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Self-organized spatial pattern determines biodiversity in spatial competition

John Vandermeer^{*,1}, Senay Yitbarek¹

Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 4809, United States

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ABSTRACT

In a simple cellular automata model it is shown that self-organization of spatial pattern in a community of strong competitors may generate a previously unrecognized mechanism of species richness determination. Employing some well-known general properties of interspecific competition, we elaborate a theoretical framework that generates both spatial mosaics and spiral waves within the same conceptual framework, dependent on the covariance of competition. We demonstrate that the qualitative nature of the spatial pattern depends on the "balance" of competition and that the number of species retained in the community depends on this spatial patterning.

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1. Introduction

Two issues that have secured semi-canonical status in ecological theory are first, that species richness tends to be related to niche diversification and second, spatial patterns are sometimes a consequence of forces inherent to the ecosystem. Species richness related to niche diversity is a direct result of expanding the classic Lotka-Volterra equations into their multiple species form and equating niche differences with competition coefficients (MacArthur and Levins, 1967; May, 1973). Self-organized spatial patterns emerge from coupling local dynamics to some form of diffusion, the most common forms being similar to Turing's famous effect (Turing, 1952; Segel and Jackson, 1972; Alonso et al., 2002). Here we consider the intersection of these two issues. We examine the process of self-organization of spatial pattern in a community of strong competitors and show how the details of the self-organizing process generate a previously unrecognized mechanism of species richness determination.

The existence of spatial pattern in biological communities is familiar. Many organisms, especially sessile forms, exist in dramatic nonrandom patterns, a phenomenon well-known to early naturalists. Such patterns can take a variety of forms, many of which are clearly a consequence of underlying habitat characteristics, but some of which are thought to be patterned at larger scales as a result of dynamic interactions at a local scale. A variety of biological phenomena can easily give rise to many such patterns (Nowak and May, 1992;

E-mail addresses: jvander@umich.edu (J. Vandermeer), senay@umich.edu (S. Yitbarek).

Bascompte and Solé, 1995; Tilman and Kareiva, 1997; Dieckmann et al., 2000), from physiological models in which patterns of vegetation are formed based on the spatial details of water usage (Klausmeier, 1999), to predator prey models that generate patches showing certain characteristics of criticality (Pascual et al., 2001; Vandermeer et al., 2008), and many other examples. Of particular interest are the models that examine patterns formed from the process of competition.

Although the literature is large and eclectic, it is nevertheless possible to generalize about the general patterns formed in spatial competition using a dichotomous classification. Some studies find the emergence of a mosaic of relatively discrete patches that retain a general qualitative structure for long periods of time even if not formally stable (Durrett and Levin, 1994, 1998; Bascompte and Solé, 1995; Sheratt, 2006; Adler et al., 2007), a pattern frequently referred to as a spatial mosaic. Other studies concentrate on the formation of so-called spiral waves (Boerlijst and Hogeweg, 1991; Johnson and Seinen, 2002; Edwards and Schreiber, 2010), based on the existence of intransitive loops (i.e., species A, beats B and species B beats species C, but species C beats species A). Here, employing some well-known general properties of interspecific competition, we elaborate a theoretical framework that generates both forms (mosaics and spiral waves) within the same conceptual framework.

A related theoretical literature is concerned with the effect that spatial pattern has on the process of competitive coexistence or exclusion (e.g., Newhauser and Pacala, 1999). In an extensive review of the literature on this topic, Bolker et al. (2003) conclude that theoretical work falls into four broad categories, (1) weak interspecific competition leading to spatial structure that in turn possibly destabilizes stable systems, (2) a colonization/competition

^{*} Corresponding author. Tel.: +1 734 764 1446.

¹ Both authors contributed equally to the manuscript.

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tradeoff, (3) the construction of a "spatial successional niche" through differential reproductive rates, and (4) interspecific competition strong and short dispersal allow "local control of the environment," what has been referred to as the Phalanx strategy (Lovett-Doust, 1981).

It is to this last situation that the current work applies. Originally applied to the case of plant competition, the basic idea can be applied to competition among any sessile (or even semi-sessile) organisms. (Durret and Levin, 1994, 1998) convincingly demonstrated this idea for a very general model. The idea is that at the edge of a monospecific cluster of individuals, the only points that really count in the dynamics are those that occur on the edge of the clump. This is because points interior to the cluster are not subjected to any interspecific competition at all. Thus at the border of two clusters composed of species A and species B, there are only three qualitative possibilities: (1) A dominates B, (2) B dominates A, or (3) A and B engage in a competitive standoff where neither is capable of displacing the other. Clearly, when possibility 3 occurs, the clusters will be stationary, and when either possibility 1 or 2 occurs, one or the other species will wipe out its competitor.

Strong interspecific competition is likely to be characteristic of many situations involving sessile organisms. Only a single tree can occupy a particular site in a forest such that if the spatial model considers the scale of an individual tree as the relevant scale, competition must be strong by definition since there is no possibility of local coexistence. Furthermore, if organisms are roughly equivalent in their ecological requirements, for example forest trees rather than forest "organisms," or ants versus insects, or insects versus all animals, the strength of competition is likely to be large in both directions, giving rise to what Yodzis (1978) has referred to as founder-controlled communities. In addition to the strong competition framework, we frame the competitive process in an effect/response framework, where a species can be a strong competitor by being a good effect competitor (having a good offense) and/or being a good response competitor (have a good defense) (Goldberg and Fleetwood, 1987). In this work we specifically consider a community of founder-controlled sessile organisms where local competitive outcomes are a consequence of relative values of effect and response competition.

We propose that spatial mosaics and related patterns are implicated in the coexistence of species, a theme that already has received substantial attention (Laird and Schamp, 2006, 2008). We first note that the tendency to form mosaics in the first place is a function of the balance, rather than the intensity, of competition, which is to say the degree to which the competitive intensity felt by species A from species B is balanced by an equal degree of competitive intensity felt by species B from species A (in the Lotka-Volterra framework, this would imply that α_{ii} is highly correlated with α_{ii}). This tendency in turn suggests a conceptual framework in which the competitive structure of a community can be conceived of as falling on a gradient ranging from highly balanced to highly unbalanced, and, as we show below, a strong mosaic structure spontaneously tends to form at the balanced extreme and the likelihood of spiral waves much larger at the unbalanced extreme. Finally we show that the number of surviving species is directly related to the position of that competitive structure on the gradient, with more species being maintained in the community when a spatial mosaic is more likely to form, which is to say, in the case of balanced competition.

2. Methods

2.1. The model

As with other spatial models of competition, effective competitive pressure occurs among neighboring cells in a spatial lattice and a single cycle of competition involves deciding which of the many species occupying a single point and its immediate neighbors will be the winner, explicitly assuming that only one individual is able to occupy a lattice point after the cycle. Frequently a dispersal kernel is added to the model, and the balance of dispersal ability and competitive ability becomes a major determinant of the winner (Bolker et al., 2003). The model described here includes only local dispersal—the entire competitive process, from implicit dispersal to competitive outcome, operates only in the Moore neighborhood.

A further complication arises with local density dependence. If competition at a point depends on the occupancy of the lattice points in the surrounding Moore neighborhood, at each competition cycle there will be up to 9 individuals contesting that point. Some literature simply ranks species in order of "competitive ability" and eliminates 8 of the individuals, leaving an individual that belongs to the species with the largest competitive ability. Clearly this is a problem in any realistic vision of competitive ability spectrum than species B, but if there are 8 individuals of species B and only one of species A, the latter could be overwhelmed by numbers. Any realistic vision of interspecific competition must allow for some local density-dependent effect unless the differences in competitive abilities are extremely large.

To motivate our argument, consider the competition scenario pictured in Fig. 1, where the numbers associated with the arrows are Lotka-Volterra competition coefficients. From a knowledge of the competition coefficients alone, it is clear that this is a case of indeterminate competition, or in the classification scheme of Yodzis (1978) a founder-controlled community (all competition coefficients > 1.0). Summing the relevant competition coefficients we see that species A has a total competitive effect of 3.5 on all other species (1.5 on C plus 2.0 on B), while species C has a total effect of 2.51. On the other hand, species A must respond to the effects of all the other species (i.e., both species B and C which sum to 3.1) and C must respond to the effects of all the others (which sum to 2.52). Based on these numbers alone we might say that species A is a better "effect" competitor while species C is a better "response" competitor, using the conceptual framework of Goldberg and Fleetwood (1987) and Goldberg and Landa (1991). The question then, if these three species all contest for a single point, being that only one can survive, might we expect A to win because it is a good effect competitor, or will C win because it is a good response competitor?

In the Lotka–Volterra sense the question is not answerable since the situation is one of indeterminate competition and thus requires knowledge of relative population densities of the three species. Assuming all competition is local, involving the individual in the central cell plus all individuals in the Moore



Fig. 1. Illustrative competitive network. Numbers indicate relative strength of Lotka–Volterra competition between any two of the three species, A, B, and C. Arrowheads indicate competitive effect. Note that A is the best "effect" competitor (with an effect of 2.0 on B and 1.5 on C for a total of 3.5) and C is the best "response" competitor (having to respond to 1.5 from A and 1.02 from B, for a total of 2.5).

neighborhood the 8 immediately surrounding cells in this formulation, each of the species has a population density ranging from 0 to 9. There are, to be sure, obvious cases-if all nine individuals belong to species A, the result at the central point will be A. But what of other combinations of individuals? For example, if there are N_A individuals of species A, N_B individuals of species B, and $N_{\rm C}$ individuals of species C, based on the competition coefficients in Fig. 1, the following relations are reasonable extrapolations of the LV framework (see Supplementary material A). The total "effect competition" for species A will be $(2.0N_B+1.5N_C)N_A=C_E$ and the total "response competition" for A will be $1.5N_C + 1.6N_B = C_R$. We then take the total competition to be $C_T = C_E/C_R$, and assert that the species with the largest C_T will indeed be the winner at that point (see Supplementary material A). This is the basic framework that motivates the model we develop and explore here, focusing on how different arrangements of competitive interactions in the competition matrix generate qualitatively distinct spatial patterns and what those patterns may imply.

Combining these observations, we incorporate both density dependence and the effect/response competition to compute "total competition" at a particular lattice point, for each of the species occurring in its neighborhood. The winner at that point is then the species with the greatest "total competition." Our formulation is arbitrary in that we seek only to devise an index that is large when the relative values of effect and response are large, and small when the relative values of effect and response are small. We formulate the idea as a ratio between effect and response, which is certainly not the only way of capturing the biological idea, but is clearly intuitive and broadly consistent with a Lotka–Volterra framework (see Supplementary material A).

Formally, in the model proposed here, the competitive effect of species i at lattice point m,n is,

$$E_i(m,n) = \sum_{x=m-1}^{m+1} \sum_{y=n-1}^{n+1} N_i(x,y) \sum_{j=1}^{s} N_j(x,y) a_{j,i}$$
(1)

where $N_i(m,n)$ is the population density (either 0 or 1) of species *i*, $a_{j,i}$ is the relative strength of the competitive effect of species *i* on species *j*. Note that the parameter *a* is conceptually related to the Lotka–Volterra competition coefficient, but not identical to it since this model framework is quite distinct from the dynamic continuous time LV model (Supplementary material A). The competitive response of species *i* at lattice point *m*,*n* is

$$R_i(m,n) = \sum_{x=m-1}^{m+1} \sum_{y=n-1}^{n+1} \sum_{j=1}^{s} N_j(x,y) a_{i,j}$$
(2)

whence the total competition for species *i* at a single point *m*,*n* in the lattice, at any point in time, is

$$C_i(m,n) = \varepsilon \frac{E_i(m,n)}{R_i(m,n)}$$
(3)

where ε is a stochastic force representing environmental variability in competitive outcome. The winning species at a point *m*,*n* is the species with the highest C. Further description of the model and its implementation is in Supplementary material A.

An alternative framework was also considered based on the well-known game of Colonel Blotto. The results were almost identical so are only reported in Supplementary material B.

2.2. Species diversity and covariance

To investigate the interplay of mosaic formation and species diversity, we examined the qualitative structure of the competition matrix and the consequent generation of mosaics as an input into the exclusion or coexistence of species. Characterizing the qualitative structure of a competitive network is not an obvious task. MacArthur was one of the first to suggest that the arrangement of competition coefficients would be important to species diversity, noting that the "connectivity" of a competitive network would likely influence the species diversity (MacArthur, 1965). Subsequently this basic idea became commonplace. It is not only the intensity of competition but also the arrangement of the coefficients in the competition matrix that is important in determining species diversity (Levins, 1968; May, 1973). More recently network theory has provided a number of useful metrics, including more sophisticated measures of the "connectivity" of a system (Solé et al., 2002). Here we follow the spirit of that evolving literature and focus on the relationship between the reciprocal pairs of competition coefficients, and especially on their quasi-statistical properties. In particular, we focus on the row and column sums of the competition matrix, classically proposed as the obvious measures of the effect competition of species *i* (the column sum of the *i*th column) and the response competition of species *i* (the row sum of the *i*th row) (Goldberg and Fleetwood, 1987). If the two are positively related, that is, if a strong effect competitor implies a weak response competitor, the covariance between the row sums and column sums will be positive (i.e., if $a_{i,i}$ is large that means $a_{i,i}$ is also large). If, on the other hand, a strong effect competitor implies a strong response competitor, there will be a negative relationship between the reciprocal pairs in the competition matrix and the covariance between row sums and column sums will be negative (i.e. if $a_{i,i}$ is large that means $a_{i,i}$ will be small). Thus, a large positive covariance implies a tradeoff between effect and response competition while a large negative covariance implies a competitive hierarchy, or, put another way, a large positive covariance implies a situation of "balanced" competition while a large negative covariance implies a situation of "unbalanced" competition.

Historically the covariance of the community matrix was constructed as an input to the general formula for species diversity generated by the structure of the community matrix, conceptualizing the competition coefficients as quasi-random variables subject to the operation of expectation (Levins, 1968, 1979). We used the row/sum component of the covariance (Vandermeer, 1972) to measure the structure of a series of randomly selected competition matrices.

We explored the behavior of the model through extensive simulations so as to relate the covariance of the matrix to the number of species remaining in the system after a short simulation of 100 iterations. For these simulations we chose the matrix containing the parameters a_{ij} from a uniform random distribution over the range 0–1. Subsequently we adjusted the covariance of this matrix by applying the formulas,

$a_{ii}(aa_justea) = \gamma(1 - a_{ii}) \tag{4}$	(4a) (4a)	$=\gamma(1-a_{ii})$	a _{ii} (adjusted)
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$$a_{ij}(adjusted) = \gamma(a_{ij}) \tag{4b}$$

$$a_{ij}(adjusted) = \gamma(a_{ji}) \tag{4c}$$

where $a_{ij}(adjusted)$ is the competition coefficient used in the simulations, *i* is not equal to *j*, and γ is a uniformly distributed random variable providing a range of average competition. Eq. (4a) alone generates a negative covariance, Eq. (4b) alone generates, on average, a zero covariance, and Eq. (4c) alone generates a positive covariance. So as to insure a broad range of covariances, Eqs. (4a)–(4c) were applied with equal probabilities for each pair of coefficients in the generation of each competition matrix.

Thus, there are three sources of stochasticity introduced in the model: first, the initial a_{ij} were taken from a uniform distribution of random numbers {0,1.0}, making the initial competition matrix a "random" matrix, second, the γ was chosen from a uniform

random distribution {1.0,1.2} to generate an additional stochastic variability and third, the ε was generated from a uniform random distribution {1.0,1.05}. Thus, while the matrix A (containing elements a_{ij}) initially contains a random assembly of elements below the diagonal, the elements above the diagonal are either a_{ij} or $1-a_{ji}$. Adjusting with $\gamma > |1|$ (equations (4)) introduces stochasticity to the symmetry of the original A matrix, and adding $\varepsilon > 1$ (Eq. (3)) adds environmental stochasticity to the determination of competitive outcome. As indicated above, our results are for γ taken from a uniform random distribution ranging from 1.0 to 1.2 and for ε taken from a uniform random distribution ranging from 1.0 to 1.05. However, in a subsequent section, we use $\gamma = \varepsilon = 1.0$ to explore the question of transient behavior of the whole system.

The model was run 300 times, 100 iterations each run, on a 100×100 lattice with periodic boundaries. This provided us with a range of covariances from highly negative to highly positive, yet still a random collection of a_{ij} since the original values were drawn from a uniform random distribution. The algorithm for constructing the matrix was (1) place random numbers selected from a uniform distribution 0-1 in the matrix, (2) set the values above the diagonal to either their reciprocal values below the diagonal, or 1 minus those reciprocal values, or no change (i.e., according to Eqs. (4a)-(4c)), (3) add variability by multiplying by a random number (uniform $\{1.0, 1.2\}$) corresponding to γ of equation set 4. The algorithm for tracking the dynamics of the system was, at each point in the lattice (1) compute response, effect, and total competition for each species, (2) multiply the total competition by ε (uniform {1.0 to 1.05}). After all lattice points had been visited, each was revisited and an occupying species was assigned based on which of the 12 species had a larger "total competition" (Eq. (3)) for that lattice. In terms of classical cellular automata, updating was synchronous (simultaneous). All simulations were done beginning with five individuals of each of 12 species allocated at random on a 100×100 lattice with periodic boundaries.

3. Results

3.1. Preliminary simulations

We begin with a set of preliminary runs to illustrate the qualitative behavior of the model. For these illustrative preliminary runs we eliminated all stochastic factors except the initial random allocation of the competition matrix (i.e., $\gamma = \varepsilon = 1$). In Fig. 2 we present two exemplary series of snapshots of a 100×100 lattice with 12 competing species after 20, 50, 80 and 100 iterations for a positive covariance Fig. 2a, and after 50, 100, 600 and 3000 iterations for a negative covariance.

In Fig. 2a, the competition coefficients were arranged so as to have a high positive covariance, which is to say effect and response competition are negatively correlated, or the competition is "balanced", or there is a tradeoff between effect and response competition a good effect competitor implies a poor response competitor. Note the clear mosaic structure, in which obvious monospecific patches appear at each stage. The way this mosaic develops depends on starting conditions, of course, but rapidly the patches that constitute the mosaic become fixed in space due to the effective standoff that exists at the borders of the patches. After only 100 iterations, the clumps are spatially fixed in perpetuity.

In Fig. 2b the competition coefficients were arranged so as to have a high negative covariance (highly negatively correlated above and below the principle diagonal of the matrix) which is to say effect and response competition are positively correlated, or the competition is unbalanced (a good effect competitor implies a good response competitor). A competitor that has a strong competitive effect in the community, will also tend to have a large competitive response, i.e., be unable to tolerate the effects of other species. This means that species will be either good or poor competitors on both the effect and response scales, which implies the possibility of at least one intransitive loop, (discussed more fully below) in the matrix. Note the presence of spiral waves,



Fig. 2. Two qualitatively distinct examples from the model on a 100×100 lattice. All cases were initiated with five individuals of each of 12 species placed randomly on the lattice. Color codes, including patterned colors, represent different species the six colors, red, black, green, blue, yellow and cyan, plus a patterned version of each color yields 12 species. Simulations based on Eqs. (1)–(3) in text, with competition matrix randomly set with application of equation 4 to create either a large or small positive or negative covariance, i.e., a case of balanced versus unbalanced competition. The precise matrices for these two simulations are presented in the Supplementary material D. (a) A strongly positive covariance generating a strong mosaic pattern. (b) A strongly negative covariance with the chance existence of an intransitive loop open red, green and open red, with the persistence of secondary loops involving open blue and cyan. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

generated by intransitive loops. In this particular case the end state is a single intransitive loop (red, yellow and black) which persist in perpetuity. The time scale for arriving at the permanent species composition is dramatically different in the case of a negative covariance compared to a positive covariance (compare time frame differences between Fig. 2a and b).

We can thus view the overall pattern of competition as ranging from an extreme in which there is a perfect balance between effect and response, meaning a tradeoff between these competitive classes, to an opposite extreme in which there is a perfect imbalance between effect and response, suggesting intransitivity somewhere in the community. The emergent spatial pattern is dramatically different depending on that covariance.

The study of intransitive loops has recently attracted considerable attention, first because it is a way in which very strong competition can be effectively moderated to allow the coexistence of species that would otherwise not coexist (Vandermeer, 2011), but second, because of its role in the creation of a backbone for further community structure (Laird and Schamp, 2006, 2008). Specifically, in continuous time dynamic models a single intransitive loop can maintain a large number of species in perpetuity even though competition coefficients among them are extremely high, strongly violating Gause's principle (Vandermeer, 2011). However, in the spatial context, our simulation experiments suggest something rather more complicated happens. Although all species involved in an intransitive loop are maintained in the system, the species not involved in the loop tend to be rapidly removed by that same intransitive loop. Thus, for example, in Fig. 2b, after 100 iterations there appear to be at least two intransitive loops—(1) yellow, red, cyan; and (2) red, yellow, black. At time=100, the yellow, red and cyan form an intransitive loop, and the yellow, red and black form another intransitive loop. By the 600th iteration. one of those loops (the red/vellow/cvan), has completely taken over the lattice. However, those three remain, apparently, in perpetuity (see the picture for 3000 iterations).

3.2. Species diversity and mosaic formation

From the initial simulations described qualitatively above, it seems that the preservation of many species goes along with the formation of strong mosaics, while the elimination of most species through competitive exclusion occurs when mosaics fail to form, perhaps a consequence of the structure of the competition matrix—positive covariance yields a semi-permanent mosaic pattern and preservation of species and a negative covariance results in a pattern that is not permanent and thus results in much competitive exclusion. To explore this generality more extensively, we ran 300 simulations and calculated both the covariance obtained from "*a*"s randomly selected and adjusted to create a large range of covariances as described above, and the number of species surviving after 100 iterations. The results of these are displayed in Fig. 3. Clearly species diversity is positively associated with the covariance of the competition matrix, which is to say species diversity is promoted by balanced competition, a tradeoff between effect and response, whereas extinction is more common in cases of negative covariances, largely associated with sometimes complicated structures of intransitive loops.

Unlike the continuous case (Vandermeer, 2011) in which a species not in the intransitive loop but competitively attacked by a member of that loop is effectively saved periodically by the oscillations in time of the species in the loop, in the discrete spatial situation the intransitive loop creates spiral patterns that effectively eliminate other species in the system. In this way, the existence of an intransitive loop tends, in our model, to dramatically reduce the species diversity. It seems that most of the cases of only 3 or 4 species persisting over the 300 simulations were cases of an intransitive loop effectively eliminating all of the other species in the system. Furthermore, a situation of competing loops sometimes occurs, increasing diversity but only within the intransitive loop, with an additional species permanently connected to both loops.

The probability that an intransitive loop will emerge in a randomly generated competition matrix is also indirectly related to the covariance of the matrix. By stipulating that reciprocal pairs must be negatively correlated (i.e., negative covariance), the stage is set for the possibility of dominance to be exerted in an intransitive fashion. So, for example, if it is stipulated that α_{12} must be \gg than α_{21} , and α_{23} must be \gg than α_{32} , a negative covariance would suggest that α_{31} must be \gg than α_{13} (considering these three species only) which would result in an intransitive loop between the three species. Thus we see a general negative relationship between more negative covariances and species diversity (Fig. 3), due mainly to the existence of a competitive hierarchy to be sure, but also, at least in some cases, due to the existence of an intransitive loop.



Fig. 3. Relationship between the number of species remaining after 100 iterations and the covariance of the competition matrix. Simulations based on the model represented by Eqs. (1)–(3). Smooth black line connects mean values of "surviving species richness" as a function of bin midpoint -1.75, -1.25, etc. ..., dashed line is best fit linear regression, significant at p < 0.001.

3.3. The transient nature of the species diversity pattern

Although the positive relationship between the covariance of competition and species diversity is quite general (i.e., extensive simulations with other parameter values always gave the same qualitative results), it is clear that the pattern is transient. However, that transience is complicated. To see the underlying pattern of the transient nature of the system, we removed the stochastic factors (i.e., let $\gamma = \varepsilon = 1$) and ran 100 simulations for each of 50, 100, 150, and 200 time steps (iterations), the results of which are shown in Fig. 4. With high positive covariance the rapid formation of a fixed mosaic insures the maintenance of all



Fig. 4. Pattern of surviving species richness as a function of covariance for different lengths of simulations, illustrating the invariance of the mosaic structures (all values of covariance above 0.7) versus the transient behavior of all other species richness values (all values of covariance below 0.3). Values computed with stochastic effects γ and ε eliminated but the competition coefficients being randomly allocated.

12 species in the system. As covariance decreases beyond about 0.3, one or more intransitive loops form and the species diversity begins to decline. Thus, the transience is due to the lower values of covariance. This dual approach to a permanent state is also visible in Fig. 2, where the lattices were chosen so as to illustrate the rapid formation of a mosaic when the covariance is positive (Fig. 2a) and the much slower elimination of most, or many, species by an intransitive loop when the covariance is negative (Fig. 2b).

The dual nature of the transience creates the potential for a zone of alternative stable states. As illustrated in Fig. 4, in the range of covariances between about 0.3 and 0.7 it is possible to either form a fixed mosaic (with the permanence of all 12 species), or a spiral-like pattern with reduced species diversity. However, this alternative state situation only occurs after the system has been running for a relatively long period of time. Depending on the organism, 200 iterations may be short (i.e., 200 months for a forest) or long (200 day for a bacteria community), so it is not possible to specify the expectation of a pattern of a simple positive relationship between covariance and species diversity (e.g., Figs. 3 or 4a) or a double plateau with a zone of alternative states (e.g., Fig. 4c or d). The generalization that species diversity, in a closed community, will increase with increasing covariance is true. But the nature of that increase may be either smooth or abrupt. This rather odd relationship is a consequence of a differential transient state depending on the covariance.

4. Discussion

Structuring communities through competitive interactions has long been a popular research topic leading to a large and diverse literature (Levins, 1968; Tilman, 2004; Roughgarden, 1983; Goldberg and Fleetwood, 1987; Perfecto, 1994). Much of that literature has been focused on the underlying argument that different species occupy different niches, thus making interspecific competition weak enough so that Lotka/Volterra/Gause competitive coexistence is a sufficient paradigm to account for species coexistence. But when competition coefficients are very large, that same classical theory predicts competitive exclusion. The resulting paradox of the plankton (Hutchinson, 1961) has always been something of a conundrum, recently receiving renewed attention mainly because of Hubbell's analysis of competitive neutrality (Hubbell, 2001). In the case of most sessile organisms (e.g., most plant communities, ants restricted by nest site location, corals, barnacles) it is likely the case that competition is either neutral or strong (i.e., with LV competition coefficients equal to or greater than 1.0 since no two individuals can occupy the same physical space). As noted earlier, a useful categorization of these competitive scenarios was provided by Yodzis (1978) who placed competitive communities along a continuum based on the average competition coefficient, ranging approximately from very small competition coefficients dominance-controlled communities to very large competition coefficients founder-controlled communities. This categorization permits a more focused approach to research on competition and community structure.

An alternative point of view suggests that species with equivalent niches might be arranged such that those that are competitively dominant are also weak in their dispersal patterns, the so-called competition/colonization tradeoff (Hurtt and Pacala, 1995; Higgins and Cain, 2002; Calcagno et al., 2006). Regardless of the importance of this issue, our focus in this article is on local interactions only. Relaxing the assumption of this local restriction is the subject of work currently in progress (Yitbarek and Vandermeer, in preparation).

In this work we have considered communities deriving pattern from local interactions alone and those that can be described as founder-controlled (those with generally very high competition coefficients), for which classical ecological theory holds that competitive exclusion should be the rule, although the vagaries of nonlinear and stochastic forces render that point of view approximate at best (Levins, 1979; Armstrong and McGehee, 1980). Yet most of the early literature effectively assumed a well-mixed community, that is, one in which individuals were free to disperse without limits, or, more formally, species interactions without geometry. Especially when considering sessile organisms, such an assumption is unwarranted. It is thus of interest to ask what changes to the underlying theory of founder-controlled communities will emerge if a specific geometry, in this case a spatial structure, is imposed on the system. A rich literature exploring this issue has emerged (e.g., Neuhauser and Pacala, 1999; Bolker et al., 2003; Chesson, 2004; Durrett and Levin, 1998; Kerr et al., 2002; Laird and Schamp, 2006, 2008; Rohani et al., 1997).

To approach this question, and motivated by field work on ground-foraging ants (Yitbarek et al., 2011; Perfecto and Vandermeer, 2011), we employ a simple cellular automata model, in which competitive interactions are all local (the object cell and the surrounding 8 cells, commonly referred to as the Moore neighborhood), and species win in competition based on their general competitive ability. Distinct from some other models (e.g., Laird and Schamp, 2006; Kerr et al., 2002), our model incorporates the idea of the effect/response tradeoff in competition.

Our most general conclusion regarding mosaic formation is that when space is involved, it is not so much the intensity of competition that matters, but rather its balance, which we measure with the covariance of the competition matrix. With a highly symmetrical matrix (i.e., balanced competition), a strong pattern of distinct clusters of monospecific individuals emerges as a stable formation, the classic idea of a mosaic pattern in which individuals of each species mainly exist within monospecific clumps (Fig. 2a). The intensity of competition matters little except at the extremely low end for this pattern to emerge.

Mosaic patterns have been reported for many sessile organisms in several different contexts (Blünthgen and Stork, 2007; Majer, 1972; Ribas and Schoereder, 2002). It is frequently difficult to discern whether or not such patterns are self-organized as they are in our model or whether they emerge from underlying habitat conditions. Here we provide a conceptual framework indicating the conditions, in a founder-controlled community structured by competition, under which a strong mosaic pattern will be expected from self-organization alone (i.e., a large positive covariance of the competition matrix).

At the other end of competitive balance are various degrees of imbalance, including intransitive loops and competitive hierarchy. Competitive intransitivity has been reported for a number of organisms that include sessile marine organisms (Jackson and Buss, 1975), lizards (Sinervo and Lively, 1996), bacteria (Kerr et al., 2002), and plant communities (Laird and Schamp, 2006). Intransitive networks generally have been identified as an important mechanism that can theoretically lead to the coexistence of multi-species communities despite intense competition among species (May and Leonard, 1975; Vandermeer, 2011). Such intransitive loops are contrasted to their opposite, transitive chains, which are the same as the classical competitive hierarchies based on "superior" competitive abilities of the best competitor species over all the other species, then the superior competitive ability of the next best competitor over all other species except the first one, and so forth. In some work competition in multi-species communities has been thought of as falling along a continuum from hierarchical organization to intransitive competition (Laird and Schamp, 2008), which is distinct from our

approach. We take the competition matrix to be metaphorically similar to the Lotka-Volterra community matrix, but look only at the local outcome of competition, similar to the competitive outcomes matrix of Laird and Schamp (2006, 2008). However, the latter authors focus their study on only the distinction between transitive and intransitive arrangements, assuming complete competitive inbalance in their competitive outcomes matrix. Thus Laird and Schamp effectively study only half of the framework presented in this work, the competitive imbalance half. Restricting our model to only negative covariances and focusing only on the question of intransitivity, we generate qualitatively the same results as Laird and Schamp (see Supplementary material C). Much of the other work implying that intransitive loops are implicated in the preservation of species diversity are concerned with smaller species assemblages and, most importantly, are strictly concerned with the contrast between intransitive loops and competitive hierarchy (Kerr et al., 2002; Boerlijst and Hogeweg, 1991; Johnson and Seinen, 2002; Edwards and Schreiber, 2010).

In addition to our use of the effect/response framework, our simulations are generally short (e.g., 100 iterations for Fig. 3), since we view our theory as relevant to transient states, albeit relatively long term transients. On the other hand, in the completely deterministic form of the model (i.e., with γ and ε both fixed at 1.0), both the mosaic patterns and the spiral waves that are generated by intransitive loops appear to be generally fixed in perpetuity as they are in the examples given in Fig. 2. Indeed, repeating our experiments for some larger communities the same general pattern emerges in which a large negative covariance generates extinction events very rapidly whereas the mosaic pattern maintains large species diversity over a much longer period.

Both mosaic formation and intransitive competition are bound to be influenced by the spatial scales at which interactions among organisms occur in an ecosystem (Durrett and Levin, 1998), an observation that has previously motivated significant theoretical interest in the role of spatially structured populations and how they relate to the coexistence of species (Frean and Abraham, 2001; Kerr et al., 2002; Laird and Schamp, 2006). While a number of studies have reported conditions under which coexistence may occur in the face of local competition (Durrett and Levin, 1998; Frean and Abraham, 2001; Vellend and Litrico, 2008), other studies have emphasized the importance of more regional forces to be important for coexistence (Huisman and Weissing, 2001). The present study departs from previous studies in emphasizing the intersecting importance of spatially constrained populations and the balance of competitive relationships in generating spatial patterns which, in turn, have an important influence on the ultimate level of species diversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2012.01.005.

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