

# Sex and space destabilize intransitive competition within and between species

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Organisms ranging from bacteria and corals to plants and vertebrates can form intransitive competitive networks, in which coexistence can be maintained because no one species or genotype is superior to all others. However, in the simplest case with three competing types, the long-term outcome may not be so clear if two of the three represent the ends of a continuous heritable trait distribution within one species, as has been recently demonstrated empirically in a short-term experiment with plants. Using simulation models of this scenario, results with asexual reproduction confirm previous studies which showed that local interactions promote coexistence. However, with sexual reproduction, genetic variance is reduced because selection fluctuates between favouring the two extremes during population cycles, while sex continually produces intermediates. Sex thus slows the response to selection when it is the strongest and therefore slows the recovery from extreme abundances, creating larger abundance fluctuations. Local interactions do not stabilize dynamics with sex because the resultant spatial patches of one species are genetically heterogeneous, such that particular phenotypes do not benefit from spatial refuges. In sharp contrast to previous models suggesting that sex or local interactions stabilize population dynamics, here sex and local interactions destabilize dynamics and increase extinction risk.

**Keywords:** genetic diversity; intransitive competition; rock–paper–scissors; species coexistence; sexual reproduction; space

## 1. INTRODUCTION

In a group of three competing species or genotypes, if A is superior to B, B superior to C and C superior to A, they are said to form an intransitive network in that no one type is superior to all others. An often-used analogy for such situations is with the children's game of rock–paper–scissors, in which rock beats scissors, scissors beats paper and paper beats rock. The potential for intransitive networks in real populations or communities has important ramifications given the potential for the maintenance of species or genotype coexistence despite strong competitive interactions, which are otherwise not generally favourable to coexistence (Huston 1994). The discovery of compelling empirical examples of such non-hierarchical competitive networks in a range of different taxa (Jackson & Buss 1975; Sinervo & Lively 1996; Huisman & Weissing 1999; Kerr *et al.* 2002; Kirkup & Riley 2004; Lankau & Strauss 2007) has sparked theoretical interest in this issue (Durrett & Levin 1997; Pagie & Hogeweg 1999; Tainaka 2001; Johnson & Seinen 2002; Yoshimura *et al.* 2006; Reichenbach *et al.* 2007; Laird & Schamp 2006, 2008). Models provide a means of exploring the long-term implications of short-term data, as well as a wider range of situations than can typically be observed empirically.

One of the best-known empirical examples of a rock–paper–scissors game involves toxin–resistance–susceptibility relationships among strains of the bacterium *Escherichia*

*coli*. Strains that produce a particular toxin (to which they are resistant) kill non-resistant strains, resistant strains that do not produce the toxin can grow faster than toxin-producing strains because they do not pay the metabolic cost of toxin production and non-resistant strains can grow faster than resistant strains by avoiding the cost of resistance (Kerr *et al.* 2002; Kirkup & Riley 2004). Coexistence of the three discrete types can be stably maintained, at least under some conditions.

In most studies of *E. coli* and other well-known rock–paper–scissors games, such as reproductive morphs in side-blotched lizards, *Uta stansburiana* (Sinervo & Lively 1996), each member of the trio is a distinct morph or strain. A very different kind of rock–paper–scissors game was recently described by Lankau & Strauss (2007), in which two of the three players in the game represent the ends of a continuously distributed trait within one species, while the third partner is a separate species. Individuals of the outcrossing annual plant, black mustard, *Brassica nigra*, produce a chemical called sinigrin. The tissue concentration of sinigrin is a heritable trait and higher levels of sinigrin confer a competitive advantage over other species. Individuals of *B. nigra* that produce low levels of sinigrin have a competitive advantage over high-sinigrin individuals, but are competitively inferior to other species (three of which were tested). In the absence of other species strong directional selection erodes genetic variation in *B. nigra*, and in the absence of genetic variation in *B. nigra* one or the other species should go extinct depending on the fixed sinigrin concentration. Lankau &

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Strauss (2007) conducted experiments using *B. nigra* from the two extremes of the sinigrin-concentration distribution, which on the surface makes this example resemble those with three discrete types. However, the fact that *B. nigra* is an outcrosser with individuals in natural populations having sinigrin concentrations continuously distributed between the two extremes raises intriguing questions (see below). In addition, given the common occurrence of genetic variability for traits that mediate competitive interactions (Aarssen 1983; Turkington & Aarssen 1984; Taper & Case 1992), this scenario is probably more general than this specific example.

If coexistence can be maintained among three players in a rock–paper–scissors game, what are the consequences of adding intermediate phenotypes between two of the strategies, particularly if such intermediates are continually produced via sexual reproduction? Models of competitive, host–parasite or predator–prey interactions suggest that genetic variation and sexual reproduction can stabilize population dynamics and enhance the probability of coexistence (Doebeli & Koella 1994; Doebeli 1995, 1996; Flatt & Scheuring 2004; Vellend 2006). However, the scenario we address is different in that we are not examining sex and variation within each of the three species, but essentially connecting two of the three via asexually or sexually reproducing intermediate phenotypes, which makes the outcome difficult to predict *a priori*. Previous theoretical and empirical studies have also demonstrated an important role for spatially structured interactions (e.g. only with immediate neighbours) in stabilizing the outcome of intransitive competitive interactions (Durrett & Levin 1997; Frean & Abraham 2001; Kerr *et al.* 2002). Plant or bacterial competition on a two-dimensional surface is highly localized, unlike, for example, the more ‘global’ competition among bacterial strains in liquid culture. It is not immediately clear how intransitive competition with intermediate phenotypes, either with sexual or asexual reproduction, might interact with the spatial scale of species interactions to determine community dynamics.

Here we present results of a simulation model addressing the consequences of genetically determined intermediate phenotypes within a single species that connect two of the nodes in a rock–paper–scissors game. Specifically, we address the consequences of asexual versus sexual reproduction and local versus global species interactions on the outcome of competition between the two species. The results reveal that with sexual reproduction, local interactions actually increase the amplitude of abundance fluctuations and therefore make coexistence less likely than with global interactions—exactly the opposite of results found for intransitive competition among three discrete types.

## 2. THE MODEL

We simulated the dynamics of two-species communities with a constant total number of individuals across species,  $\mathcal{J}$ . Individuals of species A vary in their phenotypic value for a trait ( $\phi$ ) that determines the outcome of interactions with other individuals of either species A or B. We assume haploid genetics in species A with additive inheritance. Each of  $n_L$  loci underlying the trait takes a value of 0 or 1; the phenotype is determined by the sum of these values

across loci, and can take one of  $n_L + 1$  discrete values. There is no genetic or phenotypic variability within species B.

Following Frean & Abraham (2001), each time step in the model starts with the selection of two individuals in the community; dynamics are determined by the probability that the second individual replaces the first with one of its offspring,  $\text{Pr}(2 \rightarrow 1)$ . These probabilities were determined by the identity of the species and the phenotype of species A, when relevant, as follows.

- (i) For two individuals of the same species and phenotype, there is no replacement:  $\text{Pr}(2 \rightarrow 1) = 0$ .
- (ii) For two individuals of species A, if the phenotype of individual 1 ( $\phi_1$ ) is less than the phenotype of individual 2 ( $\phi_2$ ), then  $\text{Pr}(2 \rightarrow 1) = 0$ . (In trial simulations we found no qualitative effect of allowing some replacement when  $\phi_1 < \phi_2$ .)
- (iii) Higher phenotypes of species A are replaced by an offspring of lower phenotypes with a probability, varying from 0 to 1, that increases linearly with the difference in phenotype. That is, for two individuals of species A, if  $\phi_1 > \phi_2$ , then  $\text{Pr}(2 \rightarrow 1) = (\phi_1 - \phi_2)/n_L$ . Rules (ii) and (iii) represent the cost of possessing a high phenotype in species A.
- (iv) Individuals of species A are replaced by an offspring of species B with a probability, varying from 0.1 to 0.9, which is a negative linear function of the phenotype of species A. That is, if the first individual is of species A and the second of species B, then  $\text{Pr}(2 \rightarrow 1) = 0.1 + 0.8 \times (n_L - \phi_1)/n_L$ . (We used the endpoints 0.1 and 0.9, rather than 0 and 1, to allow for the addition of nonlinear relationships between the phenotype and replacement probabilities without having to change the mean replacement probabilities across phenotypes simultaneously.)
- (v) Species B individuals are replaced by an offspring of species A individuals with a probability, varying from 0.1 to 0.9, which is a positive linear function of the phenotype in species A. That is, if the first individual is of species B and the second of species A, then  $\text{Pr}(2 \rightarrow 1) = 0.1 + 0.8 \times \phi_2/n_L$ .

The first individual is chosen at random. With global interactions, the second individual is also chosen at random such that all pairs of individuals have the same chance of competing. For the case of local interactions, the  $\mathcal{J}$  individuals are arranged in a square matrix with dimensions  $\sqrt{\mathcal{J}} \times \sqrt{\mathcal{J}}$  and periodic boundary conditions, and the second individual is chosen randomly from among the first individual’s eight nearest neighbours. That is, with local interactions, only the nearest neighbours compete directly and dispersal occurs into adjacent cells.

For the case of asexual reproduction, the offspring of individual 2 is an exact clonal copy. For the case of sexual reproduction (relevant for species A), an offspring is generated by mating individual 2 (the mother) with another individual of species A (the father) chosen at random from the population. For plants, this amounts to an assumption of widespread pollen dispersal. We assume that the loci are unlinked such that the offspring genotype is determined by randomly selecting one of the two parental alleles independently at each locus.

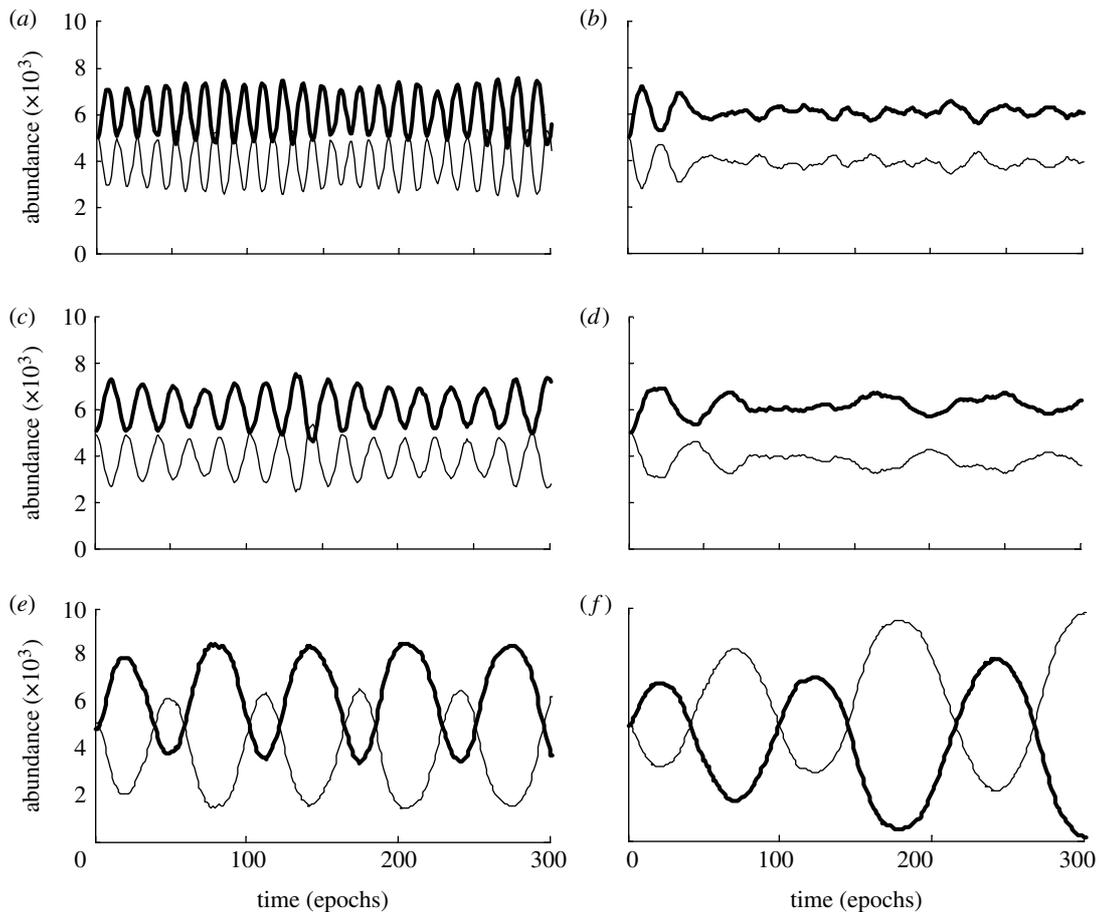


Figure 1. Abundances of species A (thick line, the genetically variable species) and species B (thin line) for the first 300 epochs (longer time periods make the shorter cycles impossible to see) in individual simulations with  $\mathcal{J}=10\,000$ . (a) Three discrete types—species B and two extreme genotypes of species A—with global interactions, (b) three discrete types with local interactions, (c) phenotypes in species A determined by 15 additive loci with two alleles each under asexual reproduction and global interactions, (d) 15 loci, asexual reproduction and local interactions, (e) 15 loci, sexual reproduction and global interactions and (f) 15 loci, sexual reproduction and local interactions.

For each of the four combinations of local versus global interactions and asexual versus sexual reproduction, we conducted 40 simulations of 1000 epochs each, with one epoch equal to  $\mathcal{J}$  time steps (i.e. every individual will, on average, have a chance of being replaced once per epoch). All simulations began with each individual assigned to one of the two species with equal probability, and within species A to each phenotype with equal probability. For each initial individual of species A, the genotype was determined by randomly selecting  $\phi$  of the loci to take a value of 1, with all other loci taking a value of 0, where  $\phi$  is the phenotype (an integer value between 0 and  $n_L$ ). This core set of simulations was repeated with 5 versus 15 loci underlying the trait in species A, and with community sizes of  $\mathcal{J}=10\,000$  versus  $\mathcal{J}=1024$ . Two additional situations were explored as well. First, we examined simulations with only one locus and asexual reproduction, which is equivalent to having three discrete non-recombining types, as in most previous models. Second, for asexual or sexual reproduction and global or local interactions in communities with  $\mathcal{J}=10\,000$ , we introduced nonlinear relationships between the phenotype and fitness in interactions between the two species. Specifically, we used quadratic functions that either gave intermediate phenotypes a relative advantage (higher probabilities of replacing B and lower probabilities of being replaced by B) or disadvantage (vice versa) relative to the linear

case. The 1000 epochs were determined *a priori* to be sufficient to characterize the model's dynamics. For all summary statistics calculated in each simulation (e.g. the mean and variance of species' abundances), we excluded the first and last 100 epochs to avoid having initial transient dynamics or dynamics during rapid declines to extinction bias the results.

### 3. RESULTS AND INTERPRETATION

Results were qualitatively the same regardless of the number of loci and the size of the community, except that in small communities high variance in abundance, when present, led to the extinction far more often than in large communities. As such, we focus on the case of large communities ( $\mathcal{J}=10\,000$ ) and 15 loci, with selected results mentioned for smaller communities.

#### (a) Competition among three discrete types

With species A represented by only the two extreme non-recombining phenotypes, intransitive competition maintains coexistence in large communities. The two species (and the two genotypes within species A) show cyclical dynamics that have shorter periods and markedly dampened amplitude (i.e. reduced temporal variance) with local interactions compared with global interactions (figures 1a,b and 2a).

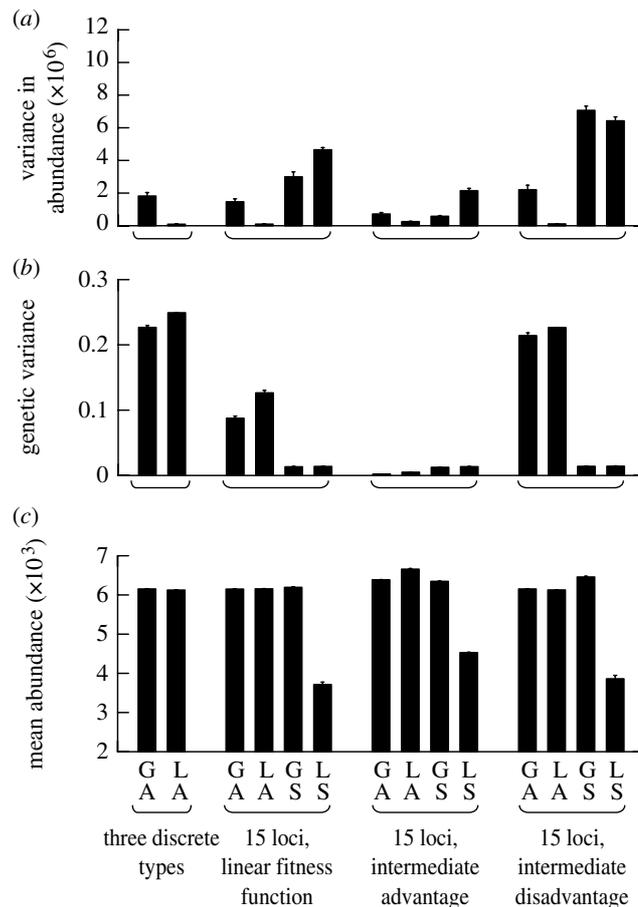


Figure 2. (a) Variance in abundance, (b) median genetic variance and (c) mean abundance in species A across 40 simulations under each of 14 parameter combinations in large communities ( $\mathcal{J}=10\,000$ ). In (b) variance was calculated after re-scaling the trait values to vary from 0 to 1. In (c) an abundance of  $5 \times 10^3$  represents equivalent abundances of the two species. Each bar represents the mean across simulations  $\pm 1$  s.e. Interactions (G, global; L, local) and reproduction (A, asexual; S, sexual).

### (b) Genetic variation with linear fitness functions

With asexual reproduction and multi-locus genetic control of the phenotype in species A, dynamics of the two species are similar, except that the cycle periods are somewhat increased (figure 1c,d). These results confirm previous models demonstrating a strong stabilizing effect of local interactions on competitive dynamics in rock–paper–scissors games (Durrett & Levin 1997; Frean & Abraham 2001; Kerr *et al.* 2002). The local interactions produce discrete patches of species or phenotypes in which losses on one side of a patch due to a superior neighbour can be balanced by gains on the other due to an inferior neighbour. The results also indicate that the main influence of intermediate phenotypes in the absence of other differences is to slow down cyclical dynamics, which can be explained as follows. With intransitive competition and cyclical dynamics, selection within species A is the strongest on the extreme phenotypes, with fluctuations back and forth depending on the abundances of each species and phenotype (figure 3a). Only with the extreme phenotypes, this allows for rapid responses to selection and similarly rapid fluctuations in abundance. Selection on intermediate phenotypes is comparatively weak despite equivalent average fitness over time, such that their addition to the population of species A reduces overall fitness variance and thereby slows down the fluctuations in abundance.

Sexual reproduction changes things considerably. Under global interactions, population cycles have greater amplitudes and longer periods with sexual than asexual

reproduction (figure 1c,e). Although sexual reproduction has traditionally been thought to increase genetic variance (Kondrashov 1993), here we find greater genetic variance with asexual than with sexual reproduction (figures 2b and 3). This is, in fact, entirely consistent with recent models demonstrating that when selection itself acts to increase genetic variance by favouring extremes, sexual reproduction can reduce genetic variance by continually creating intermediate phenotypes (Otto & Lenormand 2002). As such, when extremes of abundance create strong selection in favour of either high or low phenotypes in species A, there is more variance under asexual than sexual reproduction, thereby causing more rapid shifts in abundance back towards the long-term average when reproduction is asexual.

Things get particularly interesting with the combination of sexual reproduction and local interactions. In all scenarios discussed so far, the long-term average abundance of species A is greater than that of species B (figure 2c) because species A essentially comprises two of the three partners in the rock–paper–scissors network. However, the combination of sexual reproduction and local interactions changes the situation to one in which the opposite is true: species A is considerably less abundant than species B (figures 1f and 2c). With lowered mean abundance and high temporal variance in abundance, species A is prone to extinction, which can be seen particularly clearly in relatively small communities. In small communities ( $\mathcal{J}=1024$ ), extinction of species A

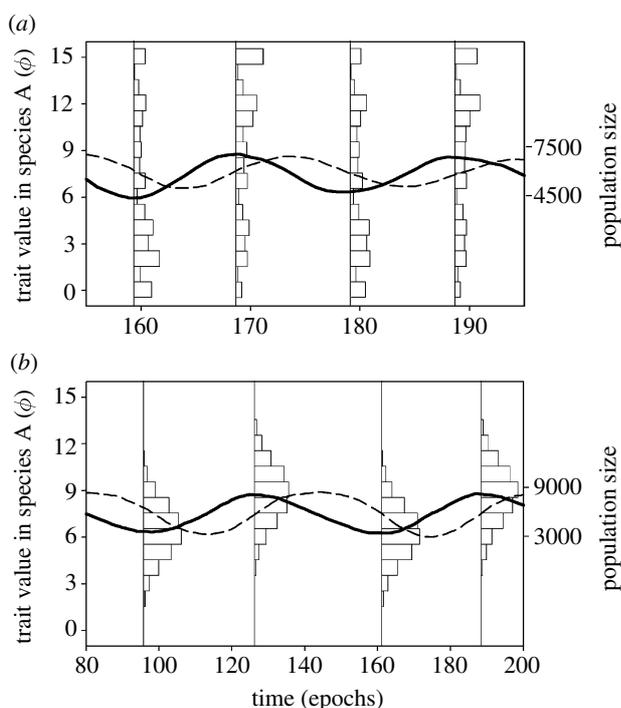


Figure 3. Changing phenotype distributions (proportional frequency histograms) during population and phenotype cycles with (a) asexual and (b) sexual reproduction in individual simulations of communities with  $\mathcal{J}=10\,000$ , 15 loci and global interactions. Solid lines show the mean phenotypic value and dashed lines show population size of species A. To allow more direct comparison, (a) and (b) have different ranges for time ( $x$ -axis) and population size (right  $y$ -axis, dashed line), which mask the differences in cycle period and amplitude seen in figure 1. After many hundreds to thousands of epochs (not shown), some phenotypes are lost due to drift under asexual reproduction, though the variance remains fairly constant. Allele fixation at particular loci under sexual reproduction occurs almost exclusively when extreme population fluctuations cause the population size of species A to approach zero (e.g. with sex plus localized interactions).

occurred in 80% of simulations with sexual reproduction and local interactions, compared with 35% or less in all other scenarios. In larger communities ( $\mathcal{J}=10\,000$ ), species A went extinct in 4 of the 40 simulations with sexual reproduction and local interactions, but never in the other scenarios.

The instability with sex and local interactions can be explained as follows. With asexual reproduction, local interactions create discrete shifting patches of species B and of different phenotypes of species A (figure 4b). Replacements of one type by another can occur only along the edges between two patches, such that individuals in patch interiors enjoy a spatial refuge (Kerr *et al.* 2002). Sexual reproduction results in patches of A and B, but not of phenotypes within species A because locally dispersed offspring are phenotypically variable (figure 4c). In the interiors of patches of species A, selection always favours lower phenotypic values. If high phenotypes occur on patch edges they enjoy a competitive advantage over species B, but since they are continually replaced by lower phenotypes from the patch interior, it is comparatively difficult for patches of species A to advance against patches of species B. This puts species A at a relative disadvantage, greatly lowering its average abundance

(figure 2c). Finally, since the same factors that caused sexual reproduction to increase the amplitude of population cycles under global interactions still apply, species A becomes prone to extinction.

### (c) Genetic variation with nonlinear fitness functions

When intermediate phenotypes have increased fitness (averaged across interactions with all other types) relative to the linear case and interactions are global, asexual reproduction leads to extinction of the extreme phenotypes and therefore greatly reduced genetic variance (figure 2b). However, with only a few intermediate very similar phenotypes remaining, selection is relatively weak leading to slightly reduced temporal variance in abundance (figure 2a). Despite reduced selection intensity, the fluctuating selection regime still maintains coexistence of two to three of the asexual phenotypes. As with linear fitness functions, local interactions greatly reduce temporal variance in abundance (figure 2a).

With an intermediate fitness advantage, the destabilizing effects of sexual reproduction are diminished because the intermediate phenotypes are not as strongly selected against when selection favours the extremes. With global interactions, variance in abundance is actually somewhat reduced relative to the asexual case (figure 2a). However, the combination of sexual reproduction and local interactions still leads to the greatest variance in abundance of the four sex-by-space combinations (figure 2a), as well as a greatly reduced abundance of species A (figure 2c). Thus, the disadvantage of sex with local interactions outweighs any advantage in terms of reduced abundance fluctuations resulting from a fitness advantage to intermediate phenotypes.

When intermediate phenotypes are at a fitness disadvantage and reproduction is asexual, selection rapidly leads to extinction of intermediate phenotypes leaving only the extremes, and thus dynamics converge on those observed with three discrete types (figure 2). With sexual reproduction, recombination continually produces relatively unfit phenotypes leading to very unstable dynamics, which show the greatest temporal variance in abundance of any scenario examined (figures 2a and 5). Even in large communities ( $\mathcal{J}=10\,000$ ), extinction of species A or B occurred in more than 97% of simulations. Since extreme phenotypes can still be produced and species A still represents two of the three nodes of the intransitive network, abundance of species A is, on average, higher with global interactions, so in this scenario species B typically goes extinct (figure 5c). With local interactions, species A goes extinct (figure 5d).

## 4. DISCUSSION

Previous models on the evolutionary dimensions of intransitive networks have focused on toxin production/resistance genes that are either on or off (e.g. Czárán *et al.* 2002), or on the growth rate or degree of competitive advantage within species (Freen & Abraham 2001; Johnson & Seinen 2002). In these cases the nodes of the intransitive network are discrete, albeit potentially evolving, which is distinct from our model with sexual reproduction in which multiple nodes in the network are intimately linked by sex and recombination. We found that

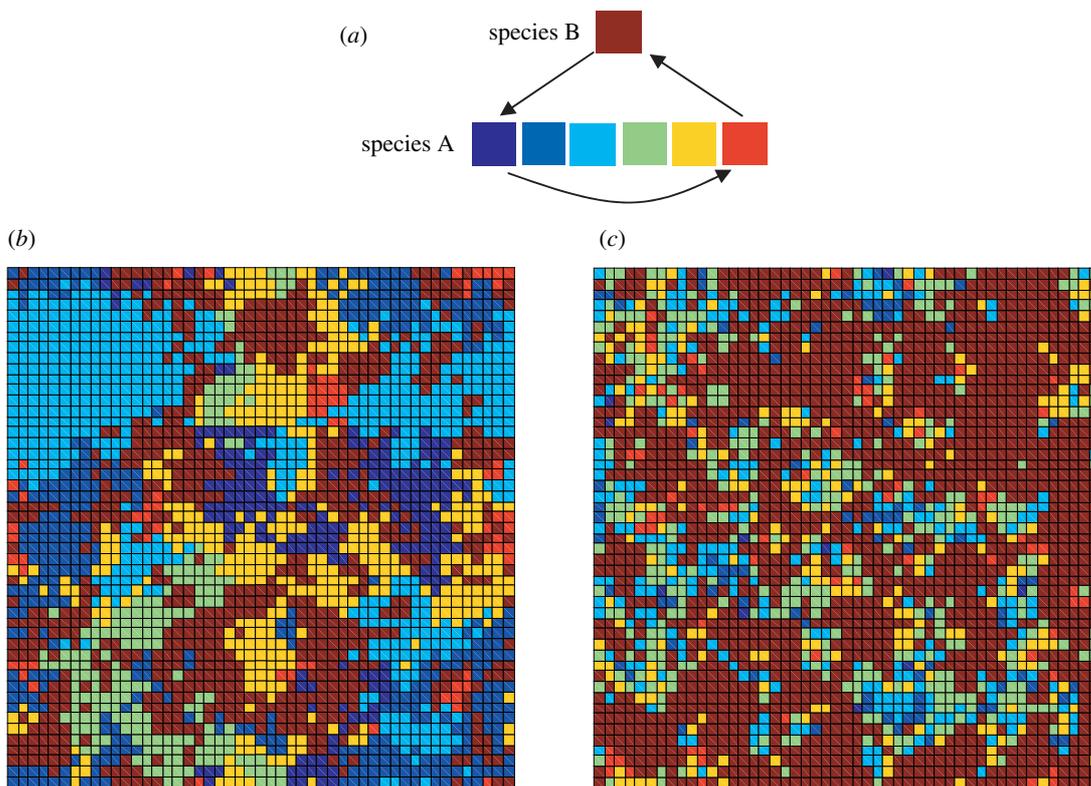


Figure 4. Spatial patterns in a  $50 \times 50$  cell portion of a community. (a) Species B and each phenotype ( $\phi$ ) of species A are represented by different colours, with dark blue corresponding to  $\phi=0$  and red to  $\phi=5$ . Spatial patterns are shown at single points in time with (b) asexual and (c) sexual reproductions. In these simulations, we used five loci giving six phenotypes for simplicity of presentation.

sexual reproduction and local interactions (i.e. ‘space’) combined to greatly destabilize population dynamics—exactly the opposite of previous studies indicating that sex and space have stabilizing effects on the dynamics of interacting species (references below).

Adding sexual reproduction with explicit genetic variation has been shown to simplify dynamics in systems of competitive, predator–prey and host–parasite interactions (Doebeli & Koella 1994; Doebeli 1995, 1996; Flatt & Scheuring 2004). In these cases, strong antagonistic interactions that result in relatively complex dynamics were ‘blurred’ with the addition of sex due to dampening of allele–frequency fluctuations (Doebeli & Koella 1994). Indeed in our model with global interactions, sexual reproduction caused slower population cycles than asexual reproduction (figure 1). However, it is precisely a shift in allele frequencies that contributes to reversals of extremes in abundance, and with sexual reproduction these shifts were slower due to reduced genetic variance (figures 2b and 3). This created abundance cycles of larger amplitude and therefore a greater risk of extinction in our model. It remains to be seen how often intransitivity in competitive networks results from within-species genetic variation with respect to competition with other species, as in the case of *B. nigra* (Lankau & Strauss 2007), but there is sufficient suggestive evidence that the phenomenon is widespread in plants (Aarssen 1983; Taylor & Aarssen 1990) to warrant greater empirical attention. It is also noteworthy that the system for which there is the most evidence for widespread genetic variation in natural systems for traits involved in intransitive competition is toxin–resistance interactions in bacteria (best studied in *E. coli*, but present in many

species), where reproduction is largely asexual, albeit with some degree of plasmid transfer and recombination (Riley & Gordon 1996; Gordon & Riley 1999). Experiments with *E. coli* have taken advantage of discrete and contrasting characteristics of carefully selected strains (e.g. Kerr *et al.* 2002), but samples from the field exhibit a continuous range of variation in toxin and resistance traits (Gordon & Riley 1999).

A repeated result found in models of rock–paper–scissors games is that coexistence is maintained more easily under spatially localized interactions than with global interactions (Durrett & Levin 1997; Frean & Abraham 2001; Kerr *et al.* 2002; Reichenbach *et al.* 2007), and indeed we see the same thing in our asexual models. Our model, in which localized interactions apply simultaneously to competition and dispersal, was initially inspired by plants, in which pollen movement is generally more widespread than seed movement (Ennos 1994), and for which competition is always highly localized (Harper 1977). *B. nigra* is pollinated by a variety of flying insects (Conner & Rush 1997) and has small hard seeds, most of which fall very close to the mother plant (J. Orrock 2007, personal communication), suggesting that local competition and seed dispersal, but widespread pollen movement, apply to this species, as well as many others. With sexual reproduction under these conditions, we find destabilized interactions and a potentially high risk of extinction (figures 1f and 5), especially when compared with the local–asexual case for which there are scarcely any abundance fluctuations at all (figure 1d). This suggests that either we are unlikely to find many cases in nature like that described for *B. nigra*, or that other factors not included in our model contribute to the stability of such

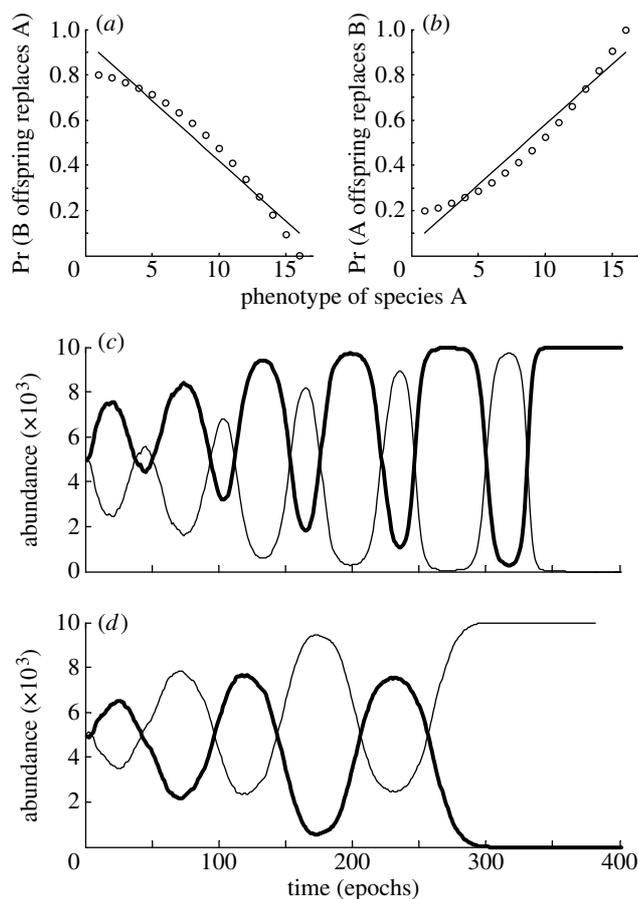


Figure 5. Extinction occurs when intermediate phenotypes have a fitness disadvantage and reproduction is sexual. Fitness of intermediate phenotypes of species A (open circles) have a disadvantage relative to the linear case (solid line) both in terms of probabilities of being (a) replaced by offspring of species B and (b) of replacing species B. (c) With global interactions species B (thin line) goes extinct and (d) with local interactions species A (thick line) goes extinct. Simulations were run with 15 loci and  $\bar{r} = 10\,000$ .

systems. In the case of *B. nigra* specifically, sinigrin has important effects not only on competitors (Lankau & Strauss 2007) but also herbivores (Traw 2002), and soil mycorrhizae (Schreiner & Koide 1993). More generally, a complex web of community interactions influences this species (e.g. Orrock *et al.* 2008) and indeed all species (Harper 1977; Huston 1994). Intransitive competitive interactions of the kind modelled here may occur in any species for which (i) genetic variation is present for the production of allelochemicals that provide a competitive advantage over other species and (ii) production of these chemicals incurs a metabolic cost. Empirical evidence supports both conditions specifically for allelochemicals (Belz 2007) and more generally for secondary chemicals involved in species interactions (Strauss *et al.* 2002). How these interactions play out in natural community contexts is less clear, and is a promising area for empirical study.

In summary, we have demonstrated that when two of the nodes in an intransitive competitive network are linked by sex and recombination, realistic assumptions concerning the spatial scale of movement and interactions result in destabilized population dynamics of the interacting species. With empirical support for the underlying premises of the model, this represents an important exception to the seeming generalizations that sex and space stabilize species interactions, though only empirical data can assess how broadly applicable the results are to natural communities.

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