

# Dominant Species and Diversity: Linking Relative Abundance to Controls of Species Establishment

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**ABSTRACT:** Ecological theories make divergent predictions about whether extant species inhibit or promote the establishment of new species and which aspects of community composition determine these interactions; diversity, individual dominant species, and neutral interactions have all been argued to be most important. We experimentally tested these predictions by removing plant biomass (0%, 7%, 100%) from boreal forest understory communities. The 7% removals were restricted to the numerically dominant species, the second most dominant species, or many low-abundance species, thereby separating the effects of species composition from those of biomass. We tested the effects of all removal treatments on seedling establishment. Competitive effects were driven by one dominant species and were inconsistent with resource complementarity, neutral, or competition-colonization models. Facilitative effects were apparent only following removal of all vegetation, of which the most dominant species comprised more than 80%. Our results indicate that numerically dominant species in a community can influence the establishment of new species more than species diversity, but the direction of interaction can shift from facilitative to competitive as community density increases.

**Keywords:** boreal forest, coexistence, colonization, competition, facilitation, resource complementarity.

## Introduction

One of the fundamental goals of ecology is to understand the processes that determine species diversity and, in turn, to understand how diversity affects ecosystem processes (Chesson 2000; Srivastava and Vellend 2005). Over the past 2 decades, threats of species loss and species invasions have motivated numerous empirical studies that quantify the effects of species loss on ecosystem processes, such as

resistance to invasion (Levine and D'Antonio 1999; Schwartz et al. 2000; Fridley et al. 2007). These studies have shown that although some ecological communities can competitively inhibit establishment of new species, other communities facilitate the establishment of new species (Smith et al. 2004; Brooker et al. 2008). Furthermore, it is not clear which attributes of community composition are most important in determining community effects on species establishment. Although several studies have shown that high species diversity limits newly establishing species (Lyons and Schwartz 2001; Kennedy et al. 2002; Levine et al. 2004), studies that explicitly test different components of the invaded community often report that the identity of the dominant species is equally or more important than diversity per se (Fargione et al. 2003; Smith et al. 2004; Emery and Gross 2007). Other studies suggest that community dynamics are largely neutral and, thus, that species establishment is not influenced by community composition (Herben et al. 2004). Thus, on the basis of empirical results to date, there are six potential ways in which communities can influence species establishment, combining the two directions of response (competitive, facilitative) and the three important elements of community composition (diversity, dominant species identity, neither). These six empirical scenarios are mirrored in the development of six hypotheses to explain the patterns, which we now examine in detail.

Studies of the competitive effect of communities on species establishment have focused almost exclusively on a resource complementarity hypothesis as a common theoretical framework (Levine and D'Antonio 1999; Fridley et al. 2007). This hypothesis posits that diversity is maintained through each species having a distinct resource niche, and as a consequence, more diverse communities are predicted to use resources more completely and thus better exclude both exotic and native invaders (i.e., limit diversity). Other models predict that species identity, not diversity, determines the resistance of a community to in-

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vaders (Chesson 2000). In particular, the competition-colonization trade-off model posits that good competitors will be poor dispersers, and this competitive ranking determines whether an invader can establish in the presence of the resident species (Tilman 1994). The most abundant species in such a trade-off are often the best competitors (Levine and Rees 2002; Harpole and Tilman 2006), which is consistent with conceptual models proposing that numerical dominance likely results from greater competitive ability (Sala et al. 1996). By contrast, Hubbell's (2001) neutral model proposes the competitive equivalence of all species, precluding a relationship between either diversity or species identity and the establishment of new species (Hubbell 2001).

Facilitation hypotheses provide fundamentally different predictions about the impacts of extant species on the establishment of new species. A number of studies have shown that facilitation may increase the realized niches of newly establishing species, and thus their probability of establishment increases if the extant community is present (Bruno et al. 2003; Callaway 2007). These studies have produced three distinct conceptual models of facilitation. First, the diversity-facilitation model proposes that more diverse communities may have higher levels of invasibility because each extant species has the potential to facilitate the establishment of new species (Bulleri et al. 2008). Second, the principal facilitator model describes a single species that facilitates others through unique functions, such as habitat stabilization or hydraulic lift, while the beneficiary species often exhibit competitive dynamics (reviewed in Callaway 2007). Third, the neighbor facilitation model does not make species-specific predictions but rather posits that facilitation is a community-wide phenomenon more dependent on context than community attributes, such as diversity and the identity of dominant species. For example, a number of models predict that facilitation replaces competition in certain situations, such as in high-stress environments (Bertness and Callaway 1994; Brooker et al. 2008).

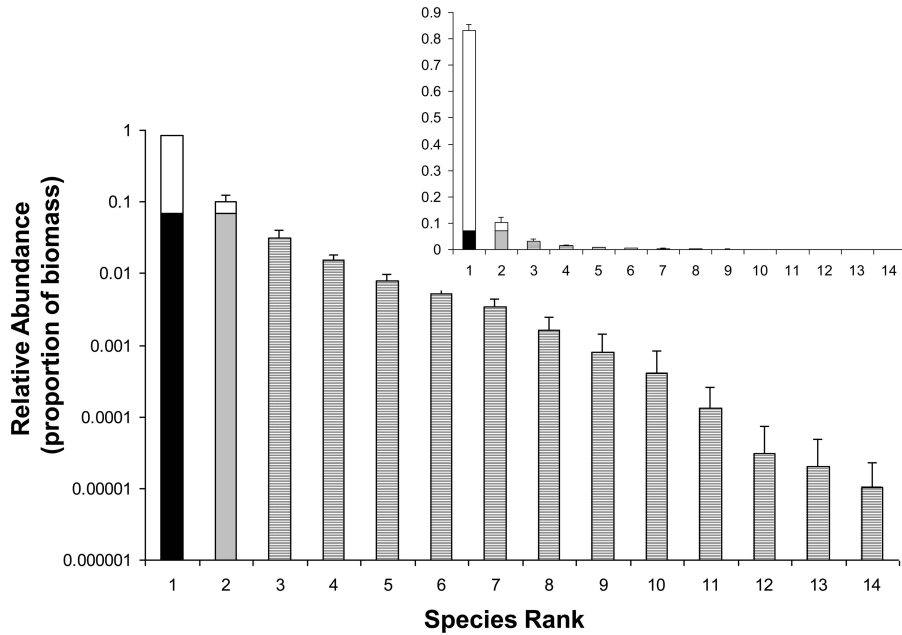
These six hypotheses can be difficult to experimentally distinguish, especially when manipulations of either diversity or a numerically dominant species necessarily result in changes in other community properties such as biomass. Here, we disentangle the relative contributions of these mechanisms by examining invasion along an experimentally imposed disturbance gradient that manipulated the identity and density of the extant community. In particular, we used the rank abundance curve of a naturally occurring plant community to generate three removal treatments that were equal in the proportion of biomass removed but differed in the number and identity of species removed (fig. 1), thereby separating the effects of biomass from those of community composition. We then added

seedlings of 12 species to test the effects of these removals on establishment dynamics.

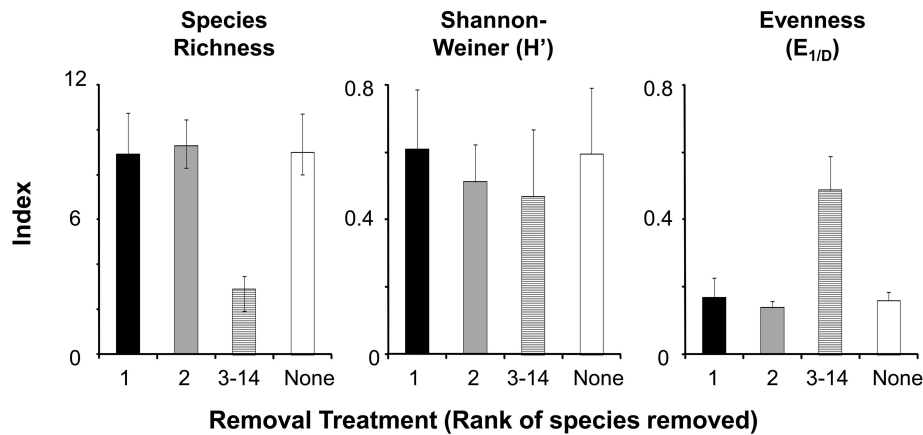
Our approach can be used to discriminate among the six hypotheses just described. For example, neutral theory and the neighbor facilitation model predict equal effects for removals of the same biomass but differ in whether the underlying interaction is competitive or facilitative (fig. 2A, 2B). The resource complementarity model posits that, on average, the relative abundance of each species reflects the availability of its resource niche (Tilman et al. 1997; McKane et al. 2002). Thus, a disturbance that eliminates many low-abundance species should allow a greater diversity of establishing species than a disturbance of similar size that affects only a single, numerically dominant species (fig. 2C). The diversity-facilitation model also relies on the importance of many low-abundance species but predicts the opposite effect of the resource complementarity hypothesis (fig. 2D; Bulleri et al. 2008). In contrast, because of the greater importance of species identity in a competition-colonization trade-off, a disturbance that affects the competitively superior species would cause the largest increase in the establishment of new species (eqq. [3.1] and [3.2] from Tilman 1994). Here, we present the numerically dominant species as competitively superior (fig. 2E), as is often the case in late successional communities (Tilman 1994; Harpole and Tilman 2006). However, unlike the other theories, the link between numeric dominance and competitive ability needs to be tested independently for a competition-colonization trade-off. We are unaware of specific predictions for the principal facilitator model and therefore used a Lotka-Volterra model to generate predictions for a species that facilitates others and in turn is negatively impacted by its beneficiaries (app. A in the online edition of the *American Naturalist*). Under the assumptions of this version of the Lotka-Volterra model, numerically dominant species are more likely to be principal facilitators. Thus, a disturbance that targets numerically dominant species should decrease seedling establishment more than a similarly sized disturbance that targets low-abundance species (fig. 2F).

We applied our design in a boreal forest understory in northern Canada. Previous work in the area has shown some facilitation by the extant community (Callaway et al. 2002) and also that community composition appears to be driven by competition for resources with little effect from herbivory (Turkington et al. 2002). Despite these general findings, no studies have examined the roles of extant species in limiting or promoting diversity in this area. Establishment was assessed with 12 species of transplanted seedlings by measuring survival over three growing seasons. The seedlings consisted of both exotic and native herbs and grasses that were functionally similar to the low-abundance species already present. Establishment is a key

**A) Removal treatments**



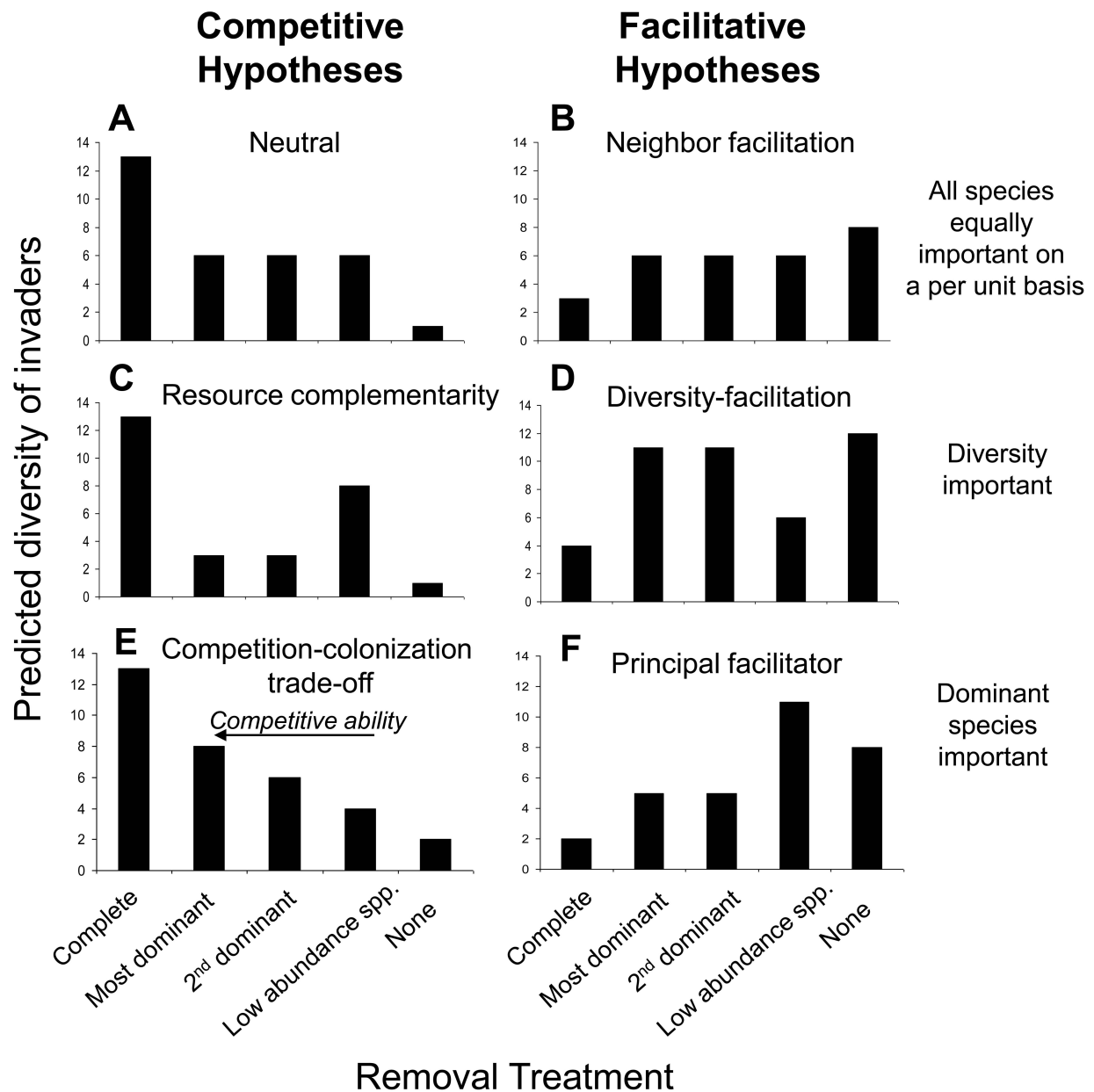
**B) Community following removals**



**Figure 1:** Removal treatment, based on the rank abundance relationship averaged over the 50 1-m<sup>2</sup> plots in the study area, and the effects of removals on community structure. *A*, Shading illustrates the removal treatment, with each removal treatment consisting of 7% of the total plot biomass. Biomass was removed by removing as many of the low-biomass species as necessary (low-abundance removal treatment; *striped bars*), most of the second-rank species (herbaceous dominant removal; *gray bars*), or a small proportion of the first-rank species (woody dominant removal; *black bars*). The inset shows the same graph with a linear Y-axis. *B*, Species richness, Shannon diversity, and evenness of the experimental plots following removal treatments, with none indicating no removal. The bar shading corresponds to the removal shown in *A*.

stage in population growth (Emery and Gross 2007), and transplanted seedlings have previously been used to test both competitive and facilitative interactions (e.g., numerous studies reviewed in Callaway 2007). It should be noted, however, that the use of transplants precludes any

effects of extant vegetation on germination of new seeds. In addition to transplanted seedlings, we used differences in resource availability among treatments and extant species' competition and colonization abilities to discriminate among potential coexistence mechanisms.



**Figure 2:** Predictions of six models from competition-based and facilitation-based hypotheses of species interactions about the effect of species-specific disturbances on the diversity of newly establishing seedlings. Disturbances (*X*-axis) involve the removal of all plants (complete), no plants (none), or an equivalent amount (7% of total biomass) of numerically dominant species or low-abundance species. Diversity of invading species (*Y*-axis) illustrates the qualitative predictions of each hypothesis and should be considered relative to other treatments in the same hypothesis. All predictions assume that each seedling is interacting only with the extant flora, not other seedlings. *A*, Neutral model. *B*, Neighbor facilitation model assumes no species-specific effects but that facilitation underlies invader establishment. *C*, Resource complementarity model whereby higher-diversity communities use more resources and thereby exclude invaders. *D*, Diversity-facilitation model, which posits that high diversity facilitates more species. *E*, Competition-colonization trade-off model predicts that better competitors exclude more species; numerical dominance is often correlated with competitive ability, as represented here with the arrow indicating the competitive ability of extant species. *F*, A principal facilitator is a single species that facilitates many others and is most likely to be a numerically dominant species.

### Study Area and Methods

The study area, near Kluane National Park in Yukon, Canada, has been described in long-term studies of the area (Krebs et al. 2001; Turkington et al. 2002). The area is semiarid, receiving a mean annual precipitation of ~230 mm, mostly falling as rain during the summer months but including an average annual snowfall of about 100 cm (Turkington et al. 2002). The vegetation at lower elevations is a patchwork of spruce and aspen forest and shrubby grasslands.

Five replicate sites were selected within aspen stands ranging in distance from 0.8 to 9 km from each other and separated by different habitat types. The central site was located at Christmas Creek near the Alaska Highway (138°13.9'W, 61°00.5'N). At each site, we selected 10 1-m<sup>2</sup> plots with similar plant communities, on the basis of the cover of the numerically dominant understory species. We first developed allometric relationships for each understory plant species by testing the relationship between biomass and specific traits, such as height or leaf area. These allometric relationships were used to estimate species-specific biomass for each individual within each plot (app. B in the online edition of the *American Naturalist*) and to generate an average rank abundance curve for all 1-m<sup>2</sup> plots (fig. 1).

We used the average rank abundance curve to generate three removal treatments that were equal in proportional biomass removed but differed in the number of species and the relative abundance of the species removed (fig. 1). These treatments had 7% of the total plot biomass removed, which was the average relative biomass of all the low-abundance species in a plot (rank 3 or higher; fig. 1). The species removed in each treatment were determined by their ranked biomass, with *Arctostaphylos uva-ursi* (woody dominant) the first rank and *Epilobium angustifolium* (herbaceous dominant) the second rank. For each plot, we first estimated the standing biomass, on the basis of the estimated biomass of each individual, and then removed individuals until 7% of the biomass was removed. In the low-abundance removal plots, we started with the individuals of species at the highest rank (lowest biomass) and moved progressively downward. If a target species had more biomass than the total biomass to be removed, plants were randomly selected from that species until the desired 7% was attained. Two additional treatments, 0% (control) and 100% removal, were also created.

Removals were done by painting the leaves of individual plants with a general systemic herbicide, glyphosate (6.8 g active ingredient L<sup>-1</sup>). Target plants were left in the plot to insure complete plant mortality and were spatially referenced so as to maintain treatments in subsequent years. Root connections were severed with a spade 15 cm

outside of the plot edge, and the buffer zone between the plot edge and the spaded line had the same removal treatment applied. Initial removals were completed in late July 2004 and were maintained until June 2006.

In mid-May 2005, 12 species of bare-root seedlings were transplanted into half of the plots (app. B). Seedling survival was monitored in August 2005 and at the start and end of the 2006 and 2007 growing seasons. In addition to the seedling additions, all plots were monitored to assess macronutrient availability, soil water content, and light availability (app. B).

### Statistical Methods

#### *Extant Community and Resources*

Following partial removal treatments, the remaining extant community within plots was assessed for three community indices: species richness, Shannon diversity, and evenness ( $E_{1/D}$ ). The evenness index ( $E_{1/D}$ ) is defined as  $1/(DS)$ , where  $S$  is species richness and  $D$  is from Simpson's index and is determined by the proportion ( $p$ ) of the total biomass occupied by each species:  $D = \sum p^2$  (Smith and Wilson 1996; Emery and Gross 2007). Differences among treatments were assessed using ANOVAs.

Species' natural colonization rates were estimated by calculating the percentage of plots that a species colonized if it were absent after the initial removal treatment. For the dominant species, this included only the complete removal plots, while many low-abundance species had the potential to colonize many plots. To test whether the different numbers of plots that could be colonized caused a bias, we redid the estimates, restricting all species to invasion into complete removal plots only. These measures were strongly correlated ( $r = 0.94$ ,  $P < .0001$ ), so we report only the first.

Species' competitive abilities were not measured directly but rather inferred from a 10-year community fertilization study by Turkington et al. (2002). Harpole and Tilman (2006) showed that species with low  $R^*$  values (the concentration of free nutrients when grown in monoculture; a low  $R^*$  indicates a high competitive ability) decrease in relative abundance when a community is fertilized, while those with high  $R^*$  values increase in relative abundance. We therefore used the change in percent cover with NPK fertilization reported by Turkington et al. (2002) to estimate relative competitive ability (RCA) of species within the community:  $RCA = \text{abundance}_{\text{control}} / \text{abundance}_{\text{fertilized plots}}$ . This RCA index scores as  $<1$  for poor competitors (species that increase following fertilization) and  $>1$  for species that decrease in relative abundance following fertilization.

Mixed models with repeated measures were used to test

for changes in resources. Initial analyses indicated that seedling addition made no difference to resource availability ( $P$  varied from .14 to .9), so we averaged plots with and without seedlings added for each removal treatment within a block. Block was included as a random effect, and the block  $\times$  treatment interaction was considered the subject for the temporal autocorrelation function, which was chosen on the basis of model fit statistics (corrected Akaike Information Criterion, Bayesian Information Criterion). For nutrients and soil moisture, if the global tests for treatment effects were significant, preplanned contrasts were used to compare partial removal treatments with each control (complete and no removal), and differences among partial removal treatments were compared using a post hoc test. Because we hypothesized that removing the woody dominant species would not affect PAR levels (its prostrate growth form meant it was shorter than the seedlings), we compared among all treatments with a post hoc test.

In these analyses and subsequent analyses, we also tested whether partial removal plots with greater amounts of biomass removed had a larger effect, because removing 7% of biomass in a plot resulted in different absolute amounts of biomass removed. Neither biomass nor a biomass  $\times$  removal interaction was statistically significant, and therefore they are not reported.

### Seedling Responses

Survival analysis was used to compare species' mortality rates in each treatment over time. The experiment was designed as a blocked split plot, with the survival time of each seedling treated as a subreplicate of the species within a plot (Allison 1995). Some removal treatments and seedling species had complete mortality. This made it impossible to consider all data in the full experimental design because of violation of analysis assumptions and because of model convergence problems. We therefore first analyzed the main effect (i.e., removal effects without species effects or interactions) by grouping all seedlings within a plot, regardless of species identity. This acts as an unbiased test of the main effect when there are no statistical interactions and will underestimate the significance of the main effects when there is an interaction (Koch 1969). After finding a significant difference between the "complete" removal and all other treatments, this treatment was removed from the analysis since it clearly influenced the effect of time in the model. We then analyzed the effect of the other removal treatments, again grouping all seedlings within each plot. We used generalized linear mixed models with a logistic link function for all survival analyses. For the first tests, degrees of freedom were determined with the Kenward-Roger correction (Littell et al.

2006). Because there was unexplained heterogeneity in the experiment (Pearson  $\chi^2/df > 1$ ), we considered covariates that showed no relationship with the treatments to avoid confounding covariate and treatment effects (we used a cutoff of  $P > .6$  from the resource results). Three covariates— $S$ ,  $NH_4$  (app. B), and initial community biomass (before removal treatment)—met this requirement and were considered. Only  $NH_4$  was significant and included in analyses. A scale parameter was also included as needed to model variance that was greater than a binomial variance (Littell et al. 2006). To analyze the full split plot model, we first removed the complete removal treatment and all species that had 100% mortality in any of the remaining treatments (app. C in the online edition of the *American Naturalist*). Sampling data were combined within each year (spring and fall census). Experimental blocks and block  $\times$  treatment combinations were included as random effects.

Species diversity was analyzed using a mixed model with repeated measures. Block was included as a random effect, and individual plots were considered subjects. Three diversity indices were generated for the transplants: species richness, Simpson's index ( $1 - D$ ), and the Shannon-Weiner index. These indices were strongly correlated ( $r_s$  ranging from 0.95 to 0.99; all  $P < .0001$ ), so we report only species richness. Diversity showed a significant time  $\times$  treatment interaction because all treatments started with similar levels of diversity. We therefore tested for significant differences in the change in seedling species richness over time using a mixed model repeated-measures ANCOVA. We also tested whether diversity showed an effect after rarefaction, with rarefaction performed at the plot level. Rarefaction was tested for a number of levels of individuals, ranging from 20 individuals, the lowest number of seedlings in a plot at the end of year 1, to two individuals, the lowest number of seedlings in a plot at the end of year 3. Rarefaction to each of these levels produced qualitatively similar results, and only the first is reported.

## Results

### Extant Community

Following removal treatments, the extant community differed in both species richness and evenness (fig. 1B). The low-abundance species removal caused both a decrease in the number of species present and also an increase in evenness since the remaining species were more similar in relative biomass (both  $P < .0001$ ). Shannon diversity did not differ among treatments ( $P = .26$ ), and the herbaceous dominant and woody dominant removals did not differ significantly in diversity or evenness (both  $P > .2$ ).

Resource availability differed among treatments for seven resources, with the complete removal treatment generally having the highest level of resource availability (fig. 3). Nitrate and calcium availability were significantly greater in the complete removal treatment than the partial removal treatments (both  $P < .01$ ), but these latter treatments did not differ from each other or from the no removal treatment (all  $P \geq .08$ ; fig. 3A). Similarly, the complete removal treatment had the most available phosphorus in the first year (all  $P < .02$ ), but this difference disappeared in subsequent years (all  $P \geq .18$ ; fig. 3B). Magnesium showed a different pattern, with the no removal treatment having higher levels than the partial removal treatments ( $P = .04$ ) and the herbaceous dominant removal containing more magnesium than the low-abundance removal treatment ( $P = .02$ ). Light availability for seedlings was highest in the complete removal and lowest in the no removal and woody dominant removal treatments (fig. 3C; all differences  $P < .02$ ), with the woody dominant showing no effect because it was shorter than the seedlings. Soil moisture showed a significant time  $\times$  removal interaction ( $F_{16,80} = 2.13$ ,  $P = .014$ ), with the complete removal treatment significantly higher than all other treatments except the herbaceous dominant removal at the beginning of the experiment. Treatment rankings in July 2005 and June 2006 were complete removal  $>$  herbaceous dominant  $>$  woody dominant  $>$  low abundance  $>$  no removal, but by 2007 there were no significant differences among treatments (fig. 3D). Potassium also showed a significant time  $\times$  treatment interaction. However, fluctuations in potassium among treatments over time suggest that this effect was due to a spurious correlation.

The colonization rates of extant species did not show the expected decrease with relative abundance that has been observed in other communities, mainly because the herbaceous dominant had a very high colonization rate (fig. 4A). When we plotted our colonization results against published data on the competitive response of species (taken from table 1 in Turkington et al. 2002), we found a strong negative correlation (fig. 4B). This negative relationship is a necessary condition for the competition-colonization trade-off model.

#### Seedling Responses

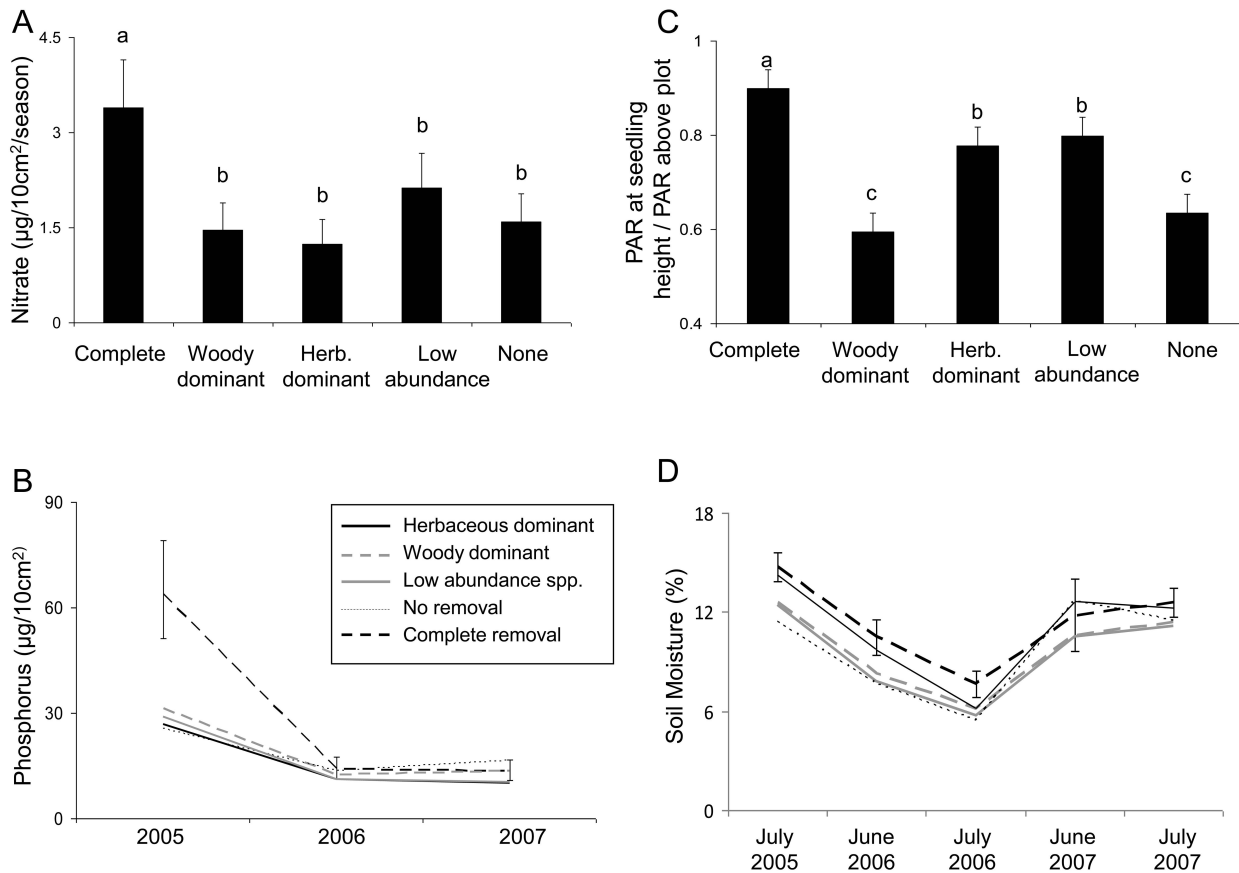
The survival rate of seedlings over three growing seasons differed among treatments ( $F_{4,74} = 19.7$ ,  $P < .0001$ ; fig. 5A, 5B). Survival was higher when the herbaceous dominant was removed compared with all other treatments (all  $P < .02$ ), and the complete removal treatment had the lowest seedling survival (all  $P < .0001$ ). The other three treatments did not differ significantly (all  $P > .29$ ).

When we excluded the complete removal treatment from our analysis and considered only those species whose seedlings had  $>0\%$  survival in all other treatments, the analysis showed two trends. First, there was a significant interaction between removal treatment and year ( $F_{6,297} = 2.23$ ,  $P = .04$ ). This interaction occurred because seedlings in the low-abundance removal treatment had a similar survival rate as seedlings in the herbaceous dominant removal treatment in the final year of the study (78% and 77%, respectively), whereas the herbaceous dominant removal treatment had the highest average survival in the other years. This interaction, along with the reduction of the species and sampling periods considered, made the difference among the partial removal and no removal treatments nonsignificant ( $P = .35$ ). Second, the species identity of transplanted seedlings had an important effect on survival ( $F_{7,141} = 12.3$ ,  $P < .0001$ ; app. C). This species effect did not change with removal treatment (interaction  $P = .23$ ), indicating that the composition of seedlings did not depend on the removal treatment. Survival did, however, change over time (year  $\times$  species interaction;  $F_{14,303} = 7.22$ ,  $P < .0001$ ) because two species (*Phleum alpinum* and *Poa compressa*) had much lower survival in the third year than in the previous year, while all other species had a higher survival in the third year.

The diversity of transplants mirrored survival trends (fig. 5C, 5D). All treatments had similar diversity of transplants at the outset of the experiment but differed in diversity over time (time  $\times$  treatment interaction;  $F_{3,91} = 3.14$ ,  $P < .03$ ). The herbaceous dominant removal treatment maintained a higher level of species richness than the other partial removal treatments ( $P < .03$ ) but was not significantly different from the no removal treatment ( $P = .12$ ). Because richness appeared to be mainly driven by the number of surviving seedlings, we used rarefaction to test for density-independent diversity effects. After rarefaction, differences among treatments became nonsignificant ( $P = .4$ ). The complete removal treatment had lower species richness than all other treatments, with three of five replicates each containing one surviving seedling of different species at the end of the experiment (fig. 5D).

#### Discussion

We found evidence of both competition and facilitation of establishing species, albeit at different levels of vegetative cover. Net competitive effects were seen at high vegetation cover, where small reductions in the biomass of the herbaceous dominant were sufficient to increase seedling survival and maintain a higher level of seedling diversity (fig. 5). Net facilitative effects, which resulted in a decrease in seedling survival and diversity following reduction of the extant community, were apparent when all vegetative bio-



**Figure 3:** Differences in resource availability among removal treatments. Note that the woody dominant was the most abundant species and the herbaceous dominant the second most abundant species in the community, so that bars are arranged as in figure 2. All graphs show mean  $\pm$  SEM. Different letters indicate significant differences ( $\alpha = 0.5$ ) among treatments. *A*, Nitrate availability. *B*, Phosphorus availability indicated a time  $\times$  removal interaction, with no significant difference 2 or more years after treatment. *C*, Proportion of photosynthetically active radiation (PAR) available at seedling height (0.10 m) compared with PAR above all plants in a plot (1.1 m). *D*, Soil moisture indicated a time  $\times$  treatment interaction.

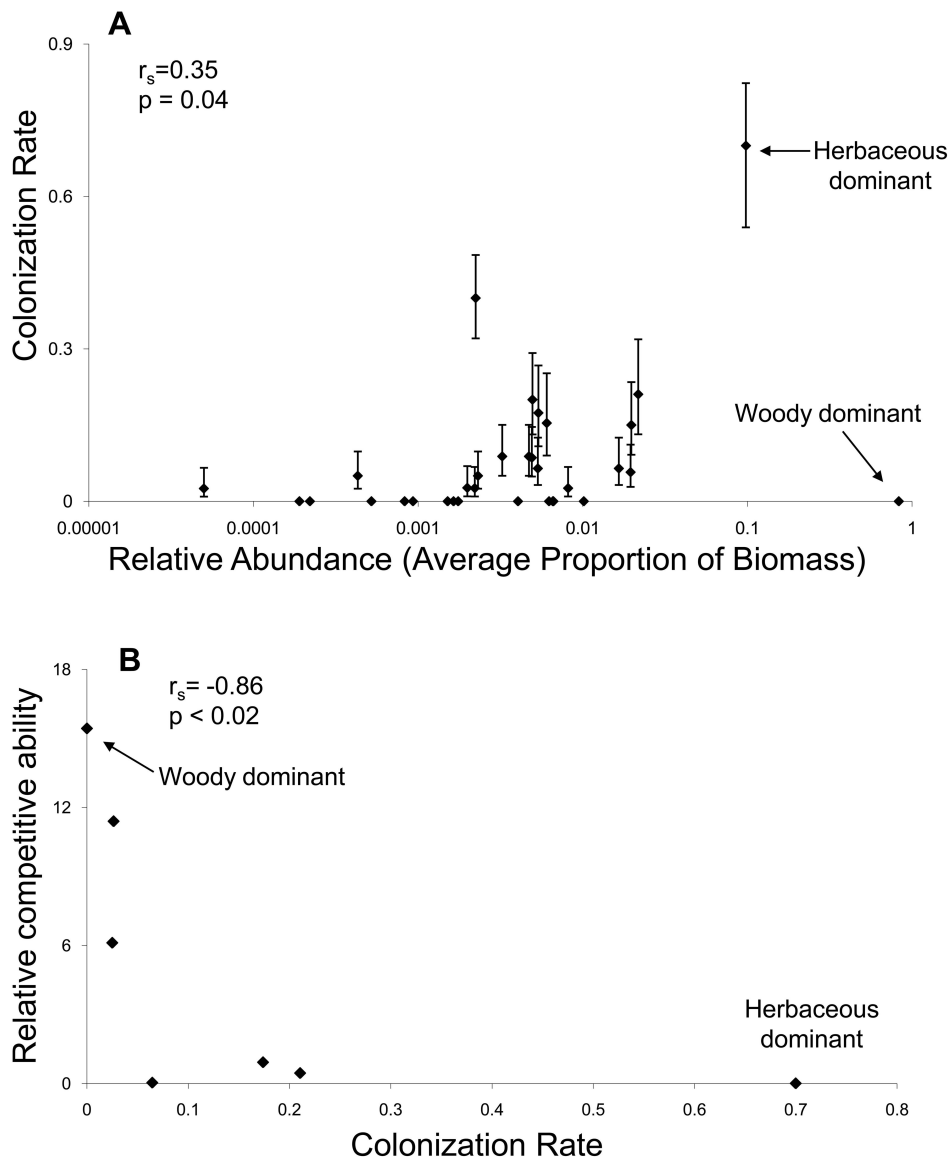
mass was removed but not following any of the partial (7% biomass) removal treatments. We consider six different hypotheses that predict distinct effects of removals on species establishment. Our results partially support several of these hypotheses, but the observed mixture of competitive and facilitative interactions were not consistent with any single model. Overall, we show that species richness has no detectable effect on species establishment in this community and that numerically dominant species have important but inconsistent effects. The different species effects detected are best understood by considering both facilitative and competitive outcomes of species interactions.

*Facilitative Effects*

Models assuming that competition for resources provides the sole limit on the establishment of new species were

not supported by our data. When all potential competitors were removed from a community, most resources became more available, but seedlings failed to establish. This facilitative effect was evident in both summer and winter, suggesting that neighboring vegetation reduced multiple stresses for new seedlings. However, despite evidence of facilitation when all extant species were removed, removal of 7% of community biomass did not result in an incremental effect (fig. 5D). Together, these results indicate that facilitative dynamics dominate seedling establishment only when disturbance levels are sufficient to remove all but the most abundant species from the community (i.e., >7% of total biomass). There have been both conceptual and mathematical models that propose that facilitation dominates at lower plant densities but switches to neutral or competitive dynamics at higher densities (Callaway and Walker 1997; Hernandez 1998). Our results support this



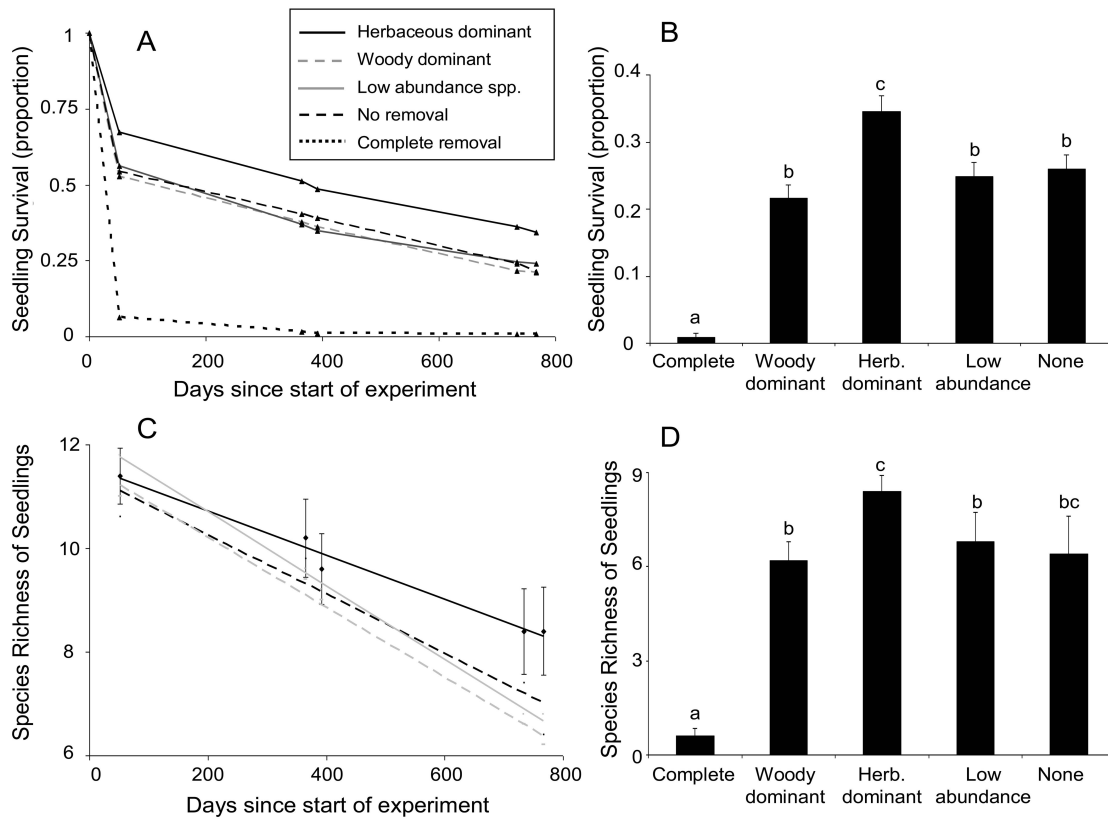


**Figure 4:** Extant species' colonization rates and competitive abilities. *A*, Colonization rates of species increased with mean abundance, except in the case of the woody dominant. *B*, Colonization was negatively correlated to species' competitive abilities, with competitive ability taken from published literature on changes in abundance following fertilization (greater increase following fertilization = poorer competitor).

hypothesis and suggest that facilitative processes may be important in early successional dynamics but play a relatively minor role when small-scale disturbances occur in intact communities. A number of studies that use removals to show strong facilitative effects may be poorly suited to detecting such changes in the relative importance of facilitation because they remove all surrounding vegetation (similar to our complete removal treatment; e.g., Choler et al. 2001; Callaway et al. 2002).

The density-dependent facilitative effects observed were

inconsistent with all facilitation hypotheses that we considered (fig. 2*B*, 2*D*, 2*F*) but do offer insight into the effects of specific species. For example, much of the literature on diversity effects focuses on species loss from a community (Hooper et al. 2005). When this species loss consists of many low-abundance species that are often considered most vulnerable, we do not see net facilitative effects (fig. 5*D*). Indeed, we removed the large majority of plant species in the low-abundance removal treatment without causing any net facilitative effects (figs. 1*B*, 5*D*). Instead,



**Figure 5:** Seedling establishment following removal treatments. Note that the woody dominant was the most abundant species and the herbaceous dominant the second most abundant species in the community, so that bar graphs are arranged as in figure 2. *A*, Number of seedlings surviving in each removal treatment at each census. *B*, Survival at the end of the experiment, with different letters indicating significantly different survival rates ( $\alpha = 0.05$ ). *C*, Species richness at each census date, with linear regression slopes fit to each treatment to model time  $\times$  treatment interactions. The complete removal treatment line is not included because it is below the values shown. *D*, Species richness at the end of the experiment, with different letters indicating significant differences in the regression slopes among treatments.

it is apparent that higher levels of disturbance (>7%) are needed to produce net facilitative effects. Because facilitation is density dependent, it is likely that the woody dominant is important to facilitative dynamics; the only other species with sufficient biomass, the herbaceous dominant, had a competitive effect on the transplanted seedlings. However, it should be noted that our experimental design did not include removals between 7% and 100% of biomass, and we therefore could not distinguish between species-specific effects and general facilitation from all neighbors at high removal levels. Previous research on facilitation by specific species (Smith et al. 2004; Rae et al. 2006) offers support for species-specific effects, whereas examples of facilitation regardless of neighbor identity (Choler et al. 2001; Callaway et al. 2002) suggest that either hypothesis is plausible.

Although it has been argued that facilitation needs to be incorporated into theories of species coexistence (Bruno

et al. 2003; Callaway 2007; Brooker et al. 2008), there has been relatively little progress. A number of models predict when species interactions will be more facilitative than competitive (Bertness and Callaway 1994; Callaway and Walker 1997), but such models do not make predictions about how these processes determine the diversity of a community or what limits a facilitative community from continually growing. More recent models, such as the facilitation  $R^*$  model (Gross 2008), provide new hypotheses about facilitation but are difficult to test. For example, Gross's model requires tests of both mortality and reproduction rates as well as information on species' competitive ranks. Similarly, density-dependent facilitation (Hernandez 1998) can be tested empirically only with a priori knowledge of which species are likely to facilitate others or through removals of various densities of all species within a community. Thus, although these models extend our conceptual understanding of how facilitation might

operate within communities, realistic experimental tests still need to be developed. Our results suggest that density-dependent facilitation may be particularly relevant and that such a mechanism would likely include numerically dominant species.

### *Competitive Effects*

Despite the importance of facilitation when all neighbors are removed, the competitive effect of removing the herbaceous dominant was large, given the disturbance level. This competitive effect informs us about the processes that limit diversity when the community is subjected to minor disturbances. For example, neutral theory requires that all species behave equally in terms of both their impacts on other species and their recruitment probabilities (Hubbell 2001); our results do not support either requirement.

Removing low-abundance species did not create "open niches" for seedling species, as predicted by the resource complementarity hypothesis. If grass species, for example, fill a specific functional niche, we would expect the removal of low-abundance species to favor grass establishment, because 28% of the biomass of low-abundance species is made up of grasses. Our results reject this hypothesis, instead showing that both alpha diversity and the composition of establishing species are unaffected by removing numerous low-abundance species. These results are inconsistent with a number of experimental communities using artificial gradients in diversity (Levine et al. 2004). However, artificial communities may not be well suited to testing invasion hypotheses because of unrealistic species composition (Fridley et al. 2007). Nonetheless, our results are also inconsistent with one field experiment that used removals to show the importance of low-abundance species (Lyons and Schwartz 2001), suggesting that the role of low-abundance species varies across communities.

Differences in seedling survival among partial removal treatments suggest that a competitive hierarchy may best explain establishment patterns in this community. One model, the competition-colonization trade-off, requires a competitive hierarchy and initially appeared to operate within the community (fig. 4B). If such a mechanism determined seedling survival, we would expect the removal of the worst colonizer to promote the greatest rate of seedling survival. We see the opposite trend, however, with the best colonizer (the herbaceous dominant) limiting seedling establishment most. This result would be unstable if a competition-colonization trade-off structured community membership, since any species that is both competitively superior and a superior colonizer would quickly displace all others in a community (Tilman 1994). Nonetheless, the high dispersability of the herbaceous dominant, *Epilobium*, and its competitive effects on other species are well known

(Broderick 1990; Hansson and Fogelfors 1998). These features of *Epilobium* are more consistent with the conceptual model proposed by Sala et al. (1996), which posits that numerically dominant species play a larger role per unit biomass than other species in a community.

Just as the herbaceous dominant appears to break the rules by having both a high colonization rate and a large competitive impact on invaders, it appears that the other dominant species, *Arctostaphylos uva-ursi*, plays a very different role in the community. Although many theories suggest that dominant species should be most effective at suppressing other species in a community (Tilman 1980; Sala et al. 1996), others suggest that avoiding competition altogether by occupying a distinct niche may lead to high abundance and even promote facilitative interactions. A number of studies support this latter hypothesis by showing that one species or group of species is facilitated by a functionally distinct species (Levine 2000; Smith et al. 2004; Valiente-Banuet et al. 2006). For example, herbaceous plants in northern Norway are facilitated by a guild of woody shrubs that include *A. uva-ursi* (Rae et al. 2006). More generally, the diverse impacts of dominant species on invasibility and ecosystem function indicate that dominant species are often critically important to community dynamics but that their roles are not always predictable a priori (Smith et al. 2004; Emery and Gross 2007).

### *Conclusion*

Seedling establishment is a key stage in population growth (Emery and Gross 2007), with early establishment results often predicting long-term patterns (Foster and Tilman 2003). Our study, which shows large species-specific effects on seedling establishment, has important implications for diversity in this boreal forest understory community and for plant community dynamics more generally.

The results highlight the importance of facilitation in early succession and illustrate that early and late successional dynamics are influenced by different processes as species interactions switch from facilitative to competitive. Our study also illustrates that numerically dominant species do not necessarily play consistent roles within communities, with one dominant limiting establishment within the community and the other likely facilitating seedlings when at low densities. Overall, our approach has provided insight into the complexity of facilitative and competitive interactions that are acting in this community and highlights the need for explicit consideration of species abundances in studies of community dynamics.

More generally, the experimental design we developed offers a framework for discriminating how facilitative and competitive processes act and interact under a range of circumstances and also for broadly distinguishing between

the effects of dominant species and diversity by using appropriate controls for biomass removed. Although the importance of dominant species has been tested (Smith et al. 2004; Emery and Gross 2007), previous studies have not linked the role of dominant species with specific predictions from theory. Our work demonstrates both the theoretical and practical importance of considering dominant species even though they contribute little to species richness. This general approach is stronger than many experiments that test single hypotheses and may act as a starting point for broader tests of theory in community ecology.

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### Literature Cited

- Allison, P. D. 1995. Survival analysis using SAS: a practical guide. SAS Institute, Cary, NC.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9:191–193.
- Broderick, D. H. 1990. The biology of Canadian weeds. 93. *Epilobium angustifolium* L. (Onagraceae). *Canadian Journal of Plant Science* 70:247–259.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. J. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119–125.
- Bulleri, F., J. F. Bruno, and L. Benedetti-Cecchi. 2008. Beyond competition: incorporating positive interactions between species to predict ecosystem invasibility. *PLoS Biology* 6:e162.
- Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. Springer, Dordrecht.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308.
- Cody, W. J. 2000. Flora of the Yukon Territory. 2nd ed. National Research Council of Canada, Ottawa.
- Cornish, P. S., and S. Burgin. 2005. Residual effects of glyphosate herbicide in ecological restoration. *Restoration Ecology* 13:695–702.
- Coupland, D., and P. J. W. Lutman. 1982. Investigations into the movement of glyphosate from treated to adjacent untreated plants. *Annals of Applied Biology* 101:315–321.
- Emery, S. M., and K. L. Gross. 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. *Ecology* 88:954–964.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the USA* 100:8916–8920.
- Foster, B. L., and D. Tilman. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology* 91:999–1007.
- Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88:3–17.
- Gross, K. 2008. Positive interactions among competitors can produce species-rich communities. *Ecology Letters* 11:929–936.
- Hansson, M., and H. Fogelfors. 1998. Management of permanent set-aside on arable land in Sweden. *Journal of Applied Ecology* 35:758–771.
- Harpole, W. S., and D. Tilman. 2006. Non-neutral patterns of species abundance in grassland communities. *Ecology Letters* 9:15–23.
- Herben, T., B. Mandak, K. Bimova, and Z. Munzbergova. 2004. Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology* 85:3223–3233.
- Hernandez, M.-J. 1998. Dynamics of transitions between population interactions: a nonlinear interaction  $\alpha$ -function defined. *Proceedings of the Royal Society B: Biological Sciences* 265:1433–1440.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638.
- Koch, G. G. 1969. Some aspects of the statistical analysis of “split plot” experiments in completely randomized layouts. *Journal of the American Statistical Association* 64:485–505.
- Krebs, C. J., S. A. Boutin, and R. Boonstra. 2001. Ecosystem dynamics of the boreal forest: the Kluane project. Oxford University Press, New York.
- Levine, J. M. 2000. Complex interactions in a streamside plant community. *Ecology* 81:3431–3444.
- Levine, J. M., and C. M. D’Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26.
- Levine, J. M., and M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *American Naturalist* 160:452–467.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis

- of biotic resistance to exotic plant invasions. *Ecology Letters* 7: 975–989.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. 2nd ed. SAS Institute, Cary, NC.
- Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function: invasion resistance. *Ecology Letters* 4:358–365.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, et al. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415:68–71.
- Parent, S., and C. Messier. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Canadian Journal of Forest Research* 26:151–154.
- Rae, D. A., W. S. Armbruster, M. E. Edwards, and M. Svengård-Barre. 2006. Influence of microclimate and species interactions on the composition of plant and invertebrate communities in alpine northern Norway. *Acta Oecologica* 29:266–282.
- Sala, O. E., W. K. Lauenroth, S. J. McNaughton, G. Rusch, and X. Zhang. 1996. Biodiversity and ecosystem functioning in grasslands. Pages 129–149 in H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze, eds. *Functional roles of biodiversity: a global perspective*. Wiley, Chichester.
- Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J. van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* (Berlin) 122:297–305.
- Smith, B., and B. J. Wilson. 1996. A consumer's guide to evenness indices. *Oikos* 76:70–82.
- Smith, M. D., J. C. Wilcox, T. Kelly, and A. K. Knapp. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106:253–262.
- Srivastava, D. S., and M. Vellend. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics* 36:267–294.
- Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist* 116:362–393.
- . 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the USA* 94:1857–1861.
- Torstensson, N. T. L., L. N. Lundgren, and J. Stenström. 1989. Influence of climatic and edaphic factors on persistence of glyphosate and 2,4-D in forest soils. *Ecotoxicology and Environmental Safety* 18:230–239.
- Turkington, R., E. John, S. Watson, and P. Secombe-Hett. 2002. The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *Journal of Ecology* 90:325–337.
- Valiente-Banuet, A., A. V. Rumebe, M. Verdu, and R. M. Callaway. 2006. Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proceedings of the National Academy of Sciences of the USA* 103:16812–16817.

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Plants in boreal forests of the Yukon Territory were studied to understand what controls biodiversity (photograph by Benjamin Gilbert).