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Emergence of structured communities through evolutionary dynamics

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H I G H L I G H T S

- Evolutionary dynamics of a community of competing species is considered.
- Model creates stable systems with > 100 species; solves complexity-stability problem.
- The emerged community has a modular structure.
- Closely related species have large niche overlap but small fitness differences.
- Relevance to many recent works on community structure, competition-relatedness, etc.

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Species-rich communities, in which many competing species coexist in a single trophic level, are quite frequent in nature, but pose a formidable theoretical challenge. In particular, it is known that complex competitive systems become unstable and unfeasible when the number of species is large. Recently, many studies have attributed the stability of natural communities to the structure of the interspecific interaction network, yet the nature of such structures and the underlying mechanisms responsible for them remain open questions. Here we introduce an evolutionary model, based on the generic Lotka–Volterra competitive framework, from which a stable, structured, diverse community emerges spontaneously. The modular structure of the competition matrix reflects the phylogeny of the community, in agreement with the hierarchical taxonomic classification. Closely related species tend to have stronger niche overlap and weaker fitness differences, as opposed to pairs of species from different modules. The competitive-relatedness hypothesis and the idea of emergent neutrality are discussed in the context of this evolutionary model.

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1. Introduction

A long standing puzzle in theoretical ecology regards the coexistence of many competing species in a single community on a confined spatial domain. This phenomenon is ubiquitous in nature, manifesting itself in many systems such as fresh-water plankton (Hutchinson, 1961; Stomp et al., 2011), tropical forests (Steege et al., 2013) and coral reefs (Connolly et al., 2014). Although the empirical identification of niches and the quantification of niche differentiation is a very difficult task in high-diversity assemblages, it seems clear that the overlap between niches of different species is substantial, as most of these species extensively utilize a common small set of resources, such as space, nutrients and water.

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This, however, makes coexistence problematic, as first noticed by Robert May in his classical 1972 paper May (1972). For a system with random degrees of niche overlap, May showed that the number of coexisting species is quite limited unless the overlaps are extremely small. This problem is known as the complexity–diversity puzzle: a complex system (in our context, many coexisting and strongly competing species) cannot be diverse, since generically there exists a combination of competitor species that will apply strong pressure on a given species and will drive it to extinction. This is a probabilistic effect: for any number of species there exists a set of interaction matrices that allow for coexistence, but the chance of a randomly picked matrix to fulfill this condition decays exponentially with the number of species (see the recent discussion in Allesina and Tang, 2012). Even if, by some miracle, the interaction parameters support a high-diversity community, any slight perturbation of the environment will lead to an altered interaction matrix and almost surely a substantial loss of diversity.

Clearly, an empirically observed collection of trees or plankton species is not a random assemblage but the outcome of a long evolutionary process during which new species appeared and old species became extinct, eventually yielding the current structure of the community. Accordingly, one would like to study an evolutionary model in order to see if, or under what conditions, the evolutionary process may “solve” the complexity–diversity problem, i.e., whether or not a set of interaction matrices supporting coexistence may appear spontaneously from the evolutionary dynamics.

Several evolutionary models have been suggested in an attempt to address the complexity–stability problem. Ginzburg et al. (1988) presented an evolutionary model based on Lotka–Volterra dynamics in conjunction with speciation events. Upon speciation, the interaction of the daughter species are set to be similar to those of the mother species modulo small, random modifications (Akçakaya and Ginzburg, 1991). The model of Ginzburg et al. is conceptually appealing in its assumptions and method yet it resulted in stable coexistence of only a very limited number of species (~ 6), too small to account for empirically observed communities. Other approaches, e.g. Tokita and Yasutomi (2003) and Yoshida (2003), were based on a similar evolutionary mechanism; however they allowed for mutualistic interactions. The inclusion of mutualistic interactions combined with speciation and extinction events applies a selective pressure towards symbiotic interactions, thereby fostering the coexistence of many species. While these models did exhibit coexistence of a large number of species (tens or more) they cannot account for ecosystems in which there is no or negligible mutualistic interactions. See further consideration in the Discussion section.

Here we propose a modified version of the Ginzburg et al. model, which does succeed in producing a stable community with many (up to hundreds of) species. Our modification is motivated by the insight that competitive interactions arise from niche overlap; the necessarily non-perfect niche overlap between a daughter and a mother species inevitably leads to weaker competition between individuals of the mother and daughter species than that of conspecific individuals. This idea is implemented by the addition of a new parameter, $h < 1$, which controls the strength of interaction between mother and daughter species relative to the intraspecific interaction. This seemingly minor change has the effect of increasing the number of coexisting species by over an order of magnitude.

The resulting model evades the theorem of May by generating a nonrandom structure for the matrix of interaction strengths. One simple way to verify this claim is by studying the community structure with a randomly shuffled version of the interaction matrix. Indeed, we find that the random shuffled system leads to the extinction of large numbers of species, reducing the system to a few coexisting survivors.

Another way of investigating the structure is via the use of standard “modularity maximization” algorithms that are designed to detect modular structure in matrices. Running an algorithm of this type (Blondel et al., 2008), we find that it succeeds in identifying a significant degree of modularity.

We can do better however since we have access to the phylogenetic history of the species in the simulation. Using the phylogenetic distance matrix and a phylogeny reconstruction algorithm to reorder the species, a unique hierarchical structure of the interaction matrix is revealed. In this structure, which arises spontaneously via the evolutionary process, the interaction matrix can be partitioned into subcommunities such that the interaction strength between two species within the same subcommunity is high while the interaction between two species from different subcommunities is low. It is moreover seen that the species within a subcommunity are phylogenetically closely related while species in two different subcommunities are only distantly related.

In the following section we describe our model and equations in detail. In Section 3 we present our results and in the last section we discuss our main findings and describe several future research directions.

2. Materials and methods

Our results emerge from simulations of the generalized competitive Lotka–Volterra model, where speciation and extinction events are allowed to change the number of species, generating an evolutionary process. Denoting the (instantaneous) number of species in the community by Q , the dynamics satisfies

$$\dot{n}_i = \alpha n_i \left(1 - \frac{n_i}{K}\right) - \frac{n_i}{K} \sum_{j=1}^Q C_{ij} n_j, \quad (2.1)$$

where n_i is the abundance of species i , α is the linear growth rate (assumed for simplicity to be species-independent), K is the carrying capacity and C_{ij} is the competition matrix.

Formally, even when a species is under strong competitive pressure and its abundance decays, the dynamics described by the deterministic Eq. (2.1) leads to decay of its abundance to infinitesimal values but it can never reach zero. This property of Eq. (2.1) is a disadvantage, since species may recover from a long period of diminishing abundance when the community structure changes during evolution, while in the real world species that undergo extinction are out of the game for good. To allow for extinction we define a threshold value n_0 , below which a species is removed forever and the corresponding row and column of the matrix C_{ij} are deleted.

Speciation events, on the other hand, involve the addition of a species to the dynamics described by Eq. (2.1). To model speciation, an existing species is chosen at random (with a probability proportional to its population size) to be the “mother” species, and its population is reduced by 5%; the individuals belonging to this 5% fraction are declared as a new, “daughter” species, that inherits most of the features of the mother species up to small modifications as described below. This implies that closely related species play a similar role in the dynamics (2.1), reflecting the similarity of their biological functions.

We illustrate this speciation process via the example of two species becoming three due to the speciation of species 1. Denoting the daughter species by the label 3, the change in the interaction matrix C_{ij} is given by

$$\begin{pmatrix} 0 & C_{1,2} \\ C_{2,1} & 0 \end{pmatrix} \Rightarrow \begin{pmatrix} 0 & C_{1,2} & h(1-\gamma)+\gamma\epsilon_1 \\ C_{2,1} & 0 & C_{2,1}(1-\gamma)+\gamma\epsilon_2 \\ h(1-\gamma)+\gamma\epsilon_3 & C_{1,2}(1-\gamma)+\gamma\epsilon_4 & 0 \end{pmatrix} \quad (2.2)$$

Our model distinguishes between the competition of the daughter species with its mother and its competition with all other species. For any species other than the mother, the daughter inherits the competition terms of its mother with small, random modifications. In particular, if $C_{\text{mother},j}$ is the interaction of the mother with species j , $C_{\text{daughter},j} = C_{\text{mother},j}(1-\gamma) + \gamma\epsilon$, where $\gamma \ll 1$ and ϵ is a random variable drawn from a gamma distribution with mean 1 and variance 1. In Eq. (2.2) we numbered the ϵ 's to emphasize that each of them is chosen independently from the same distribution. The competition matrix terms for $C_{j,\text{daughter}}$ are obtained using the same procedure.

The mother–daughter interaction terms are subject to different rules. As explained above, the mother and the daughter are usually similar in their biological functions, however some degree of niche separation appears to be a condition for successful speciation. Accordingly, we set $C_{\text{mother},\text{daughter}} = h(1-\gamma) + \gamma\epsilon$, where the

parameter $h \leq 1$ reflects the required overlap reduction. Again $C_{\text{daughter,mother}}$ is obtained similarly.

A simulation starts with a single species. Eq. (2.1) is integrated in time using a standard Runge–Kutta algorithm. Every T_s the abundance of species is checked, species for which $n < n_0$ are removed and a single speciation event occurs. The interaction matrix is then updated according to the procedure described above.

In analyzing the structure of the evolved community interaction matrix, we use, as noted above, an ordering of the species based on a reconstructed phylogenetic tree. The tree is produced by the unweighted pair group method average (UPGMA) algorithm, based on the phylogenetic distance, measured directly in the simulation.

3. Results

Having described the simulation procedure and its logic, we proceed to the analysis of the outcomes. As explained above, the critical ingredient for enabling a significant degree of coexistence is having a reduced niche overlap between the mother species and its daughter. This is illustrated clearly in Fig. 1. In the first panel the species richness as a function of time is presented for $h=1$ (i.e., full overlap). We see that, in line with the essentially equivalent results of Ginzburg et al. (1988), the species richness saturates at a very low value (5–10) of Q . Reducing h to 0.95 (panel b) increases the species richness at saturation to the range 20–50, and reducing it yet further to 0.9 (panel c) the species richness increased to 40–80.

The growth pattern demonstrated in Fig. 1 is also of interest. The number of species initially grows quite rapidly and then switches to a phase characterized by a very slow growth (or even saturation), with large fluctuations (resembling mass extinctions) in the number of species. Initially, most speciation events lead to the establishment of a new species, without driving one of the already existing species to extinction. As the community builds up and the interaction matrix grows in dimension, it becomes (in line with May's prediction) more and more difficult to increase the net number of species, until an overall balance between speciation and extinction is reached.

In the saturation phase the species richness of the system fluctuates quite strongly, oscillating, more or less, between some maximum and minimum values, on timescales which are much larger than the speciation timescale. The dynamics is thus characterized by alternating periods of increasing species richness, during which the system becomes progressively more fragile, followed by periods of diversity loss, when almost every speciation triggers the extinction of a few species.

To deepen our understanding of this behavior, we present in Fig. 2 a more detailed picture of the dynamics for one of our simulations for $h=0.95$. Now the way in which evolution shapes

the community structure, as manifested in the interaction matrix, becomes clearer. In terms of the paradigmatic framework suggested by Chesson (2013), the two factors that control the stability of the community are the degree of niche differentiation and the magnitude of fitness differences. In our competition matrix an overall measure of niche overlap is given by the average value of the nondiagonal matrix elements $\overline{C_{ij}}$ (see Kessler and Shnerb, 2015), and the fitness differences, or the level of interaction matrix heterogeneity, are expressed by the variance of all interaction matrix elements (sum over all $i, j, i \neq j$)

$$\sigma^2 = \frac{1}{Q(Q-1)} \sum_{ij} (C_{ij} - \overline{C_{ij}})^2. \quad (3.1)$$

Along the evolutionary process the strength of the average interaction initially tends to decrease in time, since species with lower interaction strengths are more likely to survive (Fig. 2, panel c), but at the same time σ^2 tends to increase. The evolutionary process, thus, promotes stabilizing mechanisms while suppressing equalizing forces. Both quantities (and also (see panel b) the overall carrying capacity of the system that increases as $\overline{C_{ij}}$ decreases) eventually saturate, reflecting the saturation of the total number of species. As seen in Fig. 3, both stabilization mechanisms increase in strength as h decreases, but the relative decrease of fitness differences appears to be more pronounced than the decrease in niche overlap.

This, however, is not the whole story. Beyond these crude indicators, there is also a subtler structure that emerges from the evolutionary dynamics (Fig. 2, panels d and e). It turns out that the interaction matrix is not random, but rather *modular*, i.e., the community is composed of a few groups of species, or sub-communities. Within each group the competition is strong but fairly homogeneous (weaker niche differentiation, smaller fitness differences) while the competition between members of different groups is characterized by weaker, but more heterogeneous, interaction terms. This hierarchical structure manifests itself in the interaction matrix (panel e) and in the bimodality/multimodality of the histogram of C_{ij} terms (panel f), with one peak associated with the interaction within a group, and the others with competition between members of different groups. Below we provide a more detailed analysis of this structure.

To confirm the indispensability of the modular structure, we compared the interaction matrix one obtains from the evolutionary process when species richness was saturated to its randomized version, i.e., to the same matrix with shuffled C_{ij} , such that $\overline{C_{ij}}$ and σ^2 are the same but the modular structure is lost. Randomization was shown to destabilize the community, leading to the loss of about 2/3 of the species.

A closer examination of the emerging interaction matrix discloses an even more interesting structure. Our simulations allow us to measure d_{ij} , the genealogic distance (shortest path along the genealogic tree, or, roughly speaking, twice the time to the most

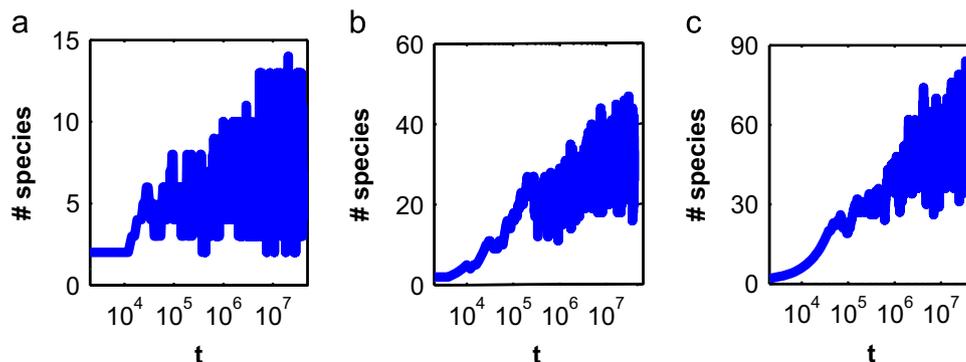


Fig. 1. Number of species as a function of time for $T_s=2000$, $N_s = 2 \cdot 10^4$ and $\gamma = 0.01$. Panel (a) $h=1$, panel (b) $h=0.95$ and panel (c) $h=0.9$.

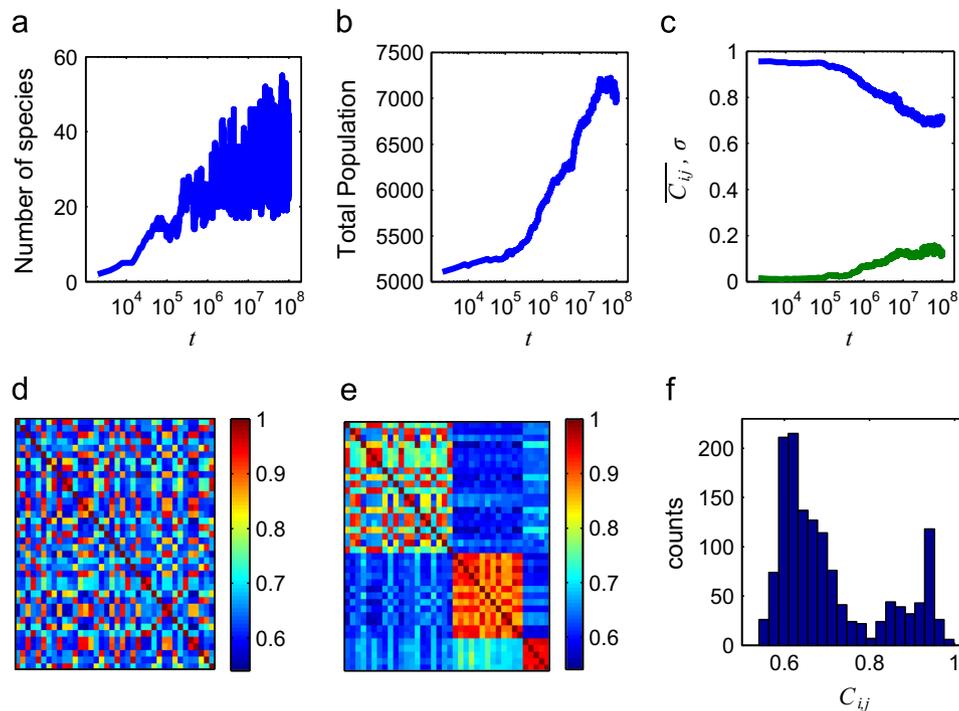


Fig. 2. An overview of the main results of the simulation for $h=0.95$ and $N_s = 5 \cdot 10^4$. The other parameters are as in Fig. 1. Panel (a) shows the number of extant species as a function of time. Panel (b) shows the total population size as a function of time. Panel (c) shows the evolution of the mean interaction strength, $\overline{C_{ij}}$ (solid blue line) and the standard deviation of the interaction strength, σ , (solid green line). Panel (d) shows a snapshot of the final interaction matrix. Panel (e) shows the same matrix as panel (d) except that it is reordered by using the Louvain method of modularity maximization. Panel (f) shows a histogram of the components of the interaction matrix. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

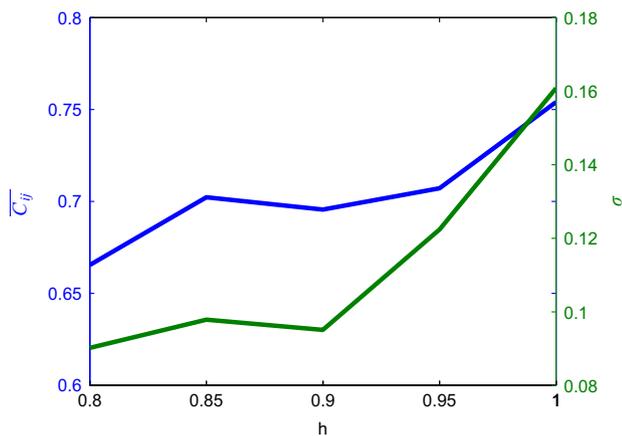


Fig. 3. The dependence of the mean interaction strength $\overline{C_{ij}}$ (solid blue line) and of the interaction strength standard deviation σ (solid green line) on the niche-overlap reduction h . All other parameters are as in Fig. 2 (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.).

recent common ancestor) for any two species in the system. Using that, we present a scatter plot Fig. 4 of C_{ij} vs. d_{ij} for any two species at the end of a single run of the simulation.

Two features of the interaction matrix emerge from Fig. 4. First, one realizes that h sets the scale for the interaction of close relatives (mother–daughter or sister species), but the interaction strength converges to a fixed value, about 0.6, for distant relatives. This is why the heterogeneity of the interaction matrix, as expressed by σ^2 , decreases with h : the smaller h is, the smaller is the difference in interaction strength between a close and a distant relative.

Moreover, Fig. 4 shows also that, for any specific history, there are “gaps” in the genealogical distance space, i.e., a histogram of d_{ij} s (and therefore of C_{ij} s) admits a few distinct peaks. This unveils the

hierarchical nature of the community, which underlies the modularity of the interaction matrix. Using the distance matrix to generate the genealogical tree, and then permuting the rows and columns of C_{ij} accordingly, one obtains Fig. 5, showing the strong relationship between the modularity of the interaction matrix and the hierarchical structure of the community. The community that emerges from the evolutionary process is thus made of “taxonomic groups” (genera, families) of closely related species. Within each group the competition is strong (high niche overlap) but with low heterogeneity, making all members of the subgroup quite equal. The inter-group matrix elements are much more diverse, but their absolute values are smaller (lower niche overlap).

3.1. Competition-relatedness

The competition-relatedness hypothesis, which can be traced back to the work of Darwin, predicts that the competition between closely related species should be typically stronger, as their niche overlap tends to be larger. Accordingly, local communities may exhibit phylogenetic overdispersion, with species being less related on average than if drawn randomly from the regional species pool.

Our work demonstrates that the premise of this argument does not entail its conclusion. Although the competition between closely related species is stronger on average, the variance of the C_{ij} s is smaller, meaning that the fitness differences are smaller. Since the coexistence stability depends on both features, one cannot conclude a priori that the community has to be overdispersed.

As an examination of this point, we consider the stability of each pair of species in the community. Every such pair, of species i and j , say, is fully characterized by the values of C_{ij} and C_{ji} . Restricting (2.1) to these two species only, one obtains a coexistence fixed point n_i^*, n_j^* , and the stability of this fixed point is given by the value of its Lyapunov exponent λ (the Lyapunov exponent is the largest eigenvalue of the stability matrix). In a realistic scenario, when the system is exposed to noise, its state fluctuates

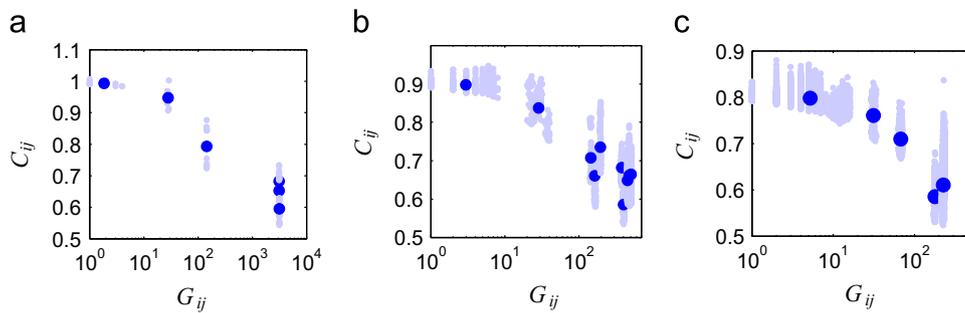


Fig. 4. Interaction strength C_{ij} vs. the genealogical distance, G_{ij} , between all pairs of species for $h=1$ (panel (a)), $h=0.9$ (panel (b)) and $h=0.8$ (panel (c)). The large dots are the "centers of mass" of the points in each cluster. All other parameters are as in Fig. 2.

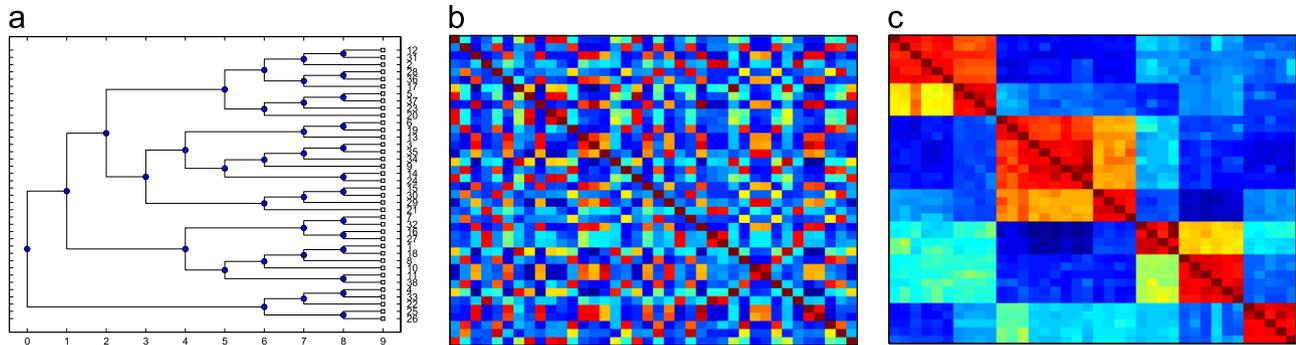


Fig. 5. Phylogenetic analysis of the interaction matrix for $h=0.95$. Panel (a) shows the reconstructed phylogenetic tree. For the sake of clarity we presented here the ultrametric version of the tree. In the corresponding phylogram (where branch lengths are drawn proportional to the genealogical distance) one observes a rapid growth of the number of lineages during the most recent period. This acceleration in lineage accumulation rate corresponds to $\gamma > 0$ as discussed in McPeck (2008). Panel (b) shows the final interaction matrix. Panel (c) shows the same matrix reordered according to the phylogenetic reconstruction. All other parameters are as in Fig. 2. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

around n_i^*, n_j^* , with a typical variation that scales like $1/\lambda$. The stability $S_{i,j}$ of such a two-species community is characterized by the chance of extinction of one of the species, which in turn depends on the distance from extinction in units of fluctuations width, so that $S_{i,j} = \min[n_i^*, n_j^*]\lambda$.

In Fig. 6 we present the value of S as a function of genealogical distance for a specific community. Clearly, the relationship is not monotonic. Although the niche overlap (as expressed in the mean value of the C_{ij}) decreases with genealogical distance, as demonstrated in Fig. 4, the stability of the pair decreases in some parameter regime as a result of stronger interaction heterogeneity. This result appears to be consistent with the outcome of recent studies (Mayfield and Levine, 2010; Godoy et al., 2014), suggesting that the increase of variance in fitness with genealogical distance may compensate for the effect of decrease in niche overlap.

3.2. Emergent neutrality

The neutral theory of biodiversity, put forward by Hubbell about 15 years ago, aimed to explain community structure by means of the assumption of perfect demographic equivalence (Hubbell, 2001; Volkov et al., 2003). In terms of Eq. (2.1), the neutral theory corresponds to the limit $C_{ij} = 1 \forall i, j$, implying that $\bar{C}_{i,j} = 1$ and $\sigma^2 = 0$ (Kessler and Shnerb, 2015). In that case, the community dynamics does not admit an attractive fixed point. Instead, any combination of n_i that satisfies the global constraint $\sum n_i = K$ is a steady state solution of Eq. (2.1), and the dynamics is dominated by demographic noise.

In Hubbell's theory the biodiversity is sustained by speciation events. With a finite carrying capacity K and without speciation, the community undergoes fixation by a single species; however the time to fixation (in units of generation) scales like K (Ricklefs, 2006). This slow, fluctuation driven, dynamics is in sharp contrast

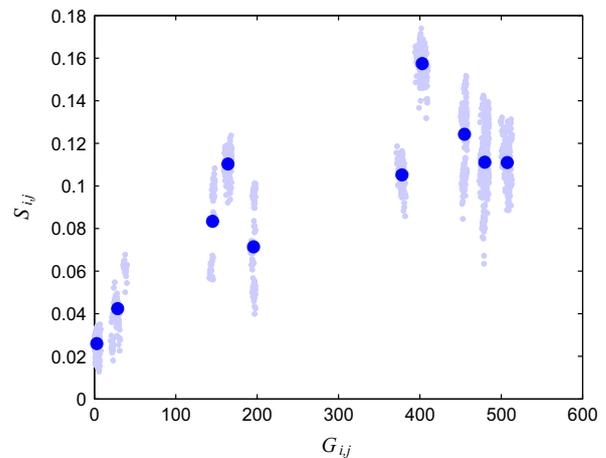


Fig. 6. Two-species community stability S_{ij} vs. the genealogical distance, G_{ij} for $h=0.9$. The large dots are the "centers of mass" of the points in each cluster. All other parameters are as in Fig. 2.

with the relatively fast dynamics associated with an attractive fixed point of Eq. (2.1) with a nonneutral C_{ij} , where the convergence time is inversely proportional to λ and is independent of K . Most of the community ecology models assume a separation between the ecological and the evolutionary timescales, such that after speciation the community reaches its new equilibrium long before the next speciation. In the neutral model the enormously long fixation times allow for a mixing of the ecological and the evolutionary scales (although this feature itself brings other problems (Ricklefs, 2006)).

Perfect neutrality is a very strong assumption that substantially restricts the possible community structure. To understand how such

a situation may emerge, possible models of “emergent neutrality” have been suggested (Scheffer and Van Nes, 2006; Holt, 2006). In essence, in these models there is a single fitness maximum (or a few maxima along a single trait axis), where inferior species go extinct and only species with fitness close to the maximum (hence with almost full niche overlap and negligible fitness differences) survive (Kessler and Nadav, 2014).

The outcomes of our model resembles, in some sense, the results of emergent neutrality models with finite range competition kernels (Scheffer and Van Nes, 2006; Vergnon, 2012). In these models the community decomposes into a few subcommunities that effectively do not interact with each other, where within any subcommunity the dynamics is, more or less, neutral. As we have seen, the model based on Eq. (2.1) yields similar results, with an emerging competition matrix which is made of strongly competing, relatively homogenous blocks.

Moreover, as the evolutionary process proceeds, not only does the number of species grow, but also the relaxation time, i.e., the time needed for the nonlinear system (2.1) to equilibrate becomes longer and longer (see Fig. 7). This feature has two implications. First, the attractive fixed point is becoming softer (the Lyapunov exponent decreases) and the dynamics resembles the neutral process for which $\lambda=0$. Second, the equilibration time after speciation is increasing steadily, such that it may overlap with T_s , eliminating the separation between the evolutionary and the ecological timescale.

4. Summary and discussion

In this paper we have analyzed the evolutionary dynamics of a community of competing species. Our model dynamics is governed solely by the competition among species and in the absence of competition any species will reach a fixed carrying capacity K , accordingly it provides an example of evolution via nonadaptive selection as defined in Borrelli et al. (2015). Upon speciation, the daughter species inherits its mother's traits up to small modifications, specifically, the strength of its competition with other species, as expressed by the relevant terms of the competition matrix. These modifications that reflect the change in niche overlap between the daughter and other species, relative to that of the mother, are taken to be uncorrelated random numbers. This effectively implies that the evolutionary process takes place in a high-dimensional trait space. In contrast, in a one dimensional trait space an increase of niche overlap with one species performance increases overlap with

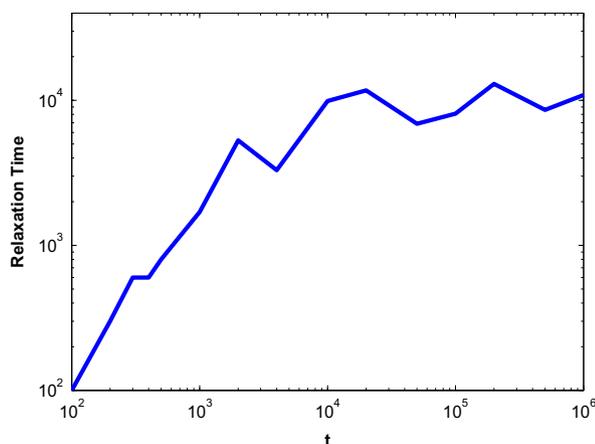


Fig. 7. The relaxation time of the system, i.e. the time needed to reach equilibrium from the current state if speciation is turned off, vs. time for $h=0.95$, $T_s=100$ and $N_s=10^4$. All other parameters are as in Fig. 2.

other, nearby species, implying correlated modifications of the C_{ij} s upon speciation.

Nevertheless, in principle the changes ε_i introduced to the interactions of the daughter species with the other species should not be completely independent, since changes to the interactions with closely related species should be similar, as would arise from an underlying niche model (Rossberg, 2006). For simplicity, we ignore such correlations here, and in view of our results, that emphasize the overwhelming importance of the mother-daughter interaction, we believe they would have only a minor quantitative effect.

As discussed above, May's complexity–diversity argument implies that even when the number of traits is very large, a random collection of species becomes unstable when there is a substantial overlap between niches. In particular, the probability that a randomly assembled community of Q species admits a feasible and stable equilibrium becomes exponentially small when Q is greater than $1/\sqrt{C\sigma^2}$.

Our aim in this paper was to find out how, or to what extent, the evolutionary process is able to “solve” the complexity–stability problem by shaping a community with nontrivial structure, such that the theorem of May is not applicable to the emerging C_{ij} matrix. We discovered that some level of niche separation between mother and daughter species (expressed, in our model, by the deviation of h from unity) is an essential feature. As pointed out by Ginzburg et al., $h=1$ (no separation on average) evolution does no better than a randomly assembled community and the number of coexisting species is ≈ 5 (recently a similar, zero-sum game model with mutations was shown to support only a few species community, Huang et al., 2012). Only when $h < 1$ does the system achieve a substantial number of species.

When evolution does work, i.e., for $h < 1$, it indeed shapes the structure of the community in a nontrivial way. As we have seen, evolution leads to an interaction matrix that supports a stable community even though the average niche overlap is above its critical value, as manifested by the collapse of the community once the (same) C_{ij} s are shuffled. The stability of the community was seen to depend on the modularity of the emerging competition matrix: the community decomposes into sub-communities, where within each sub-community niche overlap is high but fitness differences are low, while the interaction between species that belong to different sub-communities is characterized by higher fitness differences and lower niche overlap.

This modular structure within a community is related to its phylogeny. The sub-communities are, in fact, groups of closely related species, while species that belong to different sub-communities have their most recent common ancestor much closer to the root of the tree. Since the phylogeny is hierarchical, so it was found that the modules also have a modular structure. Accordingly, the hierarchical structure of biological classification, i.e., the use of taxonomic ranks like genera, family, order etc., is an emerging property of our model.

We have seen that the weakened interaction between daughter and mother species compared to the intraspecific competition of the mother is responsible for the ability of the system to generate high diversity. It is interesting in this context to consider the ability of the model of Tokita (Tokita and Yasutomi, 2003) to also produce high diversity. In this model, Tokita weakened not the interaction between the daughter and the mother, but rather between the daughter and some randomly chosen species. As far as generating diversity, this procedure is as effective as that of our model. We would argue, however, that the relative weakness of the mother–daughter interaction follows naturally from the reduced niche overlap compared to the total overlap between members of the mother species, whereas there was no clear underlying biological basis for Tokita's procedure. Although Tokita himself attributed the

success of his model to the enhancement of mutualistic interactions along the evolutionary process, we believe that $h < 1$ is a sufficient condition for the emergence of a stable community.

One line of inquiry that achieved some degree of success in generating a diverse community is based on systems with an inherent food-web structure (Drossel et al., 2001). In this case the assumption of a food-web structure imposes a particular structure on the interaction matrix which apparently lies outside the May framework. The same is true for models in which speciation appears as a result of nonlocal competition in a high-dimensional trait space with a long-range competition kernel, such as the one considered in Doebeli and Ispolatov (2010); in this case the competition matrix is ordered, reflecting the lattice-like structure of species in trait space. Yet another evolutionary model with structured competition matrix was suggested recently in Carroll and Roger (2015), where in this case the competition matrix is constrained to have a nested structure. As opposed to all these models, in our case there is no priori constraint on the dynamics, and the modular structure of the competition matrix is an emerging property.

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