

Species diversity of grasses promotes genotypic diversity of clover populations in simulated communities

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Recent studies in community genetics have demonstrated strong effects of intraspecific genetic variation on the diversity of interacting species but largely ignored the potential for effects of species diversity on genetic diversity, which could also create a positive correlation between these two levels of biodiversity. Here we investigated the role that species diversity of competitors could play in shaping the genotypic diversity of a focal species, using a modified version of an existing model of grass–clover dynamics. We simulated communities in which clover genotypes varied in their relative competitive ability when growing adjacent to different grass species. Under many parameter combinations, communities with greater species richness of grasses retained greater genotypic richness within the clover population. Increasing grass species richness effectively increased biotic environmental heterogeneity with respect to clover growth, thereby promoting the maintenance of genotypic diversity. This result depended on three conditions being met: (1) a sufficiently strong tradeoff among genotypes in their fitness when growing with different grass species, (2) partial de-coupling of competition and facilitation, with grass and clover capable of sharing microsites rather than strictly excluding one another, and (3) sufficiently high rates of clover growth and clonal spread, which allowed clover genotypes to ‘track’ the shifting mosaic of grass species. Our results demonstrate that species diversity can act as an important promoter of genotypic diversity, and they provide testable predictions concerning the conditions that promote this outcome in nature.

Genetic diversity within species and species diversity within communities are two fundamental aspects of biodiversity typically studied in isolation by population geneticists and community ecologists, respectively. One effort to link these disciplines is the emerging field of community genetics (Antonovics 1992), which integrates community ecology with evolutionary genetics by considering the interplay between distinct genetic individuals of a species with other members of the community (Agrawal 2003). Such a consideration has led to the observation of empirical relationships, most-often positive, between species diversity within communities and genetic diversity within species (Vellend 2003). The underlying causes of these correlations remain poorly understood, but could offer a deeper understanding of how these two fundamental aspects of biodiversity are maintained.

Species–genetic diversity correlations may result when common processes influence species and genetic diversity in similar ways (case 1), when genetic diversity within populations influences the species diversity of communities (case 2), or when species diversity in communities structures genetic diversity within populations (case 3) (Vellend and

Geber 2005). Both empirical (He et al. 2008) and simulation studies (Vellend 2005) have indicated parallel processes, such as immigration, disturbance, and environmental heterogeneity, can have similar, positive effects on the species diversity of communities and the genetic diversity within species (case 1, but see Puscas et al. 2008). Likewise, many studies have investigated how the genetic diversity in a foundational species influences higher trophic levels; the most common example is the effect of plant genotypic diversity on associated insect communities (case 2) (Crutsinger et al. 2006). However, much less attention has been given to investigating how the species diversity of communities may influence the genetic composition of individual species (case 3). In one of the few empirical studies to address this, Lankau and Strauss (2007) documented a ‘rock-paper-scissors’ game (i.e. intransitive competition, Taylor and Aarssen 1990) with three players: two genetic variants of the mustard plant *Brassica nigra*, one producing compounds toxic to other plants and the other not, plus heterospecific plant species in the community. While the non toxin-producing *B. nigra* variant outcompetes the toxin-producing one, the toxin-producing one outcompetes other plant species, which in turn outcompete non-toxin producing mustard plants. Thus, the presence of other plant species is necessary to maintain genetic diversity within *B. nigra*, and simultaneously, the genetic diversity

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within *B. nigra* favours the persistence of other plant species (Lankau and Strauss 2007).

A marked feature of the *Brassica nigra* system is that of positive, or facilitative, interactions, where the presence of one taxon effectively increases the fitness of another. Facilitation is increasingly recognized as an important factor, along with more widely recognized processes of competition and environmental stress, in determining the structure of communities (Brooker et al. 2008). While most often applied to the establishment of organisms, regardless of identity, where otherwise might not be possible (e.g. nurse plants), facilitation is frequently species- or genotype-specific (Callaway 1998). This identity-specific aspect of facilitation may be critical to understanding species–genetic diversity correlations. For example, if genotypes show tradeoffs in their relative fitness when in competition with different species, as suggested for genotypes of the legume white clover *Trifolium repens* in competition with different grass species (Turkington and Harper 1979a), species diversity may promote greater genotypic diversity (Vellend and Geber 2005).

At first glance, a positive species–genetic diversity correlation may seem like a necessary and obvious outcome of genotypes responding to the biotic heterogeneity provided by different co-occurring species, akin to the effect that genotypes may respond to abiotic heterogeneity. However, two factors may prevent such an outcome despite the presence of trade-offs among genotypes described above. First, the spatial distributions of co-occurring species may shift too rapidly for genotypes to ‘track’ those species with which they experience a fitness advantage. Second, because facilitation often occurs simultaneously with competition for resources or space, a qualitative prediction based only on facilitation may be obscured by the outcome of competition. A previous modelling effort incorporating both competition and facilitation in a community genetics context adopted a simplified approach, where genotypes and species interacted through positions on two niche axes, one moderating competition and the other facilitation (Vellend 2008). Although positive diversity–diversity relationships resulted under some conditions, they arose most often through a sampling effect – the increased chance, with increasing species diversity, that a species would be present that facilitated many genotypes (Huston 1997) – rather than through biotic heterogeneity, where diversity in one group imposed diversifying selection on another (Vellend 2008). In this model, the effect of facilitation was constrained by a strict zero-sum dynamic (i.e. the total number of organisms was fixed and constant); the facilitation of establishment or persistence of one individual necessarily came at the cost of reduced microsites for other genotypes or species (Vellend 2008). In other words, the effects of strict competition for space negated the possibility of species diversity enhancing genetic diversity via biotic heterogeneity.

In contrast to zero-sum dynamics, biological systems often demonstrate complementary local resource use and consequent overyielding, where biomass of each species is higher in polycultures than in monocultures and where the growth of one type is not necessarily balanced by the reduction of another. For example, grass–legume interactions frequently result in local overyielding in grasslands (Nyfeler et al. 2009). If a grass species facilitates establishment of a

new legume ramet, this need not feedback immediately to reduce the growth potential of the grass. Since genotypes of white clover *Trifolium repens* can exhibit tradeoffs with respect to fitness when growing with different species of grasses (e.g. genotype A is favoured when growing with species 1 and genotype B is favoured when growing with species 2) (Turkington and Harper 1979a, Turkington 1989), a variety of grass species could create a spatially-varied selection regime (Harper 1977), and thereby maintain intraspecific diversity within the clover population. As such, the grass–clover system may provide an ideal point of departure for exploring the theoretical conditions under which we should expect species diversity to promote genotypic diversity via biotic heterogeneity.

Here we explore the role of genotype-specific interactions with different species as a mechanism by which species diversity in a community and genotypic diversity within a population might be linked. We adopted grass–clover interactions in simulated communities to explore this hypothesis. We explicitly represent competition and facilitation between different grass species and clover genotypes in relation to a single niche axis (a clover genotype experiences relatively high growth when growing with grasses that share a similar niche position), and we explored the conditions that weaken or strengthen the species–genotype diversity relationship.

The model

The model follows the framework of clonal dynamics of clover in a matrix of grasses, as commonly observed in the field (Cain et al. 1995). We explored the effects of species richness of the grass community, the breadth of influence of a given grass species (‘niche breadth’), the rates of growth and spread of clover, and the rate of grass turnover, on the persistence of genotypes in the clover population. While the focus and terminology of the model draws from grass–legume interactions, the motivation for the model is more general, applying more broadly to communities in which two groups of potentially competing biological variants (e.g. trees vs shrubs, etc.) exhibit complementary resource use.

Model structure

The model uses as a starting point the framework of Schwinning and Parsons (1996a), who investigated the community-level consequences of oscillations between grass and a nitrogen-fixing legume, such as clover. Nutrient dynamics are not explicitly represented in the model, but are implicit in transitions between different states; for example, over time as nitrogen is depleted, grass decline and clovers increase (Schwinning and Parsons 1996b). Simulated communities were composed of a square grid of cells, each of which can take one of four states (Fig. 1a). These four states are based on field observations that clovers tend to be patchily distributed among ubiquitous grasses (Turkington and Harper 1979c). Our key addition to the framework of Schwinning and Parsons (1996a) was the incorporation of multiple grass species and clover genotypes defined by their positions on a niche axis (Fig. 1b), which mediate

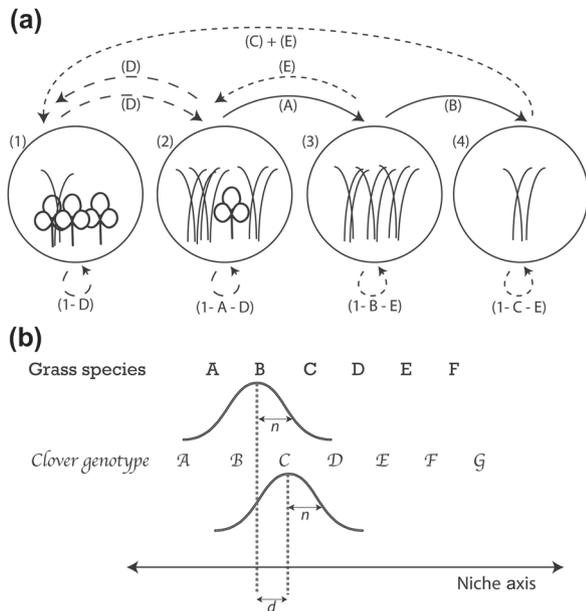


Figure 1. Model overview. (a) A schematic representation of the four possible states for each cell in the community (Schwinning and Parsons 1996a): (1) high clover/low grass, (2) low clover/high grass, (3) high grass, and (4) low grass. State transition possibilities are represented by arrows (Table 1). Solid arrows represent transitions dependent on fixed probabilities; dashed arrows represent transitions dependent on neighbouring cells (short-dash) or niche overlap (long-dash). For example, high clover/low grass cells (state 1) have two possible fates for the next time step: remain the same or convert to a low clover/high grass cell, with a probability (D) that depends on the baseline clover growth and the niche overlap. (b) Depiction of how the position of grass species and clover genotypes along a niche axis determines clover dynamics. Six grass species are shown with seven clover genotypes. The degree of niche overlap controls the relative performance of clover genotypes and is determined by dividing the difference in mean niche positions along the niche axis (d) by the niche breadth (n). Clover growth is higher when co-occurring with a grass species in which it has high niche overlap and lower when growing with a grass species with low niche overlap. For example, clover genotype C will have a higher relative growth rate when growing in a cell with grass species B than with grass species F.

the outcome of their interaction. Each cell contained only one grass species or one clover genotype, and only one of each of these if both are present in a cell. Empirical results have shown that genotypes of white clover exhibit tradeoffs with respect to their relative performance in competition with different grass species (Turkington and Harper 1979b, Mehrhoff and Turkington 1990). Possible mechanisms for these observed genotype-level response to different grass species include clover morphological structure (e.g. short and thick stoloniferous growth versus tall and sparse) and associations with particular nitrogen-fixing *Rhizobia* strains (Chanway et al. 1989).

We employed a hypothetical ‘facilitation niche axis’ (Vellend 2008) as a simple means of incorporating clover relative performance with differing grass species into our model, as follows. When the grass species and clover genotype within a cell have high niche overlap, clover performance (e.g. the probability of transitioning to clover dominance from grass dominance) is high relative to cells in which the grass

and clover have low niche overlap. Niche overlap is determined by two parameters: the relative positions of the grass and clover along the niche axis (d) and the niche breadth (n) (Fig. 1b). Niche overlap is calculated as the ratio of d to n , and thus represents the area of overlap between two Gaussian curves with means defined by the two niche positions, and standard deviations equal to the niche breadth (May and MacArthur 1972). The niche axis is bracketed between 0 and 1 inclusive, and the degree of niche overlap is maximized at a value of 1. In our model, high niche overlap results in relatively high clover growth (i.e. facilitation, Vellend 2008), in contrast to classic models of competition in which high niche overlap corresponds to reduced growth of competitors (May and MacArthur 1972).

Implemented in Matlab ver. 7.1 (The MathWorks, Inc.), the plant community is represented in a spatially-explicit grid of 50×50 (= 2500) cells, in which the grid edges are wrapped into a torus so that eight neighbouring cells surround each cell. Simulations were run for a maximum of 30 000 time steps, and two events occurred in each time step. First, the grass and clover interact within each cell, possibly resulting in a transition between one of the four possible states: clover may go extinct or invade, and grasses and clover change in abundance based on their niche overlap (Fig. 1a). Second, grasses interact with each other based on their spatial distribution and abundance, possibly resulting in species replacement within cells, but grass species richness cannot vary within a given model run (see Appendix Fig. A1 for snapshots of the community grid). The model assumes species- and genotype-specific effects of grasses on clovers but not vice versa; however, generalized effects of nitrogen fixation (by clovers) and depletion (by grasses) are implicit in the growth potential of grass in clover-dominated cells and the invasibility of grass-dominated cells by clover.

Parameters varied

We varied parameters that affected the interaction between grasses and clovers, the nature of clover dynamics, and the nature of grass dynamics. These parameters, summarized in Table 1, were chosen because of their potential to affect the fundamental nature of community dynamics and therefore the persistence and diversity of clover genotypes in the population. For instance, any link between species and genotypic diversity might be prevented if the ability of clover genotypes to spatially ‘track’ grass species is constrained by a low rate of clover growth or grass dynamics that are too fast.

Firstly, the range of niche breadths made it so that at narrow values only those genotypes that shared a nearly identical niche position with a grass species experienced a performance benefit and at the widest niche breadth all species and genotypes have overlapping niches, resulting in largely neutral dynamics. Secondly, local clover growth, defined as the probability of clover either staying or becoming abundant in a cell where it is already present (same calculation for both), depended on the degree of niche overlap between the locally co-occurring clover and grass within a range up to 0.1 below (low niche overlap) or above (high niche overlap) the baseline (Table 1). Thirdly, the rate of clonal clover spread was varied in the model via the

Table 1. Model parameters and their meanings (accompanies Fig. 1).

	Description/symbol	Value
Parameters		
	Grass species richness	1,2,4,7,10,15
	Niche breadth	0.05, 0.1, 0.5, 1, 10
	Baseline clover growth (BCG)	0.1, 0.5, 0.9
	Clover spread rate (CSR)	0,1
	Grass turnover[baseline death prob, half-range]	[0.001,0.001], [0.03, 0.03], [0.1,0.5]
Transition probabilities (Fig. 1)		
Fixed		
	Clover extinction from grass dominated cell (A)	0.3
	Transition from high grass to low grass if not invaded by clover (B)	0.08
	Global clover invasion into low grass cell (C)	0.02
	Global grass replacement when grass dies	0.01
Conditional (on niche position)		
	Local clover growth (D)	$BCG - 0.1 + 0.2 \times \text{Niche overlap}$
	Clover spreading in grass-only cell (E)	$(1-CSR) \times \text{Proportion clover neighbors} + CSR$
	Grass death (turnover rate)	$\text{Baseline} + \text{Half-range} \times \text{Proportion conspecific neighbors}$

probability of an empty cell getting colonized by clover as either equal to the proportion of neighbouring cells containing clover (low spread rate), or equal to one as long as at least one neighbouring cell contained clover (high spread rate). The local growth and spread rate can both be considered as components of average fitness in clover.

Finally, we varied the rate of grass dynamics. The diversity and relative abundances of grass species were not of interest per se as outcomes of our model, as there is no indication that clover genetic identity affects grass species identity or richness. Consequently, we specified the model to ensure that initial grass species diversity would be retained in each simulation, while allowing for different rates at which the grass species identities within cells changed, and therefore the rate at which grass species' distributions shifted through space. We set the probability of grass death within a cell, above a baseline, as proportional to the number of conspecific neighbours, thereby making intraspecific competition greater than interspecific competition, and ensuring grass species coexistence (Table 1). Once grass death occurred in a cell, it was either replaced with the species in one of the eight neighbouring cells chosen at random (local dispersal), or more rarely ($p = 0.01$) with the species in a cell chosen randomly from the entire community (global dispersal). Grass dynamics of this sort created a moving background of grass species, as is seen in natural pastures (Turkington and Harper 1979b). We varied the rate of grass dynamics via the baseline probability of grass death and the relationship between the probability of grass death and the number of conspecific neighbours (Table 1). Varying these two parameters simultaneously increased the speed at which grasses species turned-over in individuals cells, such that grass turnover was slow (~10% of grass species identities within cells changing each time step), intermediate (60%), or high (80%).

Model specifics and starting conditions

When clover spread into high grass or low grass cells, the identity of the invading clover was chosen randomly from

among the neighbouring cells, reflecting the dominance of asexual clonal spread in clover reproduction (Turkington and Harper 1979b). To reflect occasional establishment via seed (Burdon 1980), clover colonization of low-grass cells that did not get invaded by neighbouring clover occurred with a low probability ($p = 0.02$). The probability of clover extinction from grass-dominated cells was constant ($p = 0.3$), and therefore independent of grass and clover niche positions (solid lines in Fig. 1a), and high grass-cells not invaded by clover also transitioned to low-grass cells with a fixed probability ($p = 0.08$). These fixed probability values were similar to those in Schwinning and Parsons (1996a), chosen as rough approximations of field conditions; the absolute values of these parameters are not expected to be consequential – only their relative values with respect to other parameters (e.g. clover growth and spread), which we varied over a wide range. Although grass–clover interactions provided guidance, our aim was not a precise parameterization of any particular field, but a generalized treatment of dynamics among genotypes that vary in their response to interactions with other species, as is found in other biological systems as well (Vavrek 1998).

The intraspecific phenotypic diversity in populations of clover in the field is often quite high, and the likely source of this variation is genetic (Burdon 1980). Therefore, each community started with a genotypically rich clover population (clover genotypes = 50). A clover genotype is considered dead when none of the cells contain that genotype. Variation in the species richness of grasses (between 1 and 15 grass species) corresponded roughly to observations in natural pastures (Turkington and Harper 1979c). Clover genotypes and grass species were assigned evenly-spaced positions on the niche axis, taking values between and including zero and one, except in the cases when the number of grass species was 1 (niche position = 0.5), or 2 (niche positions = [0.333, 0.667]). For the initial community in each simulation, each cell was randomly assigned one of the four possible states in Fig. 1a. The identities of each grass and clover were also assigned randomly from the total pools of species and genotypes, respectively.

Response variables

The response variable representing 'genetic diversity' in each simulation was the time to reach a 50% reduction in genotypic richness. In a finite community with some global immigration, a quasi-stable equilibrium occurs when an extinction-immigration balance has been reached, and the time for a 50% reduction in genotypic richness accurately reflects relative differences among simulations in movement toward this quasi-equilibrium genotypic richness (Fig. 2). For a limited number of simulation runs, in particular those with diverse grass communities and wide niche breadths (i.e. nearly-neutral dynamics), equilibrium had not been reached at 30 000 time steps, most often because all initial clover genotypes were retained in those communities. For those limited simulations, genetic diversity is assigned a high value ($> 10^{2.5}$). We also examined as response variables the abundances of each genotype and species. Lastly, to test for deviations from randomness in the degree of niche overlap between the grass species and clover genotypes sharing individual cells at the end of each simulation, we calculated the probability of finding the observed degree of niche overlap via simulations in which clovers were randomly permuted among cells within the community.

Results

Species diversity of grasses can have a positive effect on the maintenance of clover genotypes (Fig. 3–5). Positive species-genetic diversity correlations occur with at least intermediate clover growth, a low to intermediate niche breadth, and

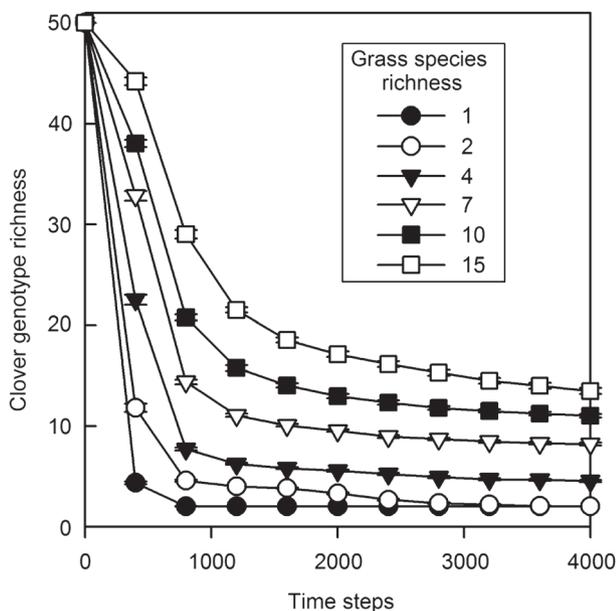


Figure 2. A simulation run showing the effect of grass species richness on mean clover genotype richness over time. A greater richness of clover genotypes from an initial pool of 50 persists in the communities with a greater richness of grass species. Standard error bars for 50 replicated communities are shown but appear small relative to the size of the symbol. In this simulation, clover growth is high ($= 0.9$), rate of clover spread is high ($= 1$), niche breadth is narrow ($= 0.05$), and grass turnover is slow.

even when grass turnover is rapid. Under these conditions, while all communities lose clover genotypes over time, the rate of loss is slower and the final genotypic richness of the clover population is higher in more grass-speciose communities (Fig. 2).

Clover growth and spread

The most prominent effect of grass species richness on clover genotype richness occurred when local clover growth was high, while at low and intermediate local clover growth the positive effect of grass species was modest (Fig. 3a). At low local clover growth, clover populations lose genotypic richness rapidly, and the positive effect of grass species richness is entirely absent under a low clover spread rate. As the growth of clover increases, the positive effect of increased grass species richness and niche breadth becomes pronounced, such that there is nearly a 100-fold increase in the time to lose the majority of clover genotypes. Interestingly, at moderate clover growth, the effect of increasing grass species richness saturates at 4–7 species. As would be predicted under an extremely wide niche breadth that is greater than the length of the niche axis ($NB = 10$), clover dynamics are effectively neutral with respect to the number of grass species, and there is consequently no relationship between grass species richness and clover genotype richness (Fig. 3a).

Increasing clover growth and clover spread rate increases both the proportion of cells in which clover is present and the proportion where clover is in high abundance (Fig. 3b). Correspondingly, in communities where clover growth is high, clovers are found in high abundance in nearly every cell of the community. However, the positive effect of grass species richness on clover genotype richness does not result only from increased clover abundance: in communities with intermediate clover growth rates, the size of the clover population was largely insensitive to grass species richness (Fig. 3b), while the genotypic richness of the clover population varied substantially with grass species richness (Fig. 3a).

At intermediate local clover growth, clover genotypic diversity remains higher for longer when clover spread is low than when it is high. This seemingly contradictory result stems from the nature of clover recruitment. The low rate of clover spread reduced the proportion of cells containing clover (Fig. 3b), and this decreased population size effectively increases the global rate of immigration because global immigration occurred only into low-grass that did not get invaded by neighbours. This increased rate of global migration leads to less predictable clover genotype composition because random clover individuals from the global pool enter into the community more often. These clover genotypes introduced from global migration in addition to those clover genotypes that share a similar niche position to the grasses present explain the increase in time to 50% genotype loss (Fig. 3a) and the increased standard error of clover genotype retention across the simulation runs, relative to high clover spread (result not shown). Although this link between local clover dynamics and global immigration may seem like a model artefact, it may not be an unreasonable representation of field conditions. Establishment of *Trifolium repens* from seed tends to be concentrated in areas of disturbance, such as molehills where clovers have been locally extirpated,

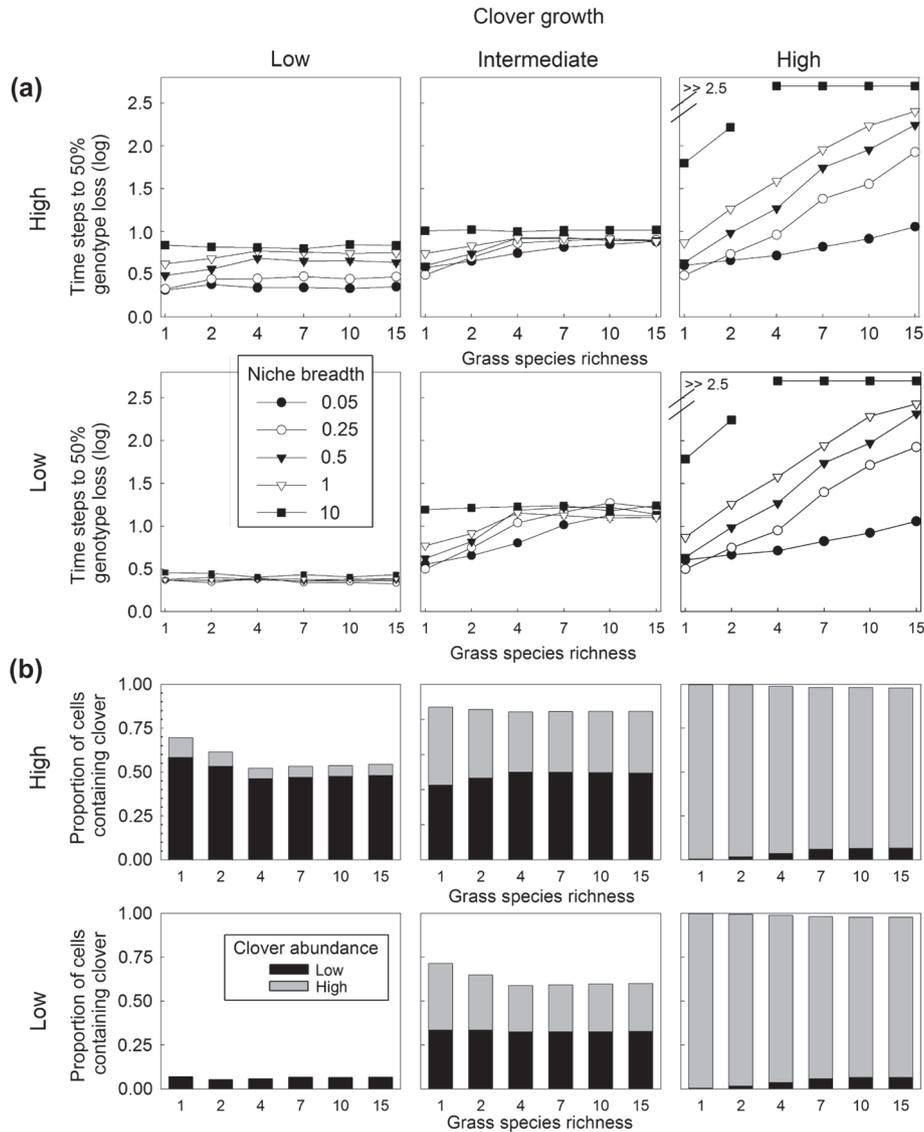


Figure 3. Effect of niche breadth, clover spread, and local clover growth on clover genotype diversity and abundance across communities with varying numbers of grass species. Local clover growth ranges from low ($=0.1$), to medium ($=0.5$), to high (0.9); clover spread ranges from low ($=0$) to high ($=1$). (a) Under many scenarios, increasing the number of grass species in the communities increases the time it takes for half of the clover genotypes to become extirpated. Each data point represents an average across 50 simulations (± 1 SE). A limited number of parameter combinations did not reach 50% genetic diversity loss in 30 000 time steps; these results appear above the hash marks. (b) The proportion of cells containing clover increases with increased local clover growth and spread, yet the positive species-genetic diversity trend does not result from increased clover abundance in more species-rich communities. Bar graphs shown for intermediate niche breadth ($=0.5$), although results are consistent across niche breadths.

and rare in undisturbed patches (Turkington et al. 1979); seedling establishment may, therefore, be inhibited by successful clonal spread.

Examination of the identities of clover genotypes retained in a given simulation reveals the mechanisms through which species and genetic diversity are linked (Fig. 4). In all cases, the clover genotypes retained shared similar niche positions with the grass species' in the community. Increasing niche breadth broadens the range of clover genotypes facilitated by each grass species, effectively increasing the number of positions along the niche axis where clover genotypes can persist, and this correspondingly resulted in greater retention of clover genotypes (Fig. 3a, 4b). Reducing local clover growth leads to lower abundance and therefore stochastic

extinction of most genotypes that do not share a nearly identical niche position with a grass species (Fig. 4c).

Rate of grass turnover

The rate at which grasses turnover had a moderate influence on clover genotype retention. As grass turnover increases, at high clover growth rate, there is a corresponding decrease in the number of clover genotypes retained for all niche breadths (Fig. 5). In all cases, the clover population retains nearly identical abundances regardless of grass dynamics (results not shown). Two other results concerning grass dynamics are worth noting. First, at high local clover growth, narrow niche breadth, and low grass species richness

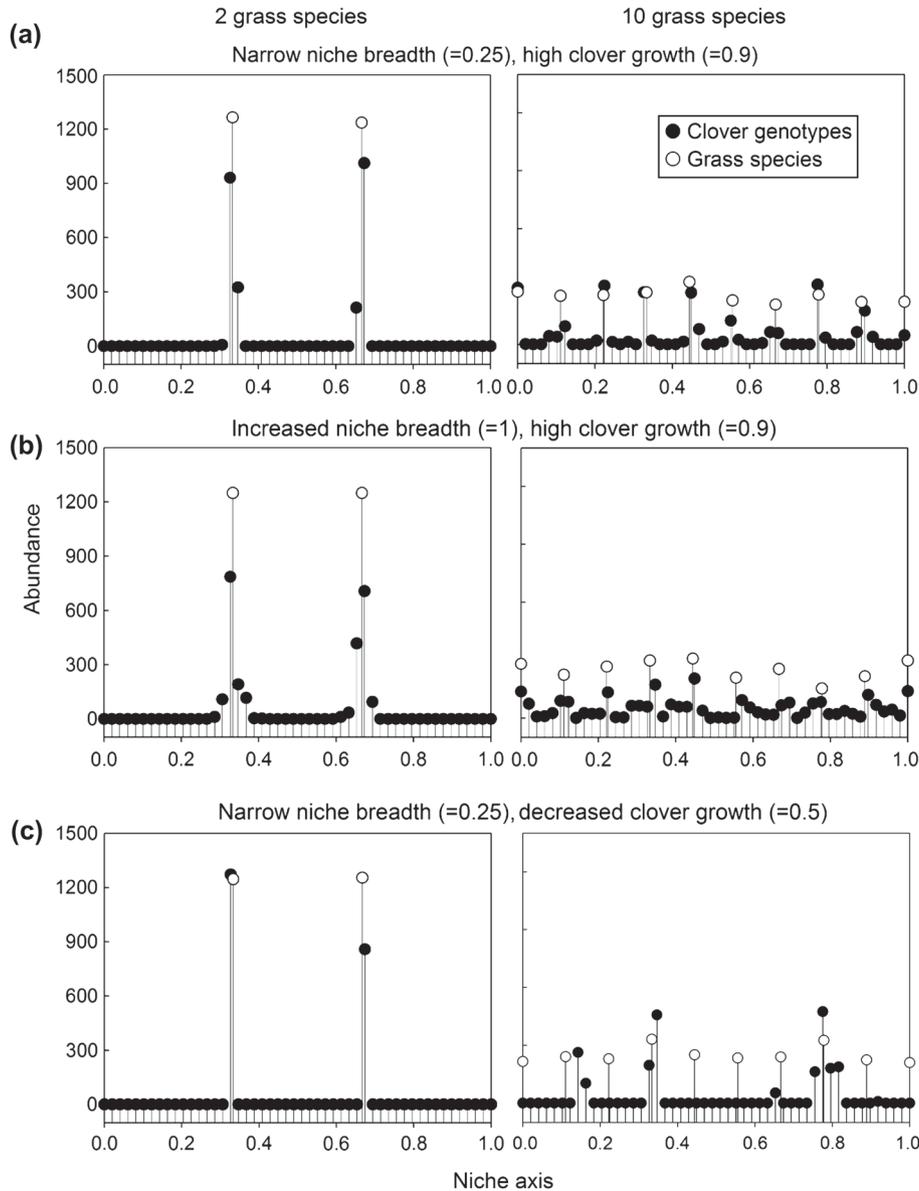


Figure 4. Abundances of grass species and clover genotypes at the final time step in representative simulation runs. Results are shown for different levels of local clover growth and niche breadths at two values of grass species richness, 2 and 10. Increased niche breadth allows for a greater spread of clover genotypes to persist around the grass species (b). As the local growth of clover decreases, fewer clover genotypes persist around fewer grass species (c).

(2–4 spp.), the fastest grass dynamics lead to the greatest genotypic diversity (Fig. 5). The negative frequency dependence of grass competition resulted in a greater evenness of grass species abundances for those communities with 2–4 grass species (thereby increasing clover genotype retention), and this effect is lost as species richness increases beyond four species. Second, although with low local clover growth the generally negative effect of increased grass turnover on clover genotype retention was not observed (Fig. 5), the mean niche difference between locally co-occurring grasses and clovers was decreased (Appendix 1 Table A1). At low local clover growth, the mean niche overlap was significantly different from random at slow and intermediate grass turnover but not at high grass turnover. This occurs at both narrow and wide niche breadths. The same trend holds at high clover growth, and the effect is even more pronounced:

the difference of niche overlap moved from highly significant ($p < 0.001$) at slow grass turnover to not significant ($p = 0.4$) at high grass turnover.

Discussion

Our model indicates that genotypic diversity in legume populations can be maintained by species diversity of interacting grasses. Diversity at these two levels of biological organization – genotypic diversity within species and species diversity within communities – can be correlated because species create a biologically heterogeneous environment, promoting diversity within a component species. In comparing our results with earlier modelling efforts (Vellend 2008), and examining the parameter combinations under which positive

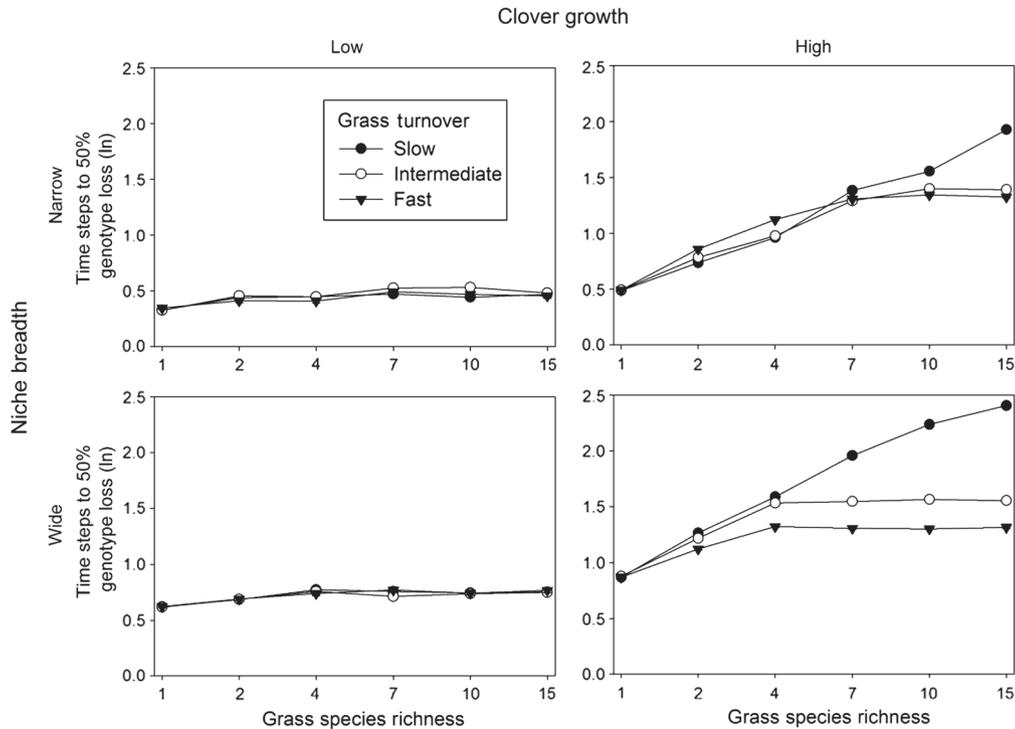


Figure 5. Effect of grass turnover rate on clover genotype diversity at different levels of local clover growth and niche breadths. In these examples, clover growth ranges from low ($=0.1$) to high ($=0.9$), and niche breadth ranges from narrow ($=0.25$) to wide ($=1$). The effect of a rapidly overturning grass population is seen only when local growth is high, regardless of the niche breadth.

species–genetic diversity correlations were found (or not), it appears that three conditions are required for this mechanism to operate. First, a tradeoff among genotypes in their response to different grass species is required; in the terminology of this model, niche breadth needs to be sufficiently narrow. Second, facilitation and competition need to be de-coupled to some degree, with facilitation allowing grasses and clovers to share physical space (this paper), rather than strictly excluding one another from individual microsites (as in Vellend 2008). Finally, clover fitness, as depicted through both growth and spread, needs to be sufficiently high relative to grass turnover to allow clover to ‘track’ the shifting mosaic of grass species. Empirical evidence provides qualitative support for each of these conditions (see Introduction), but whether or not they combine quantitatively to allow for a direct effect of species diversity on genetic diversity in the field remains an open question.

In our results, the positive species–genetic diversity correlation resulted from differential responses of genotypes to interactions with different species, a phenomenon that is not unique to *Trifolium repens* (Kelley and Clay 1987, Shaw et al. 1995, Vavrek 1998, Fridley et al. 2007). For example, different genotypes of the common dandelion, *Taraxacum officinale*, exhibited differential competitive ability against three competitor species (Vavrek 1998). Similarly, competitive ability of both the sedge *Carex caryophylla* and the grass *Koeleria macrantha* were affected by the genetic identity of the focal plant and the genetic identity of the competing species (Fridley et al. 2007). The results of our simulation may apply more broadly (when the three conditions above are met) to any system in which one group of organisms displays diversity in their response to competition with members of

a second group, whether that be at the genotypic or species level (Palmer and Maurer 1997, Iason et al. 2005).

Our model included only clonal reproduction, and therefore applies most directly to the many types of mature herbaceous vegetation, such as many grasslands, old fields, pastures or wetlands, in which seedling establishment is rare and therefore clonal growth the dominant form of reproduction (De Kroon and Van Groenendael 1997). Many of the empirical studies concerning the ecological consequences of intraspecific diversity have focused on clonally reproducing plants, such as goldenrods and evening primrose in old fields and grasslands (Crutsinger et al. 2006, Johnson et al. 2006) and seagrass in estuaries (Hughes and Stachowicz 2004). The key result of our model was that populations can locally adapt to the species identity of their competitors. Local adaptation can be influenced by sexual reproduction, especially via the addition of gene flow over larger spatial scales than clonal growth (Garant et al. 2007) and the consequent continual creation of individuals with phenotypes intermediate between those adapted to different local conditions (Vellend and Litrico 2008). Gene flow can either constrain local adaptation, via the immigration of maladapted genes, or promote local adaptation, by increasing additive genetic variance (Garant et al. 2007). Although the incorporation of additional complexities (e.g. sexual reproduction, long range dispersal, etc.) into our model could alter its predictions (as is the case for all theoretical models), we would expect similar outcomes to what we observed here as long as local selection is strong and gene flow not overwhelming (Thompson 2005).

In comparing our results with previous models (Vellend 2008), physical space and niche space emerge as important

components for predicting the effect of species diversity on genetic diversity. In our simulations, increasing the number of competing species does not necessarily constrain the available physical growing space for the focal species. Since grasses deplete soil nitrogen, thereby favouring the nitrogen-fixing clovers (Schwinning and Parsons 1996b), grasses cannot competitively exclude clovers from the entire spatial arena. Without this type of complementary resource use, increasing abundance of one group of organisms necessarily diminishes the abundance of another (i.e. zero-sum dynamics hold), and the biotic heterogeneity hypothesis is far less likely to hold (Vellend 2008). Focusing specifically on interactions between legumes and grass, the zero-sum assumption is effectively relaxed, such that 'ecological space' is created or augmented by the presence of another type. Consequently positive effects of species diversity on genetic diversity via biotic heterogeneity are found in a much wider range of conditions.

The form of facilitation incorporated in grass–clover dynamics can be considered indirect because it results from the promotion of certain genotypes relative to other genotypes growing with the same grass species, rather than relative to the same genotype growing without grass neighbours (Levine 1999). The incorporation of facilitation into traditional niche theory allows for indirect facilitation, where the addition of a new species may create or expand the realized niche of a particular species or genotype (Bruno et al. 2003). Empirical support for indirect facilitation has been found in a variety of systems at the species level (Levine 1999, Callaway and Pennings 2000, Arkema et al. 2009). Our simulations and empirical results for clover (Turkington and Harper 1979a) suggest that this same principle can operate at the genetic level: while grass may compete with clover, the exclusion of particular clover genotypes by particular grass species can facilitate the persistence of other clover genotypes. The distinction between competitor and facilitator becomes entirely relative: when the genetic diversity of the clover population is considered, the dual forces of genotype- and species-specific competition and facilitation produce a positive species–genetic diversity correlation.

Species and genetic diversity may be correlated because of direct interactions with each other, or through common processes influencing both simultaneously (Vellend and Geber 2005). When considering direct effects of one level of diversity on another, there are two contrasting theoretical frameworks for how species diversity might influence genetic diversity. Extensions of the 'diversity reduces invasibility' idea of Elton (1958) and the 'diversity begets diversity' idea of Whittaker (1975) predict effects of species diversity on non-neutral genetic diversity that are negative or positive, respectively (Vellend and Geber 2005). While a few studies have considered the possibility of within-trophic level interactions leading to an effect of species diversity on genetic diversity (Odat et al. 2004, Silvertown et al. 2009), each considered neutral genetic variation, in the form of amplified fragment length polymorphisms or allozymes. No correlation between species and genetic diversity was found in these studies. In contrast, a study of the diversity of understory species in relation to inter-individual variation in leaf chemistry in the overstory tree *Pinus sylvestris* found a positive correlation (Iason et al. 2005). These studies suggest that testing hypotheses concerning direct effects of species diversity on

genetic diversity or vice versa in empirical studies requires analyses of intraspecific variation for functional traits, rather than neutral variation. Specifically, our model indicates that relative fitness for growth rates against different competitors is a key functional trait to consider.

The aim of our model was to strike a balance between theoretical generality (interacting species on the same trophic level with a genotype \times species fitness tradeoff), and inclusion of an element of realism from a specific system (complementary resource use between the focal species and its 'community') that might provide the key to understanding when diversity in one group of organisms might directly influence diversity in a second group. Having explored a wide range of values for key model parameters under different assumptions (see also Vellend 2008), the qualitative conditions that emerge as important underpinnings of a 'diversity begets diversity' scenario seem likely to apply fairly broadly. In situations where such diversity–diversity relationships have been found, such as insects on plants (Crutsinger et al. 2006) or understory plants in relation to canopy trees (Iason et al. 2005), organisms in the 'response' group have shorter generation times than in the 'effect' group, which should allow the former to 'track' the latter (our third condition). These systems also appear to meet the other conditions concerning performance tradeoffs and space sharing.

For organisms on the same trophic level with comparable rates of temporal dynamics, such as grasses and clovers, we have shown that it is possible for diversity to beget diversity. Our simulations – with assumptions supported by empirical data – indicate that when genetic diversity within a focal species results in differential competitive ability with species of the same trophic level, a form of indirect facilitation can produce positive correlations between species diversity in communities and genetic diversity within populations. This area of research is in great need of new empirical studies. There are exceedingly few papers that have followed up on Turkington's experiments showing local adaptation of clovers to the identity of their competitors (but see Shaw et al. 1995); additional studies testing for local adaptation to competitor identity are needed to assess the generality of these results. In addition, the critical experiment of manipulating species diversity and measuring genetic diversity as a response variable has yet to be conducted. Measuring genetic variation for focal species in existing long-term species diversity manipulations (Tilman et al. 2001) could be a particularly fruitful approach in the short-term. Such studies will substantially advance efforts to link the fields of population genetics and community ecology.

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Appendix

Table A1. The p-values from a bootstrapping technique of comparing the niche positions of clovers with the niche positions of its co-occurring grasses observed at the end of simulation run to randomly swapped grasses (see methods). Dark-gray $p < 0.001$, light-gray $p < 0.05$, white p not significant. Although the effect of increasing the rate of grass turnover on time to 50% loss of clover genotypes is seen only for high clover fitness (Fig. 6 main text), the mean niche overlap between grasses and clovers decreases as rate the grass turnover increases.

Grass species	Low clover growth Rate of grass turnover			High clover growth Rate of grass turnover			
	Slow	Intermediate	Fast	Slow	Intermediate	Fast	
Narrow niche breath	2	7.44×10^{-8}	1.42×10^{-5}	2.35×10^{-1}	0.00	1.85×10^{-68}	1.50×10^{-1}
	4	4.22×10^{-6}	1.01×10^{-4}	1.42×10^{-1}	0.00	1.60×10^{-77}	1.03×10^{-1}
	7	1.96×10^{-5}	6.49×10^{-6}	6.29×10^{-2}	0.00	6.34×10^{-46}	9.77×10^{-2}
	10	2.93×10^{-5}	9.69×10^{-7}	5.20×10^{-2}	0.00	9.57×10^{-45}	7.87×10^{-2}
	15	2.33×10^{-6}	2.32×10^{-9}	3.64×10^{-2}	0.00	1.45×10^{-47}	5.51×10^{-2}
Wide niche breath	2	1.04×10^{-1}	2.22×10^{-1}	4.30×10^{-1}	9.72×10^{-288}	4.21×10^{-8}	4.01×10^{-1}
	4	2.51×10^{-2}	3.38×10^{-2}	3.19×10^{-1}	0.00	1.17×10^{-13}	3.41×10^{-1}
	7	6.27×10^{-2}	3.29×10^{-2}	3.54×10^{-1}	0.00	4.46×10^{-15}	3.07×10^{-1}
	10	6.23×10^{-2}	8.79×10^{-3}	3.34×10^{-1}	0.00	1.13×10^{-15}	2.79×10^{-1}
	12	3.16×10^{-2}	1.93×10^{-2}	2.61×10^{-1}	0.00	2.01×10^{-19}	2.74×10^{-1}

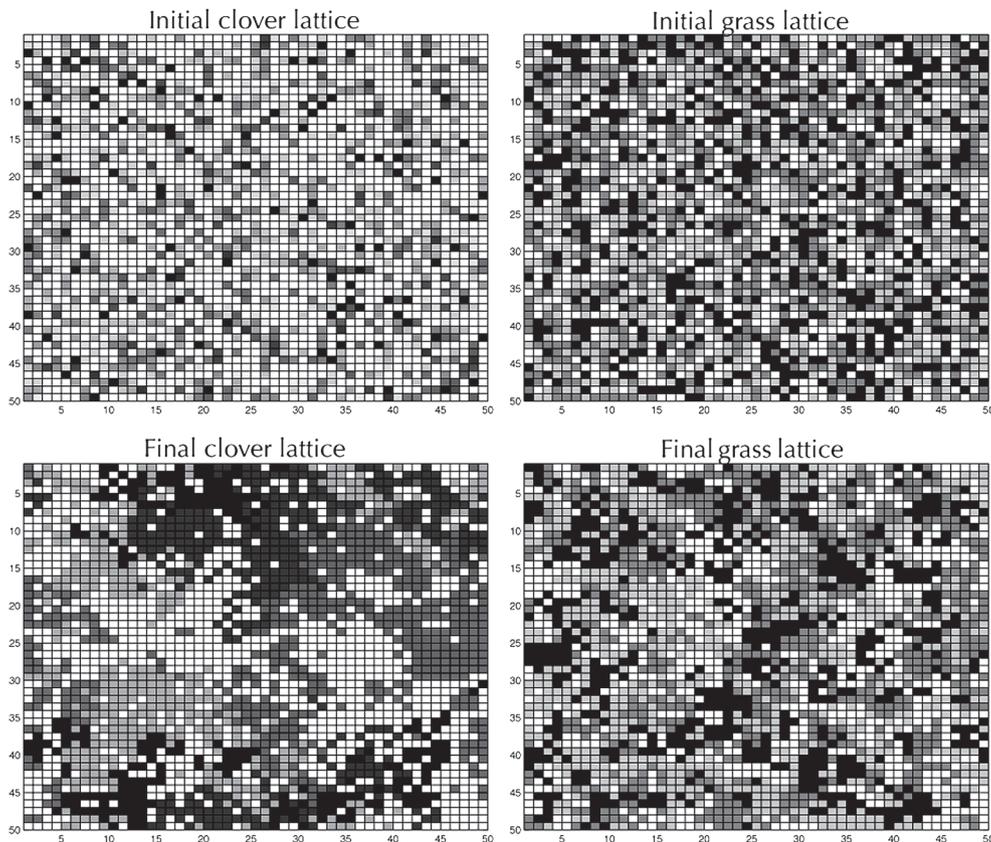


Figure A1. Snapshots of the clover and grass lattice with identities represented by shading. At the start of the simulation (top row), communities are random with respect to clover and grass abundance and distribution. Interaction and growth dynamics incorporated in the model produce the typical pattern of a clonal spread of clover in a matrix of grasses (bottom row). In this example, grass species richness is 4, niche breadth is intermediate ($\beta = 0.5$), local clover growth is intermediate ($\alpha = 0.5$), clover spread is high ($\gamma = 1$), and grass dynamics are slow.