

WEAK VS. STRONG INVADERS OF NATURAL PLANT COMMUNITIES: ASSESSING INVASIBILITY AND IMPACT

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Abstract. In response to the profound threat of exotic species to natural systems, much attention has been focused on the biotic resistance hypothesis, which predicts that diverse communities should better resist invasions. While studies of natural communities generally refute this hypothesis, reporting positive relationships between native species diversity and invasibility, some local-scale studies have instead obtained negative relationships. Most treatments of the topic have failed to recognize that all exotic invaders do not behave alike: while “weak” invaders become minor components of communities, “strong” invaders become community dominants at the expense of native species. At the same time, the specific impacts of strong invaders on communities are poorly documented yet critical to understanding implications of diversity loss. With these shortfalls in mind, we examined local-scale relationships between native and exotic plant taxa in bunchgrass communities of western Montana, USA. We found that measures of native species diversity and invasibility were positively correlated in communities with low levels of invasion where both weak and strong invaders occurred at low densities, but negatively correlated in communities with high levels of invasion where the strong invader *Centaurea maculosa* dominated. Furthermore, at both low and high levels of invasion, weak invaders tended to vary positively with native species richness while strong invaders varied negatively. Weak invaders determined positive overall relationships between native and exotic species in low invasion communities and appeared to coexist with native taxa. Strong invaders prevailed in high invasion communities, driving negative overall relationships therein. That negative relationships primarily reflected strong invader impacts was supported by the fact that negative correlations of *C. maculosa* with native species diversity and abundance held when we statistically controlled for levels of native species representing preinvasion conditions. In addition, negative associations of *C. maculosa* with native taxa varied in strength by functional group and species, with large effects on numerically dominant species, suggesting a dramatic shift in community composition and structure. The distinction between weak and strong invaders is important for reconciling conflicting results from previous studies of natural communities, and moving attention beyond the current debate surrounding the biotic resistance hypothesis.

Key words: biological invasions; biotic resistance; *Centaurea maculosa*; community properties; diversity; exotic plants; functional groups; grassland; impacts; invasibility; species richness; spotted knapweed.

INTRODUCTION

The spread of exotic species represents a profound threat to biodiversity on a global scale (Parker et al. 1999, Mack et al. 2000, Levine et al. 2003). Recent attempts to apply ecological theory to the invasive species problem have prompted increased debate over Elton's (1958) biotic resistance hypothesis, which predicts that more diverse communities should be less invulnerable (Levine and D'Antonio 1999, Naeem et al. 2000, Loreau et al. 2001, Stohlgren et al. 2003). The debate itself derives in part from conflicting results obtained from experimental studies of microcosms, which tend to indicate a negative relationship between

resident species diversity and invasibility (Levine 2000, Naeem et al. 2000, Kennedy et al. 2002, Troumbis et al. 2002), vs. observational studies and seed addition experiments conducted in natural systems, which generally show a positive relationship (Smith and Knapp 1999, Stohlgren et al. 1999, 2003, Levine 2000, Sax 2002, Brown and Peet 2003, Cully et al. 2003).

Although these outcomes may appear contradictory, in fact the two classes of studies consider complementary questions about the relationship between diversity and invasibility. Microcosm studies explore the effect of diversity on biotic resistance to invasion when extrinsic factors are controlled (i.e., all else is equal), while observational studies and seed addition experiments evaluate the influence of biotic resistance in the context of the naturally varying conditions of the real world. Taken together, results from these studies sug-

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gest that diversity per se may confer some degree of resistance to invasion, but this resistance is swamped in nature by the covariance of diversity with ecological factors that similarly promote invaders (Levine and D'Antonio 1999, Levine 2000, Stohlgren et al. 2003). Therefore, the caveat "all things being equal" may have limited applicability to natural systems, where diversity is intrinsically linked to a suite of abiotic and biotic factors, from resource supply and disturbance to propagule pressure and species dominance (Huston 1994, Robinson et al. 1995, Stohlgren et al. 1999, 2003, Levine and D'Antonio 1999, Levine 2000). Recognizing that these covarying factors can have an overarching influence on natural patterns of invasibility is essential to reconciling much of the diversity–invasibility debate (Levine and D'Antonio 1999, Shea and Chesson 2002).

However, despite the reconciliation of theory just described, the debate over the importance of diversity has been exacerbated by conflicting results obtained from studies of natural systems. Although many of these local-scale studies and most broad-scale studies have shown positive relationships between measures of diversity and invasibility (e.g., Stohlgren et al. 1999, Sax 2002, Brown and Peet 2003), several analyses of local-scale, observational data have revealed negative relationships (e.g., Stohlgren et al. 1999, Brown and Peet 2003, Cully et al. 2003). Some authors have suggested that such negative relationships indicate that biotic resistance to invasions can in fact operate in natural systems, if only at local scales (e.g., Stohlgren et al. 1999, Brown and Peet 2003), and recent studies have looked to spatial scale to explain conflicting relationships between diversity and invasibility (Brown and Peet 2003, Byers and Noonburg 2003, Cully et al. 2003). However, explanations based on spatial scale cannot reconcile conflicting results from studies of natural communities conducted at comparable local scales.

Conflicting results from studies of natural communities may instead reflect the influence of invader type and extent of invasion on patterns measured at local spatial scales (Levine and D'Antonio 1999). The majority of exotic species that establish within native communities appear to be "weak" invaders that coexist with native species as minor community components (e.g., Huston 1994, Davis et al. 2000, Brown and Peet 2003). However, crucial subsets of exotic species are "strong" invaders that attain community dominance and dramatically impact native species and processes, thereby altering preinvasion patterns (Simberloff 1981, Williamson and Fitter 1996, Levine et al. 2003). Therefore, weak and strong invaders should not be comparable in diversity–invasibility studies or theory. When strong invaders overrun natural communities, relationships between residents and invaders may be negative at local scales because of the impact of invaders on residents. In fact, those studies of natural communities reporting positive local-scale relationships between

resident and invading species appear to involve invaders that occur primarily at low abundance relative to the resident community, apparently as either weak invaders or as strong invaders in early phases of establishment (Robinson et al. 1995, Wisser et al. 1998, Smith and Knapp 1999, Stohlgren et al. 1999, 2003, Levine 2000, Brown and Peet 2003, Cully et al. 2003). In contrast, negative local-scale associations between resident and invading species have usually been reported in cases where invaders occur at high abundance (Woods 1993, Pysek and Pysek 1995, Morgan 1998, Stohlgren et al. 1999, Kedzie-Webb et al. 2001, Kolb et al. 2002, Brown and Peet 2003, Cully et al. 2003; but see Tilman et al. 1997), suggesting that such patterns may primarily reflect the impact of strong invaders on resident diversity vs. the resistance of resident diversity to invasion (Levine and D'Antonio 1999).

It is widely recognized that exotic species threaten biological diversity and the functioning of natural systems (Wilcove et al. 1998, Mack et al. 2000, Levine et al. 2003). Strong invaders are the primary basis for this threat. However, treatments of the diversity–invasibility debate have usually failed to consider that exotic invaders vary greatly in their ability to impact native systems (e.g., Brown and Peet 2003, Byers and Noonburg 2003, Cully et al. 2003; but see Levine and D'Antonio 1999, Dukes 2002). Our review of local-scale studies considering relationships between resident and invading species within natural communities suggests that the distinction between weak and strong invaders may be critical to reconciling conflicting results in diversity–invasibility studies where the impacts of strong invaders on native communities have been ignored. Such reconciliation is necessary for solidifying recent understandings of invasibility obtained from studies of natural communities vs. microcosms, and shifting invasion ecology towards understanding those factors underlying the different behavior of weak and strong invaders within natural communities.

The specific impacts of strong invaders on native communities are also poorly understood (Parker et al. 1999, Loreau et al. 2001, Dukes 2002, Cully et al. 2003). The importance of species and functional group identity to community function is widely recognized (Smith and Knapp 1999, Dukes 2002, Kolb et al. 2002), yet most studies considering effects of plant invaders treat only a limited subset of native species or treat all native species as a single group (e.g., Morgan 1998, Kedzie-Webb et al. 2001; see also Parker et al. 1999). Despite numerous studies examining ecological impacts of invading species (Parker et al. 1999, Mack et al. 2000, Levine et al. 2003), little is known about the relative sensitivity of individual functional groups and species to strong invaders under natural conditions. Such understandings would provide information on potential trajectories of species loss and inform research that examines the specific consequences of such losses on community and ecosystem function (e.g., Ostfeld

and LoGiudice 2003). Studies comparing long-term responses of native species and functional groups to strong invaders are also needed to evaluate hypotheses describing potential mechanisms of invader impact (e.g., Callaway and Aschehoug 2000), and to devise effective restoration strategies.

In this paper, we present results from an observational study of bunchgrass communities in western Montana, USA, which examines local-scale relationships between native plant taxa and weak vs. strong invaders to consider both invasibility and impact. Study communities contained weak invaders and either low or high levels of strong invaders, allowing us to evaluate the effect of invader type and extent of invasion on apparent diversity–invasibility relationships. The primary strong invader was *Centaurea maculosa* (spotted knapweed), an aggressive exotic species that impacts vast areas of western North America (Sheley et al. 2000), although a mix of other strong invaders occurred on study sites. For both low and high levels of invasion, we examined relationships between native species richness and typical measures of invasibility (i.e., exotic species richness and cover), and conducted separate analyses to examine the influence of weak vs. strong invaders on these relationships. To consider apparent impacts of *C. maculosa* on native communities, we also examined relationships between *C. maculosa* cover and occurrence of native taxa, overall and by species and functional group.

METHODS

We studied bluebunch wheatgrass (*Pseudoroegneria spicata*) grassland types (Mueggler and Stewart 1980) occurring on southwest aspects at elevations between 1300 and 1700 m. Study sites were savannas on steep slopes with scatterings of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) located within a matrix of Douglas-fir-dominated montane coniferous forest on the Lolo National Forest in western Montana (Ortega et al. 2004). *Centaurea maculosa*, a perennial forb introduced to western North America from Eurasia in the 1890s (Sheley et al. 2000), was the most prevalent exotic invader of these communities. Although *C. maculosa* has been shown to be a strong invader, dominating bunchgrass communities and impacting native species diversity (Tyser 1992, Kedzie-Webb et al. 2001, Ridenour and Callaway 2001), little is known about the specific nature of these impacts.

We chose study sites at low and high levels of invasion that were as similar as possible in terms of elevation, slope, aspect, vegetation type, and management history. Low invasion sites were located in the vicinity of *C. maculosa* infestations but contained only trace levels, approximating bunchgrass communities before *C. maculosa* invasion. High invasion sites included extensive patches of *C. maculosa* interspersed with native vegetation. Other exotic species, such as

Bromus tectorum (cheatgrass), known to be strong invaders in western North America (i.e., capable of dominating natural communities and displacing native species [Hulburt 1955, Young et al. 1972, D'Antonio and Vitousek 1992, Rice 2002]), occurred at low overall densities at both low and high invasion sites (Table 1). Both types of sites also contained weak invaders, exotic species introduced to the region primarily in the early 1900s and now established as minor components intermixed within natural communities (Lackschewitz 1991, Rice 2002). This design allowed us to examine the behavior of a mix of exotic species at two different levels of *C. maculosa* invasion.

To sample plant communities, we established four transects at each of four low and high invasion sites. Transects were oriented perpendicular to the slope and 50 m apart, and each consisted of 25 sampling stations spaced at 10-m intervals. At each sampling station, we estimated the percent cover of native and exotic plant species to the nearest 1% within a systematically oriented 0.5-m² plot. Species that occupied <1% of a plot were recorded as 0.5% cover. To provide a complete census of herbaceous species, we sampled each station twice per growing season in 2000: early during the wet period (May–June), and late during the dry period (July–August). Subsets of species in six genera were treated as morphogroups because they were difficult to distinguish in the field.

We considered only herbaceous taxa in analyses, and excluded data from plots ($n = 62$ of 800) with >25% shrub cover. Native species were assigned to the following functional groups: annual forbs, perennial forbs (including one biennial species), and perennial grasses (bunchgrasses and one tuft-forming sedge). Exotic species were grouped by type of invader, as weak or strong, using noxious weeds lists and published accounts of invasions associated with western North America (Hulburt 1955, Young et al. 1972, D'Antonio and Vitousek 1992, Rice 2002). Exotic species known to dominate natural communities and displace native species were classified as strong invaders, while those lacking evidence of such behavior were classified as weak invaders. By using literature-based information to classify invaders, we were able to a priori distinguish a subset of exotic species likely to impact native communities. While our literature-based method likely misclassified some invaders, it allowed us to avoid the pitfalls of circularity inherent in using the data in question to distinguish types of invaders. We derived cover values for native and exotic species, overall and by functional group and invader type, by summing across constituent taxa per plot and sampling period. Mean cover per plot, calculated across sampling periods, was used in analyses (mean and maximum values were highly correlated). Species richness per plot was the number of unique taxa recorded in combined sampling periods.

TABLE 1. Prevalence of exotic plant species detected within plots on low and high invasion sites in western Montana, USA, based on mean cover and frequency of occurrence.

Plant taxa	Functional group	Low invasion		High invasion	
		Cover (%)	Frequency (%)	Cover (%)	Frequency (%)
Weak invaders		0.4	40	1.5	84
<i>Agrostis interrupta</i>	AG	<0.05	<1	0.06	<1
<i>Alyssum alyssoides</i>	AF	<0.05	<1	0.4	47
<i>Arenaria serpyllifolia</i>	AF	<0.05	3	0.2	3
<i>Camelina microcarpa</i>	AF	0	0	<0.05	4
<i>Cerastium vulgatum</i>	AF	<0.05	<1	<0.05	6
<i>Dianthus armeria</i>	ABF	<0.05	<1	<0.05	1
<i>Filago arvensis</i>	AF	0.1	21	<0.05	10
<i>Lactuca serriola</i>	ABF	<0.05	<1	<0.05	5
<i>Myosotis micrantha</i>	AF	0.1	26	0.3	55
<i>Rumex acetosella</i>	PF	0	0	<0.05	<1
<i>Secale cereale</i>	AG	0	0	<0.05	<1
<i>Tragopogon dubius</i>	BF	0.1	11	0.3	20
<i>Veronica verna</i>	AF	<0.05	<1	<0.05	10
Strong invaders		1.8	45	20.2	93
<i>Bromus inermis</i>	PG	<0.05	<1	0	0
<i>Bromus japonicus</i>	AG	0	0	0.3	9
<i>Bromus tectorum</i>	AG	1.3	42	2.4	62
<i>Centaurea maculosa</i>	PF	0.4	2	17.5	68
<i>Cynoglossum officianale</i>	PF	0	0	0.2	<1
<i>Euphorbia escula</i>	PF	0	0	0.3	<1
<i>Poa compressa</i>	PG	0.06	4	0.1	3
<i>Poa pratensis</i>	PG	<0.05	<1	<0.05	3
<i>Potentilla recta</i>	PF	0	0	<0.05	1
<i>Sisymbrium altissimum</i>	ABF	<0.05	2	0.1	5
<i>Verbascum thapsus</i>	BF	0	0	<0.05	<1

Note: Species are categorized as weak or strong invaders (see *Methods*), and functional group information is given as: A, annual; B, biennial or P, perennial; and F, forb or G, grass.

Statistical analyses

We used mixed linear models (PROC MIXED; SAS Institute 1999) to evaluate relationships between native and exotic species at low and high invasion sites, respectively. To account for potential spatial autocorrelation among plots at each site, we included spherical spatial covariance terms in all models (SAS Institute 1999). To allow comparison to related studies of exotic plant invasion (e.g., Stohlgren et al. 1999, 2003, Brown and Peet 2003), we evaluated native species richness in relation to each of two commonly used measures of invasibility: exotic species richness and cover (Levine and D'Antonio 1999). To further examine relationships between native and exotic species, we repeated this analysis but split measures of invasion by type of invader (i.e., weak vs. strong). We also conducted separate tests for each native functional group. To evaluate apparent impacts of *C. maculosa*, we constructed models examining species richness and cover of native species, overall and by functional group, in relation to *C. maculosa* cover at high invasion sites. We also conducted parallel tests to examine cover of individual native species in relation to *C. maculosa* cover, limiting analyses to common species (i.e., those occurring at all sites and $\geq 10\%$ of points).

We evaluated assumptions of normality, linearity, and homoscedasticity for all dependent variables using scatterplots of residuals. Cover variables were posi-

tively skewed; transformed values (e.g., arcsine square root) showed some improvement but yielded parallel results. We therefore present results for untransformed variables. Independent variables used together in models (i.e., richness of weak and strong invaders, cover of weak and strong invaders) showed no evidence of multicollinearity, with bivariate correlations $< 22\%$ (Tabachnick and Fidell 1989). For presentation of mean values of dependent variables, we report standard errors adjusted for spatial covariance terms according to the mixed model framework previously described.

RESULTS

We identified a total of 89 native herbaceous species within plots, including 23 annual forbs, 58 perennial forbs, and 8 perennial grasses. Of 24 exotic grass and forb species detected, 13 were classified as weak invaders and 11 as strong (Table 1). Weak invaders were primarily annual forbs, whereas strong invaders tended to be perennial forb or grass species. Low invasion sites had low levels of both weak and strong invaders, while high invasion sites had 10 times the cover of exotic species, consisting primarily of the strong invader *Centaurea maculosa* (Table 1).

Measures of invasibility

Relationships between native species richness and overall measures of invasibility were opposite at low

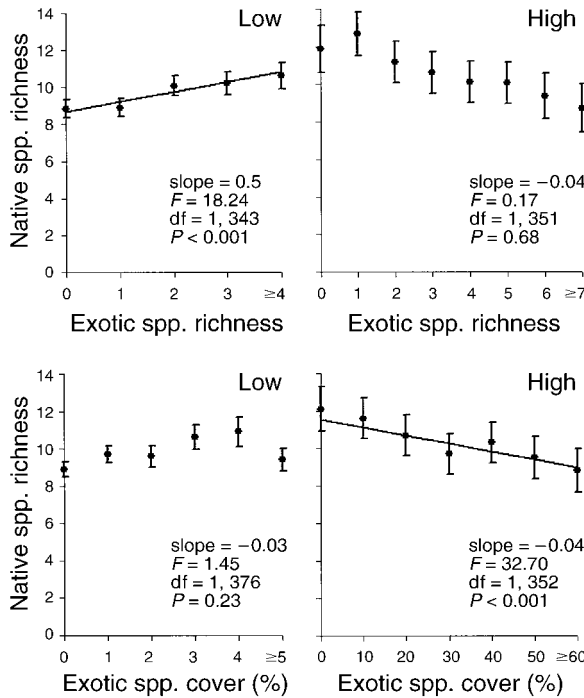


FIG. 1. Relationships between native species richness and measures of invasibility at low and high invasion sites in western Montana, USA, as determined by mixed-models analysis.

vs. high invasion sites (Fig. 1). Native species richness was positively related to exotic richness at low invasion sites ($P < 0.001$), but negatively related to exotic cover at high invasion sites ($P < 0.001$). Native species richness did not vary significantly with exotic cover at low invasion sites ($P = 0.23$), or with exotic species richness at high invasion sites ($P = 0.68$).

When measures of invasibility were split by type of invader, patterns were similar at low and high invasion sites, as native species richness tended to correlate positively with weak invaders vs. negatively with strong invaders (Table 2). Positive relationships between native species richness and weak invader species richness and cover were significant at low invasion sites ($P < 0.001$), but not at high invasion sites ($P \geq 0.56$). At both invasion levels, negative relationships between

native species richness and strong invaders were significant for strong invader cover ($P \leq 0.03$), but not for species richness ($P \geq 0.25$).

Relationships between native species richness and measures of invasibility for weak and strong invaders differed by native functional group, with consistent patterns at low and high invasion sites in most cases (Table 3). At both invasion levels, species richness of native annual forbs had significant positive relationships with weak invaders ($P \leq 0.02$), while species richness of both perennial forbs and grasses varied negatively with strong invaders ($P \leq 0.05$; except for perennial forbs in relation to strong invader cover at low invasion sites, where $P = 0.10$). In addition, annual forb richness was positively associated with strong invader richness at both invasion levels ($P \leq 0.01$), and perennial grass richness was negatively associated with weak invader cover at high invasion sites only ($P = 0.004$).

Relationships between Centaurea maculosa and native taxa

Both richness and cover of native species declined significantly ($P < 0.001$) with *C. maculosa* cover at high invasion sites (Fig. 2; species richness: slope = -0.04 , $F = 20.38$, $df = 1, 349$; cover: slope = -0.5 , $F = 70.62$, $df = 1, 320$). Similarly, significant negative relationships ($P < 0.001$) between native taxa and *C. maculosa* were evident for both perennial forb and perennial grass functional groups, with greater declines for perennial forbs (species richness: slope = -0.03 , $F = 22.79$, $df = 1, 338$; cover: slope = -0.33 , $F = 35.68$, $df = 1, 293$) than for perennial grasses (species richness: slope = -0.01 , $F = 12.55$, $df = 1, 354$; cover: slope = -0.17 , $F = 31.78$, $df = 1, 335$). In contrast, relationships between annual forbs and *C. maculosa* were weak and nonsignificant for both species richness (slope = -0.003 , $F = 0.28$, $df = 1, 336$, $P = 0.60$) and cover (slope = -0.013 , $F = 1.44$, $df = 1, 340$, $P = 0.23$).

Given that relationships between native species and *C. maculosa* differed by functional group, shifts in native community composition and structure within sites were apparent across the gradient of *C. maculosa* cover (Fig. 2). In terms of native species richness, annual and perennial forbs were each twice as prevalent as peren-

TABLE 2. Relationships between native species richness and measures of invasibility associated with weak and strong invaders at low and high invasion sites in western Montana, USA, as determined by mixed-models analysis.

Invasion level	Invasibility measure	Weak invaders			Strong invaders		
		Slope	F†	P	Slope	F†	P
Low	exotic spp. richness	0.91	25.24	<0.001	-0.05	0.85	0.85
	exotic spp. cover	0.74	14.80	<0.001	-0.05	4.99	0.03
High	exotic spp. richness	0.05	0.15	0.70	-0.24	1.32	0.25
	exotic spp. cover	0.05	0.34	0.56	-0.05	33.71	<0.001

† Degrees of freedom = 1, 372–378 and 1, 350–353 for low and high invasion sites, respectively.

TABLE 3. Relationships between native species richness by functional group and measures of invasibility associated with weak and strong invaders at low and high invasion sites in western Montana, USA, as determined by mixed-models analysis.

Invasion level	Invasibility measure	Weak invaders			Strong invaders		
		Slope	F_{\dagger}	P	Slope	F_{\dagger}	P
Annual forbs							
Low	exotic spp. richness	0.79	44.19	<0.001	0.52	10.69	0.001
	exotic spp. cover	0.62	21.98	<0.001	0.002	0.03	0.87
High	exotic spp. richness	0.17	6.44	0.02	0.29	6.20	0.01
	exotic spp. cover	0.18	13.37	<0.001	-0.005	1.29	0.26
Perennial forbs							
Low	exotic spp. richness	0.16	2.05	0.15	-0.36	5.80	0.02
	exotic spp. cover	0.07	0.33	0.57	-0.02	2.79	0.10
High	exotic spp. richness	-0.05	0.44	0.51	-0.29	4.93	0.03
	exotic spp. cover	-0.04	0.53	0.47	-0.03	26.67	<0.001
Perennial grasses							
Low	exotic spp. richness	0.002	0.00	0.97	-0.17	3.84	0.05
	exotic spp. cover	0.04	0.38	0.54	-0.03	21.93	<0.001
High	exotic spp. richness	-0.07	3.03	0.08	-0.25	11.68	<0.001
	exotic spp. cover	-0.09	8.51	0.004	-0.02	30.71	<0.001

† Degrees of freedom = 1, 364–378 and 1, 351–354 for low and high invasion sites, respectively.

ennial grasses in areas of low *C. maculosa* cover, but annual forbs alone dominated areas of high *C. maculosa* cover because of diminished representation of perennial forbs, and to a lesser extent, perennial grasses. Changes in cover of native groups were more dramatic: microsites with low *C. maculosa* cover had relatively high cover of perennial forbs, moderate cover of perennial grasses, and low cover of annual forbs, while those with high cover of *C. maculosa* had low levels of all three groups.

Of 13 native species with sufficient data for analysis, *Balsamorhiza sagittata*, a perennial forb, was the most abundant and had the steepest decline with *C. maculosa* at high invasion sites ($P < 0.001$; Table 4). The most abundant perennial grass *Pseudoroegneria spicata* also showed steep declines ($P < 0.001$). In addition, negative relationships with *C. maculosa* were apparent for the secondary bunchgrass species *Festuca idahoensis* ($P < 0.03$), and a less common forb species, the perennial *Achillea millefolium* ($P < 0.001$). Three remaining perennial species did not vary significantly

with *C. maculosa* cover ($P > 0.06$), nor did any of six species of annual forbs ($P \geq 0.10$).

To better assess whether negative relationships between native taxa and *C. maculosa* observed at high invasion sites may primarily reflect impacts of a strong invader on native communities, we repeated analyses of native species richness (overall and by functional group) and cover (overall and by functional group and species) with the inclusion of data from low invasion sites, which represented the distribution of native species in comparable communities yet to be overrun by *C. maculosa*. Models that included low invasion sites paralleled those constructed with high invasion sites alone, with comparable slope estimates and P values for *C. maculosa* (i.e., Fig. 2, Table 4).

DISCUSSION

We have demonstrated that measures of native species diversity and invasibility can be positively correlated in communities with low levels of invasion where both weak and strong invaders occur at low den-

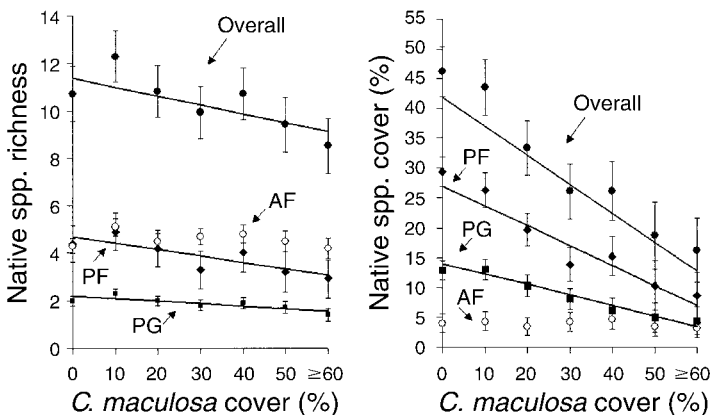


FIG. 2. Relationships between cover of *Centaurea maculosa* and native species richness and cover, overall and by functional group, at high invasion sites in western Montana, USA, as determined by mixed-models analysis. Functional group information: AF, annual forbs; PF, perennial forbs; and PG, perennial grasses (see Results: Relationships between *Centaurea maculosa* and native taxa).

TABLE 4. Relationships between cover of dominant native species and *C. maculosa* at high invasion sites in western Montana, USA, as determined by mixed-models analysis.

Plant taxa	Functional group	Intercept	Slope	F†	P
<i>Achillea millefolium</i>	PF	1.71	-0.03	15.04	<0.001
<i>Balsamorhiza sagittata</i>	PF	13.43	-0.24	41.30	<0.001
<i>Lomatium ambiguum</i>	PF	0.58	0.012	3.47	0.063
<i>Lupinus</i> spp.‡	PF	4.44	-0.028	1.51	0.22
<i>Clarkia pulchella</i>	AF	0.34	0.0004	0.06	0.81
<i>Collinsia parviflora</i>	AF	0.68	0.0008	0.11	0.74
<i>Collomia linearis</i>	AF	0.61	-0.0008	0.09	0.77
<i>Epilobium paniculatum</i>	AF	0.38	-0.003	2.80	0.096
<i>Microsteris gracilis</i>	AF	0.85	-0.0005	0.86	0.36
<i>Polygonum douglasii</i>	AF	0.15	-0.0002	0.05	0.83
<i>Festuca idahoensis</i>	PG	3.24	-0.031	4.74	0.03
<i>Poa sandbergii</i>	PG	2.24	-0.015	2.62	0.11
<i>Psuedoroegenaria spicatum</i>	PG	6.82	-0.11	27.70	<0.001

Note: Functional group information is given as: AF, annual forbs; PF, perennial forbs; and PG, perennial grasses.

† Degrees of freedom = 1, 113–355.

‡ *L. argenteus*, *L. laxiflorus*, *L. leucophyllus*, *L. polyphyllus*, *L. sericeus*, and *L. wyethii*.

sities, but negatively correlated in communities with high levels of invasion where strong invaders like *Centaurea maculosa* dominate. These results have important implications for the debate over Elton's (1958) biotic resistance hypothesis, supporting our contention that conflicting results in local-scale studies of natural communities can arise from failure to account for the prevalence of weak vs. strong invaders (e.g., Stohlgren et al. 1999, Brown and Peet 2003, Cully et al. 2003). Often absent from studies addressing the diversity-invasibility debate is the crucial recognition that exotic invaders vary greatly in their ability to impact native systems: while weak invaders become minor components of native communities, strong invaders become community dominants at the expense of native species and processes. Yet in both theoretical and empirical treatments of community invasibility, invading species are typically treated as a group with little regard to invader identity or status (e.g., Stohlgren et al. 1999, Brown and Peet 2003, Byers and Noonburg 2003).

We split measures of invasibility by type of invader and found that weak and strong invaders did not behave alike, irrespective of invasion level. Weak invaders tended to vary positively with native species, underlying the positive overall relationship between measures of diversity and invasibility observed in low invasion communities. Positive local-scale relationships between native and exotic species have been obtained in numerous diversity-invasibility studies of natural communities, opposing the predictions of the biotic resistance hypothesis (Levine and D'Antonio 1999, Stohlgren et al. 2003). Such positive relationships are thought to represent the parallel responses of native and exotic species to biotic and abiotic factors and the apparent ability of these taxa to coexist in natural communities (e.g., Sax 2002). Our results suggest that this premise may be applicable to weak but not strong invaders, as strong invaders tended to correlate nega-

tively with native species and drive the negative overall pattern between measures of diversity and invasibility observed in high invasion communities. That these negative relationships primarily reflect the impacts of established invaders on native diversity is supported by the fact that *C. maculosa*, an abundant strong invader, had negative relationships with diversity and abundance of native species that held when we statistically controlled for levels of native species representing preinvasion conditions. Our results further suggest that strong invader impacts may explain the negative relationships between native and exotic species obtained in several studies of natural plant communities, which have sometimes been treated as evidence that biotic resistance can operate at local scales in natural communities (e.g., Stohlgren et al. 1999, Brown and Peet 2003, Cully et al. 2003). Thus it appears that studies of natural communities collectively provide little evidence that Elton's biotic resistance hypothesis effectively explains invasion dynamics in the real world (Levine and D'Antonio 1999, Stohlgren et al. 2003).

At the same time, the impacts of strong invaders represent a significant force in natural communities. We found that negative relationships between *C. maculosa* and native taxa varied in strength by functional group and species, with large effects on numerically dominant species, suggesting a dramatic shift in community composition and structure. Such information on strong invader impacts is lacking yet critical to understanding implications of diversity loss on community and ecosystem function (Parker et al. 1999, Loreau et al. 2001, Ostfeld and LoGiudice 2003). The distinction between weak and strong invaders must be recognized to move invasion ecology beyond the current debate over the biotic resistance hypothesis.

Measures of invasibility for weak vs. strong invaders

In observational studies, richness and cover of exotic species in relation to community properties can provide

an index of invasibility that encompasses naturally varying conditions, but only if the invaders do not alter the preinvasion community. Weak invaders in our study were classified a priori as exotic species with no evidence of ability to dominate natural communities or displace native species. Accordingly, these invaders occurred at low levels on our study sites (Table 1), with maximum local cover values of 12%. Richness and cover of weak invaders showed positive relationships with native species richness (Table 2), indicating increased invasibility of species rich microsites, as driven by the covariance of weak invaders, primarily annual forbs, with native annual forbs (Table 3). Such positive diversity–invasibility relationships likely stem from ecological factors that similarly promote native and exotic species: in local bunchgrass systems: both native and exotic annual forbs are positively associated with fine-scale soil disturbance caused by snow melt and rodent activity characterizing much of the area surrounding perennial forb and bunchgrass plants (Antos et al. 1983, Forcella and Harvey 1983, Lackschewitz 1991; Y. K. Ortega, *personal observation*). This pattern can also explain observed negative relationships between exotic annual forbs (i.e., weak invaders) and native perennials (Table 3). Disturbance is known to increase resource availability, influence community composition, and promote exotic invasions, possibly also facilitating coexistence (Hobbs and Mooney 1985, Davis et al. 2000, Thompson et al. 2001). We found that weak invaders differentially established in areas of high native diversity, where they appeared to coexist with comparable native species as influenced by disturbance or other covarying factors.

Unlike weak invaders, strong invaders in our study were exotic species known to dominate natural communities at the expense of native species. Local cover values of strong invaders reached as high as 70% in low invasion communities and 100% in high invasion communities, possibly signaling the unique ability of strong invaders to overrun natural communities. Similarly, negative relationships between strong invaders and native species richness were observed in both low and high invasion communities (Table 2), and likely reflect the impact of *C. maculosa* and other strong invaders such as *Bromus tectorum* on native species, rather than the increased invasibility of species poor areas. Strong invaders, mostly perennial species, exhibited negative relationships with native perennial taxa (Table 3), the opposite of the relationship found between weak annual forb invaders and their native counterparts, further suggesting that different processes were at work for strong vs. weak invaders.

Negative relationships between strong invaders and native species richness were more apparent for cover than richness of strong invaders (Tables 2, 3), signifying the important role of dominance by invaders such as *C. maculosa*. Similarly, cover of exotic species in both low and high invasion communities (Fig. 1) was

driven more by cover of strong invaders ($r = 0.99$, $P < 0.001$ for both invasion levels) than by cover of weak invaders ($r = 0.36$, $P < 0.001$ and $r = 0.22$, $P < 0.001$ for low and high invasion sites, respectively), underscoring the sensitivity of abundance measures to the influence of strong vs. weak invaders. Where strong invaders are involved, invader abundance, as measured at local scales in observational studies, may be more representative of invader impact (e.g., Parker et al. 1999) than of invasibility, regardless of invasion level. In high invasion communities where strong invaders prevail, neither richness nor cover of exotic species may provide reliable measures of invasibility.

Apparent impacts of Centaurea maculosa on native communities

The primary strong invader, *C. maculosa*, appeared to differentially impact native functional groups and species, with the largest effects on perennial forbs (Fig. 2, Table 4). Overall, declines in richness and cover of native functional groups per unit of *C. maculosa* were twice as steep for perennial forbs as for perennial grasses (Fig. 2), while annual forbs did not show declines. Because native perennial forbs can account for >40% of native species richness and >60% of native species cover in areas with no *C. maculosa* (Fig. 2), the spread of this strong invader may cause a dramatic shift in community composition and structure. As *C. maculosa* invasion progresses, we expect native communities to shift away from perennial species, especially forbs. Mean cover of *C. maculosa* on our study sites was low (i.e., 17% at high invasion sites) compared to values reported elsewhere (e.g., 60–100%; Tyser 1992, Ridenour and Callaway 2001), and negative effects of *C. maculosa* on annual forbs may become evident at higher levels of invasion. However, the observed persistence of native taxa even at high densities of *C. maculosa* (e.g., Ridenour and Callaway 2001) could indicate adaptive resistance to invader impacts (Hiero and Callaway 2003).

Strong invaders such as *C. maculosa* can greatly alter natural systems by reducing diversity and abundance of native taxa (Parker et al. 1999, Mack et al. 2000, Levine et al. 2003). Given that native species and functional groups vary in their community roles, the effects of these losses on community function depend on the identity of the species or groups that are most affected (Loreau et al. 2001, Prieur-Richard et al. 2002, Ostfeld and LoGiudice 2003). Little is known about the specific roles of native taxa in bunchgrass communities of western North America, but because abundance may be an indicator of importance in plant communities (e.g., Grime 1998), declines in numerically dominant species and groups suggested by our results may amount to significant impacts on community function. Given trophic linkages, these impacts may also ripple throughout the system (e.g., Wootton 1994, Jones et al. 1998, Schmidt and Ostfeld 2003). For example, *Balsamorhiza*

sagittata, observed to be the most abundant native species in areas yet to be invaded by *C. maculosa*, produces large seeds that provide food for birds, mammals, and invertebrates. Therefore, documented declines in this plant species may signify reduced food resources for a host of consumers.

Understanding which native taxa are impacted by strong invaders also carries important implications for restoration of native systems. For example, broadleaf herbicides are the primary method for controlling *C. maculosa* (Sheley et al. 2000), yet such chemicals also suppress native perennial forbs (Rice et al. 1997, Rice and Toney 1998, Tyser et al. 1998). Therefore, use of broadleaf herbicides for control of *C. maculosa* could exacerbate the negative effects of *C. maculosa* by further shifting communities away from native forbs, an important group in many grassland systems of western North America (e.g., Mueggler and Stewart 1980). The efficacy of weed control methods for restoration must be evaluated in an ecological context that includes understandings of the impacts associated with strong invaders.

Why do strong invaders behave differently?

Numerous factors may be involved in the ability of strong plant invaders to gain community dominance and impact native systems (Callaway and Aschehoug 2000, Maron and Vila 2001, Keane and Crawley 2002, Levine et al. 2003). Although no single paradigm may serve to explain the behavior of strong invaders as a group, it is critical that this unique subset of exotic species be distinguished from weak invaders when invasion mechanisms are considered. Shea and Chesson's (2002) conceptual model of niche opportunity provides a summary of those factors potentially governing invasions that can also be used to describe the differential behavior of weak and strong invaders. According to this model, given initial propagule supply, the establishment and subsequent population growth of an invading species depends on its response to and impact on competitors, resource availability, physical factors, natural enemies, and the interactions among these factors. An invader's traits determine its response to and effect on these governing factors. In the context of this model, weak invaders, like most native species, have limited niche opportunities leading to generally low population levels and minimal impact on biotic and abiotic components of the system. Conversely, strong invaders can take great advantage of governing factors to enable relatively large population sizes and significant impacts on system components. A weak invader can also become a strong invader in another time or place if shifts in governing factors result in sufficiently expanded niche opportunities.

General understandings of when, where, and how particular governing factors interact to determine invader behavior are lacking (e.g., Maron and Vila 2001, Keane and Crawley 2002), but competitive interactions

are typically implicated as important components of invader success (Levine et al. 2003). The ability of strong invaders to impact native species has often been linked to functional differences in traits between the invaders and residents thought to impart competitive superiority (Levine et al. 2003). For example, according to the "novel weapons" hypothesis, *C. maculosa* may be a strong invader, at least in part, because it releases an allelopathic chemical that its native, Eurasian competitors have adapted to, but its new competitors have not (Callaway and Aschehoug 2000). In support of this hypothesis, greenhouse experiments have demonstrated that root exudates of *C. maculosa* differentially impact resource uptake, growth, and germination of perennial bunchgrasses from Eurasia vs. North America (Callaway and Aschehoug 2000, Ridenour and Callaway 2001, Bais et al. 2003). Future research must evaluate the relevance of the novel weapons hypothesis within natural communities while specifically addressing the differential impacts of *C. maculosa* on native taxa suggested by our study. To this end, results from observational studies of natural communities considering specific invader impacts are needed to develop predictions for testing potential mechanisms of strong invader success. Given that strong invaders appear to be uniquely capable of overrunning natural systems, they must be distinguished from other invaders in future research intended to inform the growing threat of biological invasions, as all invaders are not created equal.

Conclusions

Our study of natural plant communities indicates that although native species diversity can be positively related to local-scale invasibility where weak invaders are concerned, impacts of strong invaders on native diversity may be evident even at low invasion levels and drive negative local-scale relationships between native and exotic species within highly invaded communities. This understanding helps to reconcile conflicting results in previous studies of natural plant communities (e.g., Stohlgren et al. 1999), further suggesting that biotic resistance may not be a significant force in the real world, even at local scales. Far more pervasive is the apparent tendency of weak invaders to function like most native species in their ultimate response to abiotic and biotic factors, allowing for coexistence of these taxa within natural communities. Furthermore, recognizing the markedly different behavior of strong invaders is critical, for these exotic species take over natural communities at the expense of native diversity, thereby incurring system-level impacts. Regardless of diversity, few natural communities can escape the entry of exotic species and the impact of strong invaders. Research is needed to evaluate the ecological factors underlying the differential function of strong vs. weak invaders to enable recognition of strong invaders before invasions progress and improve

the efficacy of weed management efforts. Furthermore, the restoration of systems already threatened by strong invaders must be informed by studies that describe the specific ecological impacts of these invaders. Given the increasingly serious threat of strong invaders to diversity and function of natural systems and the difficulties associated with reversing these impacts, invasion ecology must shift away from the current debate over the biotic resistance hypothesis and develop understandings of the behavior of weak vs. strong invaders in the real world.

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