address this problem by using phylogenetically independent comparisons to investigate the habitat characteristics of plants of the Central Plains Experimental Range (Colorado, U.S.A.). We initially show that exotic species are more likely than natives to occur in riparian zones, roadsides, and disturbed sites, and less likely to occur in grassland. The relationship between exotic origins and disturbed sites disappears when phylogenetic dependence is removed from the analyses; in contrast, the other associations persist following phylogenetic detrending, indicating that aliens and their native relatives consistently differ in their ability to exploit riparian, roadside, and grassland habitats. Our results indicate that disturbed sites currently are dominated by only a few groups of related exotic ruderals, while the ability to exploit roadsides and riparian zones has been and may continue to be important for the success of many taxa of invaders.

Key words: biological invasions, comparative methods, disturbance, grasslands, phylogeny.

Résumé : Les espèces envahissantes sont souvent étroitement apparentées, et conséquemment partagent plusieurs caractéristiques de leur origine commune. Ceci tend à rendre floues les études sur l'invasion, puisque plusieurs caractéristiques non pertinentes sont susceptibles d'être corrélées avec l'origine géographique de l'espèce (indigène ou introduite). Les auteurs ont examiné cette question en utilisant des comparaisons indépendantes de la phylogénie pour étudier les caractéristiques des habitats des plantes du Central Plains Experimental Range au Colorado (U.S.A.). Les résultats montrent que les espèces introduites sont plus susceptibles que les espèces indigènes de se retrouver dans les zones ripariennes, les bords de route et les sites perturbés, et moins susceptibles de se retrouver dans la prairie. La relation entre les origines des plantes adventices et les sites perturbés disparaît lorsque la dépendance phylogénétique est éliminée des analyses; au contraire, les autres associations persistent lorsque les tendances phylogénétiques sont éliminées, ce qui indique que les espèces introduites et leurs parents indigènes diffèrent dans leurs capacités à coloniser les habitats ripariens, les bords de routes et les prairies. Les résultats indiquent que les sites perturbés sont couramment dominés seulement par un groupe restreint d'espèces rudérales introduites, alors que la capacité d'exploiter les bords de routes et les zones ripariennes ont été l'affaire, et pourraient continuer de l'être, de plusieurs taxons d'invasisseurs.

Mots clés : invasions biologiques, méthodes comparatives, perturbation, prairies, phylogénie.

[Traduit par la rédaction]

Introduction

Deliberate and accidental introductions of nonnative plants by humans have profoundly altered many natural systems. Exotics now make up 25% or more of the species of many regional floras (Heywood 1989; Vitousek et al. 1996). Most of these

exotics are innocuous, but others have significantly altered the structure and function of the ecosystems they have invaded (e.g., Mediterranean annual grasses in California: Heady 1988; Sims 1988; Heady et al. 1992; D'Antonio and Vitousek 1992; *Myrica faya* Ait. in Hawaii: Vitousek et al. 1987, 1996; Vitousek and Walker 1989). Like most well-established (naturalized) invaders, these species probably are impossible to eliminate, and may have changed the affected systems permanently.

Predicting the risk of invasion has proven to be a difficult challenge (Crawley 1986, 1987; Pimm 1987; Lodge 1993; Mack 1996). Still, most reviews agree that exotics tend to be nonrandomly distributed with respect to habitat; for example, disturbed areas are widely considered to be especially vulnerable to plant invasions (Elton 1958; Mooney and Drake 1986; Crawley 1986, 1987; Drake et al. 1989; Pimm 1991; Hobbs and Huenneke 1992; Huston 1994; Cronk and Fuller 1995). This result suggests that the ability to exploit a disturbed site

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may be an important predictor of a potential invader. Not all plants have this ability; to prosper in a disturbed site may require a ruderal life history, good dispersal ability, rapid growth, the ability to tolerate physical stresses, or other traits that can be liabilities in undisturbed environments (Grime 1979; Sousa 1984; Pickett and White 1985).

One potential problem with interpreting such patterns of invasion is that much evidence comes from case histories of one or a few troublesome species or genera, and this may present a biased perspective (for some recent exceptions see McIntyre and Lavorel 1994; Thompson 1994; Crawley et al. 1996; and Williamson and Fitter 1996). A second problem stems from the fact that exotic plants often are relatives (but for an opposing view see Williamson 1996; and Williamson and Fitter 1996). For example, even after correcting for familial species richness, Asteraceae, Brassicaceae, Poaceae, and Fabaceae contribute disproportionately many invaders (Baker 1974; Crawley 1987; Heywood 1989; Daehler and Strong 1993; Cronk and Fuller 1995; Ruesink et al. 1995; Mack 1996). Consequently, exotics can share numerous traits (including those related to habitat requirements) as a result of common ancestry, whether or not these traits are directly related to invasiveness. This may seriously confound analyses of ecological differences between natives and exotics (Felsenstein 1985; Ridley 1989; Harvey and Pagel 1991; Harvey and Purvis 1991; Gittleman and Luh 1992; Miles and Dunham 1993; Ackerly and Donoghue 1995; Ackerly 1997).

In recent years, there has been a proliferation of methods designed to address this problem (Felsenstein 1988; Brooks and McLennan 1991; Harvey and Pagel 1991; Harvey and Purvis 1991; Gittleman and Luh 1992; McKittrick 1993; Miles and Dunham 1993). These methods differ in detail, but most attempt to reduce a multispecies dataset to a set of independent contrasts, which enables tests for associations among characters without the confounding influence of relationship. Most applications of these techniques have involved analyses of evolutionary associations, usually within well-defined clades, but these methods also are proving useful to biologists who are interested in understanding the ecology and organization of complex communities (Miles and Dunham 1993; Ackerly 1997).

In this paper, we discuss the occurrence of alien plant species in a landscape still dominated by natives, the Central Plains Experimental Range in north-central Colorado. We have taken the "extended phenotype" view (Dawkins 1982), treating each plant's ability to exploit different habitats as a complex, polygenic, inherited trait, which is itself the product of numerous other traits including life history, growth rate, seed production, and dispersal. In this view, habitat requirements are not fundamentally different from other complex traits like size or behaviour. We compare the success of aliens and natives in different habitats, consider how these habitat associations contribute to invasiveness, and suggest ecological reasons for the observed patterns. Specifically, we address two principal questions: (1) Do alien and native plants have similar habitat associations, or are aliens associated with particular habitats to a greater degree than natives? (2) Do these associations persist even when the confounding influence of relationship is removed? To answer these questions, we have performed one of the first formal phylogenetic analyses comparing the aliens and natives of an entire vascular flora. To

date, only one other study (Crawley et al. 1996) has adopted a similar approach; ours is the first such investigation to consider a North American flora.

Methods

Study site and flora

This study is based on the vascular flora of the Central Plains Experimental Range (CPER) (40°49'N, 107°47'W, 1660 m ASL, ca. 60 km northeast of Fort Collins, Colorado, U.S.A.). This 6280-ha area, a research site since 1937, is set within the much larger Shortgrass Steppe Long-Term Ecological Research (LTER) site. Most of the CPER is dominated by the drought- and grazing-tolerant grass *Bouteloua gracilis* (HBK.) Lag.² and is used for grazing by cattle.

Compared with many North American grasslands, shortgrass steppe has been little penetrated by exotics (Mack and Thompson 1982; Heady 1988; Sims 1988; Mack 1989; Heady et al. 1992). Still, the 1995 CPER plant checklist includes 52 non-North American exotics (Table 1), as well as 285 species believed to be native to North America. For both natives and exotics, this tally includes locally persistent species as well as transients (Pyšek 1995), but excludes species that were planted locally but have failed to spread. Most CPER species are herbaceous dicots, graminoids, or dwarf shrubs; the only tree that occurs locally is cottonwood, *Populus deltoides* Marsh. The habitat data from the checklist allowed us to classify each plant species as primarily occurring in up to five nonexclusive habitat types: roadside (roads, trails, and their margins), riparian (watercourses, generally with trees), ravine (eroded but dry slopes and valleys), disturbed (severely physically perturbed by factors such as construction and trampling around water tanks and salt blocks), and grassland (grazed but otherwise undisturbed grassland). This checklist is available from the Shortgrass Steppe Long-Term Ecological Research Program website.³

Constructing the trees

Although detailed molecular phylogenies are rapidly becoming available for relatively small clades, the membership of most plant communities is so taxonomically diverse that reliable community-level phylogenies will not be available in the foreseeable future (Chase et al. 1993; Baum 1994). Instead, we have employed a robust analysis of two alternative but approximate classification schemes. We recognize that both of these phylogenetic trees contain errors, and therefore present them as contrasting hypotheses.

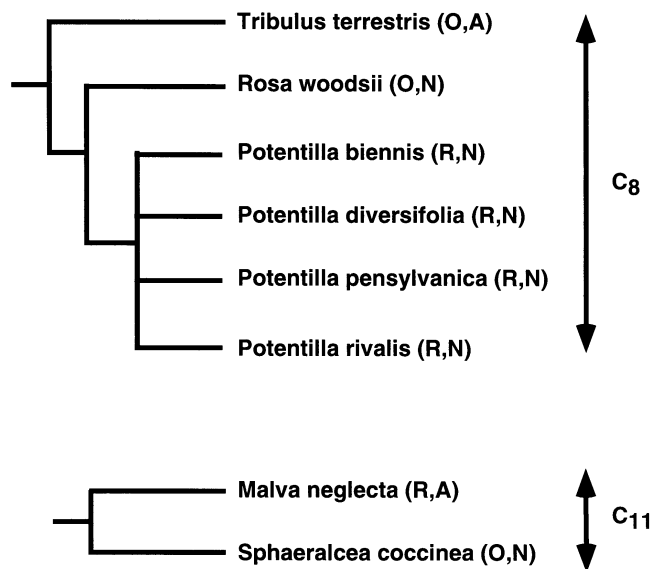
The first (FGP) classification is based on the hierarchically nested taxonomic system (species, genus, family, etc.) of the Flora of the Great Plains (Great Plains Flora Association 1986), which itself is arranged according to Cronquist (1981). This flora is unusual in that it does not subdivide Poaceae into subfamilies, tribes, or subtribes; we therefore have relied upon Clayton and Renvoize (1986) for these subdivisions. This first classification represents the resolution and accuracy available in many regional floras.

We constructed the second (Chase) classification by arranging families according to the Search II strict consensus tree of Chase et al. (1993). This tree is based on sequence data of the chloroplast gene *rbcL*, and is one of the taxonomically broadest molecular phylogenies (499 species) yet estimated for flowering plants. It is known not to be the most parsimonious possibility; however, Donoghue and Ackerly (1996) found that comparative analyses based on 7670 slightly more parsimonious variants of this tree produced very similar results. We

² Nomenclature follows Great Plains Flora Association (1986).

³ Shortgrass Steppe Long-Term Ecological Research Project. (1998, May 7). SGS Home Page. <<http://sgs.cnr.colostate.edu/sgshome.html>> (1998, May 29).

Fig. 1. Calculation of two selected phylogenetically independent contrasts from the Chase et al. (1993) tree, according to the methods described in the text. The independent variable is origin (A, alien; N, native), and the dependent variable is habitat (R, riparian; O, other). Contrast $C_8 = (0/1 - 4/5) = -0.8$; contrast $C_{11} = (1/1 - 0/1) = 1.0$. The mean phylogenetically independent contrast = $(C_8 + C_{11})/2 = (-0.8 + 1.0)/2 = 0.1$; the overall uncorrected (raw) "contrast" = $(1/2 - 4/6) = -0.17$. In this example, the phylogenetically independent contrasts indicate a positive association between aliens and riparian habitats, and the uncorrected overall contrast indicates a negative association.



omitted 11 small families⁴ containing 22 CPER species because Chase et al. did not include them or reported them as being extremely fragmented, and fused four closely related pairs of families⁵ identified by Chase et al. as mutually polyphyletic or paraphyletic. With these exceptions, this second classification is identical to the FGP tree below the familial level; it reflects the manner in which molecular techniques are changing the "traditional" view of superfamilial relationships. See Crawley et al. (1996) for a similar approach.

Statistical analyses

We have analyzed our data using a modification of the simple but robust comparative method proposed by Burt (1989) (q.v. Felsenstein

⁴ Agavaceae, Cactaceae, Equisetaceae, Geraniaceae, Juncaginaceae, Liliaceae s.l., Loasaceae, Marsiliaceae, Orobanchaceae, Plantaginaceae, and Salicaceae.

⁵ Amaranthaceae + Chenopodiaceae, Boraginaceae + Hydrophyllaceae, Brassicaceae + Capparidaceae, and Lamiaceae + Verbenaceae.

1985, 1988; Armstrong and Westoby 1993). In this method, groups of related species are defined in such a way that each group provides a single alien versus native contrast, statistically and phylogenetically independent of all similar contrasts (Fig. 1). This method is suitable for poorly known phylogenies, since it assumes no particular evolutionary model, does not attempt to reconstruct ancestral character states, does not require knowledge of branch lengths, and allows polytomies and discrete characters (Burt 1989; Felsenstein 1985, 1988; Harvey and Purvis 1991; Miles and Dunham 1993; Purvis and Rambaut 1995b).

We identified the required contrasts using the BRUNCH routine of CAIC 2.0.0 (Purvis and Rambaut 1995a, 1995b), with origin (alien or native) designated as an independent variable. This produced a unique set of phylogenetically independent contrasts for each classification. Each contrast, C_i , was evaluated as

$$[1] \quad C_i = p_{ai} - p_{ni}$$

where p_{ai} is the proportion of aliens in contrast i that have successfully occupied habitat x , p_{ni} is the proportion of natives in contrast i that have successfully occupied habitat x , and where x might represent, for example, riparian zones (Fig. 1). Each contrast ranges from -1 to $+1$; a positive value indicates that aliens are more likely to be associated with habitat x than natives, a negative association indicates the converse, and 0 indicates no net association. We conservatively followed Burt (1989) and Felsenstein (1985, 1988) in using sign tests to determine whether each set of phylogenetically independent contrasts differed significantly from zero. To test for associations in the original, uncorrected dataset, we used standard χ^2 tests (origin \times occurrence in habitat x).

Results

Raw (uncorrected) results

Aliens made up about 15% of the 337 locally recorded plant species; however, some families included many more exotics than others (Tables 1, 2; Fig. 2). In absolute numbers, more than half of the nonnative species belonged to 3 of the 54 locally occurring families (Poaceae, 27% of aliens; Asteraceae, 21%; Brassicaceae, 13%) (Table 1; Fig. 2). In addition, the proportion of species of exotic origin varied significantly among families ($\chi^2 = 33.13$, $df = 10$, $p < 0.001$; small families pooled to maintain average expected value of ~ 5). This non-random association is evidence that groups of related species may bias the raw results, and suggests that phylogenetically independent comparisons may be useful.

Grassland (85–90% of the CPER) contained the highest total number of species, followed by riparian zones and roadsides (each 1–2% of the CPER) (Table 2). Riparian and roadside habitats, roadsides and disturbed sites, and disturbed and grassland habitats shared numerous species (Jaccard coefficient > 0.2); with these exceptions, relatively few species were found in more than one habitat type (Table 2). Exotics were overrepresented on roadsides, in riparian zones, and in disturbed sites: 50% of roadside species, 28% of riparian species, and 25% of the species in disturbed sites were aliens (Tables 1, 2; Fig. 3). No exotics occurred primarily in grassland, whereas 45% of native species were recorded from this habitat (Tables 1, 2; Fig. 3). A greater fraction of natives than aliens also occurred in ravines.

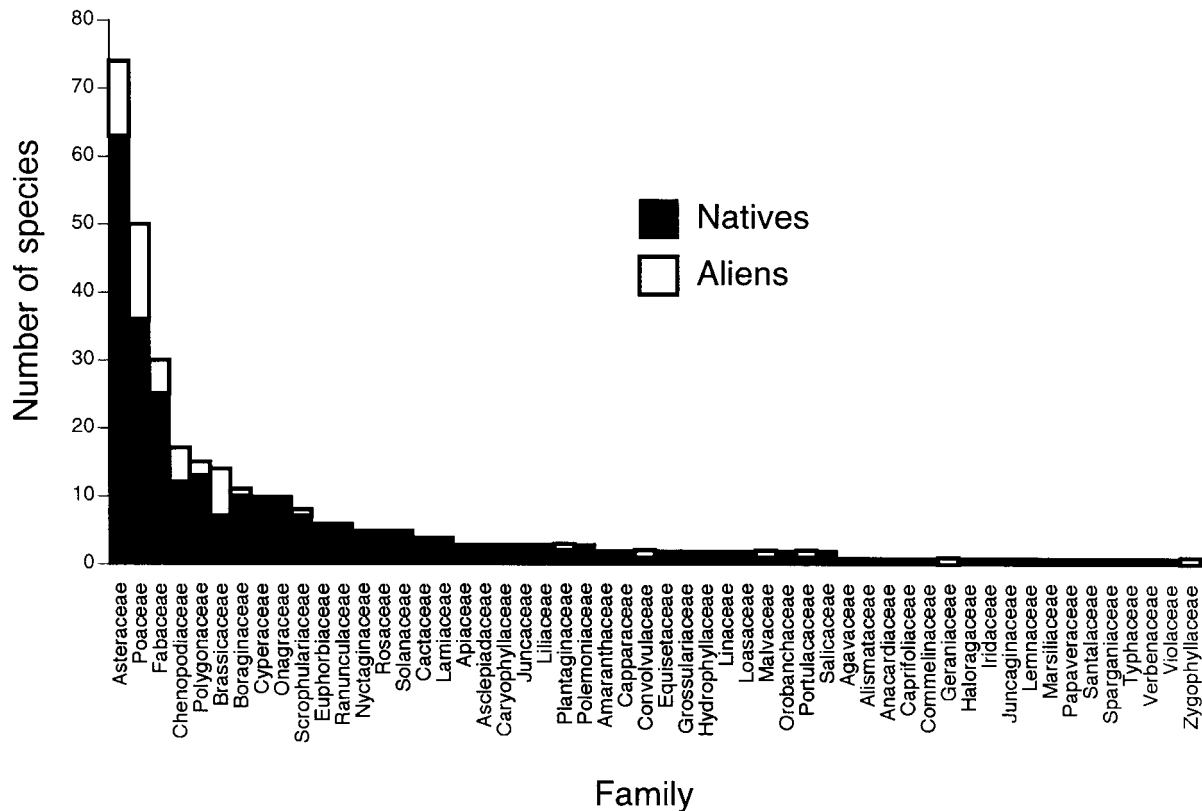
Comparative analyses

Both sets of comparative analyses generated similar numbers of phylogenetically independent contrasts: 29 for the analyses

Table 1. Life history and occurrence in each habitat type of the 52 exotic vascular plants occurring at the Central Plains Experimental Range at the time of this study.

Family	Species	Life history ^a	Habitat ^b				
			Riparian	Roadside	Ravine	Disturbed	Grassland
Asteraceae	<i>Arctium minus</i>	B	1	0	0	0	0
	<i>Centaurea repens</i>	P	1	1	0	0	0
	<i>Cichorium intybus</i>	A	0	1	0	0	0
	<i>Cirsium arvense</i>	P	1	1	0	0	0
	<i>Crepis capillaris</i>	A	1	0	0	0	0
	<i>Lactuca serriola</i>	A	1	1	0	0	0
	<i>Scorzonera laciniata</i>	A	0	1	0	0	0
	<i>Sonchus oleraceus</i>	A	1	1	0	0	0
	<i>Taraxacum officinale</i>	P	1	1	0	0	0
	<i>Tragopogon dubius</i>	B, P	0	1	0	1	0
	<i>Tragopogon pratensis</i>	B, P	0	1	0	1	0
Boraginaceae	<i>Cynoglossum officinale</i>	B	1	0	0	0	0
Brassicaceae	<i>Alyssum alyssoides</i>	A	0	1	0	0	0
	<i>Camelina microcarpa</i>	A	1	1	0	0	0
	<i>Capsella bursa-pastoris</i>	A, B	1	1	0	0	0
	<i>Chorispora tenella</i>	P	0	1	0	0	0
	<i>Descurainia sophia</i>	A, B	1	1	0	1	0
	<i>Sisymbrium altissimum</i>	A	1	1	0	1	0
	<i>Thlaspi arvense</i>	A	1	1	0	0	0
	<i>Thlaspi arvense</i>	A	1	1	0	0	0
Chenopodiaceae	<i>Chenopodium glaucum</i>	A	1	0	0	0	0
	<i>Corispermum hyssopifolium</i>	A	0	0	1	0	0
	<i>Kochia scoparia</i>	A	1	1	0	1	0
	<i>Salsola collina</i>	A	0	1	0	1	0
	<i>Salsola iberica</i>	A	1	1	0	1	0
Convolvulaceae	<i>Convolvulus arvensis</i>	P	0	1	0	0	0
Fabaceae	<i>Medicago lupulina</i>	A, P	1	1	0	0	0
	<i>Melilotus alba</i>	P	0	1	0	1	0
	<i>Melilotus officinalis</i>	B	0	1	0	1	0
	<i>Trifolium pratense</i>	P	1	0	0	0	0
	<i>Trifolium repens</i>	P	1	0	0	0	0
Geraniaceae	<i>Erodium cicutarium</i>	A	1	1	0	0	0
Malvaceae	<i>Malva neglecta</i>	P	1	1	0	0	0
Plantaginaceae	<i>Plantago major</i>	P	1	0	0	0	0
Poaceae	<i>Agropyron cristatum</i>	P	0	1	0	1	0
	<i>Agropyron repens</i>	P	1	0	0	0	0
	<i>Agrostis stolonifera</i>	P	1	0	0	0	0
	<i>Bromus inermis</i>	P	0	1	0	1	0
	<i>Bromus japonicus</i>	A	1	1	0	0	0
	<i>Bromus tectorum</i>	A	1	1	0	1	0
	<i>Dactylis glomerata</i>	P	1	1	0	0	0
	<i>Echinochloa crusgalli</i>	A	1	1	0	0	0
	<i>Elymus junceus</i>	P	0	1	0	1	0
	<i>Eragrostis cilianensis</i>	A	0	1	0	1	0
	<i>Phleum pratense</i>	P	1	0	0	0	0
	<i>Poa compressa</i>	P	1	1	0	0	0
	<i>Polypogon monspeliensis</i>	A	1	0	0	0	0
	<i>Setaria viridis</i>	A	1	0	0	0	0
	<i>Setaria viridis</i>	A	1	0	0	0	0
	Polygonaceae	<i>Polygonum aviculare</i>	A	0	1	0	1
	<i>Rumex crispus</i>	A	1	0	0	0	0
Portulacaceae	<i>Portulaca oleracea</i>	A	1	0	0	0	0
Scrophulariaceae	<i>Linaria dalmatica</i>	P	1	1	0	0	0
Zygophyllaceae	<i>Tribulus terrestris</i>	A	0	1	0	0	0

^aA, annual; B, biennial; P, perennial.^b1, occurs in this habitat; 0, does not occur in this habitat.

Fig. 2. Taxonomic distribution of native and alien vascular plant species on the CPER checklist.**Table 2.** Species occurring in each habitat type, and Jaccard similarity coefficients comparing the set of species occurring in each habitat type.

	Riparian	Roadside	Ravine	Disturbed	Grassland
No. of species					
Natives	88	37	30	44	150
Aliens	35	37	1	15	0
Total	123	74	31	59	150
Jaccard values					
Riparian	—	0.216	0.000	0.028	0.000
Roadside		—	0.010	0.243	0.023
Ravine			—	0.000	0.000
Disturbed				—	0.222

Note: Jaccard values are defined as (number of species occurring in both habitat a and habitat b) / (number of species occurring in habitat a and (or) habitat b). Total species richness is 52 aliens and 285 natives, but a given species may occur in more than one habitat type.

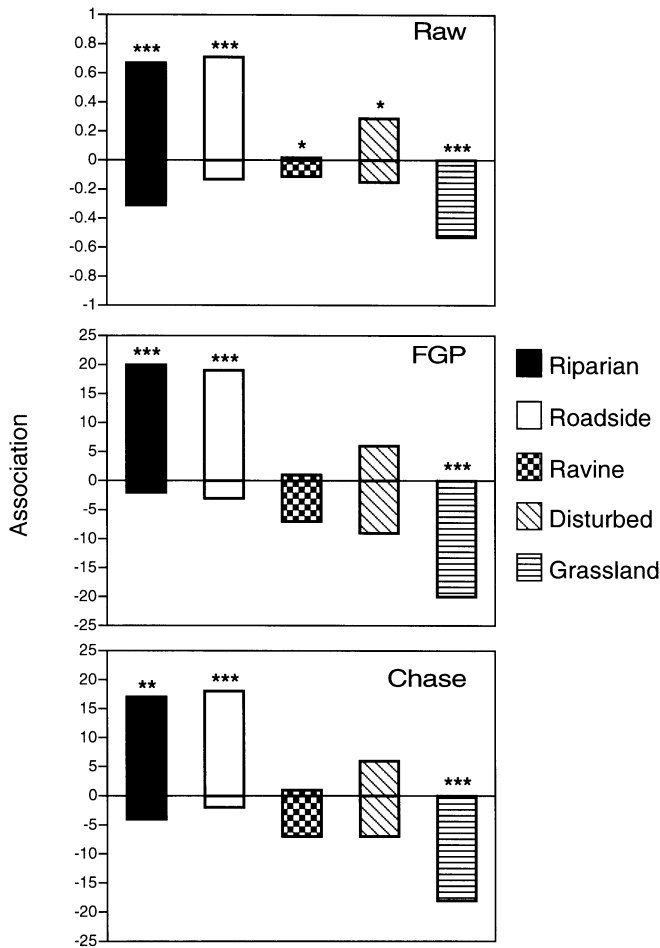
based on the Flora of the Great Plains versus 27 for those based on Chase et al. (1993). As might be expected, more than half of these contrasts (31) occurred within Poaceae, Asteraceae, or Brassicaceae; only five contrasts involved more than one family. Both comparative analyses also generated very similar trends and patterns of significance (Fig. 3). Both indicated that exotics were disproportionately likely to occur in riparian and roadside habitats and unlikely to occur in grassland habitats, whereas natives showed a marginally nonsignificant ($p = 0.07$) tendency to occur disproportionately in ravines (Fig. 3). No significant associations with disturbed sites were detected.

Discussion

Raw (uncorrected) habitat associations

Exotic plants often are especially successful at exploiting disturbed or resource-rich habitats (Elton 1958; Mooney and Drake 1986; Crawley 1986, 1987; Tilman 1987; Drake et al. 1989; Pimm 1991; Hobbs and Huenneke 1992; Huston 1994; McIntyre and Lavorel 1994; Jefferies and Maron 1997), probably because these factors can reduce the severity of competition from native vegetation. Previous studies suggest that this model applies at the CPER. As is the case in many prairies,

Fig. 3. Association between habitat and origins. Shown are uncorrected (raw) associations and phylogenetically independent contrasts based on two different classification schemes (FGP, Flora of the Great Plains; Chase, Chase et al. 1993). Raw associations illustrate the *proportion* of alien (positive values) or native (negative values) species associated with that habitat. FGP and Chase values illustrate the *number* of contrasts indicating an association with alien (positive) or native (negative) species. Significance values indicate whether each set of contrasts differs from zero (no association): *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.



belowground competition in the native-dominated CPER grassland is severe (Milchunas et al. 1992; Hook et al. 1994; Aguilera and Lauenroth 1995), but the addition of water or nutrients ameliorates belowground conditions and allows aliens to invade (Milchunas et al. 1989, 1990; Milchunas and Lauenroth 1995). Physical disturbance may have a similar effect, reducing belowground competition by breaking up the nearly continuous root network (Coffin and Lauenroth 1988; Milchunas and Lauenroth 1989; Hook et al. 1994; Aguilera and Lauenroth 1995). In addition, physical disturbance may directly favour exotics with ruderal life histories (dispersal, dormancy, phenology, etc.) while excluding competitive but disturbance-intolerant natives adapted to the surrounding, stable grassland. In contrast, the effects of grazing apparently differ from those of other forms of “disturbance.” Grazing locally reduces the abundance of exotic species, probably be-

cause it removes grazing-intolerant invaders and leads to increased belowground competition (Milchunas and Lauenroth 1989; Milchunas et al. 1989, 1990, 1992). Milchunas et al. (1990) have argued that the *absence* of grazing constitutes a disturbance in this historically grazed ecosystem.

Our results indicate that these effects translate to the landscape scale. No aliens occurred primarily in grazed but otherwise undisturbed grassland, whereas disturbed sites (areas around water sources, construction zones, etc.) supported disproportionate numbers of exotics. Exotics also were disproportionately likely to occur on roadsides, which typically are disturbed to some extent (as suggested by their high Jaccard similarity to disturbed sites), often are protected from grazing, and may trap drainage and experience runoff from the road's surface (as suggested by their Jaccard similarity to riparian habitats). Similarly, riparian habitats supported large numbers of exotics, probably reflecting both greater water availability and trampling disturbance by cattle (Valentine 1990; Fleischer 1993).

One implication of these results is that roadsides and riparian zones are acting as avenues for the initial spread of exotic species (e.g., Saunders and Hobbs 1991; Simberloff et al. 1992; Hobbs 1992; Malanson 1993; United States Congress Office of Technology Assessment 1993; de Waal et al. 1994). One case in point is cheatgrass, *Bromus tectorum* L. This Eurasian species has occupied thousands of square kilometres of the North American intermountain west, replacing native species and changing fire regimes and other ecosystem characteristics (Mack 1981, 1986; Mack and Thompson 1982; D'Antonio and Vitousek 1992). In contrast, shortgrass steppe has been relatively little invaded by *B. tectorum* or most other exotic species (Mack and Thompson 1982). To date, *B. tectorum* has been scarce in most habitats of the CPER, but its abundance has been increasing on roadsides in recent years (CPER and LTER staff, personal communication). In 1995, *B. tectorum* founded numerous large new populations in shortgrass steppe close to roads, probably because the near-record early-season rainfall in 1995 temporarily reduced water stress. Roadsides have allowed this grass to arrive, persist, and possibly to spread into the vegetation and seed banks of grassland habitats.

Phylogenetically independent comparisons between natives and exotics

In the only other study to date that has used phylogenetically independent contrasts to compare natives and exotics, Crawley et al. (1996) demonstrated that exotics in Britain differed from related natives in having larger seeds, taller stature, more pronounced seed dormancy, and smaller distributions. However, the analysis by Crawley et al. did not reveal a phylogenetically independent effect for the single habitat variable considered (altitude). In contrast, we found that associations between geographic origin and riparian, roadside, and grassland habitats all were significant even after correcting for phylogenetic confounding, indicating that the ability to exploit these habitats reliably separated aliens from related natives. Conversely, roadside and riparian habitats have been invaded by many different groups of exotics, rather than one or a few specialized clades; for these habitats, knowing the relationships of a potential invader may add little to efforts to predict its invasiveness.

Results of phylogenetically independent comparisons need

not resemble the results of uncorrected analyses (Felsenstein 1985; Ridley 1989; Harvey and Pagel 1991; Harvey and Purvis 1991; Gittleman and Luh 1992; Miles and Dunham 1993). In our study, however, these two types of analysis produced very similar results, indicating that the trends evident in the flora as a whole were not products of taxonomic biases, but instead distinguished natives from even related exotics. The chief way in which our raw and corrected analyses differed was the disappearance of the marginally significant "raw" associations between exotics and disturbed sites, and between natives and ravine habitats. As discussed below, this loss of significance probably reflects the loss of power associated with this class of test. It also suggests that, at least at this time, the weak association between exotics and disturbed sites in the raw dataset is largely attributable to a few clades of closely related disturbance-dependent species (e.g., *Kochia* and *Salsola* spp., *Melilotus* spp., *Bromus* spp.; Table 1). These may simply be the first nonnatives to exploit these habitats; their dominance may well diminish over time as more exotics arrive.

Methodological issues

Our study illustrates two difficulties associated with phylogenetically independent comparisons. First, their accuracy ultimately depends on the accuracy of the phylogeny upon which they are based. We compensated for phylogenetic uncertainty by using a method of analysis that makes the fewest assumptions possible about tree shape and branch length. In addition, we assessed the robustness of our analyses by comparing two different classification schemes; like Kelly and Woodward (1996), we found that our "phylogenetic" and "taxonomic" trees produced very similar results. Second, comparative analyses (especially robust ones) may entail significant losses of information and statistical power (Harvey and Pagel 1991; Harvey and Purvis 1991; Lord et al. 1995; Westoby et al. 1995a, 1995b). These losses are undesirable, but are costs of transforming nonindependent data into a smaller but unconfounded set of contrasts. In the FGP and Chase analyses, respectively, our methods reduced 337 species to 29–27 paired comparisons, and 34–42% of species directly contributed to no contrast whatsoever. Despite these limitations, the power of our analyses was sufficient for the identification of consistent and highly significant phylogenetically independent associations between exotic plants and roadside and riparian habitats, and between natives and grassland habitats.

Transportation biases

The ultimate reason that so many exotics prosper in roadsides, riparian zones, and (to a lesser extent) disturbed sites may reflect patterns of transportation, rather than differences in invasibility (Simberloff 1986; Heywood 1989; Rejmánek 1989; Mack 1996; Williamson 1996; Williamson and Fitter 1996). The species most likely to be transported to new sites or regions by humans probably are those already occurring in mesic regions with large human populations. These species are more likely to be adapted to wet areas or to human or cattle disturbance than to pristine, semiarid CPER habitats. Species that might thrive in undisturbed grassland (e.g., exotics from remote, semiarid regions of Eurasia) may be less likely to be transported, and perhaps unsuited to the more mesic coastal areas of North America that otherwise could act as stepping stones. Similarly, if exotics initially arrive via corridor habi-

tats, then the contrast between the high diversity of exotics in roadside and riparian areas and the apparent invasion resistance of grasslands may diminish over time as more species spread from these corridors into new territory. *Bromus tectorum* may be only one of many exotics spreading into short-grass steppe in this manner. Invasion is an ongoing process; as is true for most studies, our results most strongly capture the behaviour of the earliest invaders (~100-year time scale). In years to come, these patterns may well be modified as more invaders arrive and spread.

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