Fig. 3. Image score of receivers who obtained money on their account from donors who donated up to six times during the game (Kruskal-Wallis test, df = 5, P = 0.04, two-tailed). The figure shows the deviations from the means per group and round (averaged over all rounds) to correct for group and round effects (means ± SE, error bars).

anything (in group 6), those who donated rather rarely (less than three times, i.e., final image score of <0) showed a strong preference to give only to receivers with a relatively high image score (the mean deviations from group and round means were positive in 10 of 10 cases; $Z = 3.16$, $P < 0.01$), whereas with increasing generosity, the players appeared to be less discriminative with respect to the receiver's image score (Fig. 3). We did not find a significant correlation between the individuals' mean image score and their mean account per round (mean Spearman's r per group = −0.19; SE = 0.11; Wilcoxon test against 0: $n = 8$, $P > 0.05$, two-tailed).

Recent theoretical and experimental studies on cooperation games based on direct reciprocity support the idea that players learn from their opponents and adjust their strategy accordingly [e.g., (7, 8)]. Our results demonstrate that some form of image scoring is also used for indirect reciprocity (3–6) and hence may play a key role in the evolution of cooperation in larger groups (9).

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10. We thank the students for participating in our study; P. Aeschlimann, R. Eggler, M. Häberli, and P. Stettler for their assistance; and the Swiss National Science Foundation for support. C.W. thanks the "Berner Hochschulstiftung" and the Cloëtta Foundation for tide-over grants.

Species Diversity and Biological Invasions: Relating Local Process to Community Pattern

Jonathan M. Levine

In a California riparian system, the most diverse natural assemblages are the most invaded by exotic plants. A direct in situ manipulation of local diversity and a seed addition experiment showed that these patterns emerge despite the intrinsic negative effects of diversity on invasions. The results suggest that species loss at small scales may reduce invasion resistance. At community-wide scales, the overwhelming effects of ecological factors spatially covarying with diversity, such as propagule supply, make the most diverse communities most likely to be invaded.

Concern over the loss of species from ecological communities has stimulated renewed interest in the importance of species diversity to the functioning and stability of ecosystems (1–4). Of particular interest is the classic hypothesis that diversity enhances community resistance to biological invasions (5, 6). Support for this hypothesis has come from theoretical models (7–10) and experimental manipulations of diversity conducted in microcosms and other controlled environments (11–16). Although these studies have elegantly isolated the local or neighborhood effects of diversity on invasions, as well as the underlying mechanisms, the relevance and importance of these results for natural communities remain controversial (17–19). Factors other than diversity also influence invasions, yet most of the variation in these factors is eliminated in the relatively homogeneous experimental systems. By contrast, correlational studies of "uncontrolled" natural communities have most often shown that diverse assemblages are invaded more than their species-poor counterparts (6, 19–23). This result seems to contradict the models and experimental studies and has contributed to the impression that the relationship between diversity and invasibility defies generalization (6, 17). To address this apparent contradiction, and more generally to assess the importance of diversity to the invasion of a natural system, I performed a study coupling patterns of diversity and invasion with in situ manipulations of diversity in a natural context.

I conducted this study in the plant community bordering the South Fork Eel River in northern California. The system is dominated by *Carex nudata*, a tussock-forming sedge that provides the primary habitat for more than 60 plant species in the community. Each tussock is a discrete micro-island colonized by up to 20 perennial herbaceous plant and bryophyte species that depend on the tussock for stable substrate during winter flows (24, 25). The system is being invaded by Canada thistle (*Cirsium arvense*), common plantain (*Plantago major*), and creeping bent grass (*Agrostis stolonifera*), the propagules of which encounter numerous replicate tussocks containing varying numbers of native species.

In a survey of similarly sized tussocks over a 7-km stretch of river (26), the incidence of all three exotic plants was greater on more diverse tussocks (Fig. 1). Specifically, the presences of *Agrostis*, *Plantago*, and *Cirsium* were significantly (logistic regression $P = 0.001$, 0.008, and 0.004, respectively) and positively related to species richness (not including the invader). Although these correlations conflict with Elton's classic observation that species-rich systems are less invaded (5), they may not reflect the intrinsic effects of diversity. For example, positive correlations may result from a similar response of native and exotic species to environmental conditions (6, 19–23).
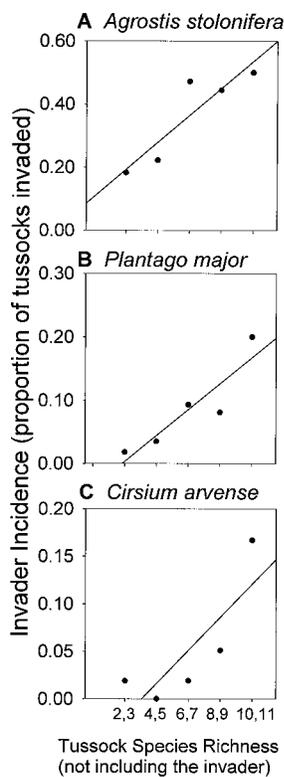
To test the effects of diversity on invasions in this system, I "invaded" tussocks in which the number of resident species was manipulated in situ. This approach left other factors that may influence invasibility free to vary (e.g., ambient nutrients and light, *Carex* stem number), but experimentally decoupled them from diversity. In late spring 1998, I removed all species from 65 randomly selected tussocks (each 350 cm²) at a single large riffle (27). Each tussock was randomly assigned to one of five species rich-

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ness treatments: one, three, five, seven, and nine native species (not including *Carex* itself), corresponding to the natural range of richness found on tussocks of that size. I determined the composition of each replicate by first defining a pool of nine native species, and then assigning species to each tussock by a separate random draw from the pool. I added all species as small transplants of similar size, maintaining a constant cover of ~90% (*28*). The experimental communities had the entire 1998 growing season to establish and then experienced natural flooding during the 1998–1999 winter. In spring 1999, I added 200 seeds of each exotic plant to the surface of the experimental tussocks. For each tussock, I counted seedlings every 3 weeks until early fall, and on the last sampling date I measured the size of the largest individual of each species (*29*).

As species richness increased, the proportion of propagules that germinated and survived the growing season significantly declined for two of the three invaders, and the size of the
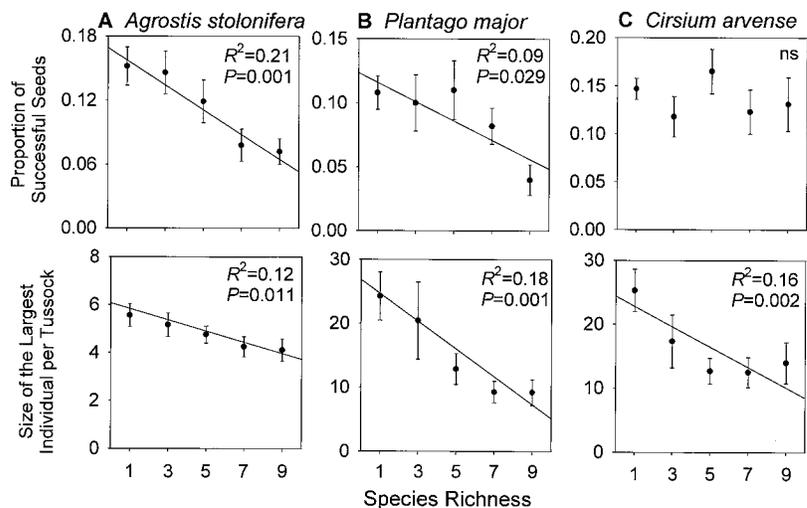
largest individual per tussock significantly declined for all three invaders (Fig. 2). Thus, even with the spatial variability of a natural system, diversity can significantly enhance resistance to biological invasions, supporting the relevance of studies conducted in more homogeneous settings (*11–16*) to complex natural communities. Additionally, for this system, the small and discrete tussocks define the "neighborhood," the spatial scale at which species interact. Thus, the results support the recently proposed hypothesis that the effects of diversity on invasions arise at the neighborhood scale (*16*).

In this study, the effects of diversity on invasion may have been mediated by resident species cover. Absolute cover was greater in more diverse treatments [$R^2 = 0.36$, $P = 0.001$; cover averaged 76%, 77%, 97%, 127%, and 138% in the one-, three-, five-, seven-, and nine-species treatments, respectively (*30*)] and, like diversity, had a negative impact on the success of *Agrostis* ($R^2 = 0.14$, $P = 0.001$) and *Plantago* ($R^2 = 0.14$, $P = 0.001$). Moreover, even 3 weeks into the experiment, results were very similar to those at the end. This suggests that the effects of diversity on invasion arose at the germination/seedling stage, a stage that is particularly vulnerable to shading by plant cover (*31*). The results in Fig. 2 were unlikely the effect of a single key resident species more often found in the high-richness tussocks (*32*). For the seven tussocks in the nine-species treatment, four different species were the most abundant resident, and their relative cover was never greater than 30%.

In this community, patterns of diversity and invasion do not reflect the intrinsic effects of

diversity operating at neighborhood scales. Hence, factors covarying with diversity, such as disturbance, propagule pressure, and species composition, are likely determinants of the community-wide patterns. It is not surprising that these factors overwhelm the local effects of diversity, because species richness explained less than 25% of the variation in invasion success in the experimental tussocks (Fig. 2). Further investigation of these covarying factors is critical, as they may be responsible for the relatively high frequency of invasions into naturally diverse communities. For this system, a more detailed analysis of the patterns of diversity and invasion suggests that they could result from spatial variation in propagule pressure (*33*). Consistent with the predominantly downstream movement of water and seeds in river systems (*34, 35*), it was the downstream tussocks that were the most diverse ($R^2 = 0.35$, $P = 0.001$) and the most invaded by *Agrostis*, *Plantago*, and *Cirsium* (logistic regression, $P = 0.001$, 0.047, and 0.025, respectively).

To further evaluate the seed supply hypothesis, I added a fixed quantity of seeds (200 for *Agrostis* and *Plantago* and 100 for *Cirsium*), more than enough to swamp natural recruitment, to tussocks varying naturally in diversity over the entire 7-km stretch of river (*36*). This manipulation equalized seed supply across the natural diversity gradient. If it were the intrinsic biotic or physical conditions of the tussocks, rather than seed supply, that covaried with diversity and drove invasion patterns, one would expect positive correlations between natural diversity and the success of added propagules. Instead, I found no correlation for *Agrostis*

Fig. 1. Natural patterns of invasion by (**A**) *Agrostis stolonifera*, (**B**) *Plantago major*, and (**C**) *Cirsium arvense* relative to the richness of species on the tussocks. Data for adjacent richness levels were pooled to better estimate the incidences because some richness levels contained as few as five tussocks. Presented are the best-fit lines from simple linear regression (*Agrostis*, $R^2 = 0.82$, $P = 0.035$; *Plantago*, $R^2 = 0.89$, $P = 0.017$; *Cirsium*, $R^2 = 0.67$, $P = 0.092$), although I also conducted more statistically powerful logistic regressions showing significant ($P < 0.01$) effects of richness on invasion by each of the three invaders (see text).

Fig. 2. Results of a direct manipulation of species richness on the invasion success and size of (**A**) *Agrostis stolonifera*, (**B**) *Plantago major*, and (**C**) *Cirsium arvense*. Presented are the proportion of seeds that germinated and survived to the end of the growing season (*29*) and a nondestructive measure of the size of the largest individual per tussock. For the grass, *Agrostis*, this measure was height (in centimeters); for the two dicots, it was the product of leaf number and maximum leaf size (in centimeters). Overall, nonlinear curves were not statistically ($P < 0.05$) better fits than linear curves; however, for *Plantago* success and *Cirsium* size, adding a squared term to the regression ($P = 0.111$ and 0.058, respectively) increased R^2 by 0.04 and 0.06. Data points are means ± 1 SE; ns, not significant.

($R^2 = 0.00$, $P = 0.985$) and *Cirsium* ($R^2 = 0.00$, $P = 0.977$), and only a very weak correlation for *Plantago* ($R^2 = 0.02$, $P = 0.033$). These results, along with the more downstream position of the diverse and invaded tussocks, suggest that propagule supply may be one important factor behind the positive correlations between diversity and invasion in this system. Additionally, the difference between these results and those in Fig. 2 may reflect other covariates that were decoupled from diversity in the experiment (e.g., species composition, physical conditions).

Although diversity tends to enhance community resistance at neighborhood scales, other factors covarying with diversity (e.g., propagule pressure in this study) may be more important in driving community-level patterns of diversity and invasion (6, 19). That the correlations between native diversity and the success of exotic species are mostly positive is reasonable, because the factors known to promote or limit native diversity are known to similarly influence invasions (6). This conclusion raises two concerns that at first may have seemed contradictory. First, the most diverse assemblages might be at the greatest risk of invasion, an important point for managing invasive species (19). Second, however, losses of species, if they affect neighborhood-scale diversity, may erode invasion resistance.

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26. The analysis included 256 tussocks of similar size (400 cm²) and plant cover (90%).
27. Because of a limited choice of riffles after the 1998 El Niño high water, the riffle at which I conducted the experiment was among the highest riffles in the system. Thus, in 1999—a year with little spring rain—the tus-socks at this site were much drier than the majority of tussocks, most of which were saturated. I minimized these differences by giving the tussocks in the experiment 1 liter of water daily. Water availability differences between the natural and experimental tussocks were not significant ($t_{1, 239} = 3.47$, $P = 0.13$).
28. The pool of transplants included *Conocephalum conicum*, *Epipactis gigantea*, *Equisetum arvense*, *Juncus covillei*, *Marchantia polymorpha*, *Mimulus cardinalis*, *M. guttatus*, *M. moshatus*, and *Panicum pacificum*. Tussocks in the one-, three-, and nine-species treatments received 9 total transplants. For treatments of five species (10 transplants) and seven species (7 transplants), I adjusted transplant size to maintain constant cover and biomass. Throughout 1998 and 1999, I carefully removed species that were not purposely planted. These species were weeded when small to prevent the weeds, or their removal, from affecting invasibility. In spring 1999, Shannon diversity, a measure incorporating both the richness and relative abundance of species, was highly correlated with planted richness ($R^2 = 0.92$, $P = 0.001$). No natural recruits were found in 10 tussocks not sown with seeds, which suggested that natural recruitment did not significantly contribute to variability in the experiment.
29. I added 200 seeds to obtain accurate per capita demographic rates. To prevent seedlings from interfering with one another, I thinned them on the 12 July 1999 and 1 August 1999 sampling dates. I thus calculated the proportion of successful seeds as (proportion that germinated and survived to 12 July) × (proportion of the 12 July unthinned surviving to 1 August) × (proportion of the 1 August unthinned surviving to 3 October).
30. Total cover, the sum of each species' cover, can exceed 100% because species' canopies overlap.
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36. I added seeds of *Agrostis* and *Plantago* to 190 tussocks using the same selection criteria as for the pattern tussocks. I added *Cirsium* to a subset (50) of these tussocks, and fewer seeds per tussock, because I had fewer seeds of this species. Seedlings were followed using the same procedures as in the diversity manipulation experiment. Seedling size yielded similar results to the proportion of successful propagules.
37. I thank W. Satterthwaite, J. Williams, R. Globus, and F. Sexsmith for assistance in the field; the University of California Natural Reserve System for stewardship and preservation of the study site; and E. Berlow, C. D'Antonio, N. Hausmann, J. McGraw, M. Power, W. Satterthwaite, W. Sousa, K. Suttle, and J. Williams for helpful comments on the manuscript. Supported by a NSF Graduate Research Fellowship and Dissertation Improvement Grant.

Homogenization of Fish Faunas Across the United States

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Fish faunas across the continental United States have become more similar through time because of widespread introductions of a group of cosmopolitan species intended to enhance food and sport fisheries. On average, pairs of states have 15.4 more species in common now than before European settlement of North America. The 89 pairs of states that formerly had no species in common now share an average of 25.2 species. Introductions have played a larger role than extirpations in homogenizing fish faunas. Western and New England states have received the most introductions, which is a reflection of the small number of native fishes in these areas considered desirable gamefish by settlers.

Establishment of exotic species and loss of native species reduces regional differences among faunas and floras, a process referred to as biotic homogenization (1, 2). Homogenization of Earth's biota is accelerating and is an underappreciated aspect of global environmental change (3). Although many biologists have expressed concern about biotic homogenization, there are few quantitative assessments of the increased similarity among biota from different regions. Furthermore, the loss of regional distinctiveness can occur because of the introduction of widespread, cosmopolitan species or the extirpation of localized, endemic species. The relative importance of these two processes in homogenizing biotic communities is poorly known.

The distribution of many fish species has increased throughout the world as a result of intentional introductions for aquaculture and angling (4). The distribution of other species has expanded because of ballast water transfers, aquarium releases, and illegal stockings (5–7). In some cases, introduced fishes have eliminated native species and reduced regional biodiversity (8, 9). The addition of cosmopolitan species and the loss of endemic species is homogenizing the world's fish faunas, but the extent of this process is poorly documented.

Here, I describe the homogenization of freshwater fish faunas across the continental United States and evaluate geographical patterns and the relative importance of introductions versus extirpations in altering fish faunas. I assembled fish faunal lists for each of the 48 coterminous United States from regional textbooks, journal articles, and state

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