

REPORT

## Rare species loss alters ecosystem function – invasion resistance

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### Abstract

The imminent decline in species diversity coupled with increasing exotic species introductions has provoked investigation into the role of resident diversity in community resistance to exotic species colonization. Here we present the results of a field study using an experimental method in which diversity was altered by removal of less abundant species and the resulting disturbance was controlled for by removal of an equivalent amount of biomass of the most common species from paired plots. Following these manipulations, the exotic grass, *Lolium temulentum*, was introduced. We found that exotic species establishment was higher in plots in which diversity was successfully reduced by removal treatments and was inversely related to imposed species richness. These results demonstrate that less common species can significantly influence invasion events and highlight the potential role of less common species in the maintenance of ecosystem function.

### Keywords

Diversity, ecosystem process, invasion, *Lolium multiflorum*, rare species, removal, resistance.

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### INTRODUCTION

Virtually every biome on Earth is currently faced with species loss at an unprecedented rate (Pimm *et al.* 1995). As a result of past and predicted species extinctions, attention to the effects of a variety of species diversity measurements on ecosystem processes has intensified in the last decade (e.g. Naeem *et al.* 1994; Tilman *et al.* 1996; Wardle *et al.* 1997; Symstad 2000). While these studies have addressed diversity, they have not investigated the intrinsic contribution of rare species to communities. A relatively small number of less common species have been the focus of keystone species investigations (e.g. Paine 1966; Terborgh 1986). These taxa warrant study because they have large impacts on ecosystem processes that are disproportionate to their abundance (Power *et al.* 1996). Overlooked in this discussion, however, is the potential contribution of less abundant species that may be at higher risk of extinction with no apparent contribution to community stability or ecosystem functions.

Concomitant with an increase in species extinctions is an ever-increasing rate of species introductions to native ecosystems (Vitousek *et al.* 1997). Indeed, exotic species invasions are a threat to regional biota (Drake *et al.* 1986; Mooney & Drake 1986; Simberloff *et al.* 1997) and ecosystem

processes (e.g. Vitousek & Walker 1989; D'Antonio & Vitousek 1992) and rival habitat loss and global environmental change as threats to diversity (Chapin *et al.* 2000). The increase in exotic species introductions coupled with native species extinctions has prompted investigation into the role of diversity in resistance to exotic species invasion, one measure of community stability (Levine & D'Antonio 1999, and references cited therein).

Here we present the results of a removal experiment designed to test the hypothesis that less common species can influence the colonization of an exotic. Removal studies have been successfully employed to manipulate and examine competitive dynamics among marine organisms (Connell 1961) and plants (Pinder 1975; Fowler 1981; Hils & Vankat 1982; McNaughton 1983; Symstad 2000). This approach offers an effective experimental alternative to the widespread use of constructed communities to address the diversity/invasibility issue (e.g. McGrady-Steed *et al.* 1997; Knops *et al.* 1999; Stachowicz *et al.* 1999; Levine 2000; Prieur-Richard *et al.* 2000), as it preserves the original community composition, dominance structure and species interactions and allows for a natural response to experimental manipulation. We conducted a field experiment in a naturally occurring plant community wherein species diversity was lowered by removal of less

abundant taxa and the resulting experimental disturbance was accounted for through the use of controls. We then examined the effects of local species reductions on the colonization success of an experimentally introduced invader.

## METHODS

### Study site

The investigation was conducted in the Sierra Nevada mountain range at Leek Spring Meadow in the El Dorado National Forest, California, U.S.A. (38°30'N, 120°14'W; altitude, 2160 m). The climate of the region is high altitude Mediterranean. The meadow is covered by snow from early November through early to mid-June with annual rainfall of 126 cm. The average temperatures for the coldest (January) and warmest (July) months are -2.7 °C and 13.8 °C, respectively (Twin Lakes climate station, 38°42'N, 120°03'W; altitude, 2389 m).

Soil samples from the 0–10 cm mineral horizon were collected from the perimeter of our experimental plot at the peak growing season in 1999. The soils are volcanic derived and slightly acidic (pH = 5.87) with 4.06% organic matter, 0.25% total nitrogen and 108 mg/kg phosphorus (P-Olsen). They also consist of 59% sand, 31.3% silt and 9.3% clay.

Leek Spring Meadow has a long history of land use. The meadow is commonly disturbed by gophers and occasionally cattle, although there has been no grazing on the site since 1995. Despite this history, the meadow is substantially less invaded by exotic species than are similar sites at lower elevations in California (K. Lyons, personal observation). It harbours one exotic species, *Spergularia rubra* (Caryophyllaceae), which is uncommon and occurred in our plots only in the first year of this study. The flora of the meadow occupies on average  $\pm 6$  cm in vertical space. We have encountered 22 species in our plot since 1996. The plant community dominants include the annuals *Madia gracilis* (Smith) Keck (Asteraceae), *Lotus purshianus* (Benth.) Clements & E.G. Clements var. *purshianus* (Fabaceae) and *Gilia leptalea* (A. Gray) E. Greene (Polemoniaceae), in addition to two perennials, *Sanicula tuberosa* Torrey (Apiaceae) and *Triteleia ixioides* (S. Watson) E. Greene ssp. *anilina* (E. Greene) L. Lenz (Liliaceae) (Hickman 1993).

### Experimental design

In 1996, an experimental plot was established in a relatively homogeneous herbaceous area of the meadow and divided into 180, 35 × 45 cm plots, including a 10-cm buffer on all sides. Sixty blocks, consisting of three adjacent plots, were initially designated. Due to the occurrence of gopher

mounds and the high percentage of bare ground, only 53 of these plots were maintained for the duration of the experiment and used in the final analyses.

In all plots, species percentage cover, disturbance and percentage of bare ground were assessed at the beginning of each season. Soil disturbance was assessed by visual inspection and rated between 1 and 3. A "1" indicated that the soil surface was smooth with no irregularity caused by gophers. A "2" was reserved for soil that was turned over in the previous year but had been compacted during winter and spring by snow and water, and a "3" indicated recent, post-snow melt disturbances.

Three treatments were assigned in a randomized, complete block design. In one treatment, richness was reduced to a randomly chosen number of species, between two and seven, by removal of the least common species (SR, species reduction). In a second plot, an equivalent biomass of the most common species (*Madia gracilis* or *Lotus purshianus* var. *purshianus*) was removed to control for the disturbance created in the SR treatment (BR, biomass reduction). The third plot was a control (C, control). After the manipulations, bare ground and disturbance were reassessed, and the 10-cm buffers were clipped to reduce seed dispersal from peripheral vegetation. The plots were treated each year from 1996 to 1998. In 1997 and 1998, *Lewisia nevadensis* (A. Gray) Robinson (Portulacaceae), an early seeding perennial that was difficult to remove, was left in all SR plots; these blocks were placed in higher treatment categories ( $n = 21$ ). As a result, there are fewer two-species and some eight-species treatment blocks in the final analysis.

We chose to remove individuals of the most common species from the BR plots because this ensured that richness was not affected by the accidental extirpation of less abundant species. This method was extremely important for geophytes and other perennials often represented by a few conspicuous, high biomass individuals. In addition, we anticipated that randomly removing species from BR plots would result in patchy disturbance that might not mimic that of the SR plots. Weeding individuals of an evenly distributed species common to every plot allowed us to more evenly distribute removal and thus any resulting disturbance.

In 1998, commercially grown seeds of the exotic *Lolium multiflorum* Lam. (annual ryegrass, Poaceae) were sown evenly at a density of 600 seeds/plot. Only one exotic species was used in order to avoid placing colonizers in competition with one another. It was determined in preliminary trials that *L. multiflorum* was an appropriate choice as it germinated and grew successfully in the meadow. In addition, it is a conspicuous annual grass that is widespread at lower elevations and easily removed prior to shattering. Throughout the 1999 field season, *L. multiflorum* plants were harvested at maturity. The number of spikelets

and seeds was positively correlated with plant number. We therefore used the number of fruiting plants as a measure of success. To ensure that *L. multiflorum* does not become permanently established at Leek Spring Meadow, we will conduct yearly harvests of any remaining individuals until the species is completely removed.

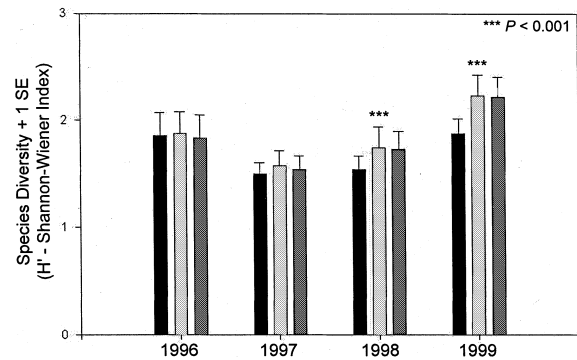
### Statistical analyses

We employed analysis of variance (ANOVA) (general linear model) and Sheffé pairwise comparisons to assess the treatment effects of species removal on diversity within and between years and on *L. multiflorum* establishment. We report the diversity as the Shannon–Wiener index ( $H'$ ) because it weights the presence of rare species, which were the focus of our removal. Simple linear regression was used to determine the relationship between experimental and natural variables and *L. multiflorum* colonization. Multiple  $r^2$  values are reported for regressions. For simple linear regression, variables were log-transformed as necessary to improve compliance with normality assumptions. All analyses were conducted using SYSTAT software, version 9.0 (SYSTAT 1998).

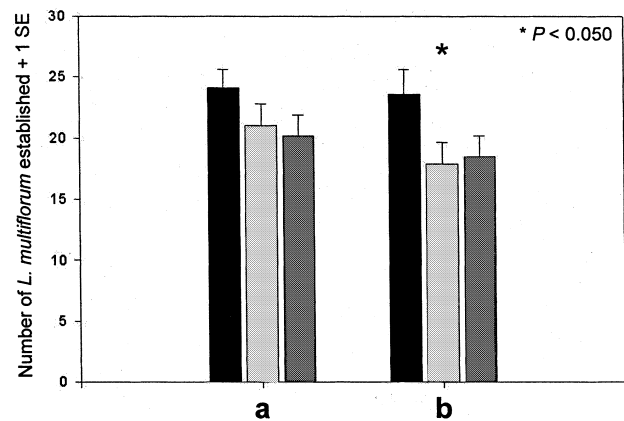
### RESULTS

Through this experimental method, we aimed to separate diversity from covarying environmental factors by deleting species on a small scale. Species diversity was successfully reduced in SR plots (Fig. 1: 1998:  $F = 28.481$ ,  $P < 0.001$ ; 1999:  $F = 74.105$ ,  $P < 0.001$ ;  $n = 53$  in all years). This reduction in diversity was not immediate, however. Diversity data collected in 1997 did not show a significant treatment effect (Fig. 1: 1997:  $F = 4.011$ ,  $P = 0.120$ ). A persistent seed bank or individuals that were missed or seeded prior to removal probably caused the lag in treatment response from 1996 to 1998. Trends reported here were consistent across all diversity measures.

Species removal treatments had a significant effect on colonization by the exotic species, *L. multiflorum*. Establishment in 1999 was higher in SR than in either BR or C plots, although this result was nonsignificant (Fig. 2a:  $n = 53$ ,  $F = 2.241$ ,  $P = 0.111$ ). We did find, however, that one-tailed Wilcoxon signed-rank analyses demonstrated that establishment was higher in SR plots than in either BR or C plots and equivalent between controls ( $n = 53$ ; SR–BR:  $P = 0.054$ ; SR–C:  $P = 0.019$ ; BR–C:  $P = 0.363$ ). When the ANOVA was performed using only those blocks in which species diversity was successfully reduced in the SR relative to the BR or C plots in both 1998 and 1999, those years in which we found overall significant treatment effects, *L. multiflorum* colonization was significantly higher in the SR plots (Fig. 2b:  $n = 38$ ,  $F = 4.218$ ,  $P = 0.018$ ).



**Figure 1** Results of 3 years of species removal on diversity. Statistical analysis was by ANOVA for within year comparisons. We find statistically significant lower diversity in 1998 and 1999 in the SR plots than in the BR and C control plots. The probability for Scheffé pairwise comparison between the SR treatment and both controls was  $P < 0.001$  in 1998 and 1999. Diversities of the control treatments (BR and C) were equivalent throughout the duration of the experiment (Scheffé pairwise comparisons: 1996:  $P = 0.637$ ; 1997:  $P = 0.531$ ; 1998:  $P = 0.537$ ; 1999:  $P = 0.767$ ). ■, less abundant species removal (SR); ▨, biomass removal (BR); ■, disturbance control (C).



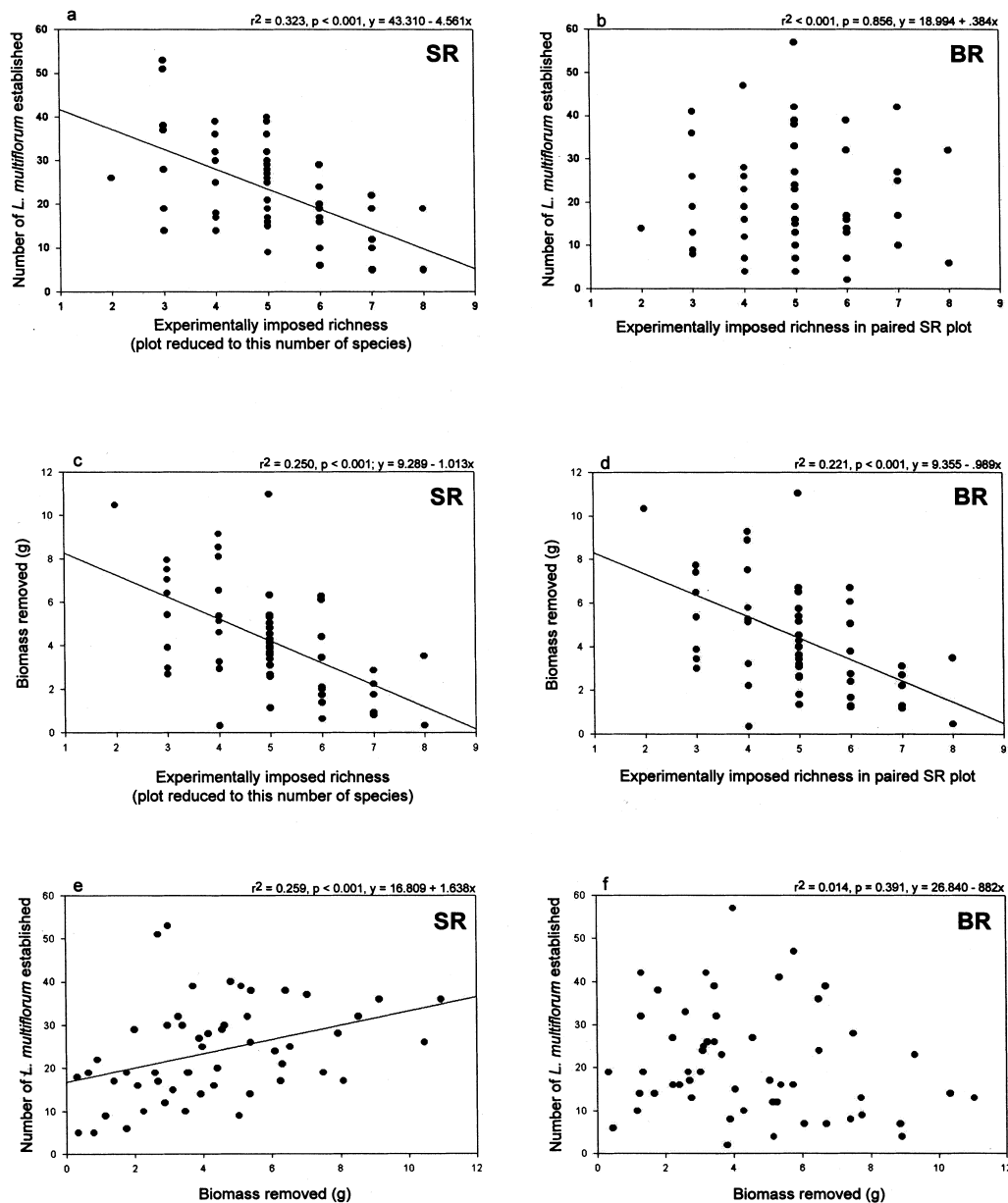
**Figure 2** Treatment effect on the establishment of the exotic *L. multiflorum*. (a) All blocks ( $n = 53$ ,  $F = 2.241$ ,  $P = 0.111$ ). (b) Establishment in blocks in which diversity was lower in the SR plots than in either the BR or C plots for two consecutive years, 1998 and 1999 ( $n = 38$ ,  $F = 4.218$ ,  $P < 0.018$ ). ■, less abundant species removal (SR); ▨, biomass removal (BR); ■, disturbance control (C).

We were concerned that the treatment effect in SR plots was driven by initial plot diversities. In other words, plots with higher diversity might be more resistant to species removal; however, we found no difference in original (1996) diversities between “effective” and “non-effective” SR treatments ( $F = 0.501$ ,  $P = 0.482$ ,  $n_{\text{effective}} = 38$ ,  $n_{\text{non-effective}} = 15$ ). In addition, differences in treatment effects were not explained by the presence of persistent perennials or *Lewisia nevadensis* (K. Lyons, unpublished data, 2000).

Our SR treatment includes low to increasingly larger species diversity reductions. We therefore analysed *L. multiflorum* colonization by linear regression to better assess the effects of incremental species removal. Among SR plots, experimentally imposed richness resulted in higher exotic species establishment (Fig. 3a). Species reduction in SR plots explained 32.3% of the variability in *L. multiflorum* density (SR:  $F = 24.358$ ,  $P < 0.001$ ). Conversely, in BR

plots, there was no significant relationship between *L. multiflorum* colonization and imposed species richness in paired SR plots (Fig. 3b: BR:  $r^2 < 0.001$ ,  $F = 0.033$ ,  $P = 0.856$ ).

Biomass removal alone had no effect on *L. multiflorum* colonization. In all years, larger reductions in species diversity required higher biomass removal from SR and, consequently, paired BR plots (Fig. 3c: SR:  $r^2 = 0.250$ ,



**Figure 3** Linear regression of experimentally imposed richness, biomass removed and *L. multiflorum* establishment ( $n = 53$ ). Effect of species removal on the number of *L. multiflorum* established in SR (a) and paired BR (b) plots. Relation between experimentally imposed richness and weight removed in 1998 in SR (c) and paired BR (d) plots. Biomass removal coupled with species removal on *L. multiflorum* establishment (e). Effect of biomass removal without species removal on establishment of *L. multiflorum* (f). Trends shown are best fit simple linear regressions. Statistical analyses were conducted using log-transformations where necessary. For clarity, data presented graphically are not log-transformed.

$F = 16.977$ ,  $P < 0.001$ ; Fig. 3d: BR:  $r^2 = 0.221$ ,  $F = 14.460$ ,  $P < 0.001$ ; only biomass removed for 1998 shown). Biomass removed from SR plots in 1998 explained 25.9% of the variability in *L. multiflorum* colonization (Fig. 3e: SR:  $F = 17.867$ ,  $P < 0.001$ ), a result confounded by species removal. Conversely, *L. multiflorum* establishment was not significantly affected by biomass removal in BR plots (Fig. 3f: BR:  $r^2 = 0.014$ ,  $F = 0.748$ ,  $P = 0.391$ ).

We also tested to determine whether initial and final plot conditions had a lasting effect on the colonization success of *L. multiflorum*. We measured plot species richness and diversity, percentage of bare ground and disturbance at the beginning of each season. None of these conditions, in 1999 or previous years, explained *L. multiflorum* success and are therefore not included as covariates in our ANOVA (Fig. 2).

During the 2000 growing season, we returned to the site to remove *L. multiflorum*; only 217 individuals were found. Establishment data from the 2000 season were not included in our analyses because we no longer maintained or observed diversity removal treatments.

## DISCUSSION

Using a species removal treatment coupled with a control for experimental disturbance and biomass removal, we were able to demonstrate that less common species can have a significant impact on invasion resistance in this montane meadow. Colonization by *L. multiflorum* was significantly higher in SR plots in which diversity was successfully reduced (Fig. 2b). In addition, incremental species reduction treatments resulted in significant increases in *L. multiflorum* colonization (Fig. 3a).

This study addresses an ongoing debate regarding the role of less common species in the maintenance of ecosystem processes. There is experimental evidence to suggest that, under natural conditions, where species differ in abundance, not all and perhaps only a fraction of the species in a community are needed to maintain ecosystem processes (Schwartz *et al.* 1999). Schwartz *et al.* (1999) assert, within the context of models developed by others (Doak *et al.* 1998; Tilman *et al.* 1998), that ecosystem processes are maximized when species abundance is equitable. This is supported empirically by Wilsey & Potvin (2000) in an experimental study where evenness among species enhanced ecosystem function.

We suggest that, under natural circumstances, where species abundance is inequitable, the contribution of less common species will be difficult to assess in the presence of common dominants, and measurements of ecosystem processes may not be sensitive enough to assess the effects of less common species. Furthermore, the magnitude of influence on specific ecosystem processes will vary among taxa and functional groups (e.g. Symstad *et al.* 1998; Symstad

2000) and the contribution of a species may not be reflected through the use of a single or small number of criteria. In our study, uncommon species, as a group, made a small but nonetheless consistent and measurable contribution to invasion resistance. These results highlight the importance of the development of new methods to accurately assess the individual and collective effects of less common species on ecosystem processes.

The effective scale and methodological approach used to assess the role of diversity in the invasion process are under intense discussion. In their review of investigations addressing the diversity/invasibility hypothesis, Levine & D'Antonio (1999) concluded that the majority of descriptive studies (e.g. Stohlgren *et al.* 1999) support a positive correlation between the diversity of a community and exotic species colonization, while manipulative approaches generally demonstrate the reverse (e.g. Stachowicz *et al.* 1999; Levine 2000).

Descriptive studies are instrumental in the development of predictive models of invasibility and can alert us to community types that are more invasion prone. Nonetheless, at any scale, uncontrolled environmental factors that determine resident species diversity as well as new species colonization make it impossible to assess the intrinsic role of diversity. In fact, Loreau (2000) has demonstrated that local effects of diversity on ecosystem processes, such as productivity and nutrient retention, may be systematically obscured due to differences in local environmental conditions. The scale and manipulative approach employed here is designed to specifically address whether changes in diversity by species loss at the neighbourhood scale can render a community or site within a community more susceptible to invasion *regardless* of initial community diversity.

Exotic species colonization is often positively correlated with anthropogenic as well as natural disturbance (Crawley 1987; Hobbs & Huenneke 1992; Loope 1992). With the exception of Symstad (2000), previously conducted plant removal studies have focused on compensatory growth of resident species within the same season of removal with no control for physical soil disturbance, a factor that could significantly affect the establishment and growth of ruderal species (Burke & Grime 1996). Surprisingly, at Leek Spring Meadow, biomass removal, in the absence of diversity reduction, did not explain the variation in *L. multiflorum* colonization (Fig. 3b,f). Furthermore, colonization among BR and C plots was equivalent (Fig. 2). We attribute this result to the small, herbaceous growth forms of the plants in this meadow and the fact that experimental physical disturbance was small and transient relative to that caused by gophers.

Disturbance by gophers has been shown to favour non-native ruderals (Hobbs & Mooney 1985, 1991), and we expected that it too would explain some variability in

colonization. Despite the large amount of gopher activity throughout the duration of the experiment, we found that natural disturbance and the percentage of bare ground, both of which are generally higher in gopher-disturbed areas, were not predictors of *L. multiflorum* colonization.

We also anticipated that exotic species success would be influenced by both natural and manipulated diversity measures as in other investigations (e.g. Stohlgren *et al.* 1999; Levine 2000), but found no significant relationship between initial and final richness or diversity and *L. multiflorum* colonization. The strong effect of our experimental manipulations on *L. multiflorum* success, compared to the lack of a clear colonization pattern with diversity, emphasizes the need to exercise caution in the interpretation of correlative studies and the use of diversity measures in general.

Richness and diversity indices are essential tools in ecology, but may inaccurately represent the contribution of a species to a community. Richness, while easily assessed at this small scale, is an inherently uninformative measure, as the presence of one or many individuals of a species yields the same increase in richness. Diversity is more informative; however, we attribute our negative results using single plot diversities to the general inaccuracy of species cover assessments and the undetectable, yet important, reductions in species abundance, combined with a failure of cover to approximate the magnitude of the contribution of a species to a community. As demonstrated for keystone species, contributions to ecosystem processes can outweigh species abundance (Power *et al.* 1996) and cover may not accurately represent the activity, community importance or interaction strength of a species.

Species deletions within a community are often assumed to create open niches (*sensu* MacArthur 1970, 1972). Our results lend credence to the fluctuating resource theory (Davis *et al.* 2000), wherein species deletions are accompanied by resource release, making a community more susceptible to invasion. The soils at Leek Spring Meadow are well drained, consisting of 59% sand, and, like other high altitude meadows in the Tahoe Basin, are primarily limited by water (Victor P. Claassen, LAWR, University of California at Davis, personal communication, 2001). At least in the short term, less common species might occupy either resource or space niches that more dominant species are unable to fill. Where the less common species are sparse or absent, limiting resources, such as water, may be more abundant.

Indeed, Theodose *et al.* (1996) showed that in high stress environments under intense competition and an attenuated growing season, less common species may be more responsive to seasonal variability in resources. In an alpine moist meadow community in Colorado, U.S.A., they found that rare and subdominant plant species had higher nitrogen ( $^{15}\text{N}$ ) uptake rates than dominant species. They concluded that less common species disproportionately appropriate

this limiting resource not only for biomass production but also as a competition strategy.

Vermeij (1991) showed that large-scale extinction events over a 20-million-year period lowered the resistance of biotas to exchange with neighbouring communities when physical or biological barriers ceased to exist. In recent times, humans have increased rates of invasion by transporting species around the planet, thereby mimicking the collapse of barriers between communities. Our experimental results suggest that invasion success can be facilitated when native species diversity is reduced. The generality of our results warrants testing under long-term conditions where the introduced exotics can be monitored and controlled and more sites and community types employed. Nonetheless, in the light of our current findings, for those habitats threatened by exotic species introductions, maintenance of diversity should be considered as a conservation priority.

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**BIOSKETCH**

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