

SPECIES COMPOSITION AND DIVERSITY AFFECT GRASSLAND SUSCEPTIBILITY AND RESPONSE TO INVASION

JEFFREY S. DUKES¹

Department of Biological Sciences, Stanford University, Stanford, California 94305 USA

Abstract. In a microcosm experiment, I tested how species composition, species richness, and community age affect the susceptibility of grassland communities to invasion by a noxious weed (*Centaurea solstitialis* L.). I also examined how these factors influenced *Centaurea*'s impact on the rest of the plant community.

When grown in monoculture, eight species found in California's grasslands differed widely in their ability to suppress *Centaurea* growth. The most effective competitor in monoculture was *Hemizonia congesta* ssp. *luzulifolia*, which, like *Centaurea*, is a summer-active annual forb. On average, *Centaurea* growth decreased as the species richness of communities increased. However, no polyculture suppressed *Centaurea* growth more than the monoculture of *Hemizonia*. *Centaurea* generally made up a smaller proportion of community biomass in newly created ("new") microcosms than in older ("established") microcosms, largely because *Centaurea*'s competitors were more productive in the new treatment. Measures of complementarity suggest that *Centaurea* partitioned resources with annual grasses in the new microcosms. This resource partitioning may help to explain *Centaurea*'s great success in western North American grasslands.

Centaurea strongly suppressed growth of some species but hardly affected others. Annual grasses were the least affected species in the new monocultures, and perennial grasses were among the least affected species in the established monocultures. In the new microcosms, *Centaurea*'s suppression of competing species marginally abated with increasing species richness. This trend was a consequence of the declining success of *Centaurea* in species-rich communities, rather than a change in the vulnerability of these communities to suppression by a given amount of the invader. The impact of the invader was not related to species richness in the established microcosms. The results of this study suggest that, at the neighborhood level, diversity can limit invasibility and may reduce the impact of an invader.

Key words: biological invasion; *Centaurea solstitialis*; competition; diversity; exotic species; grassland; functional group; invasibility; species richness; relative yield total (RYT); resource partitioning.

INTRODUCTION

Invasive species pose major threats to native species in many of the world's ecosystems (Wilcove et al. 1998, Mack et al. 2000). To a large extent, the impact of an invasive species on a native community depends on whether the invader becomes established and how abundant it becomes (the community's invasibility). But the invader's impact also depends on the community's response to a given amount of the invader (the community's "impactability"). Surprisingly, studies of community invasibility have rarely investigated the vulnerability of communities to impacts of invaders.

In 1958, Elton hypothesized that more diverse communities are less susceptible to invasion, although he did not explicitly describe a mechanism that linked these properties. Since then, several theoreticians have suggested that diverse systems should be difficult to

invade because newly arrived species are more likely to find a competitor that precludes their success (Pimm 1991), or because resource availability in these systems is low (Crawley 1987, Tilman 1999). Indeed, results of recent studies suggest that diverse systems use resources more completely (Tilman et al. 1996, Hooper and Vitousek 1998). Although several theoretical papers and observational studies have addressed Elton's hypothesis (see Levine and D'Antonio [1999] and Prieur-Richard and Lavorel [2000] for reviews), surprisingly few manipulative studies have directly tested it. Results of some experiments support Elton's proposed negative relationship between biodiversity and invasibility (McGrady-Steed et al. 1997, Tilman 1997a, Knops et al. 1999), but other results suggest a positive relationship (Robinson et al. 1995, Palmer and Maurer 1997) or no relationship (Crawley et al. 1999).

While manipulative studies have reached conflicting conclusions, observational studies have primarily reported positive relationships between native species diversity and the diversity and abundance of invaders (e.g., Planty-Tabacchi et al. 1996, Wisser et al. 1998,

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¹ Present address: Department of Plant Biology, Carnegie Institute of Washington, 260 Panama Street, Stanford, California 94305-1297 USA. E-mail: dukes@stanfordalumni.org

Smith and Knapp 1999, Stohlgren et al. 1999). Some studies of this type may have simply recorded correlations between species richness (both native and exotic) and the area of study plots. However, a recent analysis by Lonsdale (1999) of several published data sets factored out the influence of study area and still found a positive relationship between native species diversity and exotic species diversity. This remaining relationship may be the consequence of a correlation between either habitat diversity or propagule pressure (or both) and native species richness. Areas with high habitat diversity and areas that receive a great influx of propagules may be at greater risk of invasion. At the neighborhood scale, competitive relationships among species are likely to determine invasibility. Researchers have yet to describe the relative importance of biotic and abiotic factors in determining invasibility or the scales on which these factors operate. However, some researchers have begun to consider these questions (Smith and Knapp 1999, Stohlgren et al. 1999, Levine 2000).

While the relationship between diversity and invasibility remains a topic of debate, the influence of species and functional group composition on a community's susceptibility to invasion is less controversial. Several studies have demonstrated that certain species or functional types are more successful than others at suppressing a given invader (e.g., Larson and McInnis 1989, D'Antonio 1993, Roché et al. 1994, Ferrell et al. 1998) or many invaders (Crawley et al. 1999, Symstad 2000).

Because species differ in their resistance to invasion, any observed effect of diversity might be a consequence of one or both of two types of mechanisms: (1) properties of diversity driven by the collective characteristics of many resident species ("collective effects," such as niche complementarity), and (2) the increased probability that diverse communities include a species that is a superior competitor with any invading species (often termed a "sampling" or "selection" effect in literature that discusses relationships between biodiversity and other ecosystem functions (Aarssen 1997, Huston 1997, Tilman 1997b, Loreau 2000). Researchers continue to debate the relative importance and validity of these effects as "diversity effects" (van der Heijden et al. 1999, Wardle 1999).

In addition to proposing a relationship between diversity and invasibility, Elton (1958) presented evidence that disturbances can increase community invasibility. In the last few decades, results of further experimental and observational studies have confirmed that some types of disturbance favor invaders, although the mechanisms behind these relationships are rarely examined (D'Antonio et al. 1999). Soil disturbance facilitates invasion in many cases, presumably either by directly increasing resource availability or by killing or injuring plants that compete for resources (Hobbs and Huenneke 1992). In some California grasslands, the burrowing and mound-building activity of gophers

(*Thomomys bottae*) promotes invasion of Eurasian grasses (Hobbs and Mooney 1991).

Before Europeans arrived in California in the late 18th century, perennial grasses probably dominated the state's grasslands (Heady 1988). European explorers and settlers brought seeds of annual grasses and forbs, which eventually replaced the perennial grasses as dominants. Today, *Centaurea solstitialis* (yellow starthistle), a late-flowering annual from the Mediterranean region, is spreading rapidly through California grasslands (Maddox and Mayfield 1985). This noxious weed infests $>8 \times 10^6$ ha in California (Pitcairn et al. 1998), and has spread throughout rangelands in Oregon, Washington, and Idaho (Maddox et al. 1985). Although *Centaurea* is known to decrease the value of rangelands, few researchers have examined its impacts on other species or on ecosystem processes. Furthermore, plant species that successfully compete with *Centaurea* in California rangelands have yet to be identified (Thomson et al. 1996b).

I designed this microcosm experiment to study how species composition, species diversity, and disturbance affect the invasibility of grassland by *Centaurea*, as well as how *Centaurea* invasion affects productivity of the other species and of the community as a whole. I planted monocultures to study competition between *Centaurea* and species from four different functional groups. I planted polycultures that differed in species richness, but not functional group richness, to determine how species diversity affects the invasibility and response to invasion of newly constructed and one-year-old grassland communities.

METHODS

Study site and infrastructure

This experiment took place on a small hilltop in the Jasper Ridge Biological Preserve (JRBP; near Palo Alto, California, USA: 37°24' N, 122°14' W, 120 m elevation), during the 1997–1998 growing season. Grassland microcosms were contained in upright sections of polyvinyl chloride (PVC) pipe (0.95 × 0.2 m [length × diameter]) that were fitted with a PVC cap at the bottom. A polyester wick directed water at the bottom of the microcosms out a 12 mm diameter drainage hole in the cap. Each pipe section was filled to 1 cm from the top with a 1:3 mixture of sand to pulverized local soil (Francisquito series: fine, mixed, thermic Typic Haploxeralf). Topsoil from JRBP grasslands was used in substrate that filled the top 30 cm of each microcosm, and subsoil from these grasslands was used in the lower portion of each soil column. The sand was added to moderate initial nutrient availability, which I expected to be artificially high following soil pulverization. The top ~10 cm of substrate in each microcosm had been wetted and heated (80°C for 48 h) to kill weed seeds. All microcosms were kept outdoors in a large metal frame storage box, where they received ambient

TABLE 1. Species and seeding densities.

Species†	Native?	Species code‡	Seeding density (no. seeds/m ²)
<i>Avena barbata</i>	no	A1	1847
<i>Bromus hordeaceus</i>	no	A2	2197
<i>Vulpia microstachys</i>	yes	A3	2548
<i>Lolium multiflorum</i>	no	A4	1019
<i>Plantago erecta</i>	yes	E1	8057
<i>Lasthenia californica</i>	yes	E2	7643
<i>Erodium botrys</i>	no	E3	2547
<i>Microseris douglasii</i>	yes	E4	6115
<i>Hemizonia congesta</i> spp. <i>luzulifolia</i>	yes	L1	1847
<i>Lessingia hololeuca</i>	yes	L2	2962
<i>Calycadenia multiglandulosa</i>	yes	L3	5096
<i>Epilobium brachycarpum</i>	yes	L4	3567
<i>Nassella pulchra</i>	yes	P1	5701 (1911)§
<i>Elymus multisetus</i>	yes	P2	3057 (1019)§
<i>Festuca pratensis</i>	no	P3	4076
<i>Elymus glaucus</i> ssp. <i>glaucus</i>	yes	P4	4076

† Nomenclature follows Hickman (1993).

‡ The first letter of the species code represents the functional-group classification of the species: A, annual grass; E, early-season annual forb; L, late-season annual forb; P, perennial grass.

§ Values in parentheses indicate the density of seeds sown in established treatments, where different from new treatments. Differences in germination and establishment rates among these species led to differences in final plant density.

precipitation (a total of 1306 mm in the 1997–1998 season, well above the region's 667 mm annual average; see Dukes [2001b] for additional rainfall data).

Experimental design

I built 0-, 1-, 4-, 8-, and 16-species microcosms from a pool of native and naturalized plant species found in grasslands at JRBP. This species pool contained four species from each of four functional groups: annual grasses, perennial grasses, early-season forbs, and late-season forbs (Table 1). 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, become senescent aboveground in June or July. Early-season annual forbs generally die in April or May, and late-season annual forbs continue growing through the summer, finally setting seed and dying between August and 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 constructed ten replicates of each of 13 different community types for the 1996–1997 growing season. The community types included one bare soil (zero-species) treatment, eight different monocultures, two different 4-species communities (which I termed “community 1” and “community 2”), one 8-species, and one 16-species community. All polycultures com-

prised an equal number of species from each functional group. I employed a nested design, such that the 8-species community consisted of all the species in the two 4-species communities, and these eight “core” species were also grown in monoculture (Fig. 1). During the 1996–1997 season, I collected all seeds as they ripened. Because these microcosms were one year old at the beginning of this experiment, they are termed “established” microcosms in this paper. Established microcosms were sown again in the autumn of 1997 for the beginning of this experiment. At the same time, I constructed 10 new replicates of each community type (“new” microcosms) for the 1997–1998 growing season.

Half (five) of the replicates of each age and community type were designated “invaded” microcosms. These microcosms received seeds of the invasive late-season annual forb *Centaurea solstitialis*. Microcosms were arranged in a block design, with one replicate of each treatment arranged randomly in each block. Microcosms from a related experiment were also included in each block.

Seeding density and community containment

In monocultures, seeds were sown at densities estimated to be higher than necessary to maximize aboveground biomass production and to ensure 100% cover (based on density and size per individual of plants in surrounding grassland; Table 1). In polycultures, seeding densities of “resident” species (species other than *Centaurea*) were reduced according to the number of species in the community (e.g., for a 4-species community, a given species would be sown at one-quarter

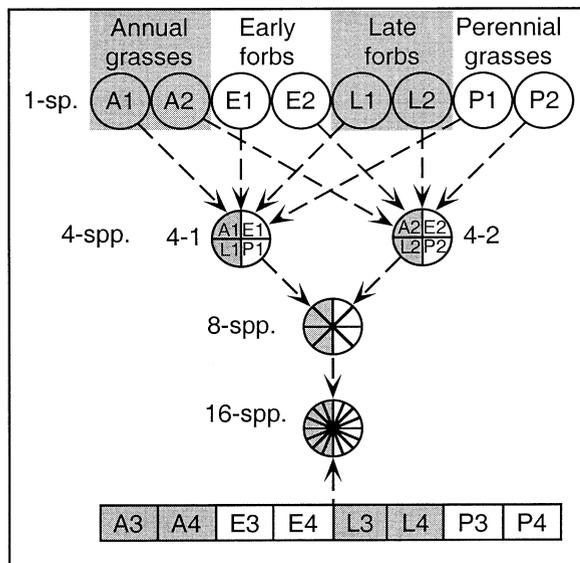


FIG. 1. Illustration of the basic experimental design. This design was used to create control communities in the new and established treatments. Each circle represents one community type. The number of sections in each circle corresponds to the number of species in that community. Arrows identify which species were used in each polyculture. Species codes are explained in Table 1. The eight species shown at the bottom were only used in the 16-species communities. Labels identify the two 4-species community types, 4-1 and 4-2. Each of the control community types shown (and a bare soil, or zero-species community, not shown) was paired with an invaded community type, which received seeds of *Centaurea* but was otherwise identical to the control. Five replicate microcosms were created of each invaded and control community type.

its density in monoculture). To compensate for survival of approximately one-third of the previous year's perennial grass seedlings, established microcosms received fewer perennial grass seeds than the new microcosms (Table 1). Litter from the 1996–1997 growing season was returned to the surface of established microcosms after seeds for the 1997–1998 season were sown. Invaded microcosms were identical to control microcosms in the composition and seeding density of resident species. All invaded microcosms received 25 plumed *Centaurea* achenes at the start of the experiment. After the seeds began to germinate, all microcosms were checked for weeds frequently and weeded as necessary. Seedlings of *Centaurea* were thinned to four evenly spaced individuals in early December of 1997, and to three individuals on 18 February 1998.

Vertically oriented cylinders made of aluminum window screening encircled each microcosm. Screens around new microcosms were raised to ~6 cm above the rims on 7 May 1998 to prevent plants in adjacent microcosms from becoming entangled. On the established microcosms, screens were raised to 6 cm from the start of the growing season to contain the previous

year's litter and to simulate shading by neighboring litter. Screens reduced the intensity of perpendicularly incoming direct radiation by 26% (LI-250, Li-Cor, Lincoln, Nebraska, USA).

The established and new microcosms were created to approximate different microenvironments in California grasslands. New communities resembled gopher-disturbed patches (which comprise an average of 26% of a nearby grassland; Hobbs and Mooney 1991), and established communities resembled undisturbed patches of grassland, where a litter layer shades seedlings, the soil column is more developed, and perennial grasses, which resprout from mature root systems, grow much larger. Soil in established microcosms had settled prior to the start of this experiment, creating more compacted soil columns.

Harvests

Reproductive biomass of all species was harvested as it ripened, to prevent the escape of seeds and associated flower parts. Nonreproductive aboveground biomass of *Centaurea* was harvested immediately after senescence of each individual until the beginning of the general harvest. In the general harvest, nonreproductive aboveground biomass of all remaining species was cut, one block at a time, after senescence of the majority of late-season forb individuals. The general harvest took place 19 August–15 September 1998. All plant material was sorted by species as it was harvested. Biomass was dried at 65°C for 48 h and weighed.

Herbivores damaged *Centaurea* seed heads in several microcosms just prior to harvest, and microcosms with extensive damage were excluded from all analyses of *Centaurea* reproductive biomass.

Measure of diversity

To assess the species and functional diversity of the different control treatments, I calculated effective species richness ($e^{H'}$), where

$$H' = -\sum p_i \ln p_i \quad (1)$$

and p_i is the proportion of total aboveground biomass made up by species i (or functional group i) at the final harvest. Effective species richness measures the number of equally abundant species necessary to obtain a given H' .

Measures of invasibility

According to Crawley (1987:429), “a community is invasible when an introduced species is able to increase when rare.” In this study, I did not define invasibility based on changes in the population size of *Centaurea*. Instead, I defined invasibility based on the competitive effects that other species had on *Centaurea*'s aboveground and reproductive biomass. In annuals like *Centaurea*, these traits are strongly correlated, and are important predictors of the potential for population increase in a field setting.

Measures of complementarity

In testing for complementarity, I analyzed this experiment as an additive design in which invaded microcosms comprised two components. Resident species were collectively treated as one component, and *Centaurea* was treated as the other component of the mixtures. Each component of the invaded microcosms was also grown in isolation (*Centaurea* grew alone in the invaded zero-species microcosms). By segregating the invaded microcosms into two components, I could use standard complementarity measures to determine which community types might have partitioned resources with *Centaurea*. I calculated relative yield totals (RYT; Harper 1977) and D_T (the proportional deviation of a mixture from its expected yield; Wardle et al. 1997, Loreau 1998) to estimate the degree of complementary resource use occurring between *Centaurea* and resident species in the invaded microcosms. Relative yields (RY) and relative yield totals were calculated using the following equations:

$$RY_{ijk} = Y_{ijk}/Y_{ik} \quad (2)$$

$$RYT_{jk} = \sum_{i=1}^2 RY_{ijk} \quad (3)$$

$$RYT_j = \text{mean}(RYT_{jk}). \quad (4)$$

For these equations, RY_{ijk} is the relative yield of component i in treatment j in block k , Y_{ijk} is the yield (above-ground biomass production) of component i in treatment j in block k , Y_{ik} is the yield of component i grown alone in block k , and RYT_{jk} is the relative yield total of treatment j in block k . I calculated D_T for the mixtures, where D_{Tj} is the value of D_T for treatment j , as follows:

$$D_{Tj} = \text{mean}(D_{Tjk}) \quad (5)$$

and

$$D_{Tjk} = \sum_{i=1}^2 (O_{ijk} - E_{ijk})/E_{ijk} \quad (6)$$

where the observed productivity, O_{ijk} is the yield of component i in treatment j in block k and the expected productivity, E_{ijk} is half of the yield of component i grown in isolation in block k ($Y_{ik}/2$).

Relative yields quantify the success of the components in a mixture relative to their success when grown in isolation. If the RY of one component of a mixture is >0.5 , then that component competes more successfully with the other component of the mixture than with itself. If a component's RY = 0.5, then it competes equally well with the other component as with itself. Relative yields <0.5 indicate that performance of the component is limited more by competition with the other component of the mixture than by competition with itself.

Relative yield totals less than one and $D_T > 0$ suggest

complementary resource use, i.e., resource partitioning among components of a mixture (but can also indicate facilitation among the components). However, overyielding (i.e., when the mixture is more productive than its most productive component) is a more stringent test for complementarity and/or positive interactions.

Measures of an invader's impact

Invasion biologists often study the susceptibility of a community to invasion (community invasibility), but less often examine the impact of the invader on that community. Less often still are the responses of different communities to a single invader compared. Impact can be measured in absolute terms (change in grams per square meter of biomass production of resident species, for instance) or in relative terms (e.g., percentage change in biomass production of resident species). Either of these measures of impact can be disentangled from invasibility by relating them to the growth of the invader. I refer to these disentangled values as "per unit invader." In this paper I calculated relative impact per unit invader (RIP) as the percentage change in biomass production of resident species divided by invader biomass. Here, I term the community property measured by RIP "impactibility."

Statistical analysis of the diversity-invasibility relationship

Because several of the data sets that I consider here have decreasing variance with increasing diversity, and because transformations of these data sets do not eliminate this characteristic, I did not use linear regression to test for significant effects of diversity. Instead, using only the mean values of each community type, I determined whether the regression slope of a given set of data was more positive than would be expected if the y -values in the data set were assigned randomly to the set of x -values (i.e., the species richness levels). To accomplish this, I randomly assigned a y -value from the data set to each x -value, recorded the regression slope of this random arrangement, and repeated the process until I had generated 999 random slopes based on the data. I then added the actual slope to this pool of random slopes. I counted the number of slopes equal to or greater than the actual slope (equal to or less than the actual slope in cases where the actual slope was less than the median slope), and multiplied this value by two to account for a two-tailed distribution. I divided this number by 1000 to arrive at a value of P that estimated the likelihood that the observed relationship between species richness and the y -value arose by chance (for a discussion of similar statistical techniques see Manly [1997]).

RESULTS

Properties of the control microcosms

The species richness treatments produced the intended species diversity and functional diversity gra-

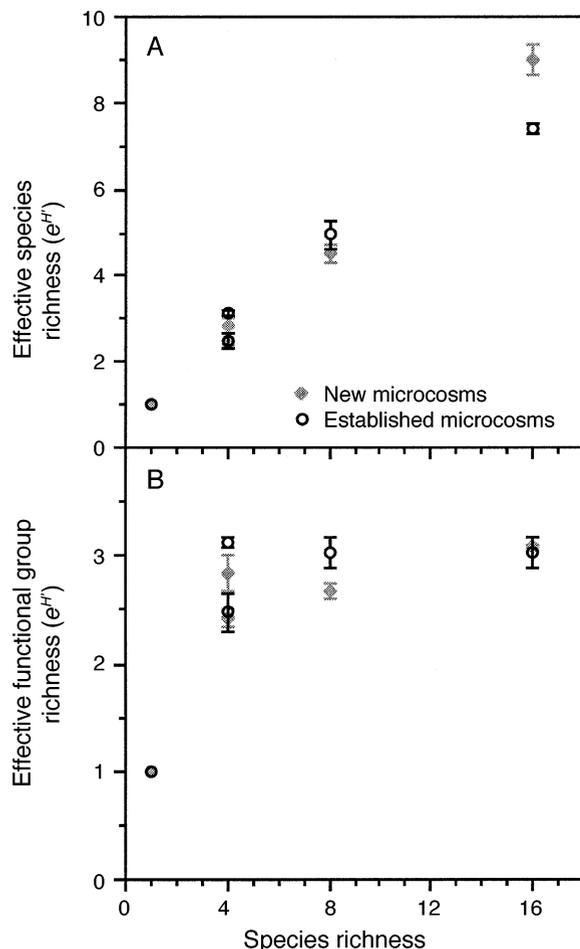


FIG. 2. Mean (± 1 SE, $n = 5$) effective richness plotted against species richness for the control communities: (A) species richness, and (B) functional group richness. In all monocultures, a single species made up 100% of aboveground biomass. Thus there was no variation in effective richness values where species richness was unity.

dients in this study (Fig. 2). Species diversity increased linearly with increasing species richness (Fig. 2A). Functional diversity increased as species richness increased from one to four species, but remained constant as species richness increased from four to 16 species (Fig. 2B). In the new polycultures, annual grasses generally contributed the greatest proportion of total biomass (Fig. 3A). In the established polycultures, late-season annual forbs and perennial grasses were the most productive functional groups (Fig. 3B).

Measures of invasibility

Biomass production of *Centaurea* varied by community type and by microcosm age, and in several cases the effect of community type depended on microcosm age (two-way ANOVA; community type effect, $F_{11,95} = 26.3$, $P = 0.0001$; microcosm age effect, $F_{1,95} = 29.6$, $P = 0.0001$; interaction, $F_{11,95} = 11.9$, $P =$

0.0001). Of the new monocultures, the two perennial grasses were the most invasible, and the late-season annual forb *Hemizonia congesta* was the least invasible (Fig. 4). Results from the established monocultures were less clear-cut, but *Hemizonia* was again among the least invasible communities, along with the other late-season forb *Lessingia hololeuca* and the perennial grass *Nassella pulchra*. Of the new 4-species communities, community 1, which contained *Hemizonia*, was less invasible than community 2, which did not. The trend reversed in the established treatment, although this difference was not significant (Fig. 4).

Reproductive biomass production of *Centaurea* was closely related to aboveground biomass (Figs. 4 and 5). Reproductive mass made up $\sim 13\%$ of *Centaurea*'s aboveground biomass in new communities, and 22% in established communities (Fig. 5). *Centaurea* allocated significantly more of its aboveground biomass to reproduction in the established communities (slopes differed; ANCOVA, microcosm age by aboveground biomass interaction, $F_{1,108} = 14.8$, $P = 0.0002$). Reproductive mass varied with the invaded community, and with the age of the different community types (two-way ANOVA; community type effect, $F_{11,70} = 22.1$, $P = 0.0001$, microcosm age effect: $F_{1,70} = 2.4$, $P = 0.13$, interaction: $F_{11,70} = 3.6$, $P = 0.0005$; Fig. 4).

Microcosm age affected *Centaurea* growth, and the proportional contribution of *Centaurea* to community biomass. Aboveground biomass production of *Centaurea* was greater in new communities than in established communities in three cases (the two perennial grass monocultures and 4-species community 2; Fig. 6A), and did not differ significantly in the other nine. In contrast, resident species generally produced less biomass in established communities than in new communities (cf. Fig. 3). For this reason, in six of the community types *Centaurea* made up a significantly greater proportion of total aboveground biomass in the established treatment (Fig. 6B). The reverse was true only in monocultures of *Nassella pulchra* and *Elymus multisetus*, which competed better with *Centaurea* as established bunchgrasses than as seedlings (Fig. 6B). The proportional contribution of *Centaurea* increased with microcosm age in the annual grass and early-season forb monocultures, 4-species community 1, and the 16-species community.

In both the new and established treatments, *Centaurea* growth was a decreasing, asymptotic function of species richness (Fig. 4). A substantial decrease in *Centaurea* growth occurred as species richness increased from zero to four species, the region in which species and functional group richness increased simultaneously. Species richness within functional groups did not affect *Centaurea* growth (randomization analysis of 4-, 8-, 16-species communities: new treatment, $P = 0.33$; established treatment, $P = 0.64$).

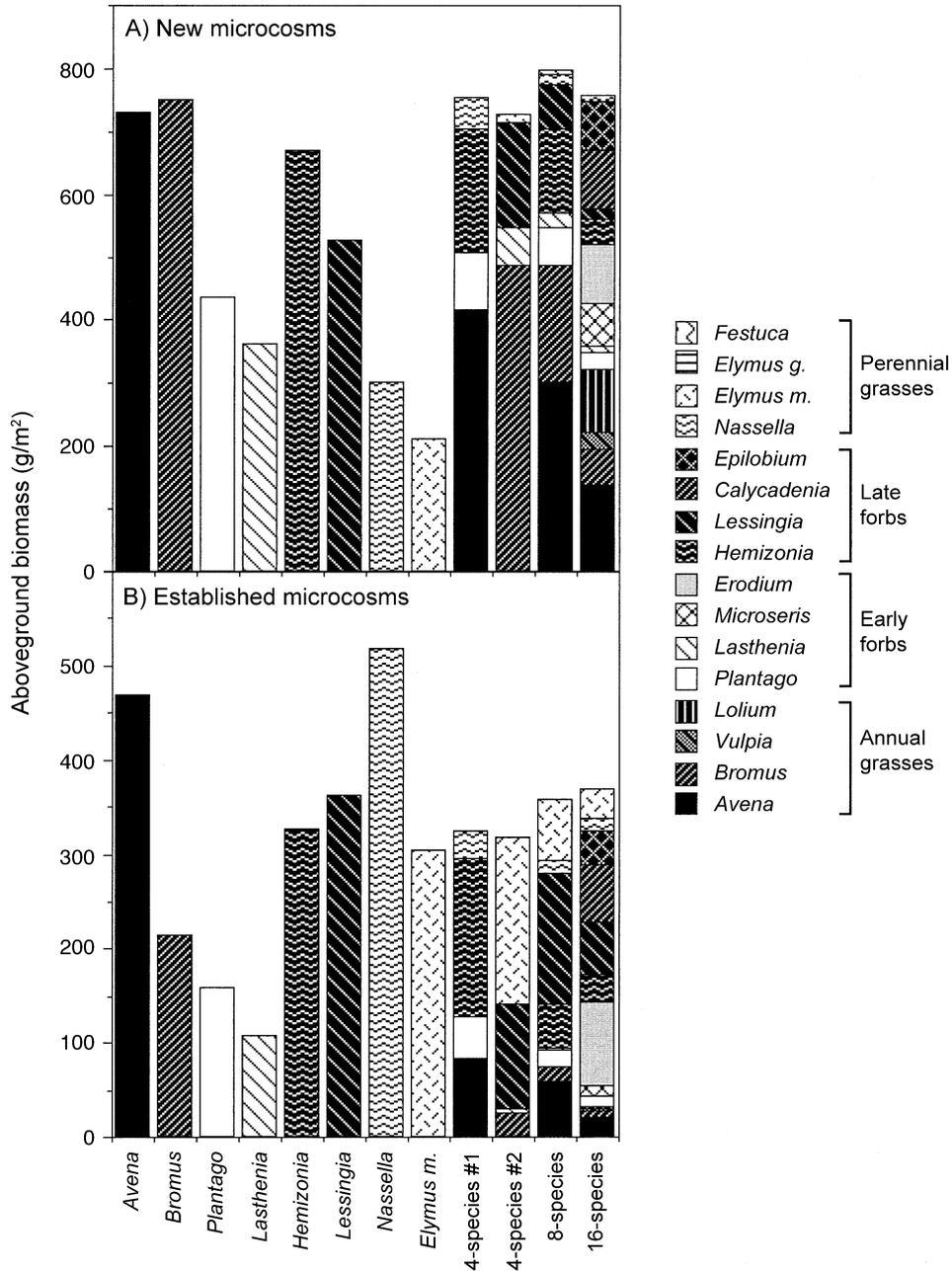


FIG. 3. Mean ($n = 5$) biomass of the control community types, by species: (A) new microcosms, and (B) established microcosms.

Measures of complementarity

Relative yield totals (RYT) were significantly greater than unity for invaded annual grass monocultures in both new and established treatments (Table 2). D_T was greater than zero in these communities, although D_T for the established *Avena* treatment was not significantly positive (Table 2). The RYT of established *Elymus multisetus* monocultures was significantly greater

than unity, but D_T was not significantly greater than zero. D_T of *Plantago erecta* monocultures was significantly greater than zero, but the RYT was not significantly greater than one. Only two invaded communities significantly “overyielded,” or outproduced both their control community and the *Centaurea* monoculture. These were the invaded annual grass monocultures in the new treatment (Fig. 7).

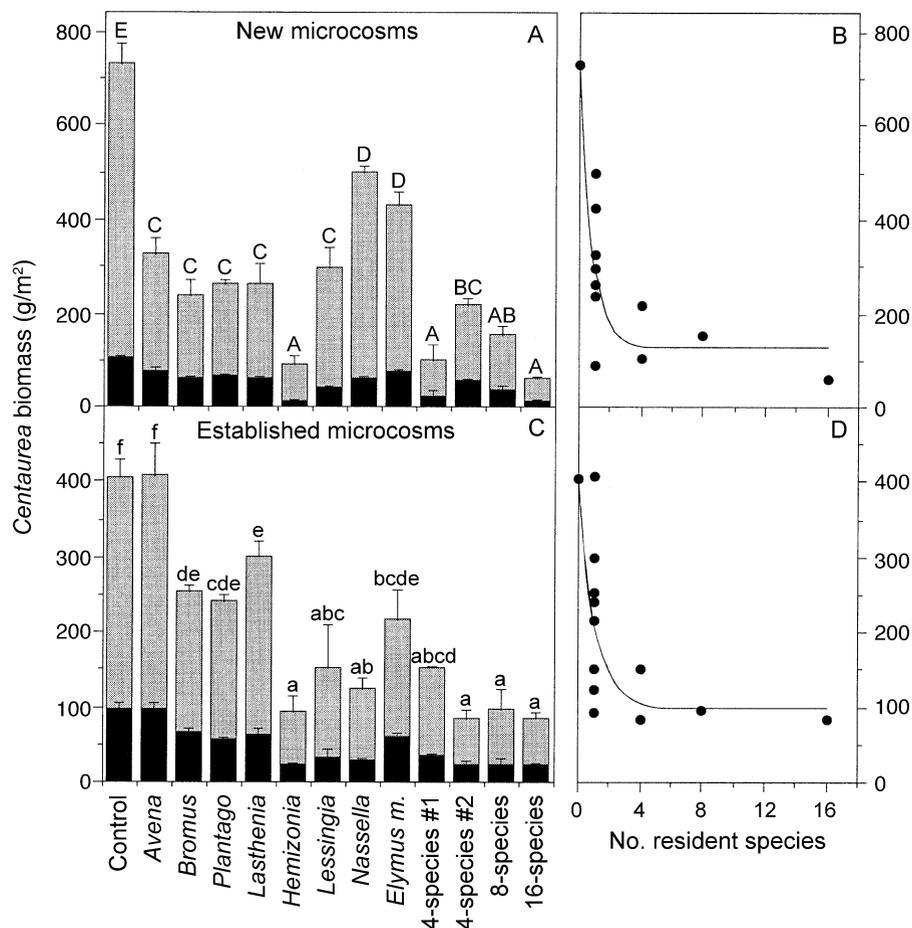


FIG. 4. Panels (A) and (C) show invasibility of the (A) new and (C) established community types, as measured by total aboveground biomass (top of columns, mean \pm 1 SE, $n = 5$) and reproductive biomass (top of black sections, mean \pm 1 SE, $n = 3-5$) of *Centaurea*. Columns that do not share a common letter differ significantly in total aboveground biomass (one-way ANOVA: new microcosms, $F_{12,52} = 38.1$, $P = 0.0001$; established microcosms, $F_{12,51} = 19.7$, $P = 0.0001$, followed by Student-Newman-Keuls post hoc test, $\alpha = 0.05$). Panels (B) and (D) show mean aboveground biomass production of *Centaurea* in (B) new and (D) established microcosms plotted against the species richness of invaded communities. Curves are best fits of the exponential function $y = a + (bc^{dx})$ to the means of each community type. These decreasing, asymptotic curves fit the data better than linear relationships or simple exponential functions: (B) $y = 128.5 + (599.1)(2.4^{-1.45x})$, $r^2 = 0.71$; (D) $y = 98.2 + (304.8)(9.1^{-0.4x})$, $r^2 = 0.53$). Randomization analysis of regression slopes confirmed that the means decreased significantly with increasing species richness in both new (slope = -17.4 , $P = 0.008$) and established (slope = -11.0 , $P = 0.016$) microcosms.

Effect of *Centaurea* on productivity

Although *Centaurea* invasion increased total biomass production (resident species plus *Centaurea*) of several monocultures, invasion did not affect total biomass of polycultures or monocultures of late-season annual forbs (Fig. 7). Competition with *Centaurea* significantly decreased production of resident species in several communities (Fig. 8). A surprising trend emerged in the new microcosms, where, on average, *Centaurea* depressed resident species growth more in simple communities than in diverse communities (Fig. 8A). This trend was not evident in the established microcosms (Fig. 8B).

These trends differ strikingly when one considers the per unit invader impact of *Centaurea* on resident spe-

cies. In the new microcosms, the relative impact per unit invader (RIP) of *Centaurea* on resident species biomass did not differ among community types (ANOVA, $F_{11,47} = 1.06$, $P = 0.42$; Fig. 9A), and there was no trend with increasing species richness (randomization analysis: $P = 0.242$). However, in the established treatment, the RIP of *Centaurea* differed among community types (ANOVA, $F_{11,47} = 2.88$, $P = 0.006$; Fig. 9B) and became increasingly negative with increasing species richness (randomization analysis, $P = 0.016$).

Individual species responses to *Centaurea* invasion varied by microcosm age, by diversity level, and by species (Table 3). Species responses across diversity levels were idiosyncratic. For instance, in new com-

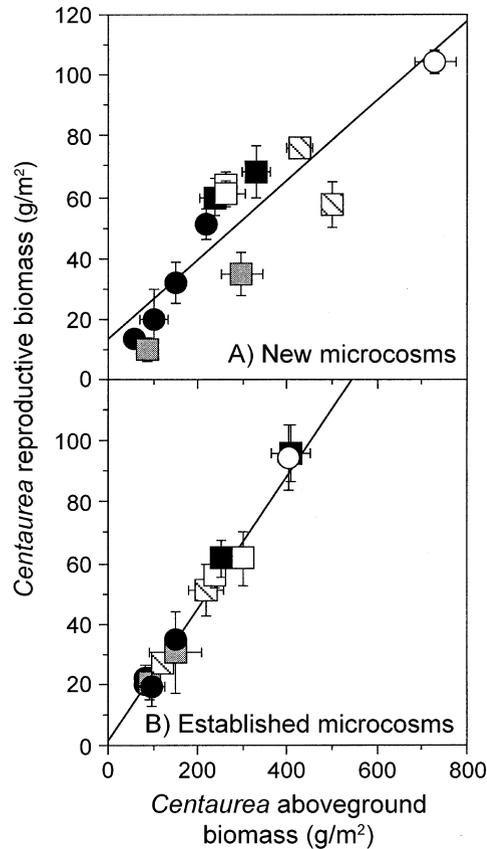


FIG. 5. Relationships between reproductive and aboveground biomass of *Centaurea* in (A) new and (B) established microcosms. Regression lines: (A) $y = 13.54 + 0.13x$; $r^2 = 0.72$, $P < 0.0001$; (B) $y = 1.25 + 0.22x$; $r^2 = 0.93$, $P < 0.0001$. Each symbol identifies mean values (± 1 SE, $n = 3-5$) of one community type. Key to symbols: open circles, bare plots; filled circles, polycultures; open squares, early-season annual forb monocultures; gray squares, late-season annual forb monocultures; black squares, annual grass monocultures; striped squares, perennial grass monocultures.

munities, the annual grass *Bromus* was unaffected by the invader at low diversity levels, and more positively affected as diversity increased (Tables 3 and 4). In contrast, early-season annual forbs were generally negatively affected by invasion, and the magnitude of their response did not change with increasing diversity (Tables 3 and 4). In the newly constructed microcosms, responses of the eight core species were significantly less negative in 16-species communities than in communities with fewer species (two-way ANOVA of transformed data ($\ln[\text{proportional decrease} + 1]$); species effect, $F_{7,116} = 4.3$, $P = 0.0003$; species richness effect, $F_{3,116} = 4.8$, $P = 0.0035$; species \times species richness effect, $F_{21,116} = 1.4$, $P = 0.13$; followed by Student-Newman-Keuls test, $\alpha = 0.05$).

Responses of most species to *Centaurea* did not vary consistently across diversity levels in the established mi-

crocosms (Table 4). However, *Bromus* and both species of perennial grasses responded more positively as community species richness increased in the new microcosms (Tables 3 and 4). A similar trend was evident for *Avena* in the established microcosms (Tables 3 and 4).

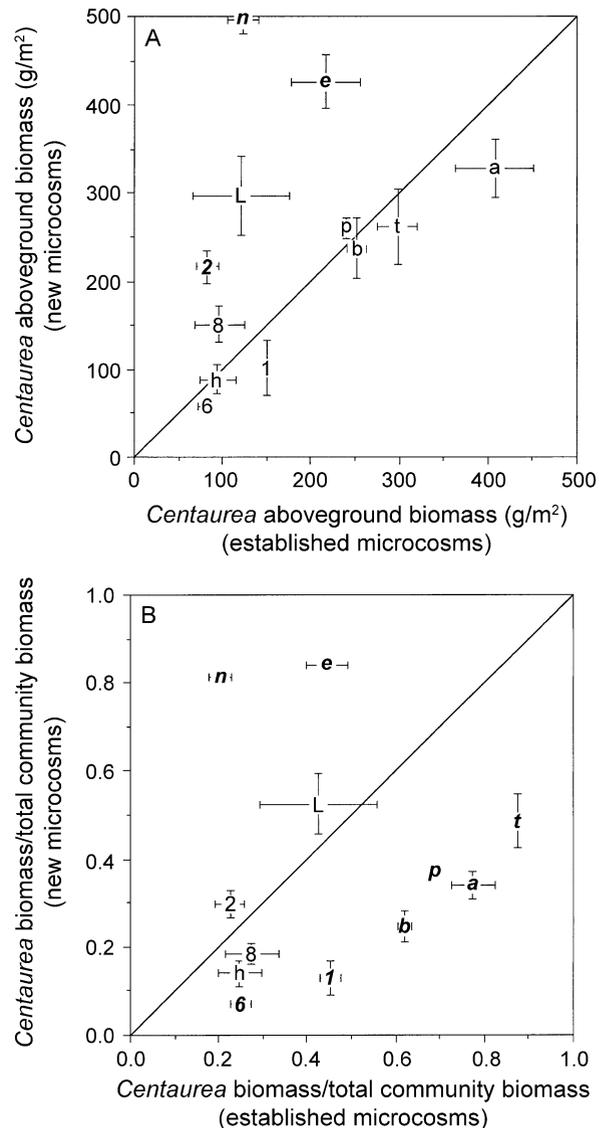


FIG. 6. (A) Absolute and (B) relative invasion success (measured as aboveground biomass production, mean ± 1 SE, $n = 5$) of *Centaurea* in new vs. established microcosms. The 1:1 line is drawn for reference. Key to symbols (letters represent monocultures; numbers represent mixed-species communities): a, *Avena*; b, *Bromus*; e, *Elymus multisetus*; h, *Hemizonia*; L, *Lessingia*; n, *Nassella*; p, *Plantago*; t, *Lasthenia*; 1, 4-species mixture in community 1; 2, 4-species mixture in community 2; 6, 16-species community; 8, 8-species community. Standard error bars are shown where standard errors are (A) > 10 or (B) > 0.02 . Italic bold characters indicate that *Centaurea* growth was significantly different ($\alpha = 0.05$) in the new vs. established microcosms, as measured by t tests followed by sequential Bonferroni correction of P values.

TABLE 2. Mean (± 1 SE, $n = 5$) relative yields (RY), relative yield totals (RYT), and proportional deviation of a mixture from its expected yield (D_T) for the invaded communities.

Community type	RY		RYT \dagger	D_T \dagger
	Community	<i>Centaurea</i>		
New microcosms				
<i>Avena</i>	0.89 \pm 0.10	0.45 \pm 0.02	1.34 \pm 0.08**	0.33 \pm 0.08**
<i>Bromus</i>	0.98 \pm 0.06	0.33 \pm 0.06	1.31 \pm 0.03**	0.31 \pm 0.02**
<i>Plantago</i>	0.79 \pm 0.06	0.36 \pm 0.01	1.15 \pm 0.06	0.07 \pm 0.06
<i>Lasthenia</i>	0.76 \pm 0.10	0.37 \pm 0.07	1.13 \pm 0.11	0.00 \pm 0.11
<i>Hemizonia</i>	0.85 \pm 0.08	0.13 \pm 0.03	0.98 \pm 0.06	-0.07 \pm 0.04
<i>Lessingia</i>	0.53 \pm 0.09	0.42 \pm 0.08	0.95 \pm 0.07	-0.09 \pm 0.07
<i>Nassella</i>	0.38 \pm 0.02	0.70 \pm 0.06	1.07 \pm 0.06	0.20 \pm 0.08
<i>Elymus m.</i>	0.39 \pm 0.04	0.59 \pm 0.03	0.98 \pm 0.05	0.08 \pm 0.05
4-species #1	0.87 \pm 0.06	0.14 \pm 0.05	1.02 \pm 0.06	0.04 \pm 0.07
4-species #2	0.73 \pm 0.12	0.31 \pm 0.04	1.04 \pm 0.09	0.01 \pm 0.06
8-species	0.83 \pm 0.06	0.21 \pm 0.03	1.04 \pm 0.05	0.07 \pm 0.05
16-species	1.01 \pm 0.06	0.08 \pm 0.01	1.09 \pm 0.06	0.13 \pm 0.05
Established microcosms				
<i>Avena</i>	0.25 \pm 0.04	1.01 \pm 0.09	1.26 \pm 0.08*	0.22 \pm 0.10
<i>Bromus</i>	0.72 \pm 0.03	0.63 \pm 0.02	1.34 \pm 0.04**	0.32 \pm 0.04**
<i>Plantago</i>	0.63 \pm 0.08	0.60 \pm 0.04	1.24 \pm 0.09	0.21 \pm 0.07*
<i>Lasthenia</i>	0.44 \pm 0.10	0.76 \pm 0.10	1.20 \pm 0.15	0.36 \pm 0.16
<i>Hemizonia</i>	0.88 \pm 0.08	0.24 \pm 0.06	1.12 \pm 0.09	0.04 \pm 0.08
<i>Lessingia</i>	0.49 \pm 0.10	0.40 \pm 0.18	0.89 \pm 0.09	-0.13 \pm 0.10
<i>Nassella</i>	0.95 \pm 0.11	0.31 \pm 0.05	1.26 \pm 0.12	0.32 \pm 0.13
<i>Elymus m.</i>	0.86 \pm 0.06	0.55 \pm 0.12	1.41 \pm 0.14*	0.35 \pm 0.16
4-species #1	0.58 \pm 0.07	0.38 \pm 0.03	0.96 \pm 0.06	-0.07 \pm 0.05
4-species #2	0.90 \pm 0.02	0.20 \pm 0.03	1.10 \pm 0.04	0.02 \pm 0.03
8-species	0.70 \pm 0.11	0.23 \pm 0.06	0.93 \pm 0.10	-0.12 \pm 0.05
16-species	0.69 \pm 0.07	0.21 \pm 0.02	0.90 \pm 0.07	-0.13 \pm 0.05

* $P < 0.05$; ** $P < 0.01$. \dagger Relative yield totals significantly different from unity and D_T values significantly greater than zero were determined using confidence intervals and were corrected using the sequential Bonferroni technique.

DISCUSSION

In this study, the late-season annual *Hemizonia congesta* suppressed the growth of *Centaurea* most effectively. Contrary to my expectations, communities in new microcosms (which grew on soil more recently disturbed) were less dominated by *Centaurea* than communities in established microcosms, because resident species were generally more productive in the new treatment. Facilitation or resource partitioning occurred between annual grasses and *Centaurea*; this observation suggests that the weed may have increased the productivity of California's annual grasslands. Results from this experiment suggest that functional diversity can limit the success of an invader, but the number of species per functional group is relatively unimportant. The observed diversity effect may result from the greater likelihood that the most competitive functional groups and/or species are included in more diverse communities. In new microcosms, diversity reduced the impact of *Centaurea* on competing species, largely by limiting growth of the invader. If this proves to be a widely observed effect of diversity, then declines in biodiversity may increase both community invasibility and the potential impact of invaders on a community.

Invasibility

In this experiment, the great variability in *Centaurea*'s success in the monocultures provides evidence that species composition strongly influences community invasibility. Indeed, community composition may have driven the observed negative relationship between diversity and invasibility. In all cases, the invasibility of a functionally diverse community equaled that of the least invulnerable monoculture of its component species. This suggests a probabilistic effect of biodiversity, such that communities with higher levels of diversity have a greater chance of containing a species that somehow limits the invader's growth. In this study, the *Hemizonia* monoculture was least invulnerable, and *Hemizonia* may have played an important role in limiting *Centaurea* growth in some of the polycultures. However, there were fewer *Hemizonia* individuals in these polycultures than in the monocultures, and these individuals contributed only a fraction of the resident community's biomass (Fig. 3). This leaves two possible explanations for the observed pattern. Either small amounts of *Hemizonia* are as effective as large amounts at suppressing *Centaurea* growth, or species other than *Hemizonia* are also involved in suppressing *Centaurea* growth in the communities. Because I constructed only

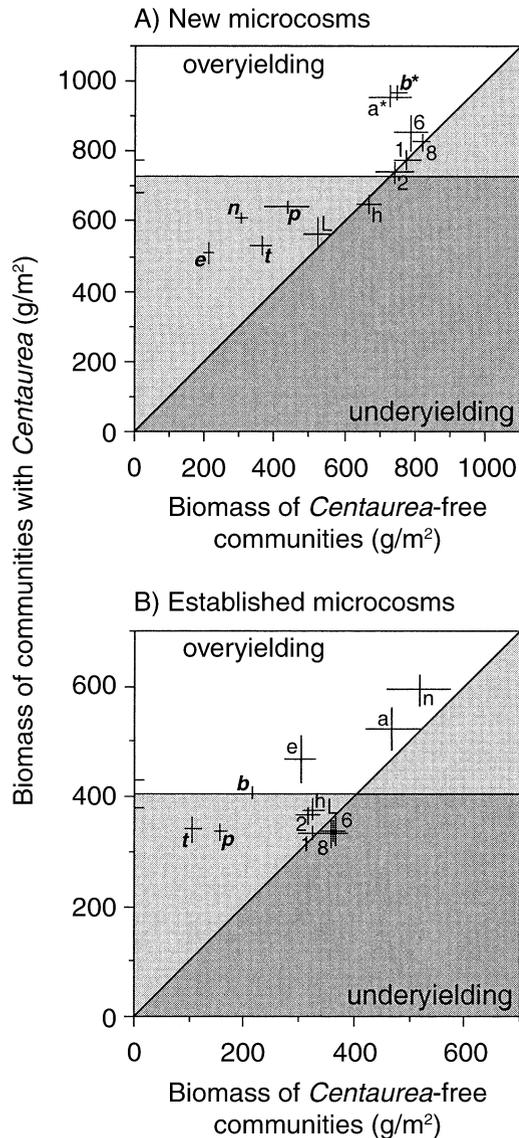


FIG. 7. Total aboveground biomass production (mean \pm 1 SE, $n = 5$) of invaded vs. control communities in (A) new and (B) established microcosms. Characters are as defined in Fig. 6. Horizontal lines indicate mean aboveground biomass production of *Centaurea* monocultures (standard errors are marked by ticks on the inside of the y-axis). Diagonal lines are 1:1 lines. Community types that fall within the white zones on the graphs outproduced microcosms of their components. Communities that fall within the dark gray zones were less productive than microcosms of their components. Communities that fall within the light gray zones outproduced one of their components. Italic bold characters indicate that *Centaurea* significantly altered community productivity ($\alpha = 0.05$, t tests followed by sequential Bonferroni correction). Asterisks indicate significant overyielding ($\alpha = 0.05$, Bonferroni-corrected t tests). *Centaurea* marginally increased productivity of the new *Avena* monoculture ($P < 0.10$).

one community type at the eight- and 16-species levels (and each of these species-rich communities contained *Hemizonia*), the diversity effect observed in this experiment cannot be definitively categorized as a collective or a selection effect. However, it is clear that removing species from the 16-species community can, depending on the identity of the species removed, either steadily increase the invasibility of the community, or have no effect whatsoever on *Centaurea*'s success.

A related study that examined resource availability in newly constructed microcosms found a positive correlation between late-season water availability and *Centaurea* growth (Dukes 2001a). If summer water

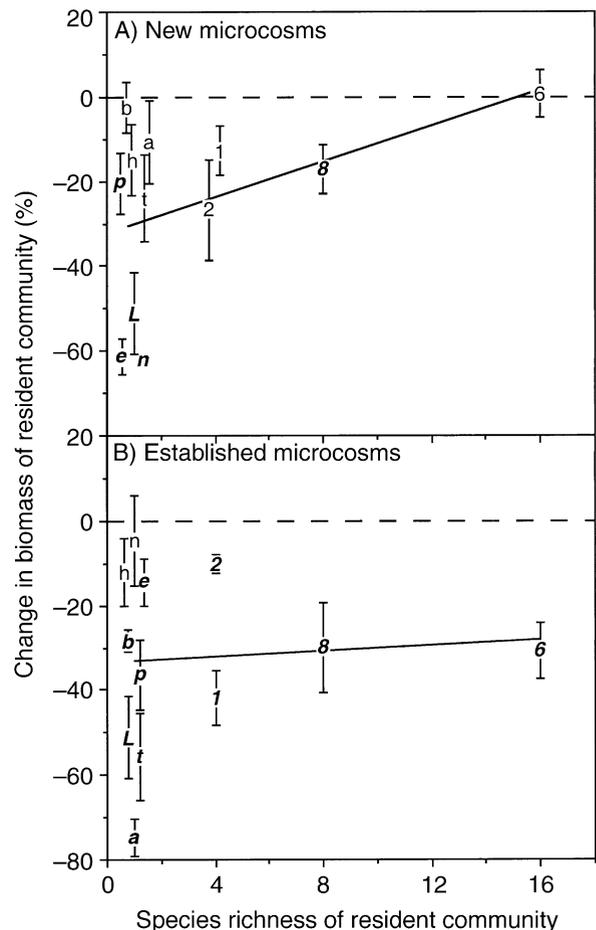


FIG. 8. Response (mean percentage change in aboveground biomass production \pm 1 SE, $n = 5$) of resident species to *Centaurea* invasion plotted against species richness of the resident community in (A) new and (B) established microcosms. Characters are as defined in Fig. 6. Values of some monocultures have been moved horizontally to improve clarity. Dashed lines mark the border between negative and positive responses. Italic bold characters indicate that responses were significantly different from zero ($\alpha = 0.05$, calculated using confidence intervals that were corrected using the sequential Bonferroni technique). Solid lines are from linear regressions of all values (randomization analyses: new microcosms, $P = 0.08$; established microcosms, $P = 0.85$).

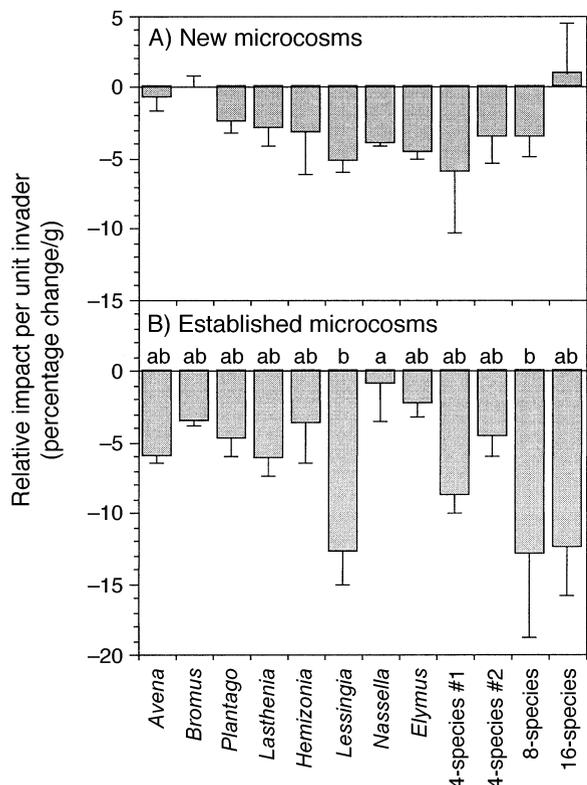


FIG. 9. Response of resident species to *Centaurea* invasion (percentage change in aboveground biomass production) divided by *Centaurea* biomass (g) in invaded microcosms (mean \pm 1 SE, $n = 5$). This measure is termed relative impact per unit invader (RIP) in the text. (A) RIP in new microcosms; (B) RIP in established microcosms. In (B), columns that do not share a common letter differ significantly in RIP (one-way ANOVA followed by Student-Newman-Keuls post hoc test, $\alpha = 0.05$).

availability limited *Centaurea* growth in this study, then mixed-species communities may have reduced availability of this resource to the level of the driest monoculture of their component species.

Linear regressions accurately predicted *Centaurea*'s reproductive biomass from its aboveground biomass (Fig. 5). However, the slope of the relationship was dependent on microcosm age. A handful of community types were responsible for the difference in slopes. Community types that decreased the slope of the relationship for new microcosms included the perennial grass monocultures, the *Lessingia* monoculture, and the invaded zero-species microcosms.

Results of recent studies suggest that the relationship between community diversity and invasibility is positive in some cases (e.g., Robinson et al. 1995, Stohlgren et al. 1999) and negative in others (e.g., McGrady-Steed et al. 1997, Knops et al. 1999, Symstad 2000). While it is too early to reconcile these seemingly contradicting results, it is possible that several mechanisms, acting on different spatial scales, cause the ob-

served patterns. Together with Dukes (2001a), this study suggests that within a neighborhood, diversity minimizes community invasibility by increasing competition for limiting resources. On larger scales, diversity often reflects spatial heterogeneity in resource availability and habitat types. This spatial heterogeneity ensures suitable habitat for a diverse array of invaders, as well as natives (see Stohlgren et al. [1999] and Levine and D'Antonio [1999] for further discussion). Hopefully, future research will not only identify the factors that influence an ecosystem's susceptibility to invasion, but will also determine the relative strengths of these factors and the scales on which they operate. This information will help to predict how changes in biodiversity and other ecosystem characteristics may alter a community's invasibility.

Currently, annual grasses overwhelmingly dominate most of California's grasslands. The results of this experiment suggest that these species are relatively poor at suppressing growth of *Centaurea*—not a surprising observation, given *Centaurea*'s great success in invading California grasslands. Dyer and Rice (1999) suggest that the replacement of perennial grasses by annual grasses as dominants in California's Valley grassland may have facilitated the later success of *Centaurea*. Results from this study support their theory, as perennial grasses were more successful than annual grasses at suppressing *Centaurea* growth in established communities. However, high seedling mortality of the annual grass *Avena barbata* in established monocultures may have contributed to this result.

Because *Centaurea* is considered a noxious weed in much of the western United States, several previous studies have evaluated species for their ability to suppress *Centaurea* growth (e.g., Larson and McInnis 1989, Prather and Callihan 1991, Roché et al. 1994, Thomsen et al. 1996a). These studies have focused on perennial grasses and legumes (Thomsen et al. 1996b), many of which were introduced from other continents. To date, few of the species studied have dramatically reduced starthistle growth. *Centaurea* and other late-season annuals require summer soil moisture for growth (Gulmon et al. 1983, Roché et al. 1994), a demand that could potentially be exploited to reduce populations of the weed. Gordon and Rice (1993) found that the late-season annual forb *Hemizonia congesta* rapidly depletes soil moisture, and suppresses growth of blue oak seedlings. In this study, *Hemizonia* competed strongly with *Centaurea*. The success of native summer-active annuals at suppressing growth of *Centaurea* may inspire the development of new weed control techniques.

The new microcosms in this experiment, which were in many respects similar to gopher-disturbed patches of grassland, were generally less dominated by *Centaurea* than the established microcosms. The invader typically produced a similar amount of biomass in both types of microcosm, but many resident species grew

TABLE 3. Proportional response (mean \pm 1 SE, $n = 5$) of the biomass of resident species in control communities to *Centaurea* invasion.

Species	Proportional change by community type			
	1-species	4-species†	8-species	16-species
New microcosms				
<i>Avena</i>	-0.11 \pm 0.10	-0.09 \pm 0.14	0.02 \pm 0.13	0.01 \pm 0.28
<i>Bromus</i>	-0.02 \pm 0.06	0.05 \pm 0.26	0.11 \pm 0.27	1.15 \pm 0.50
<i>Vulpia</i>	-0.19 \pm 0.12
<i>Lolium</i>	0.39 \pm 0.29
<i>Plantago</i>	-0.21 \pm 0.07	0.02 \pm 0.13	-0.38 \pm 0.21	-0.33 \pm 0.08
<i>Lasthenia</i>	-0.24 \pm 0.10	-0.32 \pm 0.18	-0.36 \pm 0.16	-0.16 \pm 0.28
<i>Erodium</i>	0.41 \pm 0.34
<i>Microseris</i>	0.01 \pm 0.12
<i>Hemizonia</i>	-0.15 \pm 0.08	-0.09 \pm 0.30	-0.48 \pm 0.19	0.33 \pm 0.55
<i>Lessingia</i>	-0.47 \pm 0.09	-0.91 \pm 0.05	-0.26 \pm 0.44	1.79 \pm 2.02
<i>Calycadenia</i>	0.18 \pm 0.68
<i>Epilobium</i>	-0.52 \pm 0.23
<i>Nassella</i>	-0.62 \pm 0.02	-0.02 \pm 0.12	-0.26 \pm 0.15	0.03 \pm 0.11
<i>Elymus m.</i>	-0.61 \pm 0.04	-0.26 \pm 0.14	-0.44 \pm 0.26	1.21 \pm 0.70
<i>Festuca</i> ‡
<i>Elymus g.</i> ‡
Established microcosms				
<i>Avena</i>	-0.75 \pm 0.04	0.09 \pm 0.41	-0.27 \pm 0.38	0.91 \pm 0.57
<i>Bromus</i>	-0.28 \pm 0.03	1.37 \pm 0.98	0.58 \pm 1.07	0.04 \pm 0.30
<i>Vulpia</i>	0.34 \pm 0.36
<i>Lolium</i>	-0.58 \pm 0.19
<i>Plantago</i>	-0.37 \pm 0.08	0.34 \pm 0.52	0.74 \pm 0.98	-0.11 \pm 0.33
<i>Lasthenia</i>	-0.56 \pm 0.10	1.88 \pm 1.16	0.21 \pm 0.36	0.50 \pm 0.53
<i>Erodium</i>	-0.46 \pm 0.13
<i>Microseris</i>	-0.16 \pm 0.14
<i>Hemizonia</i>	-0.12 \pm 0.08	-0.69 \pm 0.04	-0.08 \pm 0.40	1.74 \pm 2.10
<i>Lessingia</i>	-0.51 \pm 0.10	-0.09 \pm 0.23	-0.62 \pm 0.08	-0.29 \pm 0.24
<i>Calycadenia</i>	0.18 \pm 0.68
<i>Epilobium</i>	-0.52 \pm 0.23
<i>Nassella</i>	-0.05 \pm 0.11	0.06 \pm 0.25	0.19 \pm 0.24	0.33 \pm 0.41
<i>Elymus m.</i>	-0.14 \pm 0.06	-0.07 \pm 0.20	0.13 \pm 0.22	19.85 \pm 19.34
<i>Festuca</i> ‡
<i>Elymus g.</i> ‡

Note: Some species failed to germinate in some microcosms. Where these species were the only representative(s) of a functional group within the community, all data from that microcosm and its paired invaded or control microcosm were excluded from the calculations. In cases where the microcosm contained other species from the same functional group, I only excluded data from the species that failed to germinate.

† Species in two separate 4-species communities.

‡ Establishment rates of *Elymus glaucus* and *Festuca pratensis* were very poor, and these species were hard to distinguish from one another in the seeding stage. Therefore, data from these species have been omitted.

less in the established microcosms than in new microcosms (with the exception of the perennial grasses). Reduced growth of the resident species in established microcosms led to greater dominance of *Centaurea* (measured as the proportional contribution of *Centaurea* to total community biomass; Fig. 6B) in six of the community types. This result was surprising for two reasons. First, disturbances that increase resource availability (such as the recent soil pulverization in the new microcosms of this experiment) are generally thought to increase the success of invaders (Burke and Grime 1996, D'Antonio et al. 1999). Second, *Centaurea* growth is known to be strongly limited by winter shading (Roché et al. 1994), and established microcosms were more shaded (by screening and a litter layer) than new microcosms.

I can only speculate as to how *Centaurea* was fa-

vored over resident species in the established microcosms. Several mechanisms, including the following two, could potentially have led to this result: (1) In the year prior to the start of this experiment, resident species reduced the availability of limiting nutrients in their rooting zone (data not shown). Decomposing roots may have further immobilized nutrients in this zone during this experiment. *Centaurea* may be limited by different nutrients, or may grow deeper roots than resident species, thus escaping the infertile soil volume. (2) Soil compaction in the established microcosms may have limited growth of resident species more than growth of *Centaurea*.

Measures of complementarity

Measures of complementarity suggested that facilitation or resource partitioning took place between *Cen-*

TABLE 4. Parameters from linear regressions of the proportional response of the biomass of core resident species to *Centaurea* invasion against the number of resident species in a community.

Species	Regression parameters		
	<i>P</i>	<i>r</i> ²	<i>n</i> [†]
New microcosms			
<i>Avena</i>	0.9396	0.00	20
<i>Bromus</i>	0.0173	0.28	20
<i>Plantago</i>	0.5287	0.02	20
<i>Lasthenia</i>	0.9905	0.00	20
<i>Hemizonia</i>	0.9446	0.00	16
<i>Lessingia</i>	0.3833	0.06	16
<i>Nassella</i>	0.0147	0.29	20
<i>Elymus m.</i>	<0.0001	0.66	17
Established microcosms			
<i>Avena</i>	0.0190	0.27	20
<i>Bromus</i>	0.9570	0.00	20
<i>Plantago</i>	0.6823	0.01	20
<i>Lasthenia</i>	0.2443	0.07	20
<i>Hemizonia</i>	0.3750	0.05	19
<i>Lessingia</i>	0.9621	0.00	19
<i>Nassella</i>	0.5422	0.02	20
<i>Elymus m.</i>	0.0778	0.17	19

Notes: The following transformation of response values was used to calculate linear regressions: $\ln(\text{proportional biomass response} + 1)$. Mean proportional biomass responses are listed in Table 3.

[†] Data from some microcosms are excluded as described in Table 3.

taurea and species in other functional groups, but not between *Centaurea* and other late-season annuals or polycultures. The strongest evidence for resource partitioning and/or facilitation came from invaded annual grass monocultures. In the new microcosms, these communities significantly overyielded monocultures of their components (Fig. 7).

In the established treatment, one of the resource complementarity measures suggested resource partitioning between *Centaurea* and one species each of the perennial grasses and the early-season annual forbs. However, neither of these mixtures outproduced monocultures of *Centaurea*. Resource complementarity between *Centaurea* and other species in this experiment is likely a consequence of differences in phenologies and rooting depths and patterns. Resource partitioning probably did not occur when communities included late-season annual forbs, because these species have a similar phenology (summer-flowering annuals) and morphology (rosette-forming plants with deep tap roots) to *Centaurea* (Maddox 1981, Gulmon et al. 1983, Mooney et al. 1986, Chiariello 1989, Roché et al. 1994), and thus compete for resources spatially and temporally. In some of the polycultures, resource partitioning and/or facilitation took place among the resident species (Dukes 2001b), perhaps limiting the possibility of further complementarity.

The limited depth of the microcosms may have reduced resource partitioning in this study. Sheley and

Larson (1994) found evidence for resource partitioning between *Centaurea* and the annual grass *Bromus tectorum*, but also found that this resource partitioning depends on soil depth (Sheley and Larson 1995). In their study, resource partitioning occurred when soil depth was unrestricted, but not when depth was limited to 0.5 m. *Centaurea* roots are known to grow deeper than 0.95 m, the soil depth used in this study (Roché et al. 1994).

Effects of invasion on total productivity

Invasion significantly increased total biomass production of early-season forb and *Bromus hordeaceus* monocultures, as well as of monocultures of perennial grass seedlings (Fig. 7). *Centaurea* also marginally increased production of new *Avena* monocultures. The increases in production of annual grass monocultures suggest that the invasion of *Centaurea* may have increased the productivity of some of California's annual grass-dominated valley grasslands. However, two other results from this study suggest that this impact of the invader might be limited. First, *Centaurea* did not significantly increase biomass production of *Avena* monocultures in the established treatment. Relatively high seedling mortality of *Avena* in the established microcosms played some role in this result. The seedling mortality appeared to be a consequence of the hardened soil column in these microcosms, which prevented seeds from burrowing into the soil. Second, invaded polycultures did not overyield in either treatment. Thus, the effect of *Centaurea* invasion on productivity depends on the species composition and functional diversity of a given grassland community.

Community response to invasion

Invasion reduced production of resident species in all of the monocultures, but this reduction was not significant in every case. Interestingly, although *Centaurea* consistently reduced growth of one late-season annual (*Lessingia*), it did not significantly reduce growth of the other (*Hemizonia*) in either the new or established monocultures (Fig. 8, Table 3). *Hemizonia* reduced growth of *Centaurea* more than *Lessingia* (Fig. 4), and was evidently a superior competitor. It is not clear what difference between these two phenologically and morphologically similar species led to *Hemizonia*'s superior competitive ability.

In new communities, diversity marginally decreased the impact of invasion on resident species (Fig. 8). Was this trend a consequence of the reduced growth of *Centaurea* in more species-rich communities? Or, alternatively, were the species-rich communities less affected by a given amount of *Centaurea*? Diversity did not affect the relative impact per unit invader (RIP) of *Centaurea*, suggesting that any relationship between diversity and *Centaurea*'s impact in the new communities was driven by changes in invasibility (and not impactability). The trend was not consistent across all

species in the communities. Three species in particular responded more positively to *Centaurea* in more diverse communities (Table 4). Positive responses to invasion of late-season annuals in the 16-species community also contributed to the community-level result. In the established communities, impact did not vary with species richness. Interestingly, this lack of a trend was the result of two counteracting mechanisms. As species richness increased, communities became less invulnerable, but more impactable.

In another microcosm experiment, Dukes (2001a) observed a decrease in *Centaurea*'s impact on resident species as species richness increased from 4 to 16. This decrease appears to have been a consequence of declining community impactability. Results of Dukes (2001a) should not be viewed as entirely independent of the results of this experiment. While the study used separate, randomly drawn 4-, 8-, and 12-species communities, it employed the same 16-species communities as the new microcosms in this experiment.

Negative relationships between species richness and the impact of invaders suggest that declining biodiversity can reduce not only a community's resistance to invasion, but also the community's ability to persist after invasion. Hopefully, future studies of community diversity and invader impact will allow researchers to determine how frequently these properties are related.

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