Jeffrey S. Dukes

Biodiversity and invasibility in grassland microcosms

Abstract In the years since Charles Elton proposed that more diverse communities should be less susceptible to invasion by exotic species, empirical studies have both supported and refuted Elton's hypothesis. Here, I use grassland community microcosms to test the effect of functional diversity on the success of an invasive annual weed (*Centaurea solstitialis* L.). I found that high functional diversity reduced the success of *Centaurea* by reducing resource availability. An equally important, but unstudied, question is whether diversity can buffer a community against the impacts of invasive species. In this experiment, although species diversity (independent of functional diversity) did not affect the success of the invader, the invader suppressed growth of species-poor communities more strongly. Invasion of *Centaurea* also increased summer evapotranspiration in species-poor communities. These results suggest that loss of species diversity alone does not affect community invasibility, but that communities with fewer species may be more likely to decline as a consequence of invasion.

Keywords Biological invasions · California grassland · *Centaurea solstitialis* · Competition · Species richness

Introduction

An ecosystem's susceptibility to invasion is thought to be influenced by many factors, including the composition and diversity of resident species (Elton 1958; Rejmánek 1989; Robinson et al. 1995; Crawley et al. 1999; Levine and D'Antonio 1999). It is commonly hypothesized that diverse communities use resources more completely than simple communities, and are thus more resistant to invasion (Levine and D'Antonio 1999; Tilman 1999). If this is the case, diverse communities might buffer ecosystem processes against invader-driven perturbations for two reasons: (1) reduced success of invading species, and (2) reduced likelihood that an invading species will introduce some new property or process to the system (Chapin et al. 1998). Recent studies have described positive (Robinson et al. 1995; Palmer and Maurer 1997) and negative (McGrady-Steed et al. 1997; Tilman 1997; Stachowicz et al. 1999) relationships between diversity and invasibility, and in some cases have found no relationship (Lavorel et al. 1999). Relatively few studies have isolated the effect of diversity or examined the mechanisms that control these relationships (but see Knops et al. 1999; Lavorel et al. 1999; Stachowicz et al. 1999; Symstad 2000).

To better understand how diversity influences community invasibility, researchers must uncover mechanisms that link the two properties. Several mechanisms, acting on different spatial scales, may be responsible for the conflicting patterns observed in previous studies (Knops et al. 1999; Lonsdale 1999; Stohlgren et al. 1999). Microcosms allow the isolation and study of mechanisms that act on a small scale, and that contribute to larger-scale patterns observed in the field. I constructed community microcosms from a pool of native and naturalized California grassland species, in order to test the effects of species composition and diversity on invasibility, the stability of ecosystem functions after invasion, and several other ecosystem properties.

J.S. Dukes (✉)
Department of Biological Sciences, Stanford University, Stanford, California 94305-5020, USA

Present address:
J.S. Dukes, Department of Biology, University of Utah,
257 S. 1400 East, Salt Lake City, UT 84112, USA,
e-mail: dukes@biology.utah.edu,
Tel.: +1-801-5817086, Fax: +1-801-5814665

Materials and methods

This experiment was conducted outdoors during the 1997–1998 growing season at Jasper Ridge Biological Preserve (JRBP), near Palo Alto, California, USA (37°24′N, 122°14′W, 120 m elevation). Microcosms consisted of upright sections of polyvinyl chloride pipe, 0.2 m in diameter by 0.95 m high, which were filled with a 3:1 mixture of topsoil from surrounding grassland:sand.

I established 64 "control" communities from a pool of 16 grassland species found at JRBP. The pool contained four species

Table 1 Species and seeding densities in monocultures[a]

Species[b]	Native?	Functional group[c]	Seeding density (seeds m^{-2})[d]
Avena barbata	No	AG	1847
Bromus hordeaceus	No	AG	2197
Vulpia microstachys	Yes	AG	2548
Lolium multiflorum	No	AG	1019
Plantago erecta	Yes	EF	8057
Lasthenia californica	Yes	EF	7643
Erodium botrys	No	EF	2547
Microseris douglasii	Yes	EF	6115
Hemizonia congesta ssp. luzulifolia	Yes	LF	1847
Lessingia hololeuca	Yes	LF	2962
Calycadenia multiglandulosa	Yes	LF	5096
Epilobium brachycarpum	Yes	LF	3567
Nassella pulchra	Yes	PG	5701
Elymus multisetus	Yes	PG	3057
Festuca pratensis	No	PG	4076
Elymus glaucus ssp. *glaucus*	Yes	PG	4076

[a] Not all species were grown in monoculture. The seeding densities presented here formed the basis for calculating seeding densities in the polycultures. For instance, 16-species communities received seeds of all of the species listed at 1/16 the densities listed here

[b] Nomenclature follows Hickman (1993)

[c] Key to functional groups: *AG* annual grass, *EF* early-season annual forb, *LF* late-season annual forb, *PG* perennial grass

[d] Imperfect germination and establishment rates led to lower final plant densities. Final density of *Centaurea* was 96 individuals m^{-2}

from each of four functional groups: annual grasses, perennial bunchgrasses, early-season annual forbs, and late-season annual forbs (Table 1). Control communities contained 0, 1, 4, 8, 12, or 16 species. Eight species (two species from each of the four functional groups) were represented in monocultures. Each of these monocultures was replicated five times, as were bare soil (0 species) and 16-species treatments. Replicates of the 4-, 8- and 12-species treatments were created by repeating random draws of one, two, or three species from each of the four functional groups. Thus, polycultures differed in species diversity, but not functional diversity. Five "replicate" communities of 4 and 12 species were created, and four of 8 species. Monocultures were sowed at densities estimated to allow maximum biomass production for each species (Table 1). In polycultures, seeding densities were reduced according to the total number of species in the community. For instance, in four-species communities the density of each species was reduced to one-quarter its density in monoculture.

I paired each of the 64 control microcosms with an "invaded" microcosm that contained individuals of the invasive late-season annual *Centaurea solstitialis* (yellow starthistle, a major problem weed in California; Balciunas and Villegas 1999), but was otherwise identical to the control. At the beginning of the study, the invaded communities received 15 seeds of *Centaurea*, in addition to seeds of resident species (which were sown at the same density as in the control communities). Seeds in the communities germinated shortly after the rains of 10 November 1997, which marked the start of the rainy season. *Centaurea* seedlings were thinned to four evenly spaced individuals in early December 1997, and to three seedlings on 18 February 1998. Because all species grew from seed in disturbed soil that was not covered by litter, microcosms in this experiment were analogous to gopher-disturbed patches of California grassland. In grasslands at JRBP, pocket gophers (*Thomomys bottae*) cover an average of 26% of the surface with their tailings each year (Hobbs and Mooney 1991).

In the San Francisco Bay area, grassland species germinate or resprout after the first significant autumn rains, which usually fall in October or November. Most of the grasslands are dominated by introduced annual grasses, which set seed and die in May or June. Perennial bunchgrasses, which are mostly native, senesce aboveground in June or July. Early-season annual forbs generally die in April or May, and late-season annual forbs (including *Centaurea*) continue growing through the summer, finally setting seed and dying in September or October. Within these phenologically based functional groups, species are generally similar in morphology and physiology (Gulmon et al. 1983; Mooney et al. 1986; Chiariello 1989; Armstrong 1991). Among these groups, species differ in seasonal and spatial patterns of resource use (Hooper and Vitousek 1998). I collected reproductive biomass of each species as it ripened, and harvested non-reproductive aboveground biomass of all species from 19 August to 15 September 1998, immediately after the senescence of *Centaurea*. All plant material was oven-dried (65°C) for 2 days before weighing.

During the growing season, I used ion-exchange resin bags to measure soil nutrient availability in all of the 4-, 8-, 12-, and 16-species communities, and in one replicate of the 1-species and bare communities. Anion (AG-1-X8, Bio-Rad Laboratories, Hercules, Calif., USA) and cation (HCR-W2, H$^+$ form, spherical beads, 16–40 mesh, J.T. Baker, Phillipsburg, N.J., USA) exchange resin beads were mixed to achieve a 1:1 ratio of exchange capacities. Each resin bag comprised 1.5 g of air-dried resin, tightly wrapped in a section of nylon stocking, which was tied shut with a cable tie. Resin bags were soaked in 4 M NaCl for several hours and rinsed with deionized water before being placed in the microcosms. To facilitate non-destructive placement and removal of resin bags during the growing season, I shaved uniform portions off of the sides of polypropylene test tubes and pushed these tubes into the soil until the open sections of the tubes were at a depth of 6 cm. Resin bags were gently pushed to the bottom of these tubes, exposing two sides of each bag to soil, and the tubes were stoppered. These resin bags were removed, extracted in 10 ml of 2 M KCl, and replaced with a new set monthly during the growing season. Nitrate, ammonium, and phosphate concentrations of extracts were determined on an autoanalyzer.

Evapotranspiration (ET) was determined indirectly, by measuring bulk water inputs (rainfall) and outputs (leachate), and soil moisture during the growing season. For a given period, ET was calculated using the following equation: Water entering microcosm via rain-Water lost via leachate-Change in amount of water stored in soil=ET. Precipitation was measured by a tipping-bucket rain gauge located within 10 m of the experimental setup. Volumetric water content of the top 28.5 and 88.5 cm of soil was measured using time-domain reflectometry (TDR), as described (Field et al. 1997). Water availability and the volumes and nutrient concentrations of leachate were measured during the wet season for all replicates of 0, 4, 8, 12, and 16 species, and for one replicate of each single-species treatment. Lysimeters connected to the microcosms by vinyl tubing collected leachate, which was analyzed for concentrations of nitrate and ammonium on an autoanalyzer.

Results and discussion

Aboveground biomass of the single-species control communities varied widely. Annual grasses produced the most biomass, followed by late-season forbs, early-season forbs, and the perennial grass seedlings (Fig. 1A). On average, biomass production of four-species control communities was greater than that of monocultures, but there was no significant biomass trend as communities increased in diversity from 4 to 16 species (linear regression, P=0.14, Fig. 1B). This pattern is reasonably consistent with that observed in similar biodiversity experiments (e.g., Naeem et al. 1996; Tilman et al. 1997; Hector et al. 1999).
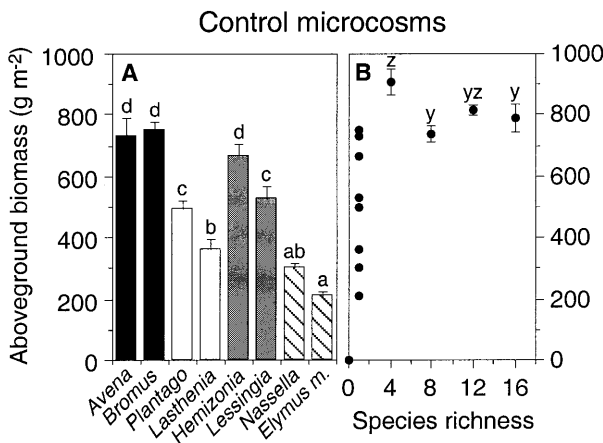
Fig. 1A, B Aboveground biomass production of control (uninvaded) microcosms (mean±SE, *n*=5). **A** Productivity of the monocultures. Bar patterns represent functional groups (*solid filled* annual grasses, *open* early-season forbs, *lightly filled* late-season forbs, *shaded* perennial grasses). **B** Productivity of all community types. In both **A** and **B**, values that do not share *letters* are significantly different (*P*<0.05, ANOVA followed by Student-Newman-Keuls post hoc test). Separate ANOVAs were conducted for the monocultures and for the polycultures, which differ in species diversity but not in functional diversity. For clarity, *error bars* have been removed from the 1-species values in **B**

Fig. 2A, B Invasibility of the grassland microcosms. Invasibility is displayed as aboveground biomass of *Centaurea* (mean±SE, *n*=5) in invaded microcosms, which was highly correlated with reproductive biomass of *Centaurea* (data not shown). **A** Invasibility of monocultures. **B** Invasibility of all community types, plotted against the number of resident species (species other than *Centaurea*) in the community. Statistical analyses, *letters* and *bar patterns* are as in Fig. 1. For clarity, *error bars* have been removed from the 1-species values in **B**

According to Crawley (1987), "a community is invasible when an introduced species is able to increase when rare." In this study, I did not focus on changes in the population size of *Centaurea*, but rather on competitive effects that other species had on *Centaurea*'s aboveground biomass. In annuals like *Centaurea*, aboveground biomass production is strongly correlated with reproductive output (J.S. Dukes, unpublished work), and as such is an important predictor of the potential for population increase in a field setting. Community invasibility, as defined by aboveground biomass production of *Centaurea*, varied widely among the single-species treatments (Fig. 2A). Monocultures of perennial grass seedlings were most successfully invaded, while monocultures of *Hemizonia congesta*, which, like *Centaurea*, is a late-season forb, strongly suppressed growth of the invader. *Centaurea* biomass in the invaded monocultures was negatively, but not tightly, correlated with biomass production of paired control monocultures (Fig. 3). Communities with four or more species (and thus all four functional groups) suppressed *Centaurea* growth as strongly as *Hemizonia* monocultures, even though these polycultures did not always include *Hemizonia*. *Centaurea* biomass remained constant as species diversity increased from 4 to 16 species (Fig. 2B, linear regression, slope=0.01, *P*=0.80, *r*²<0.01, *n*=19).

To assess whether resource depletion by the resident plant community limited community invasibility, I regressed the log of *Centaurea* biomass in invaded microcosms against water and soil nutrient availability in paired control (uninvaded) microcosms (Table 2). Community invasibility was positively correlated with water
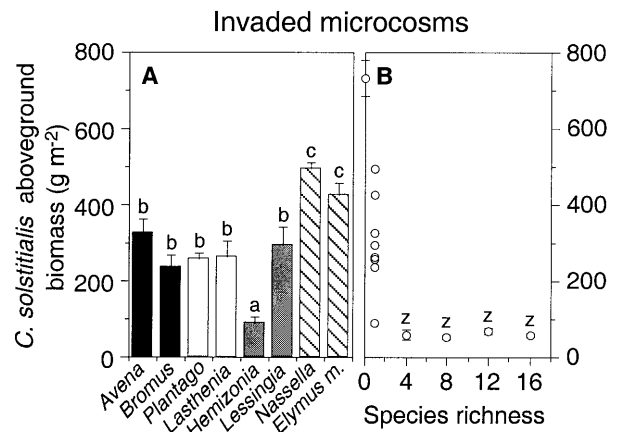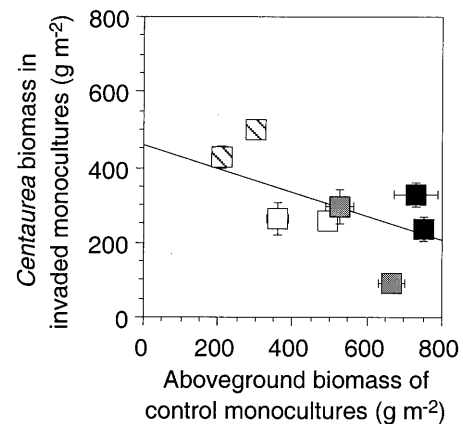

Fig. 3 Relationship between *Centaurea* biomass in invaded monocultures and productivity of control monocultures (*symbols* show means±SE, *n*=5). *Symbol patterns* represent functional groups and correspond with bar patterns described in Fig. 1. *Regression line*: *y*=457.71-0.31*x* (*P*<0.01, *r*²=0.24, *n*=40)

and nitrate availability during some parts of the growing season. Availability of these two resources is related; soil moisture levels determine the mobility of nitrate in the soil, and thus modulate nitrate capture by resin bags. *Centaurea* biomass was significantly related to nitrate availability during the late February measurement period (although the fit of the relationship was poor), and linear regressions suggested the possibility of a weak relationship (not significant after Bonferroni correction) during two subsequent measurement periods. In late February, this relationship was driven by relatively high nitrate availability in the *Nassella* and *Lessingia* monocultures and in the bare soil microcosm. The bare soil microcosm consistently had higher nitrate availability than vegetated

Table 2 Factors influencing invasibility by *Centaurea solstitialis*. Parameters are from simple regressions of the log of *Centaurea* biomass in invaded communities on resource availability in paired control communities. Values for nitrate, ammonium, and phosphate availability in the rooting zone represent the concentration of these nutrients ($\mu g\ ml^{-1}$ N or P) in extracts from ion-exchange resin bags. *Shallow water* is defined as (volumetric %) soil moisture in the top 28.5 cm of soil. *Total water* is defined as soil moisture in the top 88.5 cm of soil

Resource	Date (1998)	n^a	Slope	P value (slope)	r^2
NO_3^-	11 Jan–9 Feb	28	0.256	0.3037	0.041
NO_3^-	9 Feb–11 Mar	26	0.950	0.0010*	0.370
NO_3^-	11 Mar–7 Apr	28	2.183	0.0431	0.148
NO_3^-	7 Apr–13 May	28	0.344	0.0111	0.223
NH_4^+	11 Jan–9 Feb	28	0.133	0.5133	0.017
NH_4^+	9 Feb–11 Mar	27	–0.007	0.9648	0.000
NH_4^+	11 Mar–7 Apr	28	–0.219	0.3218	0.038
NH_4^+	7 Apr–13 May	28	–0.075	0.6921	0.006
PO_4^{3-}	11 Jan–9 Feb	28	–0.370	0.3191	0.038
PO_4^{3-}	9 Feb–11 Mar	27	–0.409	0.3297	0.038
PO_4^{3-}	11 Mar–7 Apr	28	–1.09	0.2009	0.062
PO_4^{3-}	7 Apr–13 May	28	–0.295	0.3613	0.032
Shallow water	27 Mar	32	0.009	0.7391	0.004
Shallow water	17 May	32	0.091	0.0002**	0.381
Shallow water	11 Jun	32	0.064	0.0003**	0.361
Shallow water	2 Jul	16	0.072	<0.0001**	0.807
Shallow water	15 Jul	14	0.065	<0.0001**	0.813
Total water	27 Mar	32	–0.014	0.4120	0.023
Total water	17 May	31	0.071	<0.0001**	0.522
Total water	11 Jun	32	0.06	<0.0001**	0.455
Total water	2 Jul	30	0.041	<0.0001**	0.863
Total water	15 Jul	29	0.037	<0.0001**	0.808

[a] In some cases, values for *n* are less than 28 (nutrient analyses) or 32 (soil moisture analyses) because data were missing, or because data were spurious and were therefore omitted, *Statistically significant *P* values ($\alpha=0.05$) according to the sequential Bonferroni test, **P* value is less than the critical Bonferroni value for $\alpha=0.01$

Fig. 4A, B Impact of *Centaurea* invasion on aboveground biomass of resident species (species other than *Centaurea*). To measure impact, I subtracted resident species biomass in the control microcosms from resident species biomass in paired invaded microcosms. **A** Mean (+SE, *n*=5) impacts on the monocultures. *Bar patterns* are as in Fig. 1A. Differences among treatments, although large, were not statistically significant (ANOVA, *P*=0.07). **B** Actual impacts on the polycultures. *Regression line* in **B**: $y=-140.4+8.1x$ ($r^2=0.21$, *P*=0.05)

Fig. 5A, B Impact of *Centaurea* on total community biomass. Total community biomass includes biomass of resident species and *Centaurea*. To measure impact, I subtracted total biomass of the control microcosms from total biomass of paired invaded microcosms. **A** Mean (+SE, *n*=5) impacts on the monocultures. Statistical analyses, *letters*, and *bar patterns* are as in Fig. 1A. **B** Actual responses of the polycultures. *Regression line* in **B**: $y=-82.7+8.3x$ ($r^2=0.23$, *P*<0.05)

microcosms (data not shown), and was highly invasible by *Centaurea*. When the bare microcosm was excluded from analyses, the relationship between nitrate availability and *Centaurea* growth became weak in the late February measurement period (*P*=0.02, not significant after Bonferroni correction), and subsequently disappeared (data not shown).

Invasibility was strongly correlated with soil moisture availability on several dates. This relationship was strongest for moisture in the top 88.5 cm of the soil column on 2 July 1998. Invasibility was also significantly related to water availability in the top 28.5 cm of soil on this date, and this relationship remained strong on 15 July. The relationship between summer water availability and invasibility remained highly significant when bare microcosms were excluded from the analyses (data not shown). By reducing the availability of soil moisture in the summer, diverse communities and the *Hemizonia* monoculture reduced the growth of *Centaurea*. Conversely, communities that lacked summer-active, deep-rooted species provided less resistance to invasion.

Biomass production of resident species (species other than *Centaurea*) was greater in control microcosms than in invaded microcosms. This difference varied substan-
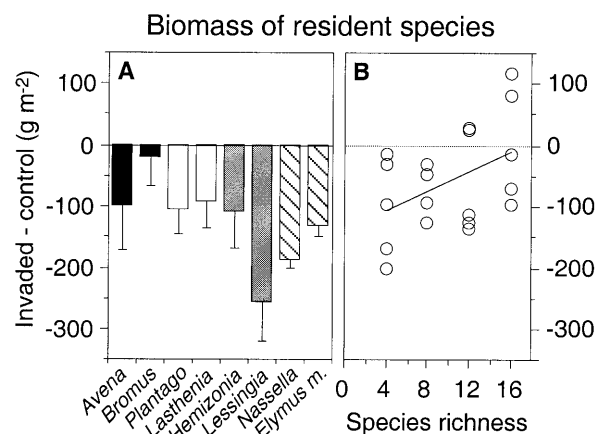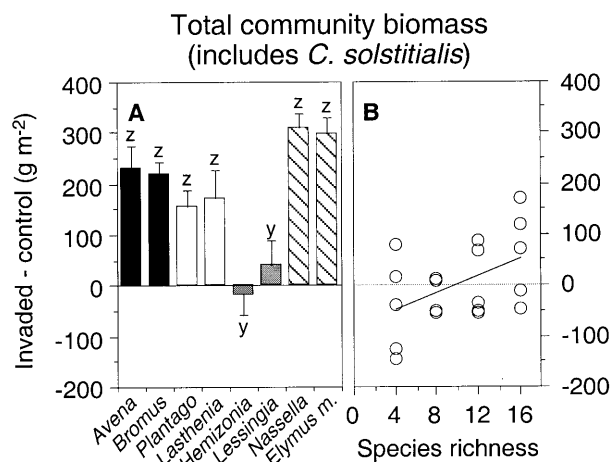
tially but not significantly among the single-species communities (Fig. 4A, *P*=0.07 ANOVA). In the polycultures, this difference was greater in simpler communities than in more diverse communities (Fig 4B). Interestingly, this pattern was not related to the success of *Centaurea*, which remained constant across the polycultures. As diversity increased, the negative impact of *Centaurea* on growth of other late-season annual forbs, and to some extent also annual grasses, decreased (data not shown).

The responses of these two functional groups were the basis for the overall trend.

Introduction of *Centaurea* significantly increased the total biomass (aboveground biomass of resident species plus *Centaurea*) of single-species communities, with the exception of late-season forb communities (Fig. 5A, P=0.0001 ANOVA). This result suggests that the invasion of a species whose functional group is not represented in a community has greater potential to increase community biomass production than the invasion of a species whose functional group is already represented. The presence of late-flowering forbs in the polycultures probably minimized the response of total biomass of these communities to *Centaurea*. The effect of *Centaurea* on total biomass of polycultures varied with the number of species in the community (Fig. 5B). Biomass of less diverse communities declined in response to *Centaurea* introduction, while more diverse communities gained biomass. Responses of resident species to the invader (Fig. 4B, discussed above) drove this pattern of increasing total biomass responses with increasing diversity.

Introduction of *Centaurea* affected community evapotranspiration rates, but did not affect nutrient availability or loss. Although *Centaurea* increased late-season (11 June–15 July) evapotranspiration (LET) from simple communities, the differences in LET between invaded and control communities decreased with increasing species richness (Fig. 6B). This trend may have been a consequence of the declining success of the invader in communities with more functional groups. Alternatively, diverse communities may have been more likely to harbor plant species that used water at the same time of year as *Centaurea*. I did not have enough data to adequately describe the effect of *Centaurea* on evapotranspiration in the different single-species communities (Fig. 6A). However, these communities can be considered as replicates of a 1-species treatment in which invasion significantly increased LET (by 2.3±0.9 mm day^{-1}, mean±95% confidence interval). This result agrees with those of other researchers studying *Centaurea* invasions on North America's West Coast, who have concluded that the weed has altered the water balance of the region's annual grasslands (Borman et al. 1992; Gerlach 2000). Nutrient capture by resin bags and inorganic N loss via leachate did not differ between invaded and control communities at any diversity level or time of year, with the exception of bare soil communities (determined by calculating the 95% confidence interval for differences between paired communities at each diversity level and date; these confidence intervals encompassed 0 in all cases).

In this study, functional diversity reduced community invasibility by reducing resource availability. However, increased species richness did not reduce invasibility when functional diversity was held constant. Interestingly, while this increased "functional redundancy" (Naeem and Li 1997) did not affect invasibility, it did decrease the impact of the invader on resident species. This result suggests that where species diversity does not affect the invasibility of a community, it may still affect the growth
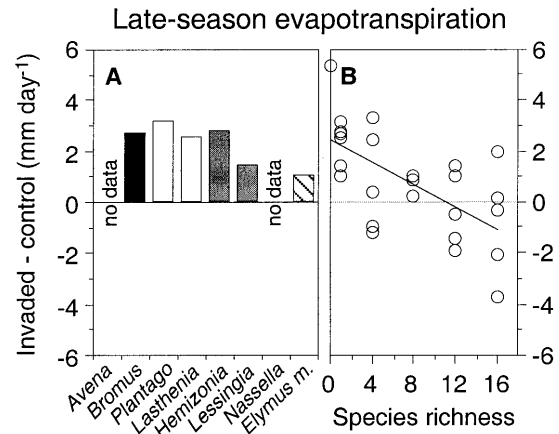

Fig. 6A, B Effect of *Centaurea* on community evapotranspiration from mid-June to late July. To obtain the plotted values, I subtracted late-season evapotranspiration of the control microcosms from late-season evapotranspiration of paired invaded microcosms. Note that in **A**, n=1, and values for *Avena* and *Nassella* are omitted due to faulty measurements. *Regression line* in **B**: y=2461.5–233.8x (r^2=0.40, P<0.001)

and persistence of resident species after invasion. This is the first study to provide evidence that species and functional diversity reduce the impact of biological invaders on resident species and on ecosystem processes such as evapotranspiration. Generalizations about the influence of diversity on the vulnerability of a community to impacts of biological invaders will be more appropriate after this relationship has been studied in other systems and environmental conditions.

Recent experiments have found both positive and negative correlations between the biodiversity and invasibility of plant communities (e.g., Robinson et al. 1995; Knops et al. 1999), but observational studies have consistently suggested that the diversity and abundance of invaders are positively correlated with native plant diversity (Pickard 1984; Planty-Tabacchi et al. 1996; Stohlgren et al. 1998, 1999; Wiser et al. 1998; Lonsdale 1999). Conclusions from this study, other experimental studies, and observational studies may be reconciled as future experiments identify the scales at which interspecific interactions and abiotic factors operate, and distinguish the relative importance of these mechanisms in determining the invasibility of an ecosystem.

References

Armstrong JK (1991) Rainfall variation, life form, and phenology in California serpentine grassland. PhD thesis, Stanford University, Stanford

Balciunas J, Villegas B (1999) Two new seed head flies attack yellow starthistle. Calif Agric 53:8–11

Borman MM, Johnson DE, Krueger WC (1992) Soil moisture extraction by vegetation in a mediterranean/maritime climatic regime. Agron J 84:897–904

Chapin FS, III, Sala OE, Burke IC, Grime JP, Hooper DU, Lauenroth WK, Lombard A, Mooney HA, Mosier AR, Naeem S, Pacala SW, Roy J, Steffen WL, Tilman D (1998) Ecosystem consequences of changing biodiversity. BioScience 48:45–52

Chiariello NR (1989) Phenology of California grasslands. In: Huenneke LF, Mooney HA (eds) Grassland structure and function: California annual grassland. Kluwer, Dordrecht, pp 47–58

Crawley MJ (1987) What makes a community invasible? In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonization, succession and stability. Blackwell, Oxford, pp 429–453

Crawley MJ, Brown SL, Heard MS, Edwards GR (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? Ecol Lett 2:140–148

Elton CS (1958) The ecology of invasions by animals and plants. Chapman and Hall, London

Field CB, Lund CP, Chiariello NR, Mortimer BE (1997) CO_2 effects on the water budget of grassland microcosm communities. Global Change Biol 3:197–206

Gerlach JD Jr (2000) A model experimental system for predicting the invasion success and ecosystem impacts of non-indigenous summer-flowering annual plants in California's Central Valley grasslands and oak woodlands. PhD thesis, University of California, Davis

Gulmon SL, Chiariello NR, Mooney HA, Chu CC (1983) Phenology and resource use in three co-occurring grassland annuals. Oecologia 58:33–42

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze E-D, Siamantziouras A-SD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127

Hickman JC (ed) (1993) The Jepson manual: higher plants of California. University of California Press, Berkeley

Hobbs RJ, Mooney HA (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. Ecology 72:59–68

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121–149

Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293

Lavorel S, Prieur-Richard A-H, Grigulis K (1999) Invasibility and diversity of plant communities: from patterns to processes. Divers Distrib 5:41–49

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

McGrady-Steed J, Harris PM, Morin PJ (1997) Biodiversity regulates ecosystem predictability. Nature 390:162–165

Mooney HA, Hobbs RJ, Gorham J, Williams K (1986) Biomass accumulation and resource utilization in co-occurring grassland annuals. Oecologia 70:555–558

Naeem S, Li S (1997) Biodiversity enhances ecosystem reliability. Nature 390:507–509

Naeem S, Håkansson K, Lawton JH, Crawley MJ, Thompson LJ (1996) Biodiversity and plant productivity in a model assemblage of plant species. Oikos 76:259–264

Palmer MW, Maurer T (1997) Does diversity beget diversity? A case study of crops and weeds. J Veg Sci 8:235–240

Pickard J (1984) Exotic plant distribution on Lord Howe Island: distrubution in space and time, 1853–1981. J Biogeogr 11:181–208

Planty-Tabacchi A-M, Tabacchi E, Naiman RJ, DeFerari C, Décamps H (1996) Invasibility of species-rich communities in riparian zones. Conserv Biol 10:598–607

Rejmánek M (1989) Invasibility of plant communities. In: Drake JA, Mooney HA, Castri F di, Groves RH, Kruger FJ, Rejmánek M and Williamson M (eds) Biological invasions: a global perspective. Wiley, Chichester, pp 369–388

Robinson GR, Quinn JF, Stanton ML (1995) Invasibility of experimental habitat islands in a California winter annual grassland. Ecology 76:786–794

Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286:1577–1579

Stohlgren TJ, Bull KA, Otsuki Y, Villa CA, Lee M (1998) Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecol 138:113–125

Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y (1999) Exotic plant species invade hot spots of native plant diversity. Ecol Monogr 69:25–46

Symstad AJ (2000) A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99–109

Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Wiser SK, Allen RB, Clinton PW, Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. Ecology 79:2071–2081