

Evolution and spatial structure interact to influence plant–herbivore population and community dynamics

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SUMMARY

An individual-based model of plant–herbivore interactions was developed to test the potentially interactive effects of explicit space and coevolution on population and community dynamics. Individual plants and herbivores resided in cells on a lattice and carried linked interaction genes. Interaction strength between individual plants and herbivores depended on concordance between these genes (gene-for-gene coevolution). Mating and dispersal among individuals were controlled spatially within variably sized neighbourhoods.

Without evolution we observed high-frequency plant–herbivore oscillations (blue spectra) with small individual neighbourhoods, and stochastic fluctuations (white spectra) with large neighbourhoods. Evolution resulted in decreased interaction strength, decreased herbivore-induced plant mortality, increased population sizes, and longer-term fluctuations (reddened spectra). Small herbivore neighbourhoods led to herbivore extinction only with evolution.

To explore the increased population size response to evolution we ran simulations without evolution while tuning plant–herbivore interaction strength from high to none. We found that herbivore populations were maximized at intermediate levels of interaction strength that coincided with the interaction strength achieved when the system tuned itself through evolution.

Overall, our model shows that the small-scale details of phenotypically variable individual-level interactions, leading to evolutionary dynamics, affect large-scale population and community dynamics.

1. INTRODUCTION

The nature of plant–herbivore interactions is that they are typically spatially localized with intensities that are, at least in part, genetically determined. A question of fundamental importance to the understanding of the ecology and evolution of populations and communities is how fine-scale detail, such as interactions between individual plants and herbivores, translates into macroscopic patterns of population dynamics and community structure.

The fluctuations of natural populations are typically characterized by reddened spectra (Cohen 1995; Pimm & Redfearn 1988; Steele 1985), that is, those in which low frequency oscillations predominate. Cohen (1995), however, has shown that in contrast, typical deterministic models of population dynamics exhibit blue spectra, dominated by higher frequencies. Several authors have argued in response that simple models may exhibit more reddened spectra through widening the tested parameter space (Blarer & Doboeli 1996), or by including delayed density dependence (Kaitala & Ranta 1996) or explicit space (White *et al.* 1996*b*). Doebeli (1996) also showed that the inclusion of

quantitative traits in an individual-based model without explicit space stabilized population dynamics for both competition and host–parasitoid systems. Capturing these low-frequency dynamics in models is fundamental to representing real populations since populations with reddened spectra have been shown to have substantially lower extinction probabilities (Ripa & Lundberg 1996).

In this paper, we examine a model of genetically variable populations in explicit space, exploring the interplay between the ecology and evolution of interaction neighbourhoods in plant–herbivore systems. To simplify the system's genetics, we restrict attention to gene-for-gene (GFG) interactions (see Flor 1955; Hartvigsen & Starmer 1995; Levin 1983). Thompson & Burdon (1992) reviewed GFG interactions and found many accounts of the mechanism involved in a wide range of agricultural systems, including pests such as rusts, smuts, mildews, fungi, bacteria, viruses, and the Hessian fly. Therefore, although the effects of explicit spatial location of interacting individuals and individual-level genetic variability have been shown to independently influence population dynamics, the interactive effect of these two factors on population and community dynamics remains unexamined for such systems.

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Our effort is exploratory, demonstrating one possible mechanism underlying reddened spectra. It is mechanistic in the spirit of individual-based models (e.g. DeAngelis & Gross 1992), but clearly not definitive.

2. THE MODEL

We study a spatially explicit individual-based evolutionary model that allows us to manipulate the size of mating and dispersal neighbourhoods independently for genetically defined plants and herbivores. Individuals reside on a two-dimensional, square lattice (L^2 ; $16 \leq L \leq 256$). Lattices of $L = 64$ are discussed predominantly, but simulations with $L = 128$ and 256 gave qualitatively similar results (see all parameter values used and tested, table 1). Individual cells contained at most one plant and a variable number of herbivores. Plant population size was determined by competition for space and the effect of herbivory. Herbivore population size was a function of plant encounter rate, feeding concordance (equivalent to individual interaction strength), and energy transfer efficiency. Biomass for plants (P) and herbivores (H) at the end of each generation was modeled as:

$$P_{i,\text{end}} = P_{i,\text{start}} - \sum_{j=1}^m (C_{ij}P_i) \quad (1)$$

$$H_{k,\text{end}} = H_{k,\text{start}} + \epsilon \sum_{l=1}^n (C_{kl}P_l) \quad (2)$$

where the energy transfer efficiency $\epsilon = 0.10$.

Each i plant (P_i) started as an adult ($P_{i,\text{start}} = 35.0$) and lost biomass through m herbivore attacks. The severity of attack was a function of concordance (C), or the matching of alleles as in gene-for-gene systems, between plants and herbivores (Clay 1996; see Mitchell's (1993) review of genetic algorithms). This individual-based approach allows diffuse coevolution (Levin *et al.* 1990), with herbivores capable of eating a variety of plant types. Each k herbivore (H_k) was born with relatively low biomass ($H_{k,\text{start}} = 1.0$) and gained biomass by successfully attacking n plants. Herbivores had the potential to consume 50% of each plant they encountered (simulations were qualitatively similar for herbivore consumption ranging from 15% to 85% of each plant). The system was energetically open in that energy was transferred from plants to herbivores with a 10% efficiency, avoiding the need to set a predefined carrying capacity.

Herbivores randomly walked to one of eight neighbouring cells per step (Moore neighbourhood) for five steps during their lifetime, for an average distance of 2.15 cells from their natal cell, and attempted to feed on all plants encountered. During each movement episode all herbivores had equal probability of being chosen, moved to a new random neighbour cell, and fed if a plant was present. Model behaviour was similar when the model was changed so that herbivores took only three steps, but increasing the number of steps only increased effective neighbourhood size and simulation time.

(a)

Mating	Species Chromosome	Interaction Chromosome
Mate 1	■ □ □ □ □ □ □ □	■ □ □ □ □ □ □ □
Mate 2	■ □ □ □ □ □ □ □	□ □ □ □ □ □ □ □
Recombinant	■ □ □ □ □ □ □ □	■ □ □ □ □ □ □ □
Mutation	□ □ □ □ □ □ □ □	□ □ □ □ □ □ □ □
Offspring	■ □ □ □ □ □ □ □	■ □ □ □ □ □ □ □

(b)

Feeding	Interaction Chromosome	Concordance (C)
Herbivore Plant	□ □ □ □ □ □ □ □	1.0
Herbivore Plant	■ □ □ □ □ □ □ □	1.0
Herbivore Plant	■ □ □ □ □ □ □ □	0.0
Herbivore Plant	■ □ □ □ □ □ □ □	0.5

Figure 1. Quantitative genetics represented by linked loci, each having 2 alleles (white or black, representing binary 0 and 1). Mating (a) occurs between individuals that have no more than one allelic difference on each of the two chromosomes. Recombination occurs between individuals at one, randomly chosen location on each chromosome. Mutation (x) occurred with equal probability after recombination to produce offspring. Feeding (b) occurred as herbivores encountered plants in cells on the lattice. Matching gene-for-gene alleles determines the level of concordance ($C = \text{number matches divided by the number of loci}$).

Individuals bore a haploid genetic representation of their phenotypes (figure 1). All individuals within a trophic level were initially identical (clones) and subsequently reproduced sexually. The role of evolution was tested by allowing mutation, recombination and selection to alter gene frequencies. Two independent chromosomes, each with linked, two-allele loci, identified species and interaction chromosomes for each individual (figure 1a). Under conditions allowing evolution, a single recombination event per chromosome at a random site between individuals occurred. The resulting chromosomes were then subjected to mutation, where each of the loci was flipped (0 to 1, or 1 to 0) with a probability of 10^{-3} . Mutation rate was correlated with the rate of evolution and showed no qualitative influence on model dynamics over the tested range of 10^{-2} to 10^{-6} . There was no explicit cost of defence in plants, but individuals with unusual genetic sequences (potentially well defended mutants) suffered the risk of increased reproductive isolation and lower realized fitness (e.g. individuals that differed

by more than one allele on one of the chromosomes were reproductively isolated).

We tested the sensitivity of the model to a range of loci involved in the quantitative traits of reproductive compatibility and interaction (e.g. defence in plants) (table 1). For these tests, we used 1, 2, 4, 8, 16, and 32 loci and ran the model for 1224 generations. This allowed us to remove the first 200 generations and produce periodograms for the remaining 1024 generations.

Herbivore reproduction occurred by random selection of a female from the entire lattice, with probability weighted by its biomass, and then selection of a male with probability proportional to biomass, from within the female's neighbourhood (the size of the neighbourhood was varied from a 3×3 neighbourhood centred on the female to the entire lattice). Offspring were placed randomly within the neighbourhood of the female and one unit of biomass was subtracted from each parent. Reproduction in herbivores continued until there were no herbivores remaining (death occurred when $H_k < 1.0$). Plants and herbivores in this model reproduced and died annually. A similar model suggested that increasing the ratio of herbivore:plant generations had little effect on population dynamics (Hartvigsen & Starmer 1995).

Chromosomes were compared for gene-for-gene synchrony between individuals to determine reproductive compatibility (figure 1*a*) and the level of concordance for feeding (figure 1*b*). Concordance (C) for feeding was calculated as the number of allelic matches divided by the number of loci between individual plants and herbivores (equations (1) and (2)) and ranged from 0.0 to 1.0 (figure 1*b*). The population-level statistic for concordance represents mean interaction strength for all herbivores that successfully fed on at least one plant.

Plants functioned as both males and females (monoecious) while herbivores were either male or female. Plant reproduction was accomplished by choosing lattice cells systematically (all cells were considered open at the beginning of each reproductive phase), choosing a plant with probability weighted by biomass within the neighbourhood of the open cell, and choosing a pollen donor with probability weighted by biomass from within the neighbourhood of the first plant. Therefore, plants with the largest biomass were most likely to be chosen to be reproductives.

Simulations began with $0.8 * (80\% \text{ of Lattice } (L) \text{ filled}) L^2$ herbivores and plants randomly dispersed on the lattice. All experiments were replicated with matching sets of initial conditions (initial random number seeds resulted in identical placement, number, and genotypes of plants and herbivores), after which only the different factors, such as plant neighbourhood size, affected model outcome. The model was written in the C programming language.

3. ANALYSES

Population dynamics were analysed by finding the difference between the number of individuals at the end of each generation and the mean, and constructing

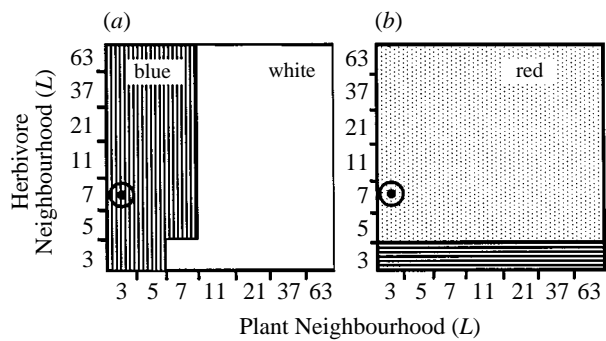


Figure 2. Herbivore population and community dynamics with (b) and without (a) evolution on a 64×64 lattice. Square neighbourhoods (L^2) were tested over a range of sizes ($3 \leq L \leq 63$). Without evolution populations either exhibited high-frequency, blue spectral oscillations (vertical pattern) or random, white spectra (no pattern). With evolution, herbivore populations exhibited low-frequency, reddened spectra (stipple pattern) or, with small herbivore neighbourhoods, went extinct (horizontal pattern). Plant populations behaved identically in all areas of parameter space except where herbivores went extinct. Under these conditions plant populations were stationary at L^2 (e.g. 4096 on $L = 64$ lattice). Bullseyes represent neighbourhood parameter settings for sample simulations in figures 3–7.

a periodogram using the fast Fourier transform algorithm (SYSTAT 7.0). Population dynamics were stationary after a transient period of approximately 100 generations in most simulations. To be conservative, we removed at least 200 generations from the beginning of each time series to avoid transient effects (see Hastings & Higgins 1994). Power spectra were categorized as being dominated by low frequency (red) or high frequency (blue), or having peaks throughout all frequencies (white) (White *et al.* 1996*a*). By using relatively long time series (usually 1024 generations) we were able to classify most periodograms within these broad categories.

To describe further the accumulation of variability in these time series we calculated the standard deviation of the natural logarithm of abundance (SDL) for the 'evolution' and 'no evolution' simulations (Pimm & Redfearn 1988). These SDLs were calculated for nested windows of size 2^g for $g = 1$ to 11 and plotted against generation (g). SDL graphs typically rise quickly and remain level for white and blue spectra (small windows capture population variability) but increase more slowly with increasing window size for reddened spectra.

4. POPULATION DYNAMICS IN RESPONSE TO EVOLUTION

Plant and herbivore populations, in the absence of external factors such as disturbance or environmental heterogeneity, exhibited a diversity of dynamical behaviours that depended on the size of plant and herbivore neighbourhoods and whether coevolution occurred (figure 2). Without evolution plants and herbivores oscillated only when plant dispersal was relatively local (blue spectra; see figure 2). Plant recruitment

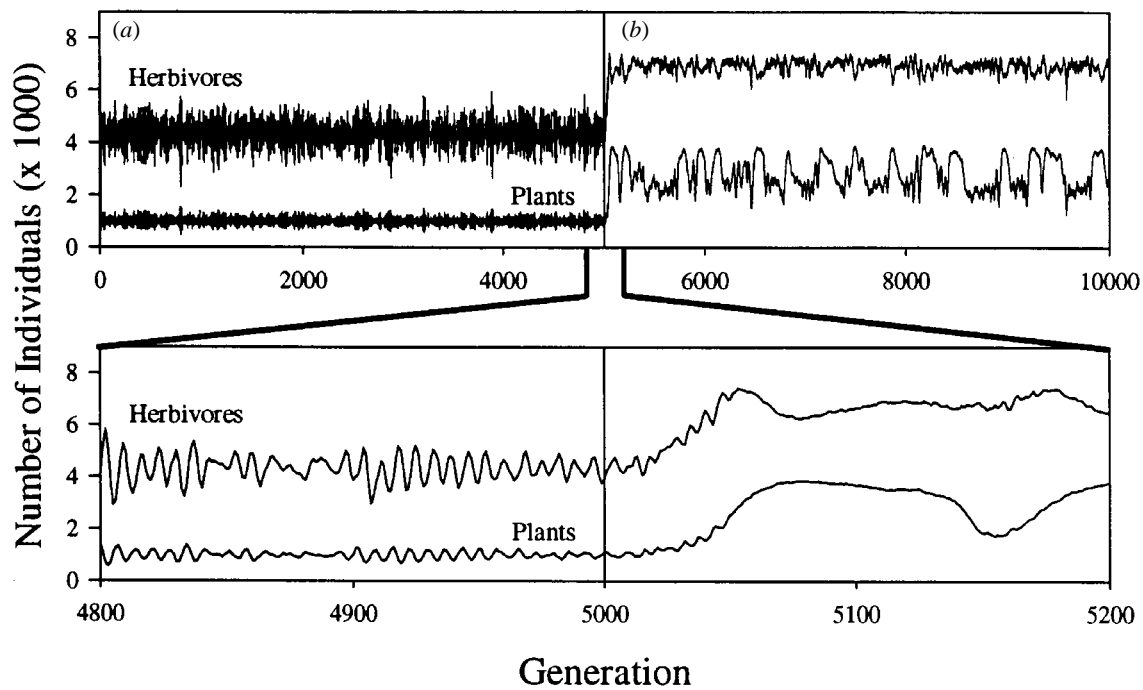


Figure 3. An example of the effect of turning evolution on, after 5000 generations without evolution (a). The transition to evolution (b) results in an increase in herbivore and plant populations and the change from coupled oscillations to reddened spectral stochastic fluctuations (default settings, table 1).

rates increased when plant dispersal distance increased (i.e. all lattice cells became available to each plant). This enabled plants to fill the lattice and break the coupled oscillations, resulting in stochastic fluctuations yielding white spectral dynamics (white area on figure 2). This suggests that the intrinsic biotic detail of how individuals use space alters population dynamics from blue to white spectra, but does not lead to reddened spectra as discussed by White *et al.* (1996a). The relative insensitivity of population dynamics to changes in herbivore neighbourhood size is likely due to the relative size of herbivore populations and their overall dependence on the plants.

The dynamics of coevolving population were quite different from this pattern (figure 2). In general, and independent of plant neighbourhood size, individual variability and natural selection allowed plants to evolve herbivore defences that ultimately reduced herbivore-induced mortality. This reduction allowed plant populations to increase in number and fill the lattice, ultimately breaking the coupled oscillations (see transition from no evolution to evolution, figure 3). However, unlike the 'no evolution' simulations that yielded blue and white spectral dynamics, the evolution simulations led to variable and delayed tracking of plant defences by herbivores, producing low-frequency, reddened spectral dynamics (e.g. figure 4e). This result was dependent on the number of loci involved in the interaction. Increasing the number of loci progressively lowered the frequency of oscillations in population dynamics (figures 4b–g). Therefore, our model strongly suggests the process of evolution, in coupled systems with quantitative traits, is sufficient to

cause low-frequency reddened spectral dynamics over time. Doebeli (1996) similarly found that sexual reproduction with genetically variable individuals changed population dynamics.

Herbivore populations went extinct when their neighbourhoods were small (3×3 cells) only under conditions allowing evolution. This result occurred on the largest tested lattices (256×256 cells), suggesting that the risk of extinction through spatial constraint at the individual level could not be allayed by using larger lattices. Since populations were persistent in the absence of evolution, extinction with evolution can not be attributed to restricted neighbourhood sizes or small population sizes (evolution with 2–16 loci consistently resulted in larger plant and herbivore populations). Therefore, results from this model suggest that herbivore populations with small neighbourhoods sustain a higher risk of extinction than herbivores that include at least some long-distance mate searching and offspring dispersal. In this part of parameter space where herbivores disperse locally, our results contradict the findings of Ripa & Lundberg (1996), who concluded that reddened spectra reduced the probability of extinction. They argued that correlated population dynamics are statistically less likely to encounter the zero boundary condition of extinction than a truly stochastic population (e.g. white spectral dynamics). This assumption, however, does not account for the mechanism causing reddened spectra. If the mechanism behind increased correlation in population dynamics is evolutionarily based, this model suggests that herbivores may, depending on how they exploit space, suffer increased extinction likelihood.

Table 1. *Parameters in model*

(The default settings and the range of tested settings are provided.)

parameter	default setting	tested settings
number of generations	≥ 1224	$\leq 10\,000$ but ≥ 1224
lattice size (L)	64	16–256
number of loci (N_{LOCI})	8	1–32
number of alleles/locus	2	*
number of mismatches for species	1	1–8 for 8 loci
number of mismatches for consumption	$= N_{\text{LOCI}}$	1–8 for 8 loci
proportion of plant eaten by herbivore	0.50	0.1–1.0
cost of reproduction	1.0	*
energy transfer coefficient	0.10	0.01–0.9
initial number of plant species ¹	1	*
plant species code (example for 8 loci)	00000000	—
plant interaction code (defence)	00000000	—
initial number of herbivore species ¹	1	*
herbivore species code (example for 8 loci)	00000000	—
herbivore interaction code (prey-type)	00000000	00000001, 00011111
(tested only for 8 loci)	—	00000011, 00111111
	—	00000111, 01111111
	—	00001111, 11111111
initial proportion of grid filled with plants and herbivores	0.80	0.05–1.0
number of herbivore steps/generation	5	0–15
plant/herbivore evolution	yes and no	all 4 combinations
plant neighbourhood	3×3	3×3 to global
herbivore neighbourhood	7×7	3×3 to global
lattice function ²	torus	*
mutation rate	10^{-3}	$10^{-2} - 10^{-6}$
new plant biomass ³	35.0	20.0–75.0
new herbivore biomass	1.0	*
plant/herbivore critical biomass	1.0	*

*Not tested.

¹This factor allows for the construction of specific food webs with variable interaction strengths among predators and prey and will be explored in the future.

²Not tested were reflecting and absorbing boundaries.

³This parameter can be changed to simulated fertilization treatments.

Our goal in this model was to investigate plant–herbivore coevolution with equal rates of mutation among interacting species. Interestingly, when we allowed plants but not herbivores to evolve, plants quickly evolved defences that resulted in herbivore extinction, independent of neighbourhood size. In contrast, if herbivores could evolve while plants were constrained evolutionarily, herbivore populations were robust in their persistence with dynamics qualitatively similar (blue spectra) to no evolution simulations. Therefore, the evolution of defence in plants drives the dynamics in our model.

In addition to the effect of evolution on herbivore population dynamics and extinction likelihood, evolution influenced how variance accumulated over time (figures 5*a,b*). The SDL describes population variability as a function of increasing length of sample period (Pimm & Redfearn 1988). Pimm & Redfearn (1988) reported that, of the 26 long-term data sets available for mammals, birds, and insects of Britain, a majority exhibited increasing SDL, a pattern indicating reddened spectra. Without evolution the last 2048 generations of runs > 5000 generations showed variability peaked between 8 and 64 generations, beyond which no added variability was observed (figure 5*a*).

With evolution, variability accumulated up to window sizes on the order of 2048 generations (figure 5*b*).

The variance peak in the SDL graphs (figure 5) occurs at longer intervals than those reviewed by Pimm & Redfearn (1988). This difference may not be surprising considering the tightly coupled coevolutionary conditions of our model, a situation likely to be more diffuse and potentially less constrained spatially in the predominantly avian populations studied by Pimm & Redfearn (1988). Our model results suggest an even more severe cautionary tale than that of Pimm & Redfearn (1988), who argued that populations studied for less than 20 years may not reveal the important patterns of population variability. Our model suggests that the intrinsic biotic factors of spatial relationships among organisms and their ability to coevolve influence population dynamics over time periods of 2000 or more years.

5. COMMUNITY RESPONSE TO EVOLUTION

As discussed above, evolution increased herbivore extinction risk only with small herbivore neighbourhoods. Herbivore populations with larger individual neighbourhoods were not at risk of extinction,

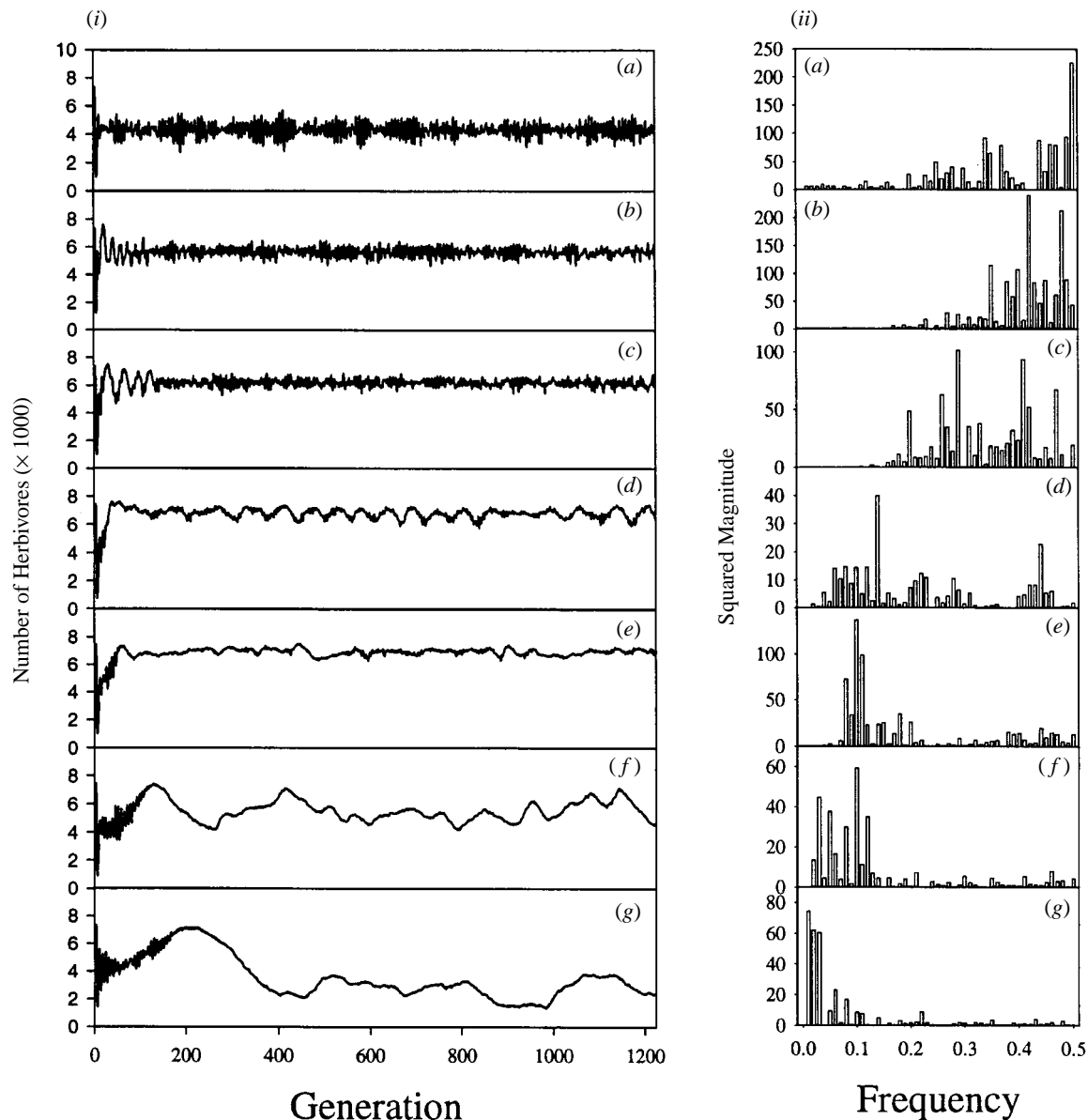


Figure 4. Herbivore population dynamics (i) for runs without evolution (a) and with evolution with 1 (b), 2 (c), 4 (d), 8 (e), 16 (f), and 32 (g) loci (default settings otherwise, table 1). Periodograms (ii) show frequency spectra for the last 1024 generations for each simulation. With evolution and increasing number of loci, observed frequencies in the population time series shift from high (blue spectra) to low (reddened spectra).

exhibited reddened spectra of low-frequency dynamics, and increased in response to evolution. Figure 3 shows the overall pattern resulting from 'switching on' individual-level mutation and recombination, resulting in plant–herbivore coevolution after 5000 generations without evolution. The transition to the low-frequency dynamics is not instantaneous as the plants evolve defences against the herbivores (figure 3b), with transients from the 5000 generations without evolution lasting fewer than 100 generations. The increase in plant and herbivore populations occurred on all tested grid sizes with 2–16 loci involved in the interaction. Interestingly, 32 loci resulted in a decrease in herbivore numbers and an increase in plant numbers. Therefore, the response of community structure and dynamics to evolution depended on how herbivores

used space and the number of loci involved in the coevolutionary interaction.

The cause of the increase in plant and herbivore populations seen in figures 3, 4 and 6 appears to lie in decreased concordance (interaction strength) between plants and herbivores that resulted in decreased herbivore-induced plant mortality. Figure 6 shows typical population dynamics with and without evolution on a 32×32 lattice. We repeatedly observed no increase in mean individual plant herbivore biomass but, because of the increase in plant and herbivore numbers, we observed increased community-level plant and herbivore biomass. A similar effect has been observed in plant–herbivore and plant–herbivore–predator systems when fertilized (Hartvigsen *et al.* 1995). Hartvigsen *et al.* (1995) grew cottonwood saplings

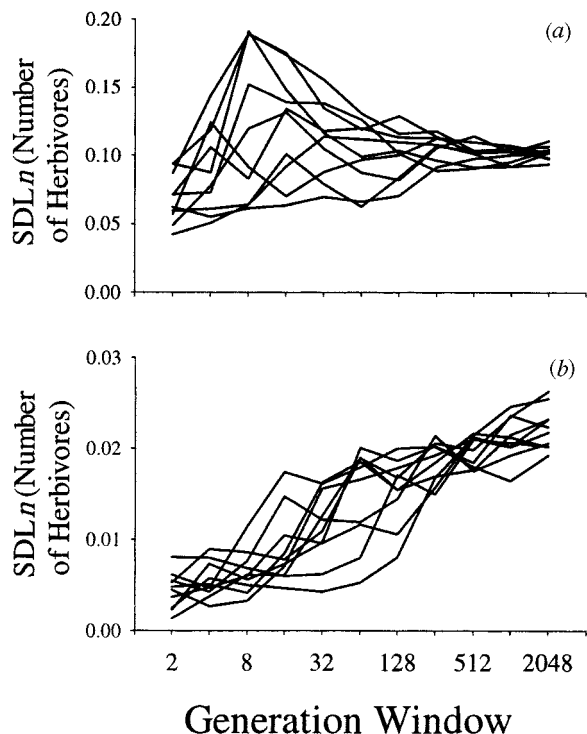


Figure 5. Nested standard deviation (SDL) of the natural logarithm of herbivore abundance (SDL). Generation windows were increased from 2 to 2048 generations using the last 2048 generations from ten 8000 generation simulations each without evolution (a) and with evolution (b).

under six different conditions: in the absence of herbivores and predators, with herbivores, and with herbivores and predators, tested under controlled and fertilized conditions. Plant fertilization only increased the growth (height, leaf area, and the number of leaves) of herbivore-free plants. Fertilization with herbivores increased herbivore population sizes but had no effect on individual plant biomass. The fertilization effect was also noted in the predator population, which reduced the herbivore population, again removing all fertilization effects. Unfortunately, as with most short-term experiments, it was not possible to observe the actual effect of fertilization on plant fitness or changes in population density over time. Therefore, our model makes a nonintuitive prediction of plant response to evolution that is similar to the Hartvigsen *et al.* (1995) fertilization result: that individual plants will not benefit from evolving defences, but that total plant biomass will increase and alter structure and dynamics of both plant and herbivore populations.

The increase in plant and herbivore populations in response to evolution appeared to have occurred in response to decreased herbivore-induced mortality and the coupled increase in plant fecundity (figure 6d), with birth rates increasing and death rates decreasing when plants evolved defences to herbivores. Interestingly, the herbivore population increased in response to the increasing plant population (figure 6b). As mean concordance (interaction strength) decreased to the level of about 40% of the 'no evolution' simulations (figures 6e,f), herbivore-induced mortality declined. Plants expanded their population

to fill the grid and the structure of the community completed its differentiation from the 'no evolution' simulations.

We conducted a controlled experiment under conditions without evolution on a 32×32 lattice to explore the effect of reducing concordance on plant and herbivore populations and community biomass (figure 7). As we incrementally altered herbivore interaction genes (see table 1) and herbivores became less adapted to feeding on plants (similar to the effect of plants evolving defence genes against herbivores) both populations of plants and herbivores increased (figure 7a). Interestingly, the maximum population size for herbivores occurred when concordance reached 37.5% of the 'no evolution' simulations where herbivore genes matched plant genes exactly (figure 1b, table 1), similar to the 40% concordance observed with evolution (vertical lines in figure 7).

Total community biomass, of course, was greatest when no herbivores were present (figure 7b). Decreases in total biomass of communities with herbivores was due to energy loss during transfer from plants to herbivores (90% loss). The non-linear decline in total community biomass appears to have been driven by the simple ability of herbivores to persist and consume plants, despite their very low feeding concordance. This suggests that plants are most negatively affected by the presence of herbivores rather than how well they are defended against attack. This result is identical to that reported from a fundamentally different coevolutionary model of how the ratio of the number of herbivore and plant generation times would affect the evolution of plant fitness (Hartvigsen & Starmer 1995). In that model the authors found that plant fitness decreased significantly between simulations without herbivores and simulations where herbivores were introduced with herbivore : plant generations of 1 : 1. Little difference in plant fitness was observed as the herbivore : plant generations increased from 1 : 1 to 250 : 1.

In a field test of the effect of local adaptation of thrips on native or novel clones of *Erigeron*, Karban (1989) found that herbivores performed significantly better on native cuttings than on other genotypes. The study, however, did not address the performance of plants relative to herbivore-free plants and, more importantly, among plants hosting variably adapted herbivores. The results presented here suggest that the evolution of plant defences reduces the impact of herbivory, resulting in increased plant fecundity, reduced herbivore-induced mortality, and dramatic changes in population dynamics. Our results also suggest that total community-level plant biomass increases with increased defence due to reduced herbivore feeding. Herbivore populations, in turn, experience a positive feedback and increase in response to increased plant biomass, despite decreased feeding efficiency. Plants are most negatively affected simply by the presence of herbivores, while long-term plant and herbivore population dynamics (in the presence of herbivores) are most affected by the interacting factors of plant–herbivore coevolution and the extent of plant mating and dispersal in space.

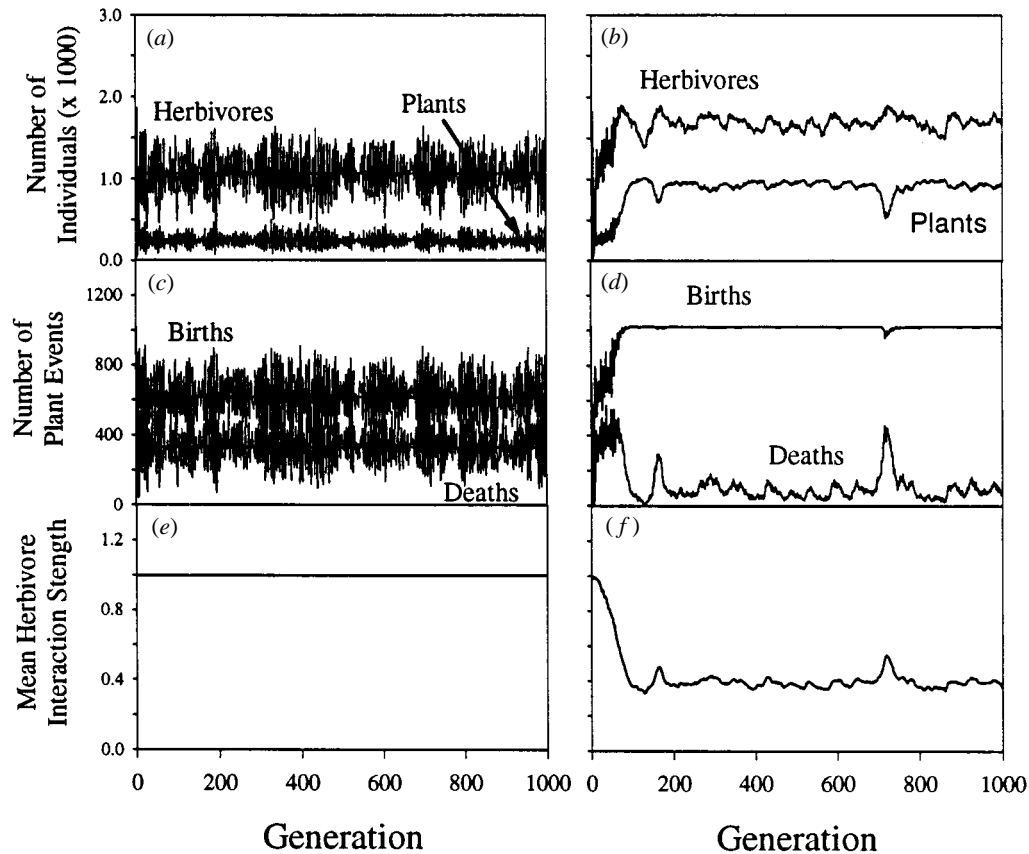


Figure 6. A comparison of typical simulations without evolution (*a, c, e*) versus simulations with evolution (*b, d, f*) on a 32×32 lattice for 1000 generations (default settings otherwise, table 1). With evolution (*b*), the initial conditions of no individual genetic variability led to oscillating transients that persisted for about 100 generations. Without evolution population dynamics were stationary throughout the simulation (*a*) while populations of plants and herbivores with evolution initially increased and then fluctuated with low-frequency, reddened spectra dynamics (*b*). With evolution, mean interaction strength between herbivores and plants (*f*) resulted in lower herbivore-induced plant mortality (*d*). Note the slight increase in herbivore interaction strength at generation 725 (*f*) that led to increased herbivore-induced plant deaths (*d*) and slightly decreased plant fecundity (*d*).

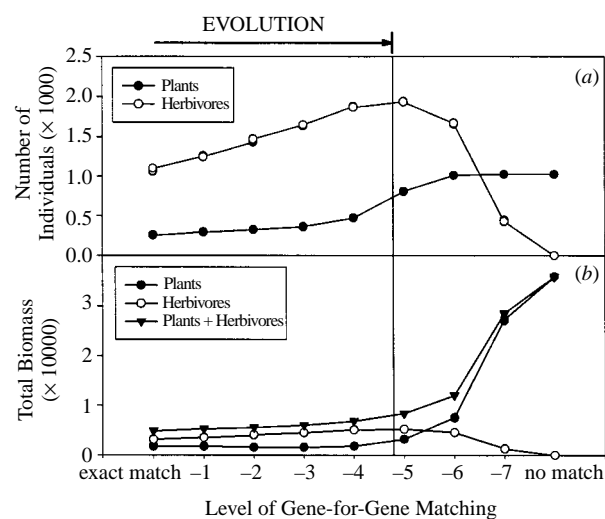


Figure 7. Changes in population and community structure are shown from an experiment with controlled reduction in level of plant-herbivore interaction strength (abscissa) without evolution on a 32×32 lattice (default settings otherwise, table 1). Interaction strength ranged from exact matches between plants and herbivores to complete mismatch where all eight interaction genes differed. Each test of herbivore feeding concordance was replicated five times (points not dithered). Herbivore population size was

6. CONCLUSION

Our model addresses the effect of individual variability on population and community dynamics through the simulated process of evolution. The results suggest that this small-scale detail (genetic variability) significantly alters large-scale community patterns and interacts with spatial dynamics operating at the level of individuals. Interestingly, observed patterns of population dynamics in nature (i.e. reddened, low-frequency spectra) were only reproduced in simulations that incorporated the process of evolution. The simplified simulations without individual variability, and thus no evolution, reproduced dynamics commonly seen in many simpler models. We, therefore, conclude that many ecological questions will have to be addressed by including processes and effects that potentially span

highest at an interaction strength 37.5% of exact gene matching (*a*) (i.e. only three out of eight genes matched). Interestingly, interaction strength between plants and herbivores evolved to a similar level of interaction strength (40%, vertical line). Due to energy transfer loss from plants to herbivores, communities without herbivores had the greatest plant and total biomass (*c*).

many hierarchical levels (e.g. genes to interacting species) in order to capture dynamics observed in nature.

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