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Local interactions, dispersal, and native and exotic plant diversity along a California stream

Jonathan M. Levine

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Although the species pool, dispersal, and local interactions all influence species diversity, their relative importance is debated. I examined their importance in controlling the number of native and exotic plant species occupying tussocks formed by the sedge *Carex nudata* along a California stream. Of particular interest were the factors underlying a downstream increase in plant diversity and biological invasions. I conducted seed addition experiments and manipulated local diversity and cover to evaluate the degree to which tussocks saturate with species, and to examine the roles of local competitive processes, abiotic factors, and seed supply in controlling the system-wide patterns.

Seeds of three native and three exotic plants sown onto experimentally assembled tussock communities less successfully established on tussocks with a greater richness of resident plants. Nonetheless, even the most diverse tussocks were somewhat colonized, suggesting that tussocks are not completely saturated with species. Similarly, in an experiment where I sowed seeds onto natural tussocks along the river, colonization increased two- to three-fold when I removed the resident species. Even on intact tussocks, however, seed addition increased diversity, indicating that the tussock assemblages are seed limited. Colonization success on cleared and uncleared tussocks increased downstream from km 0 to km 3 of the study site, but showed no trends from km 3 to km 8. This suggests that while abiotic and biotic features of the tussocks may control the increase in diversity and invasions from km 0 to km 3, similar increases from km 3 to km 8 are more likely explained by potential downstream increases in seed supply. The effective water dispersal of seed mimics and prevailing downstream winds indicated that dispersal most likely occurs in a downstream direction. These results suggest that resident species diversity, competitive interactions, and seed supply similarly influence the colonization of native and exotic species.

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Processes operating at widely varying spatial scales control the diversity of species in communities. Evolutionary diversification, geologic history, migrations, and climate operate at biogeographic scales to determine the regional species pool (Ricklefs and Schluter 1993). Within regions, dispersal regulates the fraction of this pool available to colonize different locations across the landscape, while local scale species interactions, such as competition, facilitation, and predation, control the success of arriving propagules and the persistence of

established individuals. Though all of these processes are ecologically important, we are only beginning to understand how they combine to regulate local diversity (Ricklefs 1987, Cornell 1993, Ricklefs and Schluter 1993, Huston 1999, Shurin et al. 2000).

Ecologists have used a variety of approaches to evaluate the importance of local and regional processes in controlling species diversity. Experimental community ecology has provided the most compelling support for the importance of biotic interactions, most notably

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competition, in controlling local scale diversity (Connell 1983, Goldberg and Barton 1992). In contrast, comparative approaches, where local species richness is plotted as a function of regional richness (Terborgh and Faaborg 1980, Cornell 1993, Shurin 2000, Shurin et al. 2000), have provided considerable support for the importance of the species pool and its biogeographic determinants. Many of these latter studies have found that increases in the regional species pool are accompanied by increases in local diversity, suggesting that biotic interactions do not constrain diversity and that communities are unsaturated (Cornell and Lawton 1992, Cornell and Karlson 1997, Srivastava 1999). The overriding importance of the species pool has also been suggested by a number of community assembly studies conducted in experimental microcosms (Drake et al. 1993, 1996, Fox et al. 2000). However, the relevance of microcosm studies to natural communities is controversial (Carpenter 1996). Moreover, the comparative studies have been challenged because results depend on the actual scale of "local" and "regional" diversity (Caley and Schluter 1997, Srivastava 1999, Huston 1999, Loreau 2000) and can disagree with experimental results from the same systems (Shurin 2000).

Despite these criticisms, evidence is mounting that many communities are not saturated with species. Seed sowing experiments have shown that dispersal has tremendous potential to influence species diversity (Tilman 1997, Zobel et al. 2000, reviewed by Turnbull et al. 2000). However, dispersal operating over hundreds of meters or kilometers is difficult to measure (Harper 1977, Cain et al. 2000) and thus moving from the simple seed addition experiment to demonstrating that dispersal drives community-scale patterns has proven challenging (Cain et al. 2000, Nathan and Muller-Landau 2000).

While the literature provides clear examples of where the species pool, dispersal, and biotic interactions influence local diversity, these processes are typically investigated with different methodologies and rarely examined in a single study. Consequently, their relative importance to species diversity is still far from resolved (Huston 1999). Studies that experimentally invade communities with potential colonists (Eriksson and Ehrlén 1992, Burke and Grime 1996, Tilman 1997, Shurin 2000, Zobel et al. 2000) are needed to significantly enhance our understanding of this issue (Cornell 1993, Zobel 1997). Since biological invasions, experimental or otherwise, represent increases in diversity, they provide excellent opportunities to evaluate the relative importance of processes influencing diversity.

In this study, I explore the ecological processes controlling species diversity and biological invasions in a plant community along the South Fork Eel river in northern California, USA. In this system, herbaceous assemblages of varying diversity grow on tussocks formed by the sedge *Carex nudata*. The most diverse

and invaded tussocks are located downstream. I invaded natural and experimentally manipulated sedge tussocks with seeds of three native and three exotic species to evaluate three interrelated questions: 1. Do local biotic interactions cause diverse tussocks to saturate with native and exotic species or alternatively, are the tussock communities unsaturated and seed limited? 2. Do local scale biotic interactions or processes operating at larger spatial scales, such as dispersal, control the downstream patterns of species diversity and invasions in the system? 3. Do the local biotic interactions and larger scale processes that control native species diversity also control biological invasions?

Methods

Study system

The 8-km study stretch of South Fork Eel river flows through mixed evergreen forest located on the University of California's Angelo Coast Range Reserve. The riffle or cascading sections of stream are heavily colonized by the tussock forming torrent sedge, *Carex nudata*. *Carex* is much less abundant around the long pools that separate the riffles. The sedge tussocks average 30 cm in diameter and are discrete units, separated from one another by cobbles or water depending on the season. The tussocks provide habitat for the over 60 plant species living entirely in the active river channel. These associated species, which have an average of 80–90% of their individuals on *Carex* tussocks, are mostly small perennial vascular plants and bryophytes that depend on the tussock for stable substrate during winter flood events (Levine 2000a). Among the most common are the monkeyflowers *Mimulus guttatus*, *M. cardinalis*, and *M. moschatus*, graminoids including *Juncus covillei* and *Panicum pacificum*, and many bryophytes including *Brachythecium frigidum*, and *Conocephalum conicum*. Individual tussocks contain up to 20 species, with the most diverse tussocks tending to be those downstream (see Results). The system is also invaded by a number of European plants, including Canada thistle, *Cirsium arvense*, creeping bent grass, *Agrostis stolonifera*, and common plantain, *Plantago major*, each of which is also most abundant downstream (Levine 2000b). *Carex* tussocks occur in the smaller tributaries that enter the study stretch of the Eel, but have very few associated species. See Levine (2000a) for further details of the system.

Testing for saturation

To evaluate whether local biotic interactions cause tussocks to saturate with species, and more generally, how their resistance to colonization depends on the number

of residents, I followed the performance of native and exotic plants sown onto tussocks in which I had experimentally manipulated species richness. In late spring 1998, I carefully removed all associated resident species from 55 randomly selected 350-cm² tussocks at a single large riffle (see Levine 2000b for details about tussock moisture at this riffle). Each tussock was randomly assigned to one of five species richness treatments: 1, 3, 5, 7, and 9 native species (not including *Carex* itself), corresponding to the natural range of richness found on tussocks of that size. Greater replication was allocated to species poor tussocks (18 one-species tussocks, 11 three-species tussocks, 10 five-species tussocks, 9 seven-species tussocks, and 7 nine-species tussocks) because variation in composition is typically greatest at the low end of the diversity gradient. I determined the composition of each replicate by first defining a pool of 9 native species, and then assigning species to each tussock by a separate random draw from the pool. The pool of transplants included *Conocephalum conicum*, *Epipactis gigantea*, *Equisetum arvense*, *Juncus covillei*, *Marchantia polymorpha*, *Mimulus cardinalis*, *M. guttatus*, *M. moschatus*, and *Panicum pacificum*. I added all species as small transplants of similar size. Tussocks in the 1-, 3-, and 9-species treatments received 9 total transplants yielding a total cover of ~90%. For treatments of 5 species (10 transplants) and 7 species (7 transplants), I adjusted transplant size to maintain ~90% cover and constant biomass. The experimental communities established over the 1998 growing season and then experienced natural flooding during the 1998-1999 winter. Shannon diversity in the spring of 1999 was highly correlated with the planted richness ($R^2 = 0.92$, $P = 0.001$). Throughout the experiment, I carefully weeded species not purposely planted.

In the spring of 1999, I added 200 seeds of each of six species to the surface of the experimental tussocks. These included the three most common exotic species along the channel, *Cirsium arvense*, *Plantago major*, and *Agrostis stolonifera*, and three native plants selected to match the growth forms (2 forbs, 1 grass) and abundance of the exotic species. These were *Mentha arvensis* (mint), *Mimulus cardinalis* (monkeyflower), and *Panicum pacificum* (grass). For each tussock, I censused seedling number every three weeks during summer 1999 with a final census in summer 2000. To prevent seedlings from interfering with one another, I thinned them on the 12 July 1999 and 1 August 1999 sampling dates. I calculated the proportion of successful seeds as (prop. that germinated and survived to 7/12) \times (prop. of the 7/12 unthinned surviving to 8/1) \times (prop. of the 8/1 unthinned surviving to summer 2000). No natural recruits were found in 10 interspersed tussocks not sown with seeds, suggesting that natural recruitment did not significantly contribute to variability in the experiment. On 28 August 2000, to assess plant performance I harvested three randomly located plants of

each species on each tussock, and dried and weighed them.

In the experiment, two of the native species added as potential colonizers (*M. cardinalis* and *Panicum*) were also members of the transplanted resident communities. This was unavoidable since the need for many transplants as well as many seeds limited the candidate species to those that were abundant. This did not prove problematic because I clipped all flowers off the transplants in 1998 so they did not seed into the plots. Seedlings are readily distinguished from vegetative ramets.

Documenting downstream patterns of diversity and invasion

To quantify downstream patterns of diversity and invasion, I censused the composition of 241 tussocks across 16 riffles in late spring 1999. These 16 included all but the two or three most inaccessible riffles over the 8-km study stretch. Tussocks matching a size (400 cm²) and resident cover (90%) criteria were randomly selected within each riffle. Because riffles differed in their abundance of tussocks, the number of censused tussocks per riffle varied from 9 to 21. To obtain a measure of species diversity at the riffle scale, I pooled the censuses across nine random tussocks (or all nine) within each riffle, and calculated total species richness.

Seed additions to natural tussocks

To evaluate the roles of competitive interactions, abiotic factors, and seed supply in controlling the downstream increases in species diversity and invader abundance, I added seeds of native and exotic plants to tussocks at 16 riffles along the stream gradient. These were the same 241 tussocks I censused for quantifying the patterns of diversity. To assess the importance of competitive interactions in preventing establishment, at each of the 16 riffles, I randomly selected three tussocks for which I manually removed all species but the *Carex*. I added seeds to all 241 tussocks and measured establishment and survival following the procedures described for the diversity manipulation seed addition. By adding seeds of six species that were absent from most of the tussocks, I directly tested seed limitation of tussock species richness. Based on long-term monitoring data, the chance that a tussock received even a single natural recruit of the six sown species was less than 0.5%. For *Cirsium*, a species for which I had significantly less seed than other species, I added 100 instead of 200 seeds, and did so to only three cleared and three uncleared tussocks per riffle. For all tussocks in the study, I quantified the overlying forest canopy with a spherical densiometer and percent soil moisture

by weighing tussock sediments before and after drying in late August.

Estimating water dispersal and wind transport

If tussock communities are seed limited, then increased seed deposition downstream is a likely contributor to the downstream patterns of diversity and invasion in the system. To assess the downstream movement of water dispersed seeds in the system, I released highly visible red plastic glitter as a seed mimic and observed its distribution after winter flooding. I chose to release 19 kg, or about 90 000 000 particles, comparable to my estimates of seed produced by the common monkeyflower, *Mimulus guttatus*, when it is abundant within a riffle. Glitter has been used as a propagule mimic in biomechanical studies of water transport, and behaves similarly to small seeds (Koehl and Powell 1994). Both the mass and length of the glitter particles used here (Sulyn Industries, Coral Gables, Florida) are within one eighth of a standard deviation from the mean of the seeds from eight common Eel river species. In addition, like most seeds in the system, glitter stays on the water surface until disturbed by cascading flow. Its settling velocity is two standard deviations greater than the mean for the Eel river species, making its downstream transport a conservative measure of seed dispersal in the system. I scattered the glitter at a single riffle before the winter floods in late fall 1998, corresponding to the time when natural plants have dropped their seeds. In spring 1999, at each of the consecutive riffles downstream from the point of release, I searched 131 tussocks for the presence of glitter, for one minute.

Since dispersal over several hundred meters via wind is even less likely than via water (Waser et al. 1982, Willson 1993), its estimation would require a tremendous and intractable amount of seed or seed mimic. Therefore, to quantify the possibilities of long distance seed transport via wind, I recorded wind speed and direction with an anemometer and vane (R. M. Young) wired to a data logger (Campbell Scientific). I rotated the setup among nine locations throughout the 8-km study stretch from 22 July to 16 September 2000, the period coinciding with seed release. At all locations, I placed the anemometer and vane on a tussock just above the *Carex* vegetation, the maximum height at which resident species release seeds.

Results

Tussock community saturation

In the experiment where I manipulated resident species richness, all native and exotic plants successfully invaded even the most diverse tussocks (Fig. 1). Although

this suggests that local biotic interactions cannot completely prevent the establishment of new species, tussocks with a greater number of resident species were more effective in preventing successful establishment (Fig. 1). Increasing the richness of resident plants reduced the establishment success of all three native species by half and reduced their biomass by over two thirds (Fig. 1A–C). Though effects on *Mimulus* biomass were not significant, this was due to the reduced sample size following two growing seasons of high mortality (6 of 7 nine-species tussocks had no *Mimulus* individuals by summer 2000). Similar results were found for the exotic plants. Increasing richness negatively affected the establishment success of two of the three exotic species, *Agrostis* and *Plantago*, and negatively affected the biomass of all three (Fig. 1D–F). First year effects of diversity on *Agrostis*, *Plantago*, and *Cirsium* were similar (Levine 2000b).

Because these are results from two growing seasons after the seeds were added and include the intervening flood period, they are not transient effects of diversity on the seed or seedling stage (see Levine 2000b for a discussion of why these results were unlikely to be a “sampling effect”, Huston 1997, and for other details concerning the underlying mechanisms). Nevertheless, the R^2 values never exceeded 0.20 (Fig. 1 shows standard errors). This, along with the finding that tussocks do not saturate with species suggests that the effects of accumulated diversity may be overwhelmed by sufficient propagule supply.

Seed limitation

All six species successfully established on tussocks on which they were not previously present (Table 1). Averaging across all six species, adding 200 seeds (100 for *Cirsium*) successfully established at least one individual on over 50% of the tussocks. Although this suggests that the tussocks are seed limited, the proportion of successfully establishing seeds was quite low, ranging from 0.002 for *Mimulus* to 0.06 for *Agrostis* (Table 1). In addition, there was no clear difference between the establishment rate of native and exotic species ($t_4 = 0.801$, $P = 0.468$).

Controls over downstream patterns

In natural patterns along the South Fork Eel, species richness at both the tussock and riffle scale and the richness of exotic species per tussock increased with downstream location (Fig. 2). Results of the experimental seed addition to these tussocks indicated that removing the resident species from the tussocks increased establishment two- to three-fold (Fig. 3, ANOVA $P < 0.0001$ for all species, *Panicum* $F_{1,238} = 81.59$, *Mentha*

$F_{1,238} = 287.5$, *Mimulus* $F_{1,238} = 87.08$, *Agrostis* $F_{1,238} = 120.5$, *Plantago* $F_{1,238} = 210.3$, *Cirsium* $F_{1,117} = 64.79$). With resident species present, the establishment success of all species but *Panicum* was a non-linear function of downstream location, with peak performance at around km 3 (Fig. 3, Table 2). Downstream of this point, establishment was constant or declined (Table 2). Even with resident species removed, however, establishment for all species but *Cirsium* increased from km 0 to km 3 (Fig. 3, Table 2), indicating that the increase in diversity over this stretch results from abiotic factors and not the competitive environment. Other biotic factors such as herbivory and disease rarely, if ever, killed

a seedling, and the sedges themselves showed no systematic differences over the 8-km study stretch. Because the establishment of all species but *Panicum* declined or remained constant from km 3 to km 8 on both cleared and uncleared tussocks (Fig. 3, Table 2), the increase in diversity over this stretch of river (Fig. 2) does not correspond to increasingly favorable abiotic or biotic conditions.

Decreased establishment in upstream riffles is likely due to shading in the narrower river corridor (Fig. 4A). These plants are sensitive to shading (Levine 2000a), and all but one of the riffles with canopy cover > 20% lay upstream of km 3. Slightly decreased water

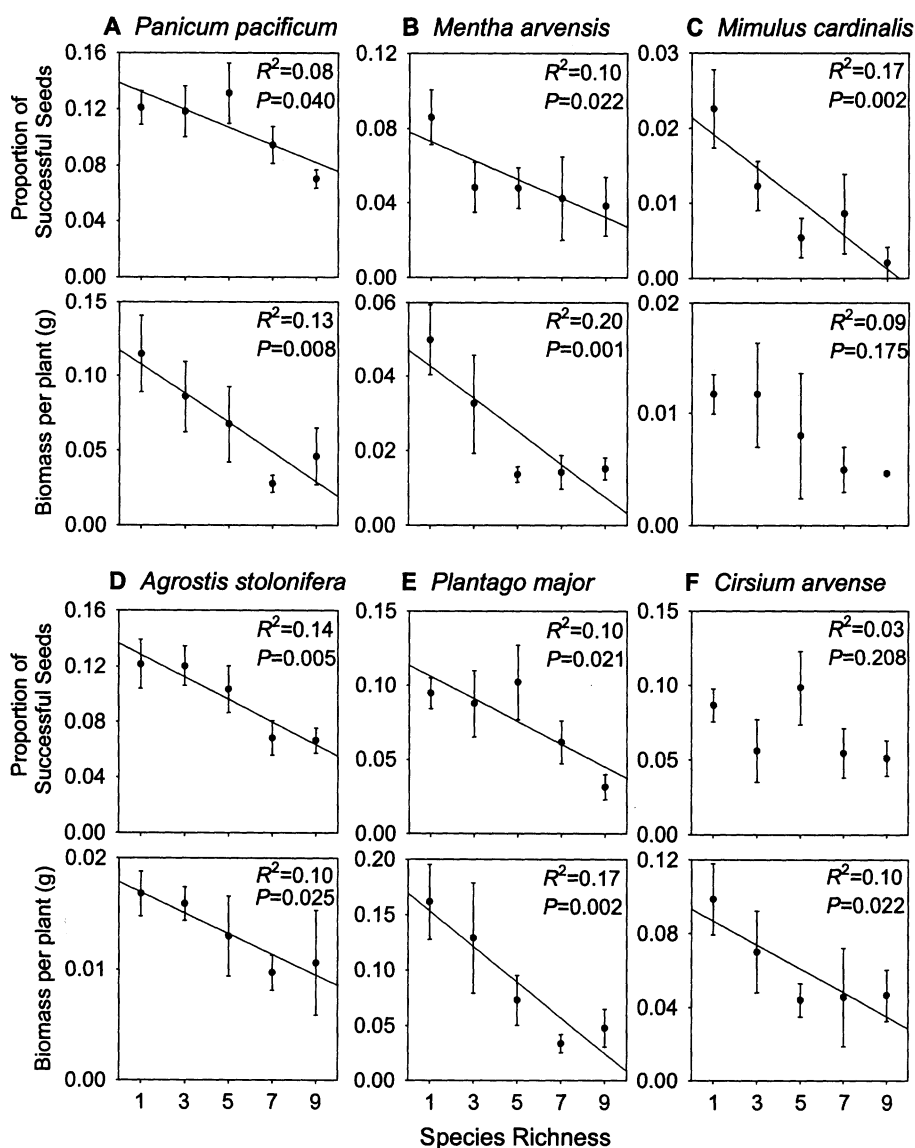


Fig. 1. Effects of a direct manipulation of species richness on the colonization success (proportion of seeds that germinated and survived to the second growing season) and final biomass per plant of three native (A–C) and three exotic (D–F) plants. Shown are means \pm 1 SE.

Table 1. Colonization by sown species not previously contained on the tussock

Added species	Proportion of successfully colonizing seeds (mean \pm 1 standard error)	Proportion of tussocks colonized by at least one individual (200 seeds added)
<i>Panicum pacificum</i>	0.043 \pm 0.002	0.600
<i>Mentha arvensis</i>	0.019 \pm 0.003	0.583
<i>Mimulus cardinalis</i>	0.002 \pm 0.001	0.111
<i>Agrostis stolonifera</i>	0.060 \pm 0.007	0.777
<i>Plantago major</i>	0.029 \pm 0.004	0.551
<i>Cirsium arvense</i>	0.017 \pm 0.003	0.424

availability may be another contributing factor (Fig. 4B). The decreased success downstream (Fig. 3) may relate to decreased tussock moisture in these locations (Fig. 4B). The most downstream locations have the greatest absolute declines in river stage over the course of the summer.

Water and wind dispersal

Following the 1998–1999 winter floods, 4 of the 131 sampled tussocks at the riffle 210 m downstream from the release riffle contained glitter released the previous fall as a seed mimic. One of the 131 tussocks 560 m downstream contained glitter, and none was found at the riffle 1110 m downstream. In addition, I located the seed mimic on substrates other than tussocks at points up to 4.5 km downstream. Overall, though the number of recovered particles represents a very small fraction of those released, these results confirm that water is capable of transporting seeds the hundreds of meters between riffles in the system and depositing them in tussocks. Because I was unlikely to recover particles buried in the resident plants, and because the settling velocity of glitter exceeds that of most Eel river seeds, these results probably underestimate the true transport of seeds in the system.

Still, dispersal might not occur in a prevailing downstream direction if wind effectively transports seeds upstream. However, the maximum wind speed recorded over nearly 2 months of 5-s interval sampling was only 6.4 m/s. Given the low height of release (\approx 40 cm) and this maximum wind speed, upstream dispersal across the 250 m between riffles most likely proceeds via strong unmeasured updrafts or a series of shorter colonization and dispersal events along the sides of pools. Furthermore, even if wind could transport seeds between riffles, aerial dispersal is more likely to occur downstream. Wind tended to blow within 20 degrees of the orientation of the channel (Fig. 5), and at only three of the nine sites (those with dashed arrows) did wind tend to blow upstream. At the six other sites, only between 0 and 11.4% of wind measures above 2.7 m/s (6 mph)

blew within 45° of the channel upstream (Fig. 5). Some of these sites, such as the starred location in Fig. 5 where none of the 97 wind measures $>$ 2.7 m/s blew upstream over the six-day recording period, provide a formidable barrier to upstream dispersal.

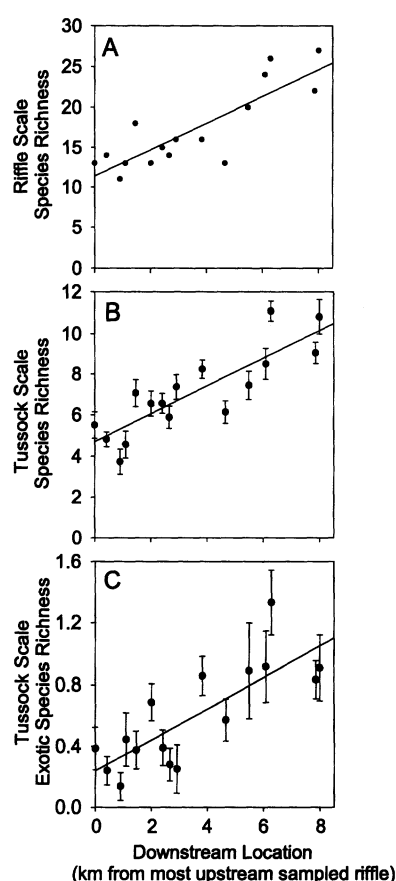


Fig. 2. Downstream increases in A. Riffle scale species richness ($R^2 = 0.716$, $P = 0.001$), B. Tussock scale species richness ($R^2 = 0.347$, $P = 0.001$), and C. Tussock scale exotic species richness ($R^2 = 0.164$, $P = 0.001$). See Methods for how these were calculated. Results for native species richness alone (Riffle scale richness: $R^2 = 0.661$, $P = 0.001$, Tussock scale richness: $R^2 = 0.317$, $P = 0.001$) were similar. Shown in B and C are means \pm 1 SE.

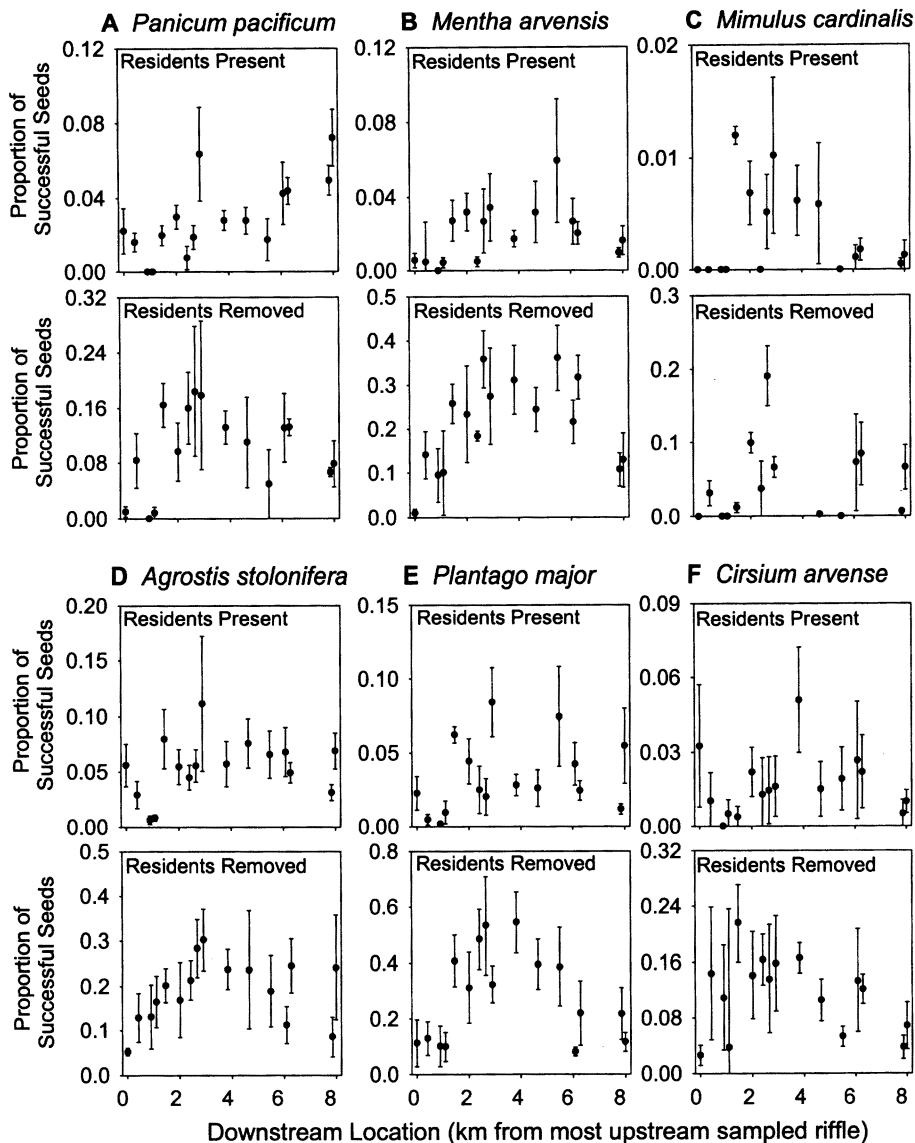


Fig. 3. Colonization success of the seeds of three native (A–C) and three exotic (D–F) species planted onto tussocks with resident species present or removed across the 8-km study stretch. Biomass per plant showed similar patterns. Shown are means \pm 1 SE.

Discussion

The results of this study indicate that although local biotic interactions reduce the success of potential colonists, the tussock communities are unsaturated. The resident plant species of the *Carex* tussocks reduced the ability of the native and exotic plants to colonize by 50 to 80% (Fig. 3). In addition, these species less successfully established on experimental tussocks with a greater richness of resident plants (Fig. 1). Negative effects of resident species diversity on the success of arriving propagules has also been found in grasslands (Knops et al. 1999, Naeem et al. 2000, Symstad 2000, Dukes 2001), freshwater ponds (Shurin 2000), marine

benthic habitats (Stachowicz et al. 1999) and microcosms (McGrady-Steed et al. 1997). Though this result has received a surge of attention from those studying the controls over biological invasions (Elton 1958, Levine and D'Antonio 1999), it also bears on native community dynamics. That systems become more difficult to colonize as they accumulate more and more species may be a common pattern of community assembly (Drake et al. 1996).

Although tussocks with more resident species were more resistant to potential colonists, all tussocks, even the most diverse had some fraction of successful colonists (Fig. 1). This means that processes influencing diversity at larger spatial scales, such as dispersal, can

Table 2. Regression results for colonization success versus downstream location

	Nonlinear regression on colonization from km 0 to km 8			Linear regression on data upstream of km 3			Linear regression on data downstream of km 3		
	R^2	P_{model}	$P_{\text{squared term}}$	R^2	P	Slope	R^2	P	Slope
<i>Panicum pacificum</i>									
Residents present	0.189	0.001	0.147	0.022	0.129	0.0044	0.123	0.001	0.0078
Residents removed	0.163	0.014	0.005	0.285	0.003	0.0586	0.058	0.268	-0.0107
<i>Mentha arvensis</i>									
Residents present	0.056	0.005	0.004	0.052	0.019	0.0083	0.013	0.298	-0.0027
Residents removed	0.381	0.001	0.001	0.351	0.001	0.0872	0.257	0.014	-0.0446
<i>Minulus cardinalis</i>									
Residents present	0.051	0.008	0.002	0.078	0.004	0.0022	0.051	0.040	-0.0014
Residents removed	0.111	0.060	0.026	0.359	0.001	0.0403	0.015	0.582	-0.0057
<i>Agrostis stolonifera</i>									
Residents present	0.030	0.059	0.031	0.035	0.056	0.0127	0.014	0.285	-0.0046
Residents removed	0.148	0.021	0.009	0.371	0.001	0.0704	0.037	0.382	-0.0174
<i>Plantago major</i>									
Residents present	0.028	0.075	0.048	0.044	0.031	0.0112	0.001	0.814	-0.0007
Residents removed	0.301	0.001	0.001	0.385	0.001	0.1378	0.361	0.002	-0.0910
<i>Cirsium arvense</i>									
Residents present	0.033	0.336	0.151	0.001	0.918	-0.0004	0.159	0.029	-0.0079
Residents removed	0.108	0.064	0.032	0.070	0.175	0.0302	0.217	0.025	-0.0215

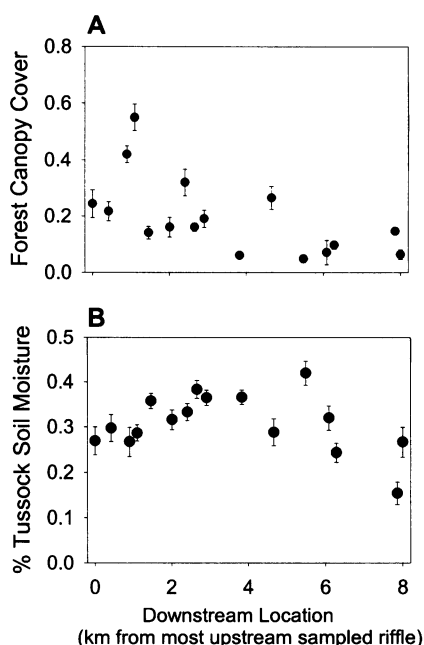


Fig. 4. A. Forest canopy cover and B. % tussock soil moisture in August 1999 as a function of downstream location. Results of regression analysis fitting quadratic equations are as follows A. $R^2 = 0.19$, $P = 0.001$, and B. $R^2 = 0.20$, $P = 0.001$. Shown are means ± 1 SE.

influence patterns of diversity in the system, potentially overwhelming the local effects of biotic interactions. This is further supported by the finding that the tus-

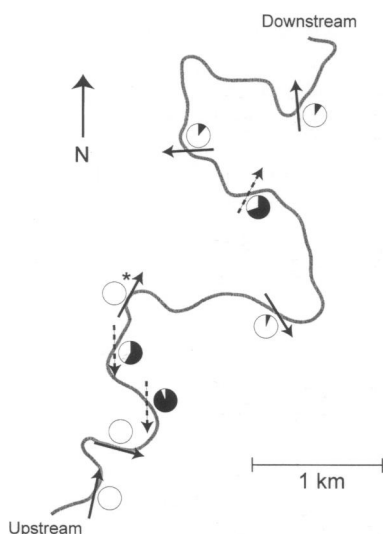


Fig. 5. Arrows show mean wind direction at nine locations along the South Fork Eel river. The black section of the pie chart at each site shows the proportion of wind measurements above 2.7 m/s that blew upstream (within a 90° arc centered on the channel). Dashed arrows indicate sites with > 50% upstream winds. At the starred site, 0 of 97 wind measures > 2.7 m/s recorded over a six-day period blew upstream.

socks were seed limited. Added seeds of all species successfully established on natural tussocks on which they were previously absent (Table 1). This lack of saturation even at the tussock scale is significant. The disproportionate support for the importance of regional controls over local diversity has been argued to result from unreasonably large areas being considered "local" in many studies (Huston 1999). Yet here, even though the small tussocks define the local scale of species interactions, they did not completely saturate with species.

The lack of saturation at the tussock scale is also important for understanding patterns of species diversity along the Eel river. In the system, downstream tussocks and riffles were more diverse than those upstream, and also contained more exotic species (Fig. 2). These patterns could be explained by: 1. An increasingly favorable abiotic environment downstream, 2. Increasingly favorable competitive conditions, or 3. Increased seed supply to downstream tussocks. Results of the seed sowing experiment indicated that from km 0 to km 3 tussocks become increasingly favorable for colonization (Fig. 3). This was found even on tussocks with the resident species removed, indicating that abiotic factors may underlie the increase in diversity over this stretch of river. However, from km 3 to km 8, the suitability of the cleared and uncleared tussocks for colonization either declined or remained constant (Fig. 3, Table 2). Thus, the increase in diversity over this stretch of river cannot be explained by abiotic or biotic features of the tussocks or their environment. Given that tussocks are seed limited (Table 1), and that water-borne seeds move unidirectionally downstream, differential seed supply is a likely explanation for the increase in diversity from km 3 to km 8. Furthermore, when seed supply was equalized across this downstream gradient in the seed sowing experiment, I did not find more colonists downstream (Fig. 3).

The role of dispersal in the system

Variation in seed supply controls the increase in diversity from km 3 to km 8 only if seeds disperse more readily downstream than upstream. This might be expected since water is typically much more effective than wind at transporting seeds long distances in rivers (Waser et al. 1982, Willson 1993, Cain et al. 2000), and all water dispersal is downstream. Indeed, differential downstream dispersal was found for the most common Eel river species, *Mimulus guttatus*, occurring along a Utah stream (Waser et al. 1982, Vickery et al. 1986). Based on the transport of the glitter seed mimic, differential downstream dispersal probably occurs with other species in the system. Even though glitter provided a conservative measure of dispersal (see Methods), water transported this seed mimic to tussocks 200 and 560 m

downstream of the release riffle over a single winter season. Another mechanism of downstream dispersal occurs when winter floods dislodge and transport entire tussocks. Nearly all riffles contain at least several tussocks that were clearly transported from upstream. One of my permanently marked tussocks dislodged by the 1998–1999 flooding, reestablished 1.1 km downstream. All resident species (orchids, monkeyflowers, and liverworts) survived the event and reproduced.

Based on measurements of wind speed and direction, and seed dislodgment rates from a past seed addition study (Levine 2000a), wind seems less likely to transport seeds the hundreds of meters between riffles and particularly unlikely to move seeds upstream. Wind speeds were low overall, never exceeding 6.4 m/s, and at only three of nine locations did wind tend to blow upstream (Fig. 5). The annual flooding is also a barrier to wind dispersal. Even if a seed is blown upstream, it must stay in place over the winter flood period. Based on a past experiment where I added seeds to tussocks before and after the winter floods (Levine 2000a), I estimate that winter flooding removes at least 99.7% of the seeds deposited the previous fall. This makes airborne dispersal particularly difficult in this system, and is probably why I find evidence for seed limitation (Table 1) even within riffles where seed sources are nearby. Upstream dispersal, which is critical to the long-term persistence of riverine populations, most likely proceeds via rare updrafts or a chain of shorter colonization and dispersal events between the sparse tussocks along the sides of pools. I have also collected seed rain throughout the system, though identifying which seeds are from other riffles and thus quantifying the external seed input is impossible.

Inferences from mathematical models

Mathematical models incorporating key features of the Eel river plant community also support the hypothesis that seed supply may drive downstream patterns of diversity in the system. These models explore the spatial and temporal dynamics of communities occurring in a linear series of patches (riffles) connected by dispersal, with dispersal occurring in a prevailing downstream direction. This work has pointed to the importance of the habitat's periodic disturbances in maintaining seed supply driven gradients in diversity. The South Fork Eel river plant community is flooded annually, and though a typical winter of floods removes less than 0.5% of the tussocks and kills only a small fraction of the resident plants, the system was nearly reset by the catastrophic 1955 and 1963 floods. Accounts of the study stretch before and after these 100–1000 year interval events indicate that the flooding removed 70–90% of the tussocks, likely leaving only small source populations of the various species. Following such an

event, the further downstream the riffle, the more likely it is to contain an upstream source of any given species. My modeling work suggests that because of this, dispersal strongly drives downstream increases in diversity. This result is robust to changes in demographic rates, dispersal abilities, and competitive interactions. Major flooding may also be important because the dislodged tussock assemblages are differentially deposited downstream.

Flooding disturbance may be a key process allowing dispersal to drive downstream increases in diversity, though this does not exclude abiotic factors and competition from contributing to these gradients. In other studies, these factors, along with disturbance and dispersal have been suggested to influence downstream patterns of plant diversity in rivers (Nilsson et al. 1994, Pollock et al. 1998).

Relationships between species diversity and invasions

In this study, native and exotic species responded similarly to resident species diversity (Fig. 1), seed augmentation (Table 1), and the abiotic and competitive environment encountered over the 8 km study stretch (Figs 2, 3). These similarities between native and exotic species may be quite general, considering that many habitats favorable for a diversity of native species also contain numerous exotic species (Stohlgren et al. 1999; see Levine and D'Antonio 1999 for review). Moreover, Thompson et al. (1995) have found that in the British Isles and the Netherlands, expanding exotic and native species are functionally identical.

If native and exotic species tend to respond similarly to environmental gradients, we may more confidently apply our knowledge of native species diversity to understand exotic species invasions, and vice versa. For example, comparative studies testing local versus regional control over species diversity (Cornell 1993) may hold the answer to a brewing question in the study of biological invasions. A number of recent studies have indicated that species diversity enhances resistance to biological invasions at small neighborhood scales (Knops et al. 1999, Stachowicz et al. 1999, Naeem et al. 2000, Symstad 2000, Dukes 2001), but whether this applies to the scale of entire communities is unknown. From the diversity literature, we know that increases in the species pool tend to be accompanied by proportional increases in local species diversity (Cornell 1993, Huston 1999, Srivastava 1999), and this suggests that at the scale of entire communities, more diverse systems might not better resist colonization or invasion.

Similarly, biological invasions may help ecologists better understand the controls over native species diversity. Plots of local versus regional richness (see Introduction) have fueled current debates over whether

communities are saturated with species. However, recent reviews of this approach (Huston 1999, Srivastava 1999), modeling studies (Caswell and Cohen 1993, Loreau 2000), and experimental tests of the conclusions (Shurin 2000), have raised questions about what these comparative studies can accurately conclude. Biological invasions provide an unequivocal test of community saturation. Species introductions are manipulations of the species pool, and the fact that few communities, even the most diverse, are free of biological invasions is strong evidence that communities are not saturated with species. Experimental invasions, such as those conducted in the current study provide similar conclusions. Unsaturated patches in the landscape have been found in temporary ponds (Shurin 2000), prairies (Tilman 1997), calcareous grasslands (Zobel et al. 2000, but not in Burke and Grime 1996), woodlands (Eriksson and Ehrlén 1992) and in many other seed addition experiments (reviewed by Turnbull et al. 2000). Further examining the similarities between the processes controlling native diversity and those influencing exotic species invasions should significantly enhance our understanding of both of these prominent issues in ecology.

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