

# On the origin of phylogenetic structure in competitive metacommunities

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## ABSTRACT

**Question:** Under what circumstances are local communities and metacommunities phylogenetically clustered, overdispersed or random assemblages in terms of phylogenetic relatedness?

**Methods:** An individual-based eco-evolutionary model was used to explain the link between system properties, ecological and evolutionary processes, and phylogenetic patterns in a spatially explicit competitive metacommunity. We simulated adaptive radiation dictated by local ecological dynamics (intra- and inter-specific competition) and dispersal. Phylogenies were constructed from the resulting metacommunities and phylogenetic community structure was analysed.

**Conclusions:** Phylogenetic clustering, dictated by the relative rate between eco-evolutionary processes such as colonization, invasion, and local radiation, are more likely if both intra- and inter-habitat heterogeneity is high. The amount of dispersal between habitats is also an important structuring parameter, but mainly so if intra-habitat heterogeneity is high and inter-habitat heterogeneity is low. Our results are based on a more rigorous and quantitative analysis of the ecological and evolutionary conditions dictating the phylogenetic signal and explain the continuous variability of phylogenetic clustering and overdispersion found in natural systems.

*Keywords:* assembly, community, competition, ecology, evolution, phylogenetic structure.

## INTRODUCTION

The assembly and diversification of biological communities and metacommunities has caught the interest of ecologists and evolutionary biologists for decades. It is now well known that natural communities are the products of local ecological processes, evolutionary contingencies (Ricklefs, 1987; Ricklefs and Schluter, 1993; Brown, 1995; Keddy and Fraser, 1999; Urban and Skelly, 2006), and neutral processes (MacArthur and Wilson, 1963, 1967; Hubbell, 2001). The relative effects of these processes at different temporal and spatial scales are, however, often unknown.

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As molecular methods and phylogenetic inference statistics have advanced, phylogenetic structure analysis has been used extensively to study the evolutionary signal in ecological community assembly processes. Today, there is a classic dichotomy, originally introduced by Webb *et al.* (2002), for the quantification and interpretation of phylogenetic community structure. With a suitable regional or global species pool as a reference, a local community can either be assembled non-randomly from closely related species (a ‘clustered community’) or from species more unrelated than a random assemblage [an ‘overdispersed community’ (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009; Pausas and Verdu, 2010)]. Given a mapping between traits influencing niche position and phylogenetic relatedness, these non-random patterns have been interpreted as signals of ecological processes. Phylogenetic clustering and overdispersion have been interpreted as signals of ‘habitat filtering’ and ‘competitive exclusion’, respectively (Webb *et al.*, 2002).

This approach has some limitations (e.g. Losos, 2011). Although traits often are assumed, implicitly or explicitly, to be conserved (positive relationship between ecologically relevant traits and species relatedness), studies have shown examples of traits being labile (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2004; Wiens, 2004; Wiens and Donoghue, 2004; Wiens and Graham, 2005; Ackerly *et al.*, 2006). The results from phylogenetic structure analysis are also dependent on both statistical approaches and on the taxonomic and spatial scales (Webb, 2000; Cavender-Bares *et al.*, 2006; Kembel and Hubbell, 2006; Silvertown *et al.*, 2006; Swenson *et al.*, 2006; Kraft *et al.*, 2007; Graham and Fine, 2008). Furthermore, community assembly is determined by both ecological and evolutionary processes and biogeographical contingencies. These effects act in concert and do not fit within the dichotomized framework of two contrasting ecological processes (Emerson and Gillespie, 2008; Vamosi *et al.*, 2009).

Emerson and Gillespie (2008) and Vamosi *et al.* (2009) made important attempts to explain the several processes that ought to be involved in phylogenetic structuring and found that competition, habitat filtering, speciation, and dispersal among habitats indeed play important roles. Some theoretical attempts have also been made to explain observed patterns (e.g. McPeck, 2007; Stegen and Hurlbert, 2011). Surprisingly few formal and more rigorous theories have, however, been formulated to explain how these processes actually structure local communities tied together by dispersal. Here we use an individual-based simulation approach to understand the link between ecological and evolutionary assembly processes and the phylogenetic patterns in metacommunities. Parameters of the model dictate individuals’ strength of competition for common resources, local and regional habitat properties in an abstract resource landscape, and dispersal propensity. We use this model to study the macro-evolution of metacommunities driven by the interaction between local ecological processes, evolutionary contingencies, biogeography, and dispersal. Our approach allows us to reinterpret and formalize recent attempts to synthesize this critical interplay (Emerson and Gillespie, 2008; Vamosi *et al.*, 2009) and we formulate a coherent theory for the origin of the phylogenetic structure of metacommunities.

## METHODS

We use an individual-based model to simulate the dynamics and evolution of large communities in five discrete habitats in space. These habitats can be reasonably well defined bona fide habitat types, large enough to harbour a full competitive community, or, for example, ponds, lakes, islands or forest fragments (Leibold and Norberg, 2004; Urban, 2004; Thompson, 2005). We will use the term ‘habitat’ throughout. The individuals are asexual and defined by

their continuous and heritable trait ( $z$ ) (McGill *et al.*, 2006), which specifies their ability to utilize the resources in any given habitat. Inspired by several similar earlier models of the evolution of resource specialization (Christiansen and Loeschke, 1980; Brown and Vincent, 1987; Dieckmann and Doebeli, 1999), we let each habitat be characterized by a unique, continuous (Gaussian) resource distribution. Hence, an individual optimally adapted to one habitat, maximizing its local resource acquisition, is less fit in the other habitats. Furthermore, the trait values dictate the strength of competition for resources within a habitat – similar values among individuals imply strong competition. To summarize, the fitness (expected number of offspring) of a focal individual is a function of its trait value, the traits of all other individuals occupying the same habitat, and the local resource distribution. By introducing mutations (small changes in individual trait values) and dispersal between habitats, a metacommunity will emerge from a single ancestral type through the processes of local adaptation, evolutionary branching, and dispersal, all according to the rules of the eco-evolutionary processes (Brown and Pavlovic, 1992; Geritz *et al.*, 1998; Nilsson and Ripa, 2010). The model thus allows for the full adaptive radiation of one or more clades, all with a common ancestor. It represents the full evolutionary potential of the initially invading type, its *bauplan* (Vincent and Brown, 2005), with all its corresponding, inherent, trade-offs. To emphasize this macro-evolutionary interpretation, we use the concept of a fitness generating function, or  $G$ -function (instead of ‘fitness function’) (Vincent and Brown, 2005).

### The model

Our simulations proceed in alternating phases of reproduction and dispersal, completing one cycle each generation (time step). In the reproduction phase, we first calculate the fitness of each individual in the metacommunity. We use a fitness generating function ( $G$ -function) derived from the classical Lotka-Volterra competition model:

$$G(z, \mathbf{z}, z_{\text{opt}}) = 1 + r \left( 1 - \frac{\sum_j \alpha(z, z_j)}{K(z, z_{\text{opt}})} \right) \quad (1)$$

where

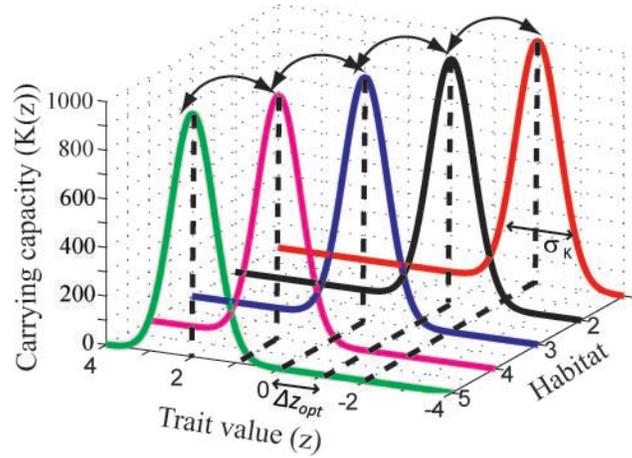
$$K(z, z_{\text{opt}}) = K_0 e^{-\frac{(z_{\text{opt}} - z)^2}{2\sigma_k^2}} \quad (2)$$

and

$$\alpha(z, z_j) = e^{-\frac{(z - z_j)^2}{2\sigma_a^2}}. \quad (3)$$

This function describes the fitness of an individual possessing a particular trait value ( $z$ ) within a particular habitat (defined by  $z_{\text{opt}}$ , see below). Fitness is also a function of the traits of all other individuals in the same habitat (denoted by the vector  $\mathbf{z}$ ). The parameter  $r$  denotes the intrinsic growth rate (equal for all individuals),  $K(z, z_{\text{opt}})$  is the carrying capacity, as experienced by an individual with trait value  $z$  in a habitat characterized by the point  $z_{\text{opt}}$  of maximal carrying capacity, and  $\alpha(z, z_j)$  is the competition coefficient between the focal individual and its competitors.

We define a local resource distribution, implicitly, by mapping a Gaussian carrying capacity (equation 2) on the continuous trait axis.  $K_0$ , equal in all habitats, denotes the maximal carrying capacity (at  $z = z_{\text{opt}}$ ). The resource availability falls off symmetrically as  $z$



**Fig. 1.** The metahabitat, defined by five Gaussian functions, illustrated by different colours. Each habitat – resource distribution – is defined in the trait dimension  $z$  by its  $z_{\text{opt}}$  and  $\sigma_K$  values.  $\Delta z_{\text{opt}}$  denotes the difference between neighbouring habitats and carrying capacity is the maximum equilibrium population size of one clonal species with a certain  $z$  trait within a habitat, given no interactions from species with alternative  $z$ -values. Black arrows between habitats illustrate the stepping-stone dispersal algorithm.

deviates from  $z_{\text{opt}}$  according to the width of the resource distribution ( $\sigma_K$ ). We use five habitats, defined by five resource functions with differently located resource peaks. The resource optima ( $z_{\text{opt}}$ ) are equally spaced along the trait axis at a distance  $\Delta z_{\text{opt}}$  from each other (Fig. 1). If  $\Delta z_{\text{opt}} \neq 0$ , we get five different resource distributions ('habitats') displaced along the  $z$ -axis. If  $\Delta z_{\text{opt}} = 0$ , all five habitats have identical resource distributions. As an individual only uses and competes for resources in one of the habitats at a time, this system can be viewed as five distinct habitats, linearly ordered along the trait axis, with different or identical resources, respectively.

The competition coefficient ( $\alpha$ ) describes the effect by a competitor ( $z_i$ ) on a focal individual ( $z$ ). Note that in equation (1), the effect on individual  $z$  is summed over all  $z_i$ . Consequently, the fitness of each individual is affected by all other individuals in the same habitat. We standardize the competition coefficients so that, for a focal individual  $i$ ,  $\alpha_{ii} = 1$  and  $0 < \alpha_{ij} < 1$  ( $z_i \neq z_j$ ). In equation (3),  $\sigma_a$  represents the strength of competition ('degree of niche separation') between individuals (given constant trait values). The larger  $\sigma_a$  is, the more neighbouring (in trait space) individuals negatively influence the fitness of the focal individual. When  $\sigma_a$  is small, competition occurs mainly between individuals with very similar trait values, which can be interpreted as a case of narrow ecological niches. Put another way, a small  $\sigma_a$  (relative to  $\sigma_K$ ) means there are many available niches within a single habitat.

To finish the reproduction phase, each individual produces a number of offspring drawn from a Poisson distribution with a mean equal to the individual's fitness (equations 1–3). Note that negative fitness values for any given individual, because of density dependence or maladaptation to its habitat, leads to zero offspring. Each offspring inherits the  $z$ -value of its parent, unless they mutate with a probability  $\mu$  ( $\mu = 10^{-3}$ ), to a slightly different trait value

from their parents (the deviation follows a normal distribution with zero mean and standard deviation of 0.02). After reproduction, the parent generation is discarded.

All offspring are born into the habitat of their respective parent, but disperse with a probability ( $d$ ) during the dispersal phase to one of the neighbouring habitats (stepping-stone dispersal; Fig. 1). Individuals in central habitats will disperse with probability  $d/2$  to one of the two possible neighbouring habitats, and individuals in the peripheral habitats will disperse with probability  $d$  in one direction only. The dispersal phase completes one generation (time step) and thereafter the reproduction–dispersal cycle is repeated.

### Simulations

At the beginning of each simulation, the middle habitat was seeded with ten optimally adapted,  $z = 0$ , individuals. Different model parameter combinations were simulated for 40,000 time steps in 100 replicates. The default settings in all runs, unless otherwise stated, were  $r = 1$ ,  $K_0 = 1000$ ,  $\sigma_K = 0.5$ ,  $\sigma_a = 0.2$ ,  $\Delta z_{\text{opt}} = 1$ , and  $d = 10^{-5}$ . The mutation process, with mutant traits close to their parents, together with the evolutionary process driven by the  $G$ -function, generated a clustered distribution of trait values along the trait axis (Fig. 2 and Fig. 3). All individuals with similar traits (no gaps  $> 0.1$  between traits of any two ‘neighbouring individuals’) and common ancestry were defined as a cluster (irrespective of in which habitat the individuals occur). Here, phenotypic trait values and ‘genotypes’ are the same and the clusters of genotypes we approximate to species. For each time step, the number of clusters and their mean trait value were registered; when a gap  $> 0.1$  in a cluster was detected, it was registered as a branching event (one cluster branching into two). We also registered extinctions, i.e. events when all individuals in a cluster went extinct because of low fitness, demographic stochasticity, or both. Note that cluster merging was not allowed – if two clusters converged in trait space, they were still considered as two distinct clusters due to their different origin. In other words, we tracked and registered adaptation (clusters travelling in trait space), speciation (branching points), and extinction in time and space. By calculating the generations past between branching points, we constructed a phylogeny of the extant species in the final metacommunity from the raw data created by the simulations.

### Phylogenetic analysis

We used the method described in Webb *et al.* (2008) to analyse the phylogenetic structure, here defined by the net relatedness index (NRI) value, of the simulated metacommunities. The NRI is based on the mean phylogenetic distance between all species in a local community compared with a null model that is randomly assembled from the global pool of available species. The NRI is defined as:

$$NRI = \frac{MPD_{\text{rndsample}} - MPD_{\text{sample}}}{sd(MPD_{\text{rndsample}})} \quad (4)$$

where  $MPD$  is mean phylogenetic distance (here measured in generations),  $sd$  denotes standard deviation, the subscript *sample* denotes values derived from the phylogenetic tree of the analysed local community, and *rndsample* denotes values derived from randomly assembled null model phylogenies. The null model used here (#2) constructs a random

phylogenetic tree by assigning species to the habitats by random draws from the phylogeny pool. Positive NRI-values indicate a clustered phylogeny where locally co-existing taxa are more related to each other than expected by chance. A negative NRI-value indicates an over-dispersed phylogeny where co-existing taxa are less related to each other than would be expected by chance. We also calculated the nearest taxon index [NTI (Webb *et al.*, 2008)] but the NTI-values were qualitatively similar to the NRI-values and not reported here.

We focus on two response variables, the phylogenetic structure within communities and differences in structure among communities. We measure the metacommunity phylogenetic clustering as the mean NRI-value taken across all local communities. The difference among communities, the metacommunity *heterogeneity*, is measured as the standard deviation (S.D.) of the local community NRI-values.

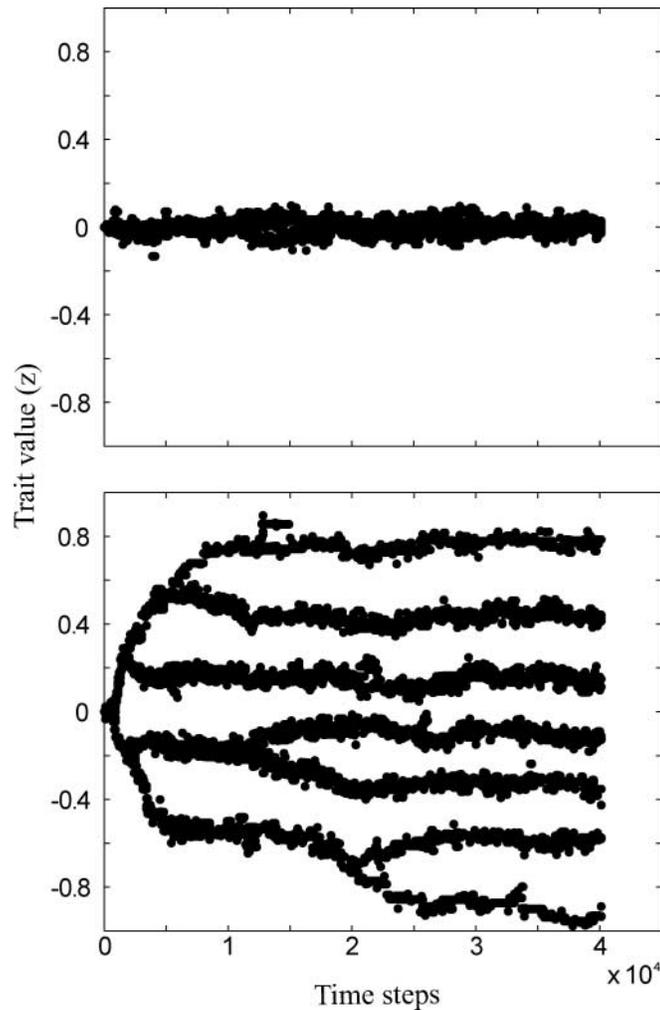
## RESULTS

The eco-evolutionary dynamics in our model is dictated by four critical parameters:  $\sigma_K$ , the breadth of the resource distribution in each habitat;  $\sigma_a$ , the width of the resource utilization function and therefore the strength of competition;  $\Delta z_{\text{opt}}$ , the distance (in trait space) between resource peaks and therefore the difference in resource distributions among habitats; and  $d$ , the dispersal rate. These parameters affect the system properties and ultimately metacommunity assembly processes. We also identify three main structuring processes that affect the community build-up: local adaptive radiation, colonization of unoccupied habitats, and invasion of already established communities. Below we first describe each of the processes and how they are dictated by the model parameters. Then, we present how each of the parameters affects phylogenetic community and metacommunity structure (NRI). We also describe the causal link between parameters of the model, system properties, processes, and phylogenetic patterns in a overarching framework.

### Major processes

#### *Local adaptive radiation*

A single phenotypic cluster will initially evolve to the peak of the resource distribution. Once there, however, it will experience disruptive selection due to heavy competition for the most utilized resources. Selection will favour phenotypes on alternate sides of the focal species trait (where unutilized resources may be available) and evolutionary branching may occur (Geritz *et al.*, 1998). The two emanating clusters will subsequently evolve to new points in trait space where further branching may occur, driven by the same mechanisms as described above. This local adaptive radiation can in this particular model continue *ad infinitum*, given infinite local population size. The limited population size of our simulations does, however, put an upper bound to local species richness. As the local number of species increases, the size of each population (species cluster) decreases and the disruptive selection becomes weaker. As a consequence, newly emerging clusters are prone to stochastic extinctions and evolutionary branching may be prohibited altogether (Johansson and Ripa, 2006; Claessen *et al.*, 2007; Johansson *et al.*, 2010). The parameter  $\sigma_a$  determines the strength of competition between individuals within a habitat. Compared with the width of the resource distribution,  $\sigma_K$ , this parameter can be viewed as representing niche width. If  $\sigma_a$  is larger than or close to  $\sigma_K$ , competition strength will be high even between individuals utilizing different ends of the



**Fig. 2.** Simulation output for one habitat only. When the ratio between  $\sigma_K$  and  $\sigma_a$  is close to one ( $\sigma_K = 0.5$  and  $\sigma_a = 0.47$ ), no branching will occur within the 40,000 time steps (top panel). When the ratio is large ( $\sigma_K = 0.5$ ,  $\sigma_a = 0.2$ ), branching is possible within the 40,000 time steps (bottom panel). Simulations are started with ten individuals with trait values equal to  $z_{\text{opt}} = 0$  and  $K_0 = 1000$ .

local resource spectrum. Consequently, there will only be room (in terms of niche space) for one species (phenotypic cluster) and no branching will occur in the local community (Fig. 2a). If, on the other hand,  $\sigma_a \ll \sigma_K$ , local evolutionary branchings are facilitated (Fig. 2b). This is a well-known result from adaptive dynamics (Geritz *et al.*, 1998; Dieckmann and Doebeli, 1999). In both cases in Fig. 2, the end community is not an ESS community (Brown and Vincent, 1987), i.e. the co-existing species are not positioned on peaks of the fitness landscape. Instead, they are ‘caught’ at branching points and branching is inhibited or much delayed due to demographic stochasticity. For our purposes, we regard them as evolutionary endpoints, although further diversification would be likely if population sizes were much larger.

*Colonization of unoccupied islands*

The fate of an individual dispersing to an empty habitat depends primarily on its fitness after arrival, which depends on how well its phenotype matches the local resource distribution. Such pre-adaptation is more likely if the difference between habitats is small (a small  $\Delta z_{\text{opt}}$ ) and/or the local resource distribution is large (a large  $\sigma_K$ ). In principle, the ratio between  $\Delta z_{\text{opt}}$  and  $\sigma_K$ , together with dispersal ( $d$ ), will determine the colonization rate of unoccupied islands. When  $\Delta z_{\text{opt}}$  is large in relation to  $\sigma_K$  (i.e. habitats are well separated in trait space), peripheral habitats will only be successfully colonized by individuals with trait values acquired through local adaptive radiation in neighbouring habitats, such that individuals from the most marginal species match the resource distribution in the receiving habitat. This typically takes some time (Fig. 3a). On the other hand, when  $\Delta z_{\text{opt}}$  is small compared with  $\sigma_K$ , the colonization will happen almost instantaneously (Fig. 3b). Species in the central habitat are pre-adapted to the peripheral habitats and colonization is less dependent on local ecology and radiation in the donor habitat (but may be dispersal limited).

*Invasion of established communities*

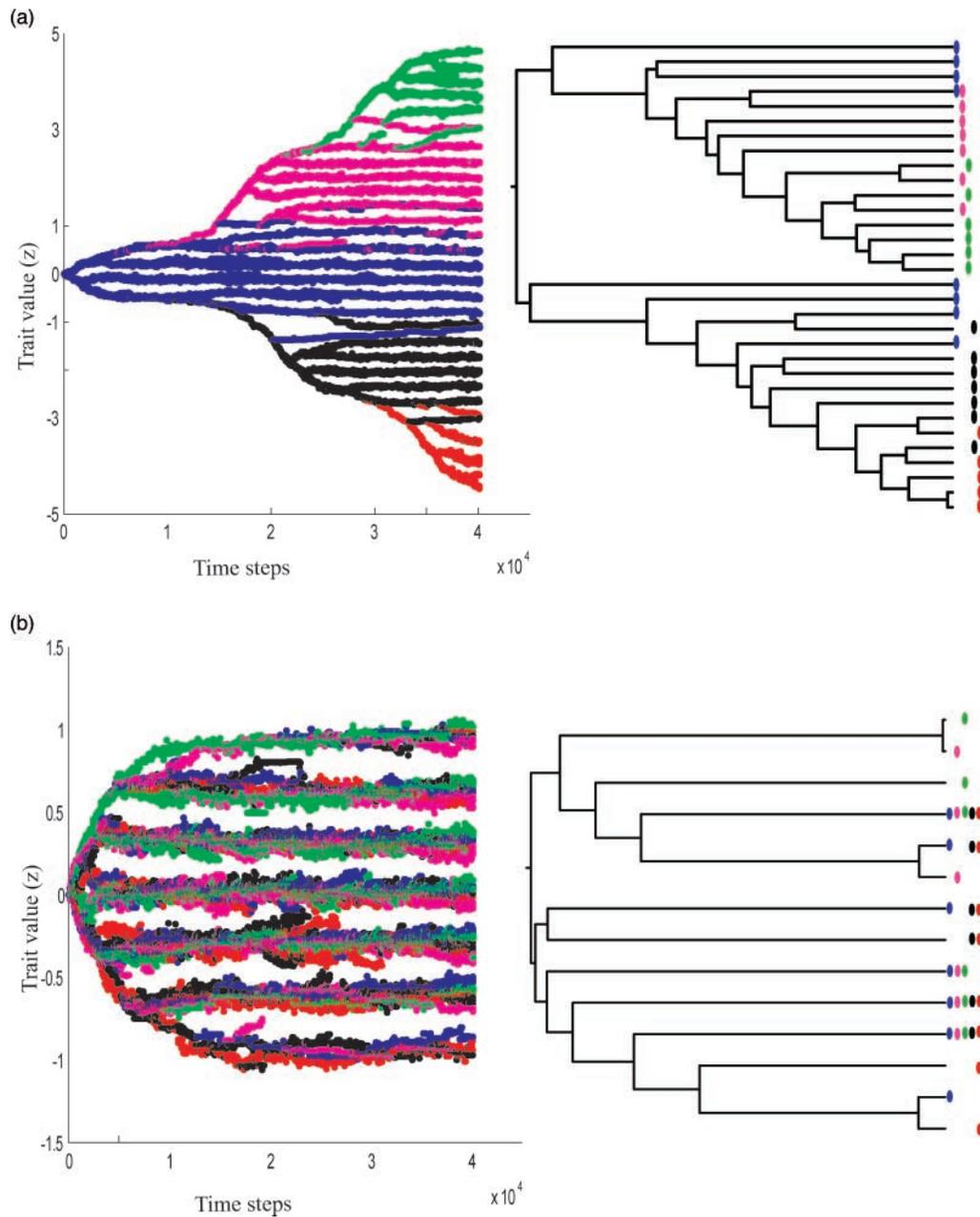
For an invasion to be successful, the migrating individual has to be pre-adapted, just like above, but there must also be niche space available in the receiving habitat. This is facilitated if there are many available local niches ( $\sigma_K/\sigma_a$  is high), although niche space will naturally be depleted as local species richness builds up – through local adaptive radiation or a succession of invasions. Dispersal also affects the invasion process, but if a species is not pre-adapted or if niche space is unavailable because of competition in the recipient habitat there will be no invasion, irrespective of the dispersal rate. Hence, the effect of dispersal is somewhat secondary and most pronounced when pre-adaptation is likely ( $\Delta z_{\text{opt}}/\sigma_K$  is low) and there is plenty of niche space within each habitat ( $\sigma_K/\sigma_a$  is high).

**Phylogenetic structure**

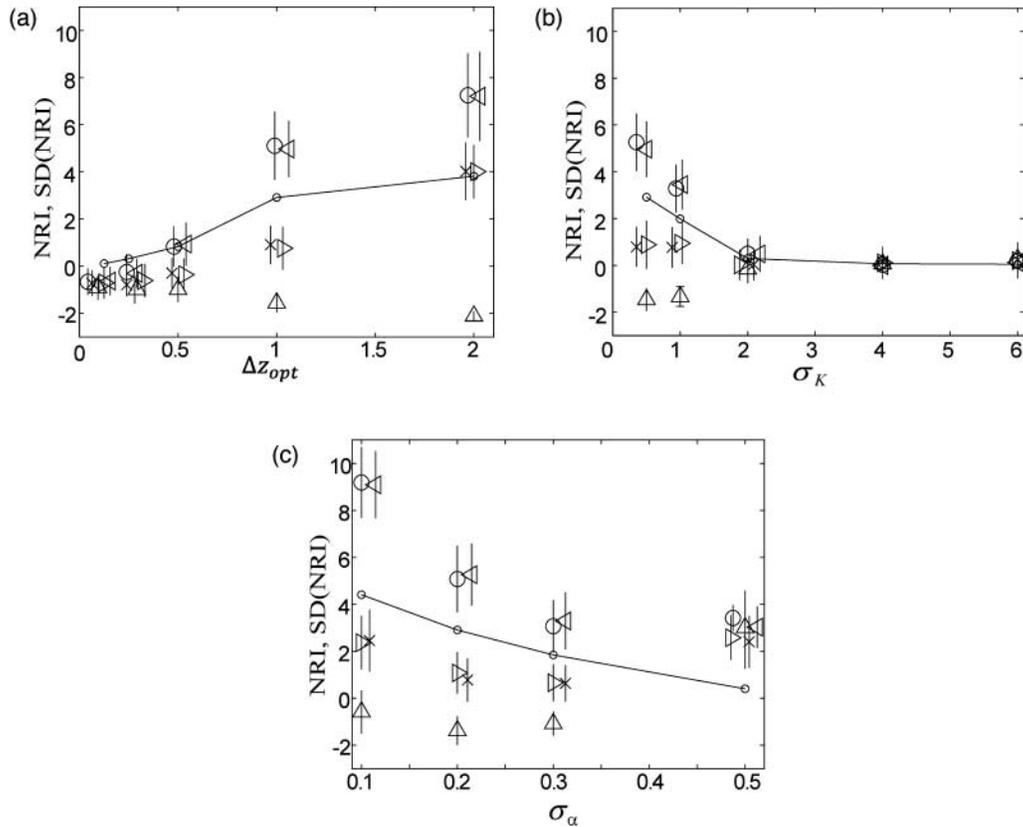
Before we present a more synthetic theory on how general system properties affect the degree of phylogenetic clustering, we present the effect of each main model parameter by itself. The difference between habitat resource peaks ( $\Delta z_{\text{opt}}$ ) has a major impact on the average degree of phylogenetic clustering (mean NRI) as well as the variation among local communities. Both increase as the habitat difference increases (Fig. 3, Fig. 4a). The large variation between local communities is due to the sequential pattern of an increasing degree of clustering in peripheral communities and an increasing degree of over-dispersion in the central community.

The width of the resource distributions ( $\sigma_K$ ) has the opposite effect (Fig. 4b). Mean metacommunity clustering decreases towards zero and the variation among communities decreases as  $\sigma_K$  increases. A higher  $\sigma_K$  increases the resource overlap between peripheral and central habitats, which promotes colonizations and invasions and thereby prevents phylogenetic clustering.

Competition strength ( $\sigma_a$ ) affects the structure in similar ways as the width of the resource distribution,  $\sigma_K$ , does. Mean clustering and among-habitat variation both decrease with increasing  $\sigma_a$  (Fig. 4c). Strong local competition, i.e. little available niche space, hampers local adaptive radiations as well as invasions from neighbouring habitats. At the



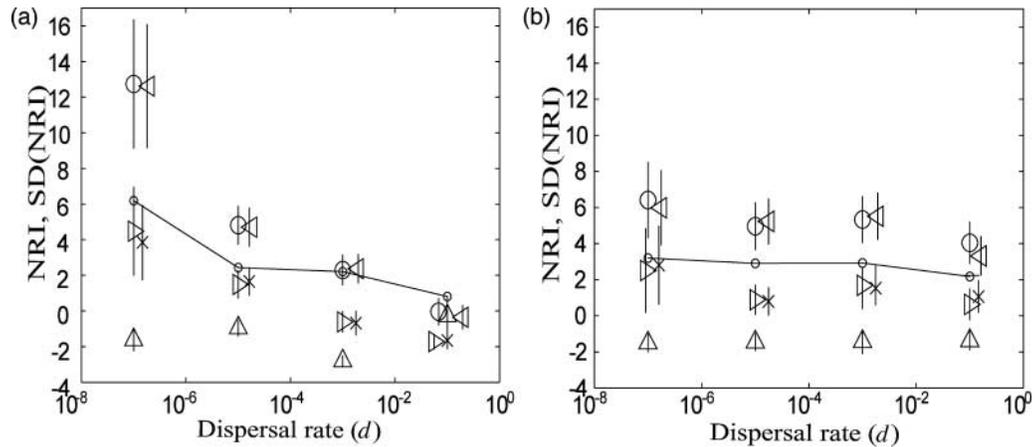
**Fig. 3.** Simulation output (left) with corresponding phylogenetic tree (right) for high (2 in (a)) and low (0.125 in (b))  $\Delta z_{\text{opt}}$ -values. Other parameters have default values ( $K_0 = 1000$ ,  $\sigma_K = 0.5$ ,  $\sigma_a = 0.2$ ). Each dot in the simulation output corresponds to an individual in time (x-axis) and trait space (y-axis) and colour indicates habitat occupancy. The phylogenetic tree is derived from extant clusters (group of individuals with continuously distributed  $z$ -values) after 40,000 time steps and their relatedness. Nodes and branch lengths in the tree are derived from branching points and time steps between branching points, respectively. Colour coding of leaves in the phylogeny denotes habitat occupancy.



**Fig. 4.** NRI (net relatedness index) values with error bars (s.d.) for the five habitats. Upright triangles denote the central habitats, circles and left-pointing triangles are the two most peripheral habitats, crosses and right-pointing triangles denote the semi-peripheral habitats. Small circles connected by black lines show the metahabitat heterogeneity defined by the standard deviation of the mean NRI for the five habitats. Points are binned and separated horizontally for clarity; clusters of points have the same x-value. Results for (a) varying  $\Delta z_{opt}$  (0.125, 0.25, 0.5, 1, and 2), (b) varying  $\sigma_K$  (0.5, 1, 2, 4, and 6), and (c) varying  $\sigma_\alpha$  (0.1, 0.2, 0.3, and 0.5). Other parameters have default values ( $\sigma_\alpha = 0.2$ ,  $\sigma_K = 0.5$ , and  $\Delta z_{opt} = 1$ ).

same time, colonizations of empty habitats occur with roughly the same rate. The total effect is a slightly decreased average level of clustering but a marked homogenization across habitats – they are all colonized relatively early in the phylogeny.

As indicated above, the effect of dispersal rate ( $d$ ) is subordinate to other parameters. In some parts of parameter space an increased rate of dispersal has an effect, whereas in other parts there is no effect (Fig. 5). When dispersal does have an effect, it decreases mean phylogenetic clustering and community variation (Fig. 5a). The central community is over-dispersed regardless of dispersal rate, while the peripheral community structure tends towards random or slight over-dispersion as dispersal rate increases.

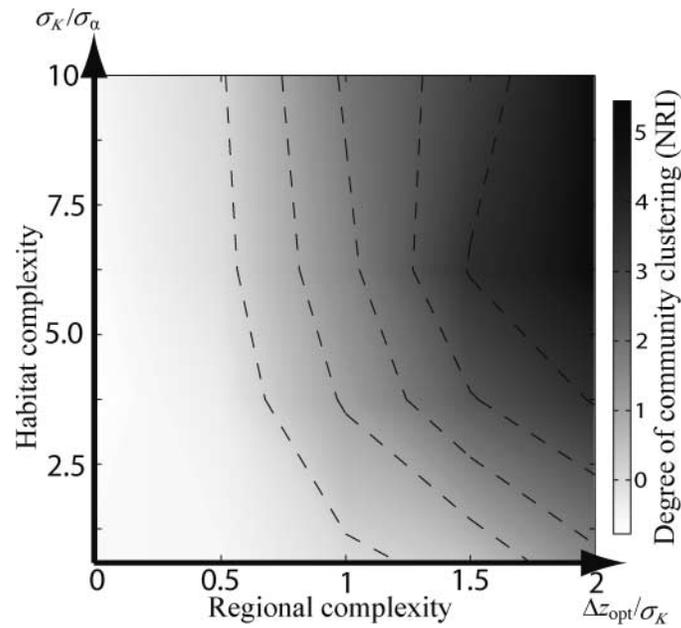


**Fig. 5.** NRI (net relatedness index) values with error bars (s.d.) for the five habitats. Upright triangles denote the central habitats, circles and left-pointing triangles are the two most peripheral habitats, crosses and right-pointing triangles denote the semi-peripheral habitats. Small circles connected by black lines show the metahabitat heterogeneity defined by the standard deviation of the mean NRI for the five habitats. Points are binned and separated horizontally for clarity; clusters of points have the same x-value. Dispersal varies between  $10^{-7}$  and  $10^{-1}$  with increments of  $10^2$ . (a) Other parameter values are fixed at  $\sigma_a = 0.2$ ,  $\sigma_K = 2$ , and  $\Delta z_{opt} = 2$ . (b) Other parameters fixed at default values ( $\sigma_a = 0.2$ ,  $\sigma_K = 0.5$ , and  $\Delta z_{opt} = 1$ ).

### Synthesis

Dispersal aside, three main parameters dictate the tendency towards phylogenetic clustering or over-dispersion: the width of the local competition kernel,  $\sigma_a$ , the width of the resource distributions,  $\sigma_K$ , and the difference in the location of the resource distribution in the habitats,  $\Delta z_{opt}$ . These parameters are measured in the same unit and should be considered in relation to each other. First, the quotient  $\Delta z_{opt}/\sigma_K$  is a measure of habitat differences. If the locations of the resource peaks are close to each other ( $\Delta z_{opt}$  small) and the width of the resource distributions large (high  $\sigma_K$ ), the habitats are similar. The reverse is of course true if  $\Delta z_{opt}/\sigma_K$  is large. This quotient can thus be interpreted as spatial heterogeneity at the regional scale (across all habitats) and we define it as *regional complexity*. Second, the quotient  $\sigma_K/\sigma_a$  is a measure of the amount of available niche space within a habitat, as argued above. We therefore think of it as a measure of *habitat complexity*.

In Fig. 6 we illustrate how the phylogenetic structure of the metacommunity is affected by these system characteristics. High degrees of phylogenetic clustering are found when both regional and habitat complexities are high. If the regional complexity is high, colonization is more difficult, but once it has occurred, the local habitat will be dominated by closely related species that have evolved *in situ*. If the habitats are similar (low regional complexity) and there is little room for local radiation, phylogenetic clustering is less likely (lower left-hand corner in Fig. 6). Notably, the non-monotonic increase in the degree of clustering towards the upper right corner of parameter space (Fig. 6) implies that the major assembly processes presented above are non-linear functions of habitat- and regional-complexity. Note also that the degree of clustering illustrated in Fig. 6 represents mean values across all



**Fig. 6.** A graphical summary illustrating our conceptual understanding of the link between model parameters and model system properties. The quotient  $\Delta z_{\text{opt}}/\sigma_K$  is the regional complexity (x-axis). The quotient  $\sigma_K/\sigma_a$  is the habitat complexity (y-axis). The contours indicate the mean degree of phylogenetic clustering (NRI value) across all habitats.

habitats and that individual habitats can be more or less clustered under the same regional and habitat complexities (cf. Fig. 4).

## DISCUSSION

Phylogenetic clustering and over-dispersion have been associated with ‘habitat filtering’ and ‘competitive exclusion’, respectively (for original discussion, see Webb *et al.*, 2002). If species through their close phylogenetic relatedness share relevant ecological traits, habitat filtering may dictate a community to contain a subset of closely related species from the available pool as specific traits are required in a particular environment. On the other hand, since shared traits (through close relatedness) implies ecological similarity, this subset of species should not co-exist because of competitive exclusion. The very same positive coupling between relatedness and ecological similarity would consequently lead to two opposing predictions (or grounds for explanation of observed patterns). Here we show how the contradicting predictions can be reconciled in a general framework for the link between the attributes of the metacommunity and the phylogenetic signal (Fig. 6). For example, Fig. 6 shows how relatively strong competition (close to the origin along the y-axis) can lead to weakly or rather strongly clustered metacommunities by moving along the axis of regional complexity (the x-axis). Local and regional complexity affects the phylogenetic structure in concert and on a continuous scale supporting earlier argumentation about phylogenetic structure in a spatiotemporal eco-evolutionary context (Cavender-Bares *et al.*, 2004; Swenson *et al.*, 2006; Emerson and

Gillespie, 2008; Vamosi *et al.*, 2009). Our results, although derived more formally, are also consistent with the dual role of competitive exclusion suggested by Mayfield and Levine (2010).

Our interpretations of the results in Fig. 4 and the theoretical formulization presented here hinge on our understanding of the relative role of different assembly processes during different biotic and abiotic circumstances. We identify three major processes – local radiation, colonization, and invasion – that determine the phylogenetic community structure. We conclude that colonization and invasion are negatively related to regional complexity and that local radiation is positively related to local habitat complexity. This is supported by empirical studies showing that island size (Losos and Schluter, 2000) and habitat heterogeneity (Hobohm, 2000; Roos *et al.*, 2004; Hughes and Eastwood, 2006) are positively related to local radiation rate. Also, when interpreted in relation to migration (colonization and invasion), local radiation rate explains community and metacommunity diversification (Losos and Schluter, 2000; Hughes and Eastwood, 2006).

The decreased clustering with increased dispersal rate (Fig. 5a) shows that physical distance between habitats in itself can affect the metacommunity structure. This underscores the fact that phylogenetic analysis is highly scale-dependent and that organisms, having different dispersal propensity, are structured at different geographical scales. Notably, the effect of dispersal on structure is, however, restricted to specific parts of parameter space. This is a possible explanation of the absence of an effect of dispersal on phylogenetic structure in empirical research (reviewed in Vamosi *et al.*, 2009).

Similar to our results, Kembel and Hubbell (2006) found wide variation in phylogenetic structure in plant communities among habitats. These results were mainly interpreted in an ecological framework of habitat filtering and competitive exclusion. Although we do not refute these interpretations, our data invite additional explanations to variation in structure among communities. Our results show that although different local communities have assembled under identical local ecological circumstances, some may be over-dispersed while others are clustered (Fig. 4). We conclude that habitats can be structured by evolutionary processes and historical biogeographical contingencies. When successful colonization- and invasion-events are rare, because of, for example, physical distance or abiotic differences, and local radiation rate is high, newly established communities are clustered because of the high internal relatedness (compared with other species in the metacommunity). Along the same lines of explanation, old and fully diversified communities will be over-dispersed. To this end, it is important to consider also the effects that an evolutionarily dynamical species pool and its adaptive radiation process may have on local community structure. Typically, phylogenetic structure analysis assumes a fixed global or regional species pool. This assumption may be appropriate when studying small local communities that have a negligible effect on its surroundings. However, in a metacommunity where local habitats are connected by dispersal, local structure will also be affected by the evolutionary trajectory of the regional or global species pool. Consequently, the variation among local communities does not necessarily mean that different assembly processes have structured the communities. Rather, the temporal scale of the adaptive radiation process of both the local and global community and historical biogeography may explain the patterns.

There have been attempts to model the evolution of metacommunities (e.g. McPeck, 2007; Stegen and Hurlbert, 2011). Those studies, however, aimed to answer questions about species diversity and co-existence. Also, in contrast to McPeck (2007), who use predefined parameters for speciation, and Stegen and Hurlbert (2011), who use parameters for environmental filtering and successful dispersal, we model metacommunity evolution by individual-based

ecological dynamics. We make no assumptions about the evolutionary lability of traits, speciation rate, successful migrations or species distribution in space or time. Similar to McPeck (2007), we assume that resources are distributed in space, resources differ between habitats, organisms utilize resources according to their traits, and individuals compete according to trait similarity and niche width. The habitats are reasonably distinct and there is stepping-stone dispersal between them. The model organisms are explicitly defined by their ability to utilize resources and their ecological interactions. The density-dependent competition for resources determines fitness, which in turn dictates the rate of adaptation, local radiation, and patterns of local and global co-existence. Our simulations allow for stochastic demographic effects, especially when population sizes are small and the fitness landscape is shallow (see, for example, Ripa *et al.*, 2009). Consequently, all relevant processes considered important in community assembly (Vellend, 2010) are subsumed in our approach. In addition, our approach encompasses differences in habitat and regional heterogeneity, properties that affect metacommunity assemblages (Hanski and Gaggiotti, 2004; Holt, 2005; Holyoak *et al.*, 2005). We do not, however, consider a range of realistic complications such as environmental stochasticity, explicit genetic mechanisms, sexual reproduction, age structures or trophic interactions. In addition, multiple traits, possibly with various trade-off structures, are most likely involved in the determination of co-existence and adaptive radiation in most systems (Leimar, 2009). Despite these simplifications, we argue that the model used here captures the link between properties of a system and the processes that determine phylogenetic structure, and that our results will help empiricists to evaluate data, considering ecological processes, evolutionary contingencies, and biogeography.

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