



Effects of diversity on diversity: consequences of competition and facilitation

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Diversity in one group of species or genotypes is often correlated with diversity in a second group – prominent examples including native vs exotic species, and genetic diversity in a focal species vs species diversity in the rest of the community. I used simulation models to investigate the roles of competition and facilitation among species or genotypes in creating diversity–diversity relationships, with a focus on facilitation, which has received little theoretical attention. When competitive interactions dominate, increasing diversity in one group reduces diversity in the second group via filling of available niche space. Facilitation can create positive diversity–diversity relationships via a sampling effect, whereby a strong facilitator of the second group is more likely to be present as diversity increases in the first group, and also via one group acting as a source of biotic heterogeneity (i.e. diversifying selection) on the second group. However, the biotic heterogeneity effect is expected only under restricted conditions – with asymmetric facilitation, only during a transient period, or only over a small range of species diversity levels – and therefore seems unlikely to operate within trophic levels in natural communities. More generally, the simultaneous operation of competition and facilitation results in several different diversity–diversity relationships and underlying mechanisms. The results clarify the potential roles of positive and negative interactions in creating diversity–diversity relationships, and in determining the outcome of community dynamics in general. This study also highlights some important difficulties in incorporating facilitation into ecological theory for communities with many species.

Relationships between patterns of biodiversity in two or more co-occurring groups, such as different taxa, different trophic levels, native vs exotic species, or species diversity vs genetic diversity, are of great interest in ecology (Vellend 2005, Lamoreux et al. 2006, Fridley et al. 2007, Longmuir et al. 2007). The interest is due to the potential these relationships hold for advancing our understanding of a variety of fundamental issues, including the determinants of community invasibility (Levine 2000, Fridley et al. 2007), the outcome of trophic interactions (Longmuir et al. 2007), the potential for using some groups as surrogates for biodiversity in other groups (Lamoreux et al. 2006), and simultaneous ecological and evolutionary community dynamics (Vellend 2005, Vellend and Geber 2005). The strength and direction of such diversity–diversity relationships varies tremendously among systems and scales of observation, but is often significantly negative or positive. At the most general level, correlated patterns of biodiversity have two potential explanations. Diversity in different groups may be correlated either because each responds independently to the same external variable, such as resource supply, spatial heterogeneity, environmental stress, etc., or they may be correlated because of direct effects of diversity in one group on diversity in the other group (Vellend and Geber 2005). Within each of these broad

classes of explanation, a long list of specific mechanisms may be at work.

In this paper I take a theoretical approach to understanding the processes by which diversity in one group may causally influence diversity in another group on the same trophic level. The most visible manifestation of this general issue in the recent literature has been a focus on the relationship between species richness in potentially competing native vs exotic species (reviewed by Fridley et al. 2007). At a local scale (e.g. plots of a few m² or less), native–exotic richness relationships vary from strongly negative to strongly positive. A common mechanism underlying negative relationships appears to be resistance to invasion by exotics at high native richness due to increased efficiency of resource use. This interpretation is an intuitive extension of classic niche theory (MacArthur and Levins 1967, Chase and Leibold 2003, Tilman 2004), and has some experimental support (Levine 2000, Fridley et al. 2007). Proposed explanations for positive native–exotic richness relationships include common responses to external variables, and facilitation of exotic species by native species (Fridley et al. 2007). The former explanation is fairly simple and straightforward, and is not considered further here. The potential for facilitation to underlie positive diversity–diversity relationships is intriguing, but has received

virtually no quantitative theoretical treatment. Although ecologists have increasingly recognized the importance of positive interactions in communities (Bruno et al. 2003, Brooker et al. 2007), it is not clear that facilitation will necessarily result in a positive relationship for species richness between the two groups (Stachowicz and Byrnes 2006); for example, facilitation between particular pairs of species may create indirect negative interactions with other species, and therefore make negligible contributions to diversity per se. While the ‘diversity begets diversity’ hypothesis may be straightforward to envision working across trophic levels (Siemann et al. 1998, Potts et al. 2003, van der Heijden et al. 2003), it is more difficult to envision working within a trophic level.

A group of studies, seemingly unrelated to those on native and exotic species diversity, begin by identifying one focal species for which genetic variation appears to have important ecological consequences (Turkington 1989, Hughes and Stachowicz 2004, Whitham et al. 2006, Crutsinger et al. 2008). These studies then examine associations between genetic diversity within the focal species and species diversity in the rest of the community, with genetic diversity typically considered only within the focal species. In some respects these studies are, in fact, conceptually identical to the native–exotic studies described above. In both cases, individuals with potentially important functional differences in a community are recognized as belonging to one of two groups – natives vs exotics or a focal species vs the rest of the community. Within each of the two groups, different variants are recognized as either species or genotypes. A key question in both cases is how diversity in one of the two groups influences diversity in the other.

For the case of causal effects of species diversity on genetic diversity, Harper (1977) offered a hypothesis that is similar to the facilitation hypothesis for native and exotic species. If one plant species shows local adaptation to the species identity of its neighbors, as demonstrated for white clover *Trifolium repens* in relation to co-occurring grass species (Turkington 1989), then grass species diversity may represent spatial heterogeneity and thus diversifying selection from the point of view of white clover. Species diversity should, therefore, increase genetic diversity. Essentially different grasses facilitate different clover genotypes. However, translating this verbal model into quantitative form raises some difficulties. First, positive interactions in their simplest form lead to instability and a runaway process of positively interacting types increasing without limit (May 1973). One realistic way to control this is by assuming finite space (Molofsky et al. 2001), but since plants (and organisms in many other communities) often compete for space if nothing else (Hubbell 2001), the outcome of species-to-genotype facilitation, plus competition for space, is difficult to predict a priori. Finally, it is not obvious how one would generalize from the grass–clover example, or from two-species models of positive interactions (Molofsky et al. 2001, Travis et al. 2005), to specify the nature of facilitative interactions between each pair of species or genotypes in a community model with many species. For competition, this is simplified in a reasonably realistic way by assigning each species or genotype a position on a niche axis (e.g. food item size for animals) and then relating the

strength of competition to proximity on this niche axis (MacArthur and Levins 1967). To my knowledge no similar approach has been used for facilitation.

In sum, the confluence of ideas and results in the literature on native–exotic richness relationships (Fridley et al. 2007), species–genetic-diversity correlations (Vellend and Geber 2005), and positive community interactions (Bruno et al. 2003, Brooker et al. 2007), point to some key gaps in our knowledge. First, is facilitation a plausible mechanism for creating positive diversity–diversity relationships, and if so how might it work? Second, how do simultaneous competition and facilitation interact to determine diversity–diversity relationships? These are the central questions that this paper begins to address.

Methods

The models presented here characterize the outcome of competition and facilitation within and between two groups of biological variants on the same trophic level. The two groups could represent either native vs exotic species, or the species in a community (except one focal species) vs genotypes within that focal species. Throughout the Methods and Results I adopt terminology from the latter example, referring to the two groups as the community, within which variants are species, and the focal species, within which variants are genotypes. Note that the group representing species in the community does not include the focal species.

Two versions of the model were explored. In model 1, competition and facilitation between each pair of species or genotypes was symmetrical and reciprocal, with the strength and direction of interactions determined by the positions of each species and genotype on two niche axes, one determining the strength of competition, the other the strength of facilitation. In model 2, facilitation was asymmetric: species could facilitate genotypes depending on their respective positions on the facilitation niche axis, but genotypes did not facilitate species or themselves. All models presented are spatially explicit simulations in which each cell of a 100 × 100 square grid is occupied by a single organism. Reproduction in the focal species was strictly asexual so that the model could equally represent native vs exotic species as well as genetic diversity in a focal species vs species diversity in the rest of the community, and also reflecting the use of non-recombining clonal genotypes in many empirical experiments on genetic diversity (Turkington 1989, Hughes and Stachowicz 2004, Crutsinger et al. 2008).

Model 1. Reciprocal interactions

In this model, each species in the community or genotype within the focal species was characterized by its position between 0 and 1 on two niche axes. According to classic niche theory (MacArthur and Levins 1967), the first niche axis determines the degree of competition between types, representing traits such as prey size in animals or rooting depth in plants. Competition between each pair of types was symmetrical, and was either strong or weak (defined

quantitatively below). Niche breadth on the ‘competition’ niche axis (NB_C) was defined such that if the distance between two types on the niche axis was $<NB_C/2$, competition was strong; otherwise competition was weak (Fig. 1).

Theoretical ecology provides some well-studied approaches for modeling competition among many species, with simplifications (e.g. a single niche axis) that retain some key biological realities (e.g. similar types compete more strongly than different types). My goal was to devise a similar approach for facilitative interactions. To this end, I used a second niche axis that determined the degree of facilitation between types, in much the same way as the first niche axis determined the degree of competition. This axis represents both the effect of an organism on its environment and the response of the same organism to the environment, thus sharing a conceptual similarity with the idea of niche construction (Olding-Smee et al. 2003). For example, the niche axis might represent the pH toward which a particular plant genotype or species changes the soil in which it is growing. It might also represent a one dimensional characterization of the composition of the soil biota on which different plant types have different effects and responses (Bever 2003). The model assumes that the particular value of the axis toward which a genotype or species causes the environment to change is also the value at which that genotype or species experiences maximal fitness. That is, the model assumes positive feedbacks, as have been demonstrated for plant–soil interactions in a variety of cases

(Bever 2003), and which may have important effects on patterns of species diversity (Reynolds et al. 2003). Interestingly, even if the effect on, and response to, the local environment are decoupled as independent traits, selection strongly favors species or genotypes for which these are the same – i.e. types with positive feedbacks – so effectively this assumption of the model is an outcome if this assumption is relaxed. Similar to the competition niche axis, if the distance between two types on the facilitation axis is $<NB_F/2$, facilitation is strong; otherwise facilitation is weak. The assumptions of this part of the model are likely unrealistic in their specifics, but there is considerable empirical evidence for positive plant–soil feedbacks (Bever 2003) and for facilitation both within species (Sommer 1992, Malkinson and Jeltsch 2007) and between species (Bruno et al. 2003). The goal here was to incorporate a process that quantitatively represents in a simple way conditions that might generate a scenario in which diversity begets diversity within a single trophic level.

Each cell in the 100×100 square lattice contained a single individual organism, and the fitness of each individual depended on the niche positions of its eight nearest neighbors (five for edges, three for corners). The background probability of individual survival was 0.5; competition reduced the survival rate, while facilitation increased it. Specifically, the survival probability of an individual was equal to $0.5 - I_C P_C + I_F P_F$. I_C and I_F are competition and facilitation coefficients, respectively, and P_C and P_F are the proportions of neighbors with niche positions $<NB_C/2$ units from the focal individual on the competition axis, and $<NB_F/2$ units from the focal individual on the facilitation axis, respectively. A single neighbor could be both a competitor and facilitator in which case these effects cancel out. All individuals that die in a given time step are replaced by an asexually produced offspring of a randomly chosen individual from those that survived (i.e. dispersal is effectively global). Cells are updated simultaneously. Models were also run with local dispersal (i.e. empty cells replaced by an asexual offspring of an immediate neighbor), producing very similar results concerning diversity–diversity relationships (results not shown).

All simulations began with 20 genotypes and 1–40 species in a 100×100 cell lattice (10 000 individuals). At the start of each simulation, half the individuals were species from the community, the other half were genotypes from the focal species, and each species or genotype started with equal relative frequency within their respective groups. For a given set of simulations the niche positions of the species were chosen randomly from a uniform distribution between 0 and 1 for both axes (Fig. 1). The niche positions of the 20 genotypes were also chosen randomly from a uniform distribution with a midpoint of 0.5, but the potential genotypic range (PGR) was varied among sets of simulations. PGR determined the range of niche values from which genotypes were chosen (Vellend 2006); the smallest PGR was 0.1 (0.45–0.55), and the largest was 1 (0–1, same range as that for the species in the community). Within a given set of simulations, niche breadths were assumed to be the same for all species and genotypes, and for the two niche axes ($NB_C = NB_F$). In different sets of simulations, NB was varied from 0.05–1.0. For all parameter combinations, sets of simulations were run for three scenarios of competition

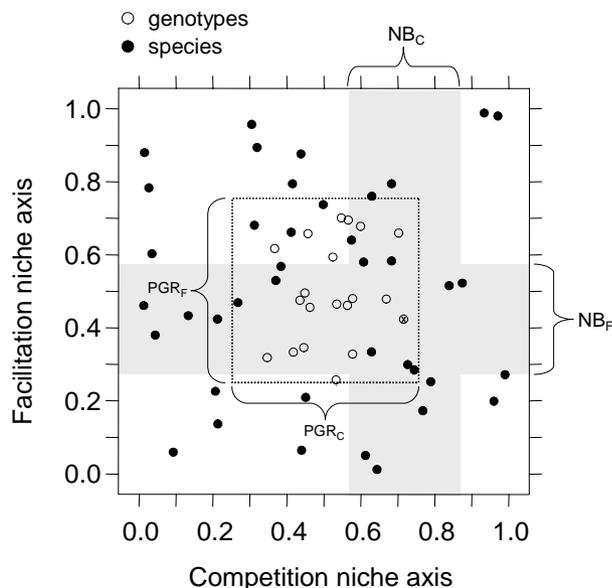


Figure 1. The set-up of model 1 with symmetric interactions. Niche positions for 40 species were chosen randomly between 0 and 1 for the two niche axes, and for the 20 genotypes within a niche space centered on [0.5, 0.5] and whose extent was determined by the potential genotypic ranges on the two axes (PGR_C and PGR_F). For the genotype marked with an X, competition is strong with all other types within the vertical grey stripe (defined by the niche breadth on the competition axis, NB_C), and facilitation is strong with all other types within the horizontal grey stripe (defined by NB_F).

and facilitation: (1) $I_C = 0.4$, $I_F = 0$; (2) $I_C = 0$, $I_F = 0.4$; and (3) $I_C = I_F = 0.4$. That is, simulations were conducted under only competitive interactions, only facilitative interactions, or both at equal strength.

The only stable equilibrium level of diversity in stochastic simulations is a single genotype or species, so simulation results were analyzed after 2000 time steps, at which point clear differences among parameter combinations had emerged, and beyond which changes in output variables were relatively slow.

Model 2. Asymmetric facilitation

Model 2 assumed that species facilitated genotypes but not vice versa, and was motivated by the failure of model 1 to capture Harper's (1977) biotic heterogeneity hypothesis (Results), the common occurrence of unidirectional facilitative effects (Brooker et al. 2007), and empirical evidence suggesting that some plant communities consist of separate groups that either provide or receive facilitative effects, but not both (Valiente-Banuet et al. 2006). Model 2 was identical to model 1 except for the following changes. First, there was no explicit competition niche axis; rather, competition was strong within but not between pairs of species ($I_C = 0.2$), and the genotypes competed equally strongly with each other but not with species in the community. This ensured stable coexistence of species in the community and of at least one genotype of the focal species with the rest of the community, aside from the effects of stochastic drift. With respect to facilitation, a given genotype's survival was increased via facilitation by species with similar positions on the facilitation niche axis ($I_F = 0.35$), but genotypes had no facilitative effects at all, and species were not facilitated at all. Thus, with sufficiently small NB_F , different stably-coexisting species facilitate different genotypes, thereby potentially contributing to genotype coexistence and diversity. For model 2, simulations were run both with the facilitation niche positions assigned randomly between 0–1 (as for model 1), and also with niche positions evenly spaced on the same interval. The main difference between randomly and evenly spaced niche positions is that with low species richness, at least some genotypes will be facilitated when niche positions are evenly spaced, but not necessarily when they are randomly spaced.

Results

Model 1. Competition

With only competition in model 1, species richness had a negative effect on genotypic diversity under all parameter combinations (Fig. 2a) except when both species and genotypes had the same potential range in niche space ($PGR = 1$) and large niche breadths ($NB_C = 1$), in which case species and genotypes were nearly neutral. Trends of population size with species richness closely mirrored those for genotypic richness (Supplementary material Appendix 1). As in previous models of multispecies competition on a single niche axis (Scheffer and van Nes 2006, Vellend 2006), species and genotypes persisted at evenly-spaced niche positions ('viable niches', Fig. 3a–b), with the spacing

depending on niche breadths. With few species in the community, the viable niche positions were filled mostly by genotypes in the focal species; with many species, less niche space was available for genotypes to fill (Fig. 3a–b). Increasing NB_C decreased species and genetic diversity via a reduced number of viable niches; increasing PGR increased genetic diversity by broadening the number of viable niches genotypes may occupy.

Model 1. Facilitation

Under the full range of parameter combinations explored in model 1 with only facilitative interactions, species richness had a positive effect on genotypic richness (Fig. 2b). Surprisingly, however, these results were not due to high species diversity representing a source of spatial heterogeneity and diversifying selection from the point of view of the genotypes. Rather, two entirely different mechanisms were involved. First, with relatively low PGR , increasing species richness increases the probability that at least one species will act as a facilitator for one or more genotypes (Fig. 3c–d). This is akin to 'sampling' effects identified in research on the ecosystem consequences of species diversity (Srivastava and Vellend 2005), which have been hypothesized to underlie some positive relationships between native and exotic species diversity via facilitation (Bruno et al. 2003, Fridley et al. 2007). In this case, species select for genotypes along a single portion of the niche axis, in distinction to the biotic heterogeneity hypothesis, which would predict different species favoring different genotypes at multiple positions along the niche axis. The second mechanism was a consequence of the dependency of the outcome of positive interactions on initial species and genotype frequencies. Since in these simulations the summed abundances of species and genotypes were initially the same (each occupying half of the cells), low species richness meant that each species began at relatively high frequency. In the extreme, with species richness = 1, half of the cells were initially occupied by the one species, compared to 1/40 cells for each genotype (20 genotypes filling 1/2 of the cells). Since all species and genotypes facilitate themselves, positive feedback favors the dominance of whichever type begins at high frequency. At low species richness, the eventual dominance of one or more species dramatically reduces both the total number of individuals (Supplementary material Appendix 1) and genotypes in the focal species' population, often to zero (Fig. 3c). With similar initial numbers of species and genotypes, initial relative frequencies are also similar, such that more genotypes are likely to persist in the long run (Fig. 3d); if, in addition, PGR is low, then there will be strong facilitation among genotypes but low facilitation among species (on average), such that genotypes may drive species extinct (Supplementary material Appendix 1).

In contrast to competition, facilitation as implemented here resulted in a single stretch along the niche axis where species and genotypes persist (Fig. 3c–d). The positive feedbacks that result from facilitation mean that wherever there is an initial cluster of species or genotypes along the facilitation niche axis (positions were assigned randomly), the frequencies of types at that position rapidly increase at

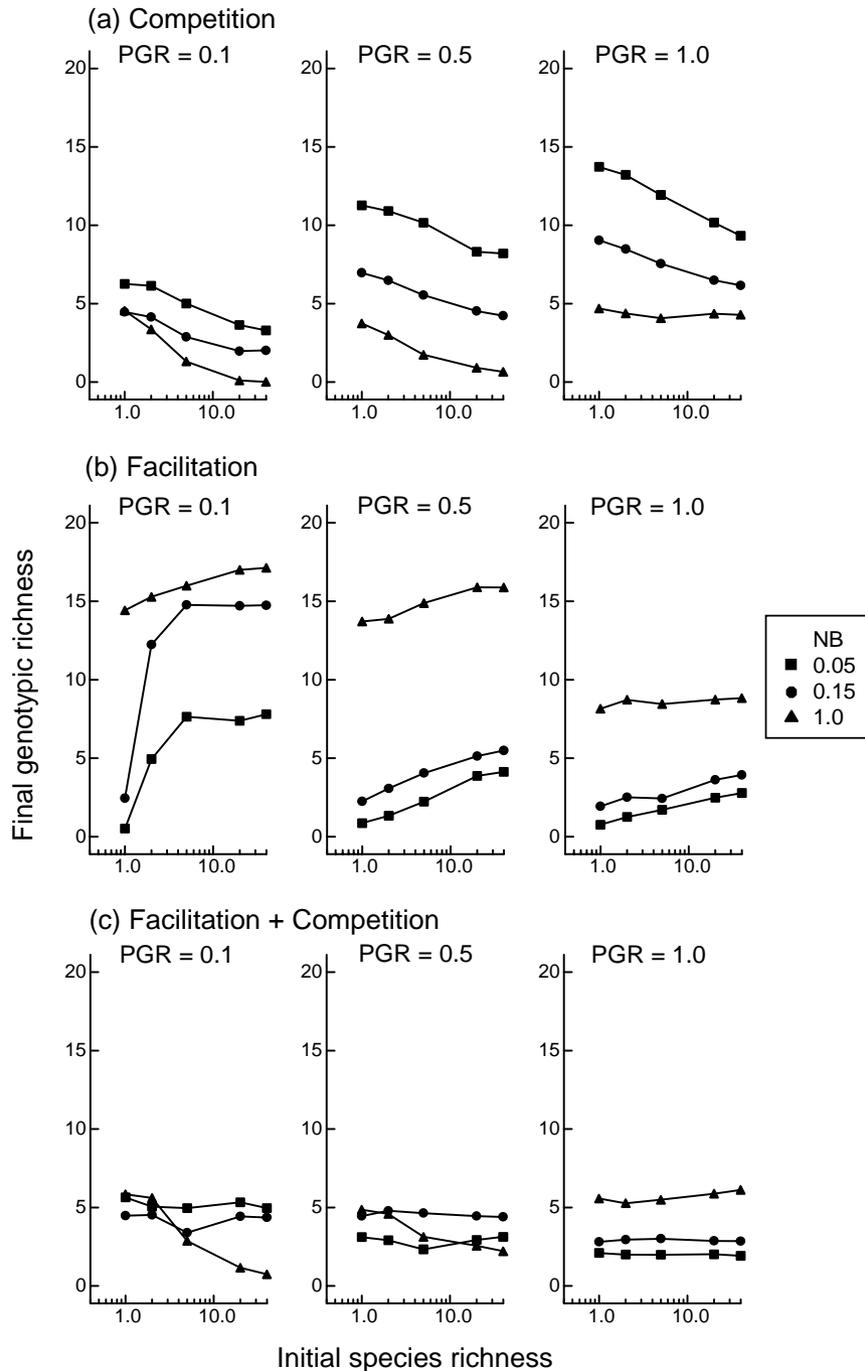


Figure 2. Effects of initial species richness on final genotypic richness in model 1 under competition only (a), facilitation only (b), and both competition and facilitation (c), at different levels of potential genotypic range (PGR) and niche breadth (NB). Each data point represents an average across 100 simulations after 2000 time steps.

the expense of other types. The remaining cluster of species and genotypes are effectively neutral, so that in the long term eventually one will drift to dominance, but for a potentially very long time there will be coexistence of similar types (Hubbell 2001, Scheffer and van Nes 2006). The promotion of rapid dominance by positive interactions prevents the situation hypothesized by Harper (1977) in which genetic diversity is maintained via each competitor species effectively facilitating different genotypes of the focal species.

Model 1. Competition and facilitation

With both competition and facilitation in model 1, species richness most often had no effect on genotypic richness (Fig. 2). Diversity at both levels was lower with both competition and facilitation than with either type of interaction alone because competition and facilitation constrain diversity in different ways. Facilitation resulted in essentially one viable niche position on the facilitation niche axis; within that viable facilitation niche, competition

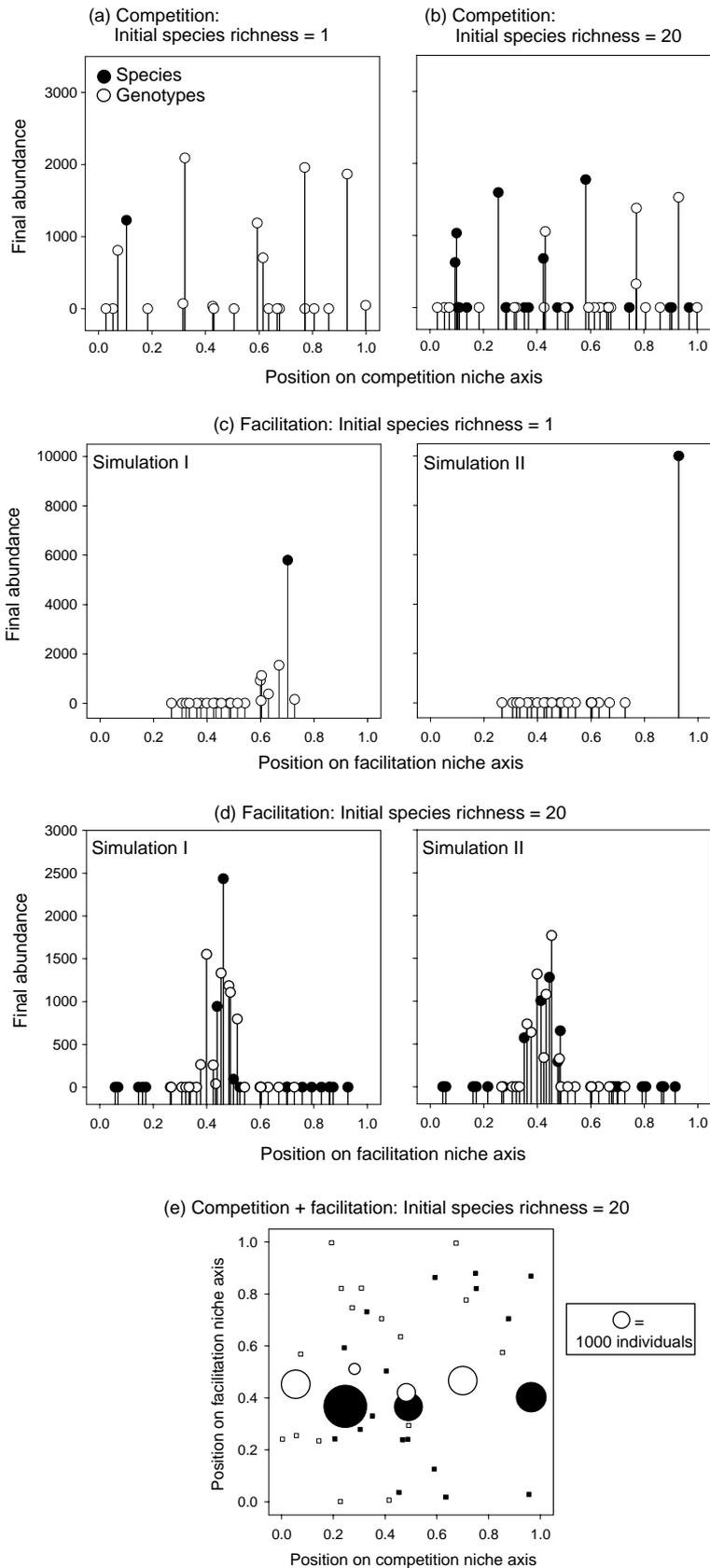


Figure 3. Abundance of each species and genotype after 2000 time steps in individual simulations of model 1 at different levels of initial species richness for competition only (a)–(b), facilitation only (c)–(d), and both competition and facilitation together (e). In each case $PGR = 1$ and $NB = 0.3$. In panel (e), the diameter of each circle is proportional to final abundance, with the small squares indicating abundance = 0.

caused species and genotypes to be evenly spaced along the competition niche axis (Fig. 3e). The negative and positive effects of species richness on genotypic richness via competition and facilitation, respectively, cancel each other out in most cases, with competition dominating to create a negative relationship only at low PGR and high NB.

Model 2. Competition with asymmetric facilitation

For most of the parameter range explored for model 2, genotypic richness declined with species richness (Fig. 4). Under some situations with high potential genotypic range (PGR) and low niche breadths (NB), there was a weakly unimodal relationship of genotypic richness on species richness, and this was more pronounced with genotypes evenly spaced on the facilitation niche axis (Fig. 4). Although monotonic positive relationships were never found after 2000 time steps, such relationships were generated during the first few hundred time steps with high PGR and low NB (Fig. 5).

At least three mechanisms mediated the effect of species richness on genotypic richness in model 2. First, as hypothesized by Harper (1977), species richness can act as a source of diversifying selection on the genotypes when NB is small and PGR large (Fig. 6). This creates the monotonic positive relationships found during a transitory period in community dynamics and also the increase phase in unimodal relationships (Fig. 5). Second, since intraspecific competition is greater than interspecific competition for all species, increasing species richness means that each species (including the focal species' population as a single unit) must eventually make up a smaller proportion of the total community (Supplementary material Appendix 1). Small population size of the focal species causes genotypic richness to decrease via drift, such that species richness has a negative effect on genotypic richness. The influence of this mechanism is weakened by large niche breadths, which lead to strong facilitation of all of the genotypes and therefore a large focal species' population relative to the rest of the community (Supplementary material Appendix 1). Finally, facilitation of genotypes by species potentially increases

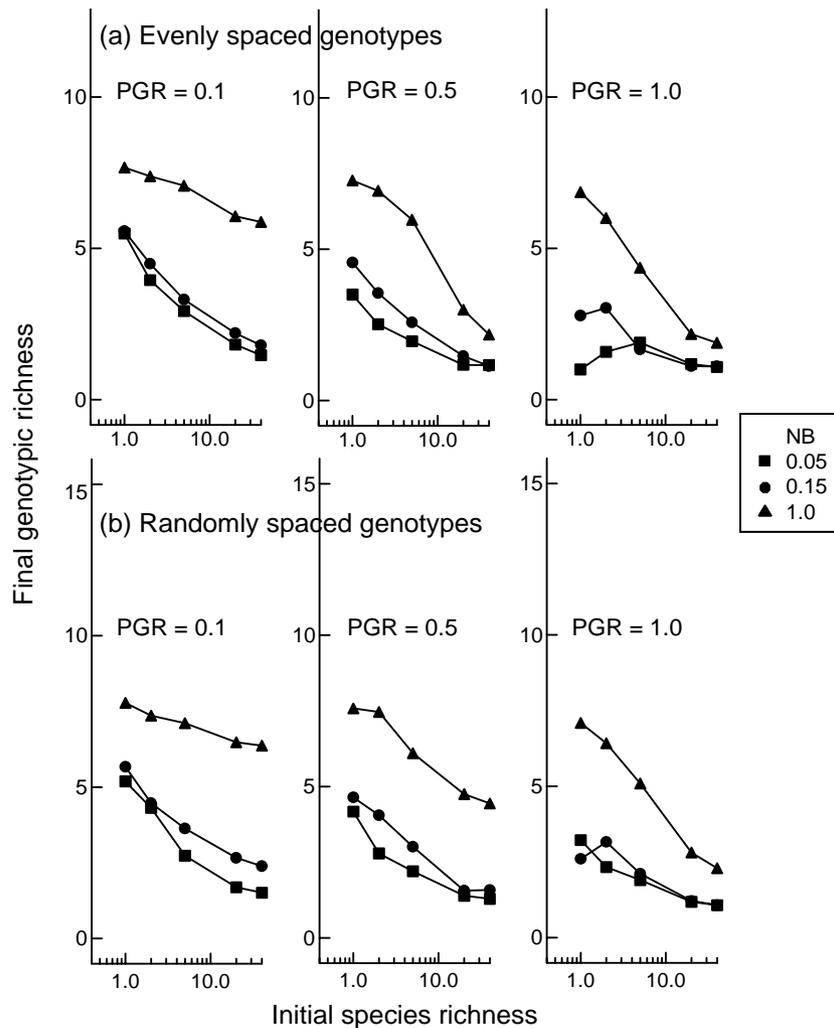


Figure 4. Effects of initial species richness on final genotypic richness in model 2 with evenly spaced genotypes (a), or randomly spaced genotypes on the facilitation niche axis (b), at different levels of potential genotypic range (PGR) and niche breadth (NB). Each data point represents an average across 100 simulations after 2000 time steps.

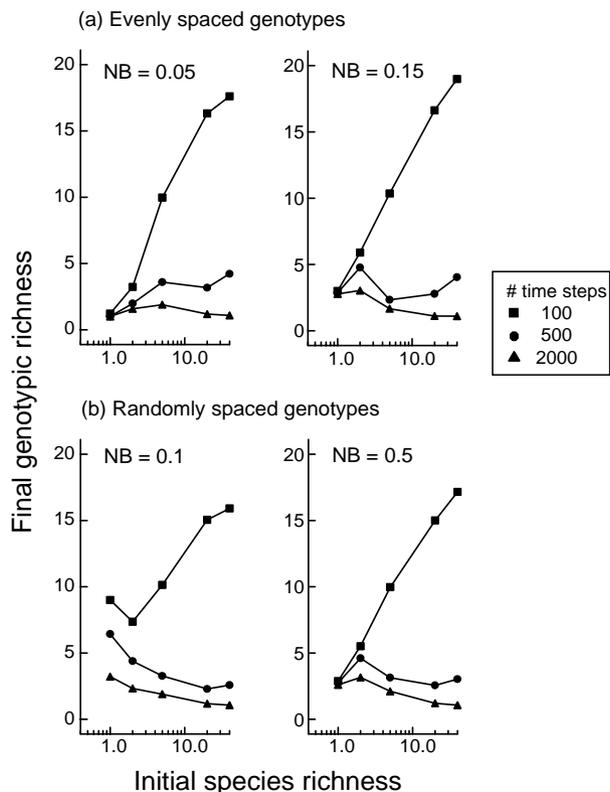


Figure 5. Effects of initial species richness on final genotypic richness in model 2 with evenly spaced genotypes (a), or randomly spaced genotypes on the facilitation niche axis (b), at three time points, 100 time steps, 500 time steps, and 2000 time steps. PGR = 1 for all results shown in this figure. Each data point represents an average across 100 simulations.

fitness differences among the genotypes, thereby decreasing genotypic richness as species richness increases. For example, with random niche positions and low NB, a single species may facilitate no genotypes at all, in which case all genotypes have the same relative fitness, and diversity may be lost only slowly due to drift. Increasing species richness increases the probability that some genotypes will be facilitated while others are not. When this happens, facilitation increases the average fitness of genotypes, but at the same time strongly favors some genotypes over others, thereby increasing the rate at which genotypic richness is lost. Essentially facilitation can eliminate an equalizing effect (*sensu* Chesson 2000) on diversity maintenance, and this effect is most pronounced when going from one to a few species. These three mechanisms can interact to create a variety of patterns at different times during community assembly, including positive, negative, unimodal, U-shaped, and fluctuating relationships of genotypic richness on species richness (Fig. 4, 5).

Discussion

The models presented here were fairly simple, but nonetheless revealed a variety of different diversity–diversity relationships, with several interacting mechanisms mediating the effect of diversity in one group on diversity in a

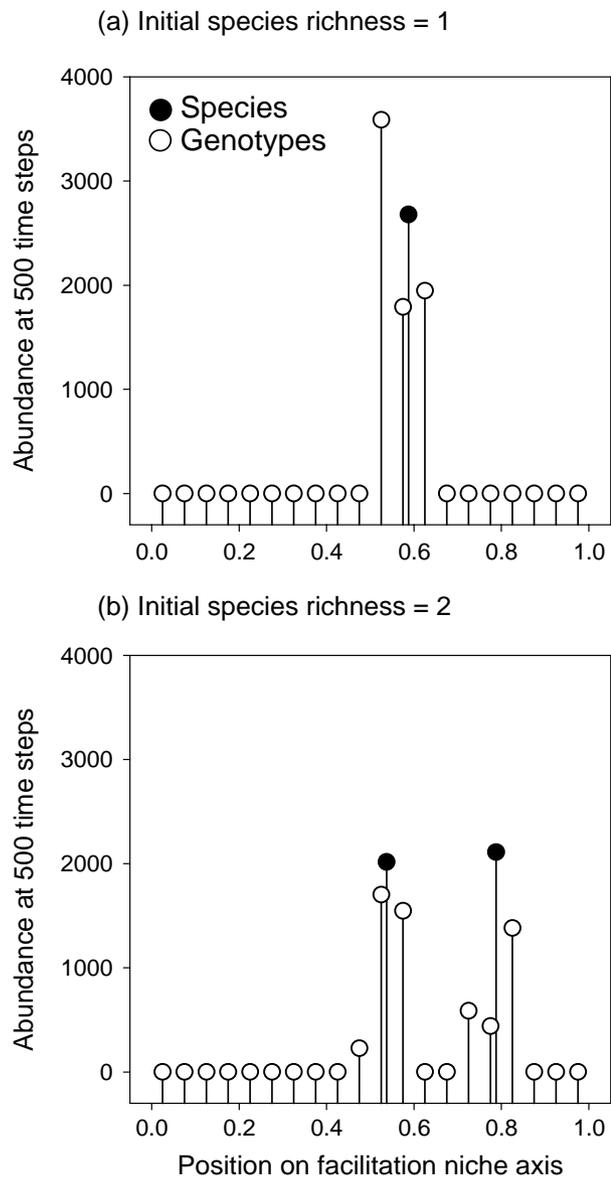


Figure 6. Abundance of each species and genotype after 500 time steps in individual simulations of model 2 with initial species richness = 1 or 2. In each case PGR = 1 and NB = 0.15.

second group. The effects of competition were straightforward and consistent with many previous models, but the consequences of different kinds of facilitation were more complex, pointing to some novel theoretical possibilities and highlighting important empirical and theoretical challenges to fully integrating facilitation into the conceptual core of ecology.

Outcomes of competition and facilitation

In the models presented here competition for limited niche or physical space typically resulted in negative diversity–diversity relationships (Fig. 2, 4). In the case of limited niche space, this result is essentially the same as those derived from different implementations of classic niche theory, in which diversity is limited by competition (May

1973, Chase and Leibold 2003, Tilman 2004). By filling niche space and using resources more fully, high diversity communities inhibit the invasion or persistence of additional types more so than low diversity communities. In the case of limited physical space, diversity in one group does not influence diversity in the second group directly, but rather indirectly via a negative effect on the total abundance of the second group. These models thus provide a plausible mechanism for negative relationships between native and exotic species diversity, often found at small scales (Fridley et al. 2007), as well as for the few documented examples of negative relationships between species diversity and genetic diversity (Vellend and Geber 2005). These results are not novel, but they do provide a basis of comparison for looking at the outcome of facilitative interactions, which have received very little theoretical attention to date (Bruno et al. 2003, Brooker et al. 2007).

With only facilitation, the results of model 1 (symmetrical interactions) provide theoretical support for the suggestion that facilitation may create positive diversity–diversity relationships if increasing diversity in one group increases the probability that a strong facilitator of the other group will be present (Bruno et al. 2003). With a relatively small PGR, some species facilitate the genotypes and some do not (Fig. 3c), much as some native species facilitate the establishment of invaders while others do not (Stachowicz and Byrnes 2006). However, the model did not produce the phenomenon of a diverse group of species representing a source of diversifying selection for a focal species (Harper 1977).

The potential positive effect of diversity on diversity via biotic heterogeneity (Harper 1977) appears to require that the two groups of species or genotypes are drawn from fundamentally different trait distributions – in this case, providers and receivers of facilitative effects. However, apart from transient dynamics, even with removal of the potentially unrealistic assumption of positive feedback leading to dominance and the addition of completely asymmetrical facilitation (model 2), positive diversity–diversity relationships due to biotic heterogeneity were found only under the limited conditions of large potential genotypic ranges, small niche breadths, and a narrow and low range of species richness (Fig. 5). Essentially a model was built specifically to explore the biotic heterogeneity hypothesis, and still it failed to produce this phenomenon under most circumstances. This suggests that while Harper's (1977) biotic heterogeneity hypothesis is at least theoretically plausible within trophic levels, such as plants, it is unlikely when accompanied by competition for space, given the restrictive conditions required to generate the predicted outcome. The biotic heterogeneity hypothesis may apply in situations not represented by these models if, for example, facilitation increases the number of individual organisms within a trophic level that can occupy each unit of space. Across trophic levels (e.g. producers and consumers) or between groups of mutualists (e.g. plants and pollinators), the biotic heterogeneity hypothesis may apply more broadly, given the lack of competition between the two groups, and the presence of specialization in such interactions. For example, if insect herbivores or pollinators are to some degree specialized on different plant species or genotypes, plant diversity may beget insect diversity

(Siemann et al. 1998, Potts et al. 2003), or if different mycorrhizal fungi benefit different plant species, fungal diversity may beget plant diversity (van der Heijden et al. 1998). However, within trophic levels native and exotic species often compete for space and share very similar characteristics (Meiners 2007), as do different species and different genotypes within plant communities (Aarssen 1983), in which case it is unlikely that facilitation would create a diversity–diversity relationship via biotic heterogeneity.

In a controversial paper, Emerson and Kolm (2005) suggested that species diversity within plants or arthropods on islands has a positive effect on the rate of speciation (i.e. the generation of genetic diversity and additional species) within those same groups. This suggestion, based on a correlation between total species richness and endemic species richness, has been sharply criticized given equally or more plausible explanations for the pattern (Kiflawi et al. 2007, Pereira et al. 2007). The results of the models presented here also suggest that Emerson and Kolm's (2005) hypothesis is unlikely on theoretical grounds: new and old species on islands presumably compete, in which case diversity is most likely to inhibit additional diversity, and it is improbable that new and old species differ in the specific ways required for diversity to beget diversity within a trophic level. In contrast, the conclusion of Valiente-Banuet et al. (2006) that the diversity of ancient plant lineages in Mediterranean ecosystems is maintained by more recent lineages appears more theoretically plausible. In this case, there is a clear distinction in ecological traits between the two groups, with species in recent lineages able to establish in open conditions and subsequently facilitate species in ancient lineages, which would generally be unable to establish otherwise (Valiente-Banuet et al. 2006).

The case of grass species vs clover genotypes remains intriguing in that there is strong potential for positive interactions, and the resource requirements of the two groups are to some degree decoupled. Clovers (and legumes in general) fix nitrogen; grasses do not. Increased soil nitrogen facilitates grass growth (Schwinning and Parsons 1996), and different grasses may selectively favor different clover genotypes (Turkington 1989). However, by depleting nitrogen, grasses create conditions that facilitate establishment of nitrogen-fixers in general – in this case clover – and all plants in such systems ultimately compete for space (Schwinning and Parsons 1996). It remains to be tested empirically whether the general model presented here (model 2) provides a reasonable caricature of these interactions, and whether grass–clover interactions can lead to a positive effect of grass species diversity on clover genetic diversity. With grass species richness varying from one to a few species, the results of this paper indicate that this is at least theoretically plausible.

Challenges in the study of facilitation

One goal of this study was to advance the goal of bringing facilitation into mainstream ecological theory (Bruno et al. 2003, Brooker et al. 2007) by constructing a model in which competition and facilitation could be represented in a closely comparable way. In model 1, similarity on

one niche axis determined the strength of competition; similarity on a second niche axis determined the degree of facilitation. Representing competition this way has a long theoretical tradition, with a firm basis in models and data on resource competition (MacArthur and Levins 1967, Tilman 2004). To my knowledge, this is the first study to represent facilitation in this way, and it highlights some important challenges in constructing simple and general models of facilitation in communities with many species or genotypes. Two-species models of positive interactions need only make the distinction between conspecifics and heterospecifics from the perspective of any one individual (Molofsky et al. 2001), but this is difficult to generalize to multi-species communities without assuming that all heterospecifics are equivalent. Assigning positions on a 'facilitation niche axis' (envisioned here as the effect on, and response to, some aspect of growing conditions) circumvents this problem, but is admittedly an oversimplification, and without further assumptions leads to dominance via positive feedbacks, which is likely unrealistic in most systems. Nonetheless, it represents a novel perspective and a starting point for considering how positive interactions between species or genotypes on the same trophic level might be treated before resorting to highly complex models based on the idiosyncratic details in any particular community.

Some more general theoretical challenges involved with modeling facilitation include extreme sensitivity to initial conditions (May 1973), the likelihood that the strength and importance of facilitation depend in complicated ways on successional stage, density and abiotic conditions (Bruno et al. 2003, Brooker et al. 2007), and the difficulty in specifying the mechanism of facilitation in a way that is analogous to the role of resources in models of competition. Nonetheless, the widespread presence of facilitative interactions in nature indicate that ecological theory needs to integrate facilitation to a far greater degree than it has to date (Bruno et al. 2003, Lortie et al. 2004, Brooker et al. 2007). The models in this paper illustrate that facilitation can have a variety of community consequences via selection effects, biotic heterogeneity, and changes in the mean and variance in fitness among species or genotypes depending on the diversity of facilitating types and their initial frequencies. Changing diversity in one group typically has multiple and simultaneous effects on diversity in a second group. A more complete picture of concurrent competition and facilitation will require consideration of factors such as changes in the direction and strength of interactions depending on life stage (e.g. seedlings vs adults) or density, and interactions with disturbance or stress, which may continually perturb communities from equilibrium and increase the importance of facilitation (Callaway et al. 2002). Development of general community models of competition and facilitation, and experimental studies of the underlying mechanisms of facilitation, remain significant challenges to ecologists.

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