

Coexistence under positive frequency dependence

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Negative frequency dependence resulting from interspecific interactions is considered a driving force in allowing the coexistence of competitors. While interactions between species and genotypes can also result in positive frequency dependence, positive frequency dependence has usually been credited with hastening the extinction of rare types and is not thought to contribute to coexistence. In the present paper, we develop a stochastic cellular automata model that allows us to vary the scale of frequency dependence and the scale of dispersal. The results of this model indicate that positive frequency dependence will allow the coexistence of two species at a greater rate than would be expected from chance. This coexistence arises from the generation of banding patterns that will be stable over long time-periods. As a result, we found that positive frequency-dependent interactions over local spatial scales promote coexistence over neutral interactions. This result was robust to variation in boundary conditions within the simulation and to variation in levels of disturbance. Under all conditions, coexistence is enhanced as the strength of positive frequency-dependent interactions is increased.

Keywords: stochastic spatial model; positive frequency dependence; effects of scale

1. INTRODUCTION

The outcome of interactions between species or genotypes is not fixed for many ecological interactions but rather depends upon the frequency of occurrence of each species in a community. For example, niche partitioning will result in negative frequency dependence within systems of competition (Ayala 1971; Antonovics & Kareiva 1988). Predation (Clarke 1969), parasitism (May & Anderson 1983) and mutualism (Bever 1999) can also result in negative frequency dependence. These same interactions can also generate substantial positive frequency dependence. For example, preferential predation on rare morphotypes (Futuyma & Wasserman 1980) and host specificity within mutualistic interactions (Bever 1999) can generate positive frequency dependence.

The general predictions of frequency dependence have long been known for well-mixed systems: negative frequency dependence promotes coexistence whereas positive frequency dependence leads to loss of diversity (Kimura & Ohta 1971). However, for sessile organisms such as plants, frequency dependence can occur over small spatial scales. For example, positive frequency-dependent selection observed between genotypes of *Allium vineale*, which results from interactions with its soil community, occurs over a spatial scale of centimetres (Ronsheim 1996; Bever *et al.* 1997). It has generally been shown that the dynamics in systems with such strong spatial structuring can be quite different from those of well-mixed systems (Hassell *et al.* 1991; May & Nowack 1992; Silvertown *et al.* 1992; Durrett & Levin 1994; Molofsky 1994; Molofsky *et al.* 1999). For example, the inclusion of spatial structure can result in several novel and distinct behaviours in frequency-dependent systems (Molofsky *et al.* 1999).

Here we show, with a stochastic cellular automata model, that positive frequency dependence will permit the

coexistence of two species, even when the initial species distributions are random. Furthermore, we show that coexistence is enhanced as the strength of positive frequency dependence is increased. This stability under positive frequency dependence results from the formation of bands which are stable over time. We compare the dynamics that result when the interactions occur over local scales and when interactions occur over the entire grid.

2. MODEL DEVELOPMENT

The model was developed for two species competing on a two-dimensional grid. Each location on the grid contains one of the two species. The dynamics develop from the application of transition rules in concert over the entire grid. The transition rules involve the interaction of two processes, interspecific interaction and dispersal. For a given cell, each of the processes depends upon the proportion of each species in the surrounding cells over some finite distance: hence, each process is frequency dependent. However, the outcome of interspecific interactions in the local neighbourhood can be positively dependent upon the proportion of each species in its surrounding neighbourhood, while the outcome of dispersal is always strictly proportional to the number of each species in the local neighbourhood (we assume no decline in dispersal with distance). In order to investigate the effect of the changing scale of interspecific interactions and dispersal, we constructed general rules that are scale neutral. The size of these two scales can vary from one square to the size of the entire grid. At this large size, the model reduces to a stochastic model without spatial structure.

The probability of a site being occupied by a particular species, such as species 1, is given by the equation

$$P_1 = H_1 \times D_1 / (H_1 \times D_1 + H_2 \times D_2), \quad (1)$$

where H_1 and H_2 represent the habitat qualities in the local neighbourhood resulting from frequency dependence

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for species 1 and 2, respectively, and D_1 and D_2 represent the numbers of individuals of the two types that dispersed into the target cell from the dispersal neighbourhood. We assume that, at the end of each generation, individuals produce a fixed number of offspring that are dispersed uniformly over the entire dispersal neighbourhood. The spatial scale of dispersal is then completely adjustable. The probability of establishment of species 2 is calculated in a similar manner.

The quality of a habitat controls the frequency dependence and is determined by the following equation:

$$H_1 = 0.5 + a(f_1 - 0.5). \quad (2)$$

The 'habitat quality' of a cell is a measure of the relative likelihood of establishment of a single propagule of species 1 relative to a single propagule of species 2. The parameter f_1 is the proportion of species 1 in the adjacent cells over some predefined neighbourhood scale. The spatial scale of frequency dependence can be varied by adjusting the range of neighbouring cells used to calculate the frequency of each type in the neighbourhood. The parameter a represents the strength of frequency dependence and can vary between -1 and $+1$. If $a = 0$, then $H_1 = 0.5$ and neither positive nor negative frequency dependence occurs. In this case, each species establishes in proportion to their relative frequency in the dispersal neighbourhood. This is the neutral case which is equivalent to the voter model (Holley & Liggett 1975) and is also equivalent to a model of random drift (Wright 1943). Positive frequency dependence occurs when $a > 0$. For example, if $a = 1$, H_1 simplifies to f_1 . Given strong positive frequency dependence ($a = 1$) and given that the dispersal and interaction regions are equal, the probability of a cell being occupied by species 1 becomes

$$P_1 = D_1^2 / (D_1^2 + D_2^2). \quad (3)$$

We investigated small neighbourhoods of five squares (the centre and all squares sharing a side) or nine squares (the centre and eight adjacent squares) and the large neighbourhood that spanned the entire grid. We included the five-square neighbourhood because it had been extensively analysed by Molofsky *et al.* (1999).

Although the model greatly simplifies ecological interactions, analytical solutions are still not possible (except under the restricted conditions already explored in Molofsky *et al.* (1999)). However, we can quantitatively investigate the probability of long-term coexistence by simulating multiple initial conditions using a spatially explicit stochastic model in which the probability of species 1 establishing at a given square is determined by the probability calculated by equation (1) for that square. The simulations are run for three types of boundary conditions: (i) torus, (ii) reflective boundaries, and (iii) absorbing boundaries. In the torus, the borders on one side wrap around to the opposite side, which generates a doughnut in each direction. In the case of reflective boundaries, we assume that all individuals have equal fitness regardless of location and, therefore, individuals located near the boundary disperse the same number of offspring onto the grid near where they would have dispersed off the grid. Similarly, in calculating habitat quality, we assume that habitat neighbourhoods

extending beyond the boundary experience the individuals that are present in the mirrored distribution adjacent to the boundary. Finally, we investigate the case of absorbing boundaries. In this case, we assume that individuals arriving at the boundary are killed and that, when these cells are included in calculations, they have the effect of reducing the overall neighbourhood size by the number of uninhabitable cells.

We also investigated the effect of disturbance in our simulations. By disturbance, we mean the probability d that a given site will be unoccupied in each generation. The probability of establishment of the two species is then adjusted by this probability as follows:

$$P_1' = (1 - d)P_1, \quad (4)$$

where P_1' is the adjusted probability of establishment of species 1. Calculation of the neighbourhood values for each target cell remain as described above. Note that increasing our disturbance parameter has the effect of reducing the overall density within the grid. For example, a simulation run on a 100×100 grid will have 10 000 individuals when $d = 0$, but 7500 when $d = 0.25$.

We used our model to investigate a series of different scenarios. We used the five-square neighbourhood for investigating the influence of the strength of positive frequency dependence on long-term coexistence within a 100×100 grid. Under these conditions, we observed the phenomenon of long-term coexistence through the formation of stable bands. We first describe the phenomenon of band formation and then test whether it can lead to increased likelihood of long-term coexistence relative to random drift. We do this by evaluating the probability of coexistence of the two types for 100 000 generations in simulations initialized with random arrangements of equal proportions of the two species on the grid. We monitor the proportion of cases in which the two types coexisted, albeit at unequal frequencies, for 100 initial arrangements. We first compare the probability of coexistence with the torus boundary condition, the five-square neighbourhood and no disturbance under random drift ($a = 0$), weak positive frequency dependence ($a = 0.1$) and strong positive frequency dependence ($a = 1$). The significance of the differences was tested with goodness-of-fit tests.

Finally, we tested these three levels of frequency dependence ($a = 0$, $a = 0.1$ and $a = 1$) in a full factorial combination with all three boundary conditions (torus, reflective and absorbing) and four levels of disturbance ($d = 0$, $d = 0.1$, $d = 0.25$ and $d = 0.5$). We used the nine-square neighbourhood for these simulations and monitored the probability of coexistence over 100 000 generations for 100 random initial arrangements. The proportions of initial conditions that coexisted were analysed with a logistic regression using all main effects and interactions as predictors.

3. RESULTS

(a) *Coexistence through coalescence into stable bands*

Strong positive local frequency dependence ($a = 1$) with local dispersal (i.e. the five-square neighbourhood) on a 100×100 grid resulted in two qualitatively different

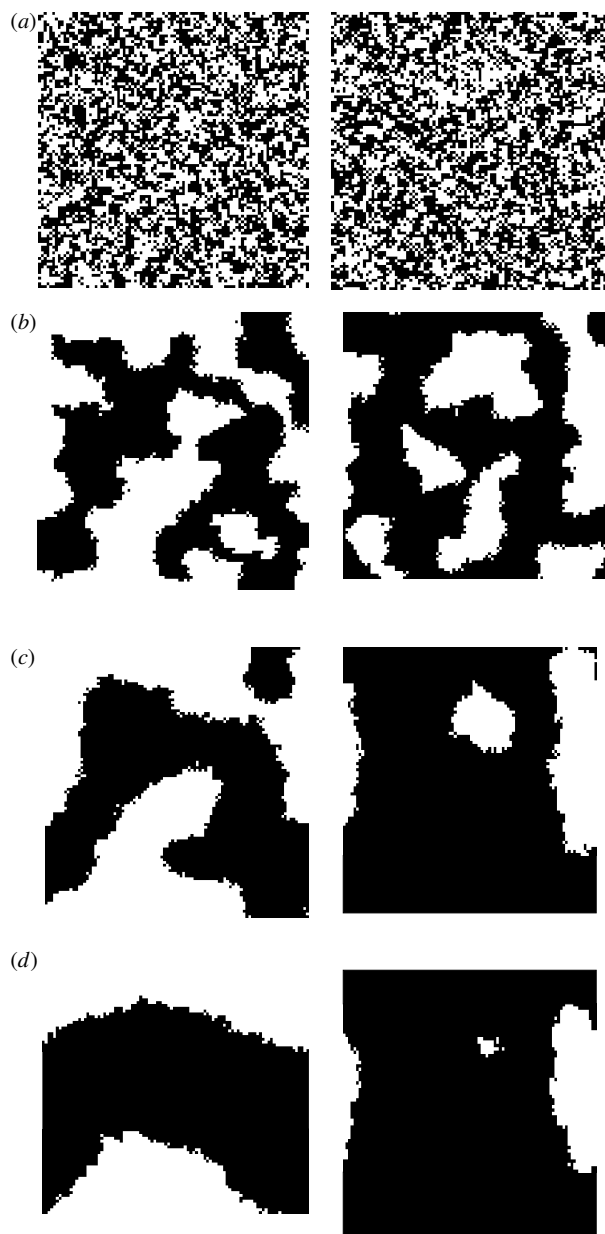


Figure 1. The outcome of strong local positive frequency dependence ($a = 1$) for two different initial distributions of species on a 100×100 grid. Simulations were run for 2000 generations or until extinction occurred. Figures on the left-hand side illustrate the development of clusters and the aggregation of clusters in order to create stable bands and figures on the right-hand side illustrate clustering leading to extinction of one species. (a) Initial distribution of both species on the 100×100 grid. (b) The pattern that develops after 100 generations. After 100 generations, the two species aggregate into irregular clusters. (c) The pattern that develops after 500 generations for the two initial distributions. On the left-hand side large aggregates have coalesced into a snake-like bands. Local positive frequency dependence causes the concave curves of the cluster to flatten, resulting in a progressive straightening of the edges. On the right-hand side aggregates have formed with the white species confined to distinct clusters. (d) The patterns that develop after 1000 generations. On the left-hand side, species have developed that can be maintained indefinitely. On the right-hand side the white species is being driven to extinction by the black species.

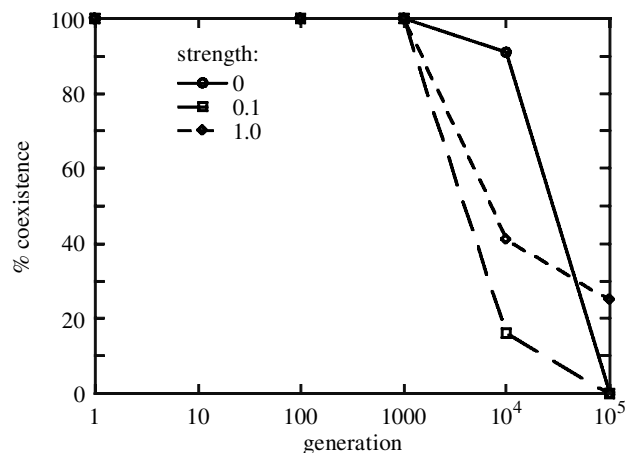


Figure 2. The percentage of simulations where two species persist for three different strengths of positive frequency dependence ($a = 0$, $a = 0.1$ and $a = 1$) for different time intervals for the five-square neighbourhood simulated on a 100×100 grid. At 10 000 generations, coexistence was more likely in the neutral case ($a = 0$) than in strong positive frequency dependence ($a = 1$) ($\chi^2_1 = 17.7$ and $p < 0.0005$) and in the strong positive frequency dependence case than in weak frequency dependence ($a = 0.1$) ($\chi^2_1 = 7.7$ and $0.01 > p > 0.005$). At 100 000 generations, coexistence was substantially more likely under positive frequency dependence than either random or weak frequency dependence ($\chi^2_1 = 21.0$ and $p < 0.0005$ for both random and weak frequency dependence).

outcomes that depended upon the initial stochastic arrangement of individuals on a grid: extinction or the production of bands which were stable over long time-periods (figure 1). Thus, for some initial conditions, positive frequency dependence leads to long-term coexistence of two species. For both situations (extinction and coexistence) strong positive local frequency dependence created clusters (figure 1). With local dispersal, these clusters cannot be invaded by the minority type. Whether extinction or long-term coexistence occurs depended upon the geometry of the clusters. As a result of positive frequency dependence, the border of these clusters always moved from the concave side to the convex side. When the clusters were highly curved, the outer type engulfed the inner type quickly driving it to extinction (figure 1). However, for certain initial conditions, the borders of the cluster flatten. When this straightening occurred, bands could form in either direction across the array and the two types coexisted (figure 1). The flattening of clusters to form bands occurred in both the five-square and the nine-square neighbourhoods and with all three types of boundary conditions.

(b) Effect of strength of frequency dependence

In order to examine the degree to which positive frequency dependence enhances coexistence quantitatively, we varied the strength of frequency dependence ($a = 0$, $a = 0.1$ and $a = 1$) and determined the proportion of initial conditions that resulted in coexistence of both species for different time-scales (figure 2). Remarkably, 100% of the initial conditions coexisted over 1000 generations under strong positive frequency dependence occurring at a local scale, whereas under similar frequency dependence

Table 1. *Logistic regression analysis with boundary conditions (torus, reflective and absorbing boundaries), strength of frequency dependence ($a = 0$, $a = 0.1$ and $a = 1$) and disturbance ($d = 0$, $d = 0.1$, $d = 0.25$ and $d = 0.5$) as main effects*

(Significant interactions are shown. n.s., non-significant.)

source	d.f.	χ^2	p -value
intercept	1	197.1	0.0000
frequency (F)	1	93.1	0.0000
boundary (B)	2	9.6	0.0084
disturbance (D)	1	8.2	0.0042
$F \times B$	2	7.3	0.0259
$D \times B$	2	3.1	n.s.
$F \times D$	1	1.4	n.s.
$F \times D \times B$	2	2.2	n.s.
likelihood ratio	24	34.0	0.0844

occurring over the scale of the grid, extinction resulted in 100% of the cases within 15 generations. Clearly the process of clumping itself can contribute to effective coexistence over relatively long periods, even if bands do not form.

By 10 000 generations, the cases of positive frequency dependence in which bands did not form had become extinct and, as a result, a greater proportion of cases were extinct under local positive frequency dependence than under random drift (figure 2). The two processes of drift over local scales and patch formation under positive frequency dependence can be distinguished by examining their spatial patterns. In the former case, patches formed but were constantly broken up, whereas in the latter case, large clusters grew resulting in large autocorrelations between sites (figure 1). In generation 10 000, clustering, which was defined as the probability that two adjacent cells are the same type, was higher in the case of strong positive frequency dependence ($a = 1$) than in the neutral case ($a = 0$) ($\bar{x} = 96.6$, s.d. = 0.49 and $n = 35$, and $\bar{x} = 76.5$, s.d. = 7.9 and $n = 80$ for $a = 1$ and $a = 0$, respectively).

However, by 100 000 generations all of the initial conditions under random drift resulted in extinction, while a substantial proportion of initial conditions under strong positive frequency dependence coexisted (figure 2). In all of these cases, the long-term coexistence resulted from band formation by positive frequency dependence.

(c) *Interacting effects of strength of frequency dependence, boundary conditions and disturbance*

Positive frequency dependence increased the likelihood of coexistence under all boundary conditions and disturbance levels (table 1). The probability of coexistence increased across all simulations, from 1.3% for $a = 0$ to 1.4% for $a = 0.1$ and to 16.3% for $a = 1$. In fact, the strength of frequency dependence was the strongest determinant of coexistence (as demonstrated by the largest χ^2 -value in table 1). The boundary condition had a significant but smaller effect (table 1). The absorbing boundary condition, which most closely simulates natural communities, resulted in the highest probability of coexistence with the torus resulting in the lowest. This result makes sense since connecting borders under the torus had the

effect of decreasing spatial structure. The probability of coexistence also significantly decreased with increasing levels of disturbance (table 1). Specifically, the overall probability of coexistence decreased from 10.7, 7.4 and 5.9% to 1.3% as disturbance increased from $d = 0.0$, $d = 0.1$ and $d = 0.25$ to $d = 0.5$, respectively. The interactions between these three factors were generally weak (as demonstrated by the small χ^2 -values in table 1). There was a significant interaction between boundary condition and frequency dependence because the torus condition resulted in slightly higher levels of coexistence than the reflective or absorbing boundary condition for the neutral case ($a = 0$), but this did not hold for cases where the frequency dependence was positive.

4. DISCUSSION

Frequency-dependent processes can drive dynamics between species and between genotypes. Positive frequency dependence has received less attention than negative frequency dependence because non-spatial models of positive frequency dependence do not permit coexistence. However, the theoretical expectation from non-spatial models is at odds with the many examples of positive interactions in communities (Bronstein 1994; Bertness & Leonard 1997; Callaway & Walker 1997; Hacker & Gaines 1997; Holmgren *et al.* 1997). Our study demonstrates that a stochastic spatial model of positive frequency dependence between two species can generate self-organized linear boundaries of each species that can be maintained over long time-scales. Although only approximately one-quarter of the random initial distributions generated stable banding patterns, the likelihood of stable borders forming due to local positive frequency dependence would increase if the initial distribution of species was biased, with one species being more frequent in a given area due to either historical factors or weak environmental gradients. Second, in our simulations we did not have any physical structure besides the hard edges in the reflective and absorbing boundaries. Interestingly, with the addition of this minimal physical structure, positive frequency dependence was more likely to maintain the two types. We can then infer that the stability of boundaries between species and the probability of long-term coexistence would be enhanced with increasing physical complexity of the environment.

Empirically, our results suggest that sharp and stable boundaries between species or genotypes may simply result from local positive frequency dependence rather than environmental dependence and may not require environmental variation. Such sharp and long-maintained borders are frequently observed in hybrid zones between sister species and between different ploidy levels where hybrid sterility maintains strong local positive frequency dependence (Barton & Hewitt 1989; Felber & Bever 1997). Sharp and stable boundaries between community types such as the forest and grassland borders of central USA and the African savannahs may also be the result of local-scale frequency dependence (Greig-Smith & Chadwick 1965; White 1971).

It is informative to compare the outcomes of local positive frequency dependence with those of random drift. In the case of random drift, two species can be maintained

over intermediate time-scales leading to 'effective' coexistence (Molofsky *et al.* 1999). The larger the area, the slower the time for extinction to occur. However, given a long enough time interval, extinction will always occur. In contrast, local positive frequency dependence leads to two alternatives, either extinction or stable band formation, with the chance of extinction increasing with larger areas. This tension between achieving self-organized bands or extinction results in two contrasting results if the strength of local positive frequency dependence is varied. As local positive frequency dependence becomes stronger, extinction occurs unless stable bands form. However, under weaker local positive frequency dependence, the two species can be maintained for long time-periods even if the ultimate outcome will be extinction. In ecological communities, these discrepancies can be resolved through examination of the spatial pattern over time. If clusters of individuals form and disintegrate over time, then neutral or weak local positive frequency dependence may be responsible, but if larger clusters are formed and are maintained over time, then local positive frequency dependence may be responsible. Discrepancies in the mechanisms responsible for the pattern require experimental documentation.

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