

LETTER

Predicting rates of interspecific interaction from phylogenetic trees

Scott L. Nuismer* and Luke J. Harmon

Department of Biological Sciences
Institute for Bioinformatics and
Evolutionary Studies (IBEST)
University of Idaho Moscow, ID,
USA

*Correspondence:

E-mail: snuismer@uidaho.edu

Abstract

Integrating phylogenetic information can potentially improve our ability to explain species' traits, patterns of community assembly, the network structure of communities, and ecosystem function. In this study, we use mathematical models to explore the ecological and evolutionary factors that modulate the explanatory power of phylogenetic information for communities of species that interact within a single trophic level. We find that phylogenetic relationships among species can influence trait evolution and rates of interaction among species, but only under particular models of species interaction. For example, when interactions within communities are mediated by a mechanism of phenotype matching, phylogenetic trees make specific predictions about trait evolution and rates of interaction. In contrast, if interactions within a community depend on a mechanism of phenotype differences, phylogenetic information has little, if any, predictive power for trait evolution and interaction rate. Together, these results make clear and testable predictions for when and how evolutionary history is expected to influence contemporary rates of species interaction.

Keywords

Coevolution, competition, macroevolution, mutualism, phylogenetic tree, trait evolution.

Ecology Letters (2015) 18: 17–27

INTRODUCTION

It is now widely accepted that ecology depends, at least in part, on the evolutionary history of interacting species as well as their ongoing evolution (Schoener 2011). Although efforts to understand the role ongoing evolution plays in ecology can capitalise on experimental techniques (Yoshida *et al.* 2003; Hairston *et al.* 2005; Friman *et al.* 2014), evolution's historical importance must frequently be discerned through integration of phylogenetic information (Webb *et al.* 2002; Mouquet *et al.* 2012; Cadotte *et al.* 2013). As phylogenies have become increasingly available at the scale of entire ecological communities, studies have begun to explore the extent to which evolutionary history explains ecological processes and patterns (Ives & Godfray 2006; Rezende *et al.* 2007; Verdu & Valiente-Banuet 2011; Rafferty & Ives 2013; Hadfield *et al.* 2014). This emerging framework of ecophylogenetics has now been used to study the extent to which phylogenetic trees can help predict community assembly (Kembel 2009; Cadotte *et al.* 2013), the structure of interaction networks (Rezende *et al.* 2007) and even ecosystem function (Cadotte *et al.* 2009; Srivastava *et al.* 2012). However, we still lack a mechanistic, process-based framework for predicting when phylogenies will have explanatory power. In other words, when will knowing the phylogenetic history of taxa add to our understanding of contemporary ecological and evolutionary processes, and when will it not?

Although ecophylogenetic analyses have been quite successful in many cases, they generally rely on statistical or phenomenological models to merge ecological and phylogenetic information. For instance, Ives & Godfray (2006) developed a

statistical approach for estimating the extent to which variation in the strength of host–parasitoid interactions can be explained by the phylogenies of the interacting species. This approach, and subsequent variations and extensions (e.g. Rezende *et al.* 2007; Rafferty & Ives 2013; Hadfield *et al.* 2014), assume phylogenetic trees have predictive power because they capture patterns of species' similarity and differences in some suite of unknown traits that influence species interactions (Webb *et al.* 2002; Ives & Godfray 2006; Mouquet *et al.* 2012; Rafferty & Ives 2013). Put differently, such approaches rely on 'phylogenetic signal' in species' traits – close relatives are more phenotypically similar for key traits than distant ones (Blomberg *et al.* 2003). However, empirical studies of trait evolution on trees suggest that traits vary tremendously in their phylogenetic pattern, with some traits showing close correlations between trait distance and phylogenetic distance, and others showing weak or no relationships between these metrics (Blomberg *et al.* 2003; Harmon *et al.* 2010). In addition, phylogenetic signal has proven to be a slippery concept (Losos 2008), with weak or no connection to any particular ecological process (Revell *et al.* 2008). These statistical approaches can be useful as predictive tools. However, their reliance on phylogenetic signal may be misplaced if species interactions have driven the evolution of the traits mediating contemporary ecological interactions.

Developing a more comprehensive understanding of the conditions under which phylogenetic information has explanatory power requires a unification of studies of trait evolution, community ecology and phylogenetics (McGill *et al.* 2006; Ives & Helmus 2011; Mouquet *et al.* 2012; Cadotte *et al.* 2013; Pillar *et al.* 2013). To date, such a synthesis has proven

difficult, and there is currently only a tenuous connection between common metrics of community phylogenetics (e.g. phylogenetic diversity, phylogenetic community structure and phylogenetic signal) and the processes that occur in evolving communities. As a particular example, consider *Anolis* lizards, perhaps one of the most famous examples of adaptive radiation (Losos 2009). Species interactions among anoles involve, among other things, competition for perch sites (Williams 1972). These ecological interactions, in turn, influence evolution of limb length (and other traits) in anoles (Losos 2009), and macroevolutionary studies suggest competitive interactions have had a strong influence on the macroevolutionary patterns of divergence across anole species (Mahler *et al.* 2010; Rabosky & Glor 2010). Despite all this, most phylogenetic comparative studies of trait evolution in anoles use a model of trait evolution that assumes that change along each branch of a phylogenetic tree is independent of change along every other branch (e.g. Brownian motion, Ornstein–Uhlenbeck or early-burst models; see below for more details). In other words, even in clades like anoles, where there is wide agreement that species interactions affect evolution, macroevolutionary models of species' traits do not account for ecological interactions.

Our goal here was to quantify the circumstances under which phylogenies will have explanatory power for predicting interaction rates and ecosystem functioning. In particular, we develop and analyse mathematical models that move beyond phylogenetic signal to explore how specific ecological and evolutionary mechanisms influence the role evolutionary history plays in contemporary community ecology. To this end, we merge established models of ecological interaction and coevolution (e.g. Roughgarden 1996; Gavrillets 1997; Nuismer *et al.* 2013), with existing models of trait evolution on phylogenetic trees (Hansen & Martins 1996; Hansen 1997). We then use these models to address a set of three key questions that link phylogenetic trees, coevolution and contemporary rates of species interaction: (1) Does the topology of the phylogenetic tree connecting interacting members of a community influence interaction rates? (2) Is the influence of phylogenetic distance on interaction rates the same for different types of species interactions? (3) Is the functional relationship between traits of interacting species an important determinant of whether or not phylogenetic distance matters? Answering these specific questions will allow us to evaluate when and where phylogenies matter for predicting the level of ecological interactions among species.

MODEL DESCRIPTION AND ANALYSIS

Predicting interaction rates for communities of related species

We begin by developing a model describing the interactions that occur among n species within a community. We will then extend this model so that the n species evolve along the branches of a phylogenetic tree. These n species are assumed to belong to a single trophic level or guild, such that all interactions among community members are of the same ecological form (e.g. all competition, or all mutualism). We assume individuals encounter a single individual within each discrete and

non-overlapping generation. This encountering individual is chosen at random from within the community and can thus be from the same species or from a different species. The probability that any particular encounter imposes fitness consequences on the focal individual depends on trait values. Specifically, we assume the fitness outcome of encounters depends on a single key trait (such as body size, beak shape, coloration or phenology). Effects on the fitness of the focal individual are positive for mutualistic interactions and negative for competition models.

We will consider two different functional relationships between the traits of interacting individuals and the probability the encounter results in fitness consequences: phenotype matching and phenotype differences. These two functional forms of interaction have been widely used in coevolutionary models (e.g. Abrams 2000; Nuismer *et al.* 2013) and demonstrated to be relevant for a variety of species interactions. Although both types of interactions can apply both across and within a trophic level, here we focus on interactions within a single trophic level. For interactions mediated by a mechanism of phenotype matching, the probability, P_{ij} , that an encounter has fitness consequences declines as the phenotypes of the individuals become more dissimilar:

$$P_{ij} = \text{Exp}\left[-\alpha(z_i - z_j)^2\right] \quad (1)$$

In eqn 1, α measures the effect of individual phenotypes, z_i and z_j , on the outcome of encounters between individuals. Specifically, if α is small, individual phenotype matters little for the outcome of interactions; if α is large, however, the outcome of interactions is very sensitive to individual phenotypes. Examples of interactions mediated by a mechanism of phenotype matching include Mullerian mimicry in *Heliconius* butterflies (Kapan 2001) and resource competition in *Anolis* lizards (Losos 2009).

In contrast to phenotype matching, interactions mediated by phenotype differences are more likely to have fitness consequences when the phenotype of one individual exceeds that of the other:

$$P_{ij} = \frac{1}{1 + \text{Exp}[\alpha(z_i - z_j)]} \quad (2)$$

As stated earlier, α measures the importance of individual phenotypes, z_i and z_j , for the outcome of encounters between individuals. Examples of interactions mediated by a mechanism of phenotype differences include body size in situations where the larger individual in any particular contest tends to win, such as competing species of fig wasp (Moore *et al.* 2008), and competition among plant species mediated by herbivore resistance (Koricheva *et al.* 2004; Agrawal & Fishbein 2008).

With functions describing how the traits of individuals influence their probability of interaction in hand, we can proceed to predict the rate of interaction between any two species i and j given some statistical distribution of trait values for the two species. Before moving forward, however, we make two key assumptions. First, we assume the parameter α is sufficiently small for eqns 1 and 2 to be accurately approximated by their first-order Taylor series expansions

(Nuismer *et al.* 2013). Second, we assume that interactions among all species within the community are mediated by the same phenotypic mechanism (i.e. phenotype matching or phenotype differences) and that α is constant across all possible pairs of interacting species. With these assumptions, and our earlier assumption of random encounters, the expected rate of interaction between any two species i and j , $\bar{P}_{i,j}$, is as follows:

$$\bar{P}_{i,j} = f_i f_j \left(1 - \alpha (\bar{z}_i - \bar{z}_j)^2 - \alpha (\sigma_{z_i}^2 + \sigma_{z_j}^2) \right) \quad (3a)$$

for phenotype matching and:

$$\bar{P}_{i,j} = f_i f_j \left(\frac{1}{2} - \frac{\alpha}{4} (\bar{z}_i - \bar{z}_j) \right) \quad (3b)$$

for phenotype differences (see supporting online material for full derivation). In these expressions, f_i and f_j are the frequencies of the two species within the community, \bar{z}_i and \bar{z}_j are the population mean phenotypes for the two species, and $\sigma_{z_i}^2$ and $\sigma_{z_j}^2$ are the within-population phenotypic variance for each of the two species.

Often, gathering the information required to apply (3) to real communities with large numbers of species will be prohibitively costly, labour intensive, or impossible because we do not know the key traits responsible for the outcome of interactions or their statistical distribution within the interacting populations. For this reason, indirect techniques that use phylogenetic information as a surrogate have become a popular alternative. In order for phylogenetic information to be used, we must first express contemporary rates of interaction as a function of a statistical distribution of trait values within a community of related species. This statistical distribution defines the likelihood that various combinations of traits have evolved, and depends upon the forces that have driven trait evolution over the history of the community. For the time being, we will calculate expected rates of interaction without specifying the details of the trait distribution itself. When interactions are mediated by phenotype matching, the expected rate of interaction between any species i and j is as follows:

$$\hat{P}_{i,j} = f_i f_j \left(1 - \alpha (\mu_i - \mu_j)^2 - \alpha (\sigma_{\bar{z}_i}^2 + \sigma_{\bar{z}_j}^2 - 2\sigma_{\bar{z}_i, \bar{z}_j}) - \alpha (\sigma_{z_i}^2 + \sigma_{z_j}^2) \right) \quad (4a)$$

and when interactions are mediated by phenotype differences it is as follows:

$$\hat{P}_{i,j} = f_i f_j \left(\frac{1}{2} - \frac{\alpha}{4} (\mu_i - \mu_j) \right) \quad (4b)$$

(see supporting online material for full derivation). In eqns (4), μ_i and μ_j are the expected population mean phenotypes for species i and j , $\sigma_{\bar{z}_i}^2$ and $\sigma_{\bar{z}_j}^2$ are the variances in population mean phenotypes for species i and j , and $\sigma_{\bar{z}_i, \bar{z}_j}$ is the covariance among population mean phenotypes for species i and j , all taken over evolutionary replicates. These quantities can be calculated from a known phylogeny using any number of popular models of phenotypic evolution (e.g. Brownian motion, Ornstein–Uhlenbeck and others; see below for worked examples). In contrast, the frequencies of the species within the

community, f_i and f_j , the phenotypic variances of the species, $\sigma_{z_i}^2$ and $\sigma_{z_j}^2$, and the sensitivity of the interaction to phenotypes, α , must be directly measured if quantitative prediction of interaction rates is the goal.

In addition to predicting the rate of interaction between any pair of species i and j , eqns (4) can be used to predict the overall rate of interaction within the community by averaging interactions across all pairs of species. For communities where interactions are primarily mediated by a mechanism of phenotype matching, the overall rate of interaction within a community is as follows:

$$\bar{\bar{P}} = \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \left(f_i f_j \left(1 - \alpha (\mu_i - \mu_j)^2 - \alpha (\sigma_{\bar{z}_i}^2 + \sigma_{\bar{z}_j}^2 - 2\sigma_{\bar{z}_i, \bar{z}_j}) - \alpha (\sigma_{z_i}^2 + \sigma_{z_j}^2) \right) \right) \quad (5a)$$

where all variables are defined as above and the double summation represents an expectation taken over all possible species pairs within the community (see supporting online material for full derivation). For communities where interactions are primarily mediated by a mechanism of phenotype differences the overall rate of interaction within the community is as follows:

$$\bar{\bar{P}} = \frac{1}{2} \quad (5b)$$

(see supporting online material for full derivation).

Expressions (4–5) provide an immediate and valuable insight into the role phylogenetic information plays in shaping contemporary rates of interaction within communities. Specifically, expression (5b) reveals that the overall rate of interaction within communities where phenotype differences predominates will be completely independent of phylogeny – that is, eqn 5b contains no terms that depend on the shape of the phylogenetic tree and, in particular, species' trait variances and covariances. The simple reason is that for every species that performs well in interactions there must, by definition, be a species that performs poorly. To take a concrete example, if competition is mediated by body size such that large species are superior competitors to small species, large species will experience reduced rates of interaction/competition, whereas small species will experience increased rates of interaction/competition. These positive and negative impacts on interaction rate exactly cancel each other out when averaged over all species within the community. As a consequence, the expectation is that phylogenetic relationships play no role in determining overall rates of interaction when interactions depend on a mechanism of phenotype differences. In contrast, for pairwise rates of interaction, or overall rates of interaction in communities where phenotype matching predominates, the pattern of evolutionary relationships among species may have predictive power through its influence on the quantities μ_i , $\sigma_{\bar{z}_i}^2$, and $\sigma_{\bar{z}_i, \bar{z}_j}$. To move beyond this qualitative statement, we next develop evolutionary models of phenotypic evolution that predict how these quantities have been shaped by various evolutionary processes. Once these models have been specified, we can provide robust conclusions about the

potential importance of evolutionary history in shaping contemporary rates of interaction, and, consequently, the role that phylogenetic trees can play in predicting patterns of species interactions in communities.

Phylogenetic trees, trait evolution and interaction rate

The most widely used methods for modelling the evolution of species' traits on phylogenetic trees assume Brownian motion, which can result from random genetic drift (Felsenstein 1973), or an Ornstein–Uhlenbeck process, which can result from a combination of random genetic drift and stabilising selection (Lande 1976). It is worth mentioning that evolution can follow either a BM or an OU model under a wide range of other scenarios [e.g. BM from selection that varies randomly from one generation to the next; OU reflecting the movement of peaks on an adaptive landscape; see Hansen & Martins (1996) and Hansen (1997) for a more in-depth discussion]. In the next sections, we will derive results for predicting species interactions when species evolve along the branches of a phylogenetic tree according to these two simple models of evolution. In the final section of the study, we will move beyond these simplifications and derive results for a model where species do not evolve independently, but instead coevolve over the evolutionary history of the clade.

Evolution by random genetic drift (Brownian motion)

We next consider the expected pattern of species interaction rates when traits evolve along the branches of the tree according to genetic drift (following a Brownian motion model). Under this scenario, we can use expressions (4) to predict the expected rate of interaction between any pair of species i and j . For the model of phenotype matching, the predicted rate of interaction is as follows:

$$\hat{P} = f_i f_j \left(1 - 2\alpha \frac{G}{N} (\tau - t_{i,j}) - \alpha (\sigma_{z_i}^2 + \sigma_{z_j}^2) \right) \quad (6a)$$

and for the model of phenotype differences it is as follows:

$$\hat{P} = \frac{f_i f_j}{2}. \quad (6b)$$

where G is the additive genetic variance, N is population size, τ is the total amount of time from clade origin to present and $t_{i,j}$ is the time from clade origin to the most recent common ancestor of i and j (see supporting online material for full derivation).

Comparing (6a) and (6b) reveals that the scope for phylogeny and shared ancestry to influence rates of interaction differs substantially depending on the mechanistic basis of interactions. This is because the rate of interaction between any pair of species within communities structured by a mechanism of phenotype matching depends on the phylogenetic tree, and in particular, on the time since their most recent common ancestor, $\tau - t_{i,j}$. Specifically, the expected rate of interaction between any pair of species i and j inevitably decreases with their evolutionary divergence. Thus, for a mechanism of phenotype matching, we expect rates of interaction to be higher between more closely related pairs of species (Fig. 1). In contrast, the rate of interaction in communities structured by a mechanism of phenotype differences is independent of branch lengths (no $t_{i,j}$ terms) and thus independent of the details of phylogenetic relatedness; only the relative frequencies of the species within the community matters.

If interactions within a community are mediated by a mechanism of phenotype matching, we can also predict how phylogeny will influence the overall rate of interaction (if interactions depend on phenotypic differences we already saw that phylogeny has no explanatory power). Specifically, when trait means evolve through a process of Brownian motion, eqn 5a predicts that the overall rate of interaction will be:

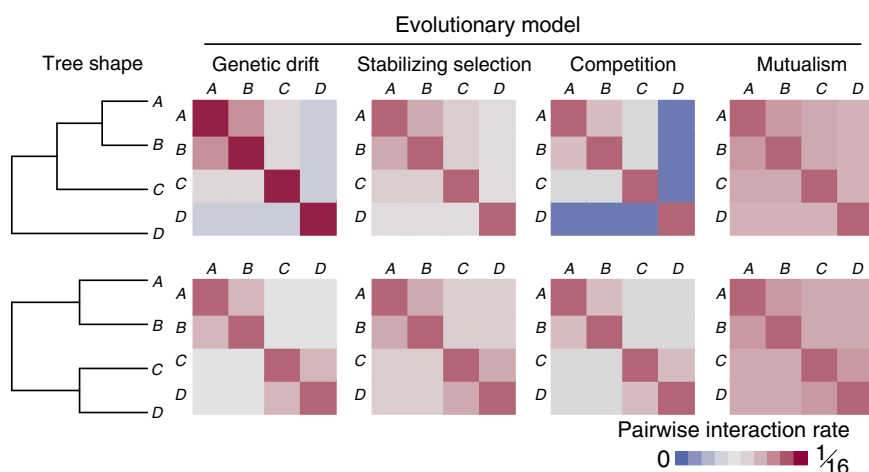


Figure 1 Interaction rates between all possible pairs of species within a four species community {A, B, C, D} for two alternative phylogenetic trees, one pectinate (top row) and one balanced (bottom row) and four different models of evolution/coevolution (columns). The shortest branch lengths for each tree were 10 000 generations, with longer branches multiples of 10 000 generations as needed to render the trees ultrametric. All evolutionary/coevolutionary models used the following parameters: $G = 1$, $N = 1000$, $\sigma_{z_i}^2 = \sigma_{z_j}^2 = 1$, $\alpha = 0.01$, and $z_0 = 10$. For the Ornstein–Uhlenbeck, Mutualism and Competition models, $\gamma = 0.00001$ and $\theta = 10$. For the Mutualism model $S = 0.00003$ and for the Competition model $S = -0.00003$.

$$\bar{P} = \sum_{i=1}^n \sum_{j=1}^n \left(f_i f_j \left(1 - 2\alpha \frac{G}{N} (\tau - t_{ij}) - \alpha (\sigma_{z_i}^2 + \sigma_{z_j}^2) \right) \right) \quad (7)$$

This result shows that overall rates of interaction will depend on the structure of the phylogenetic tree, and in particular will be greatest in communities within which species have originated recently (Fig. 2). We see this effect for both the total age of the clade and the relative timing of speciation events within clades; both young clades and old clades that have young subclades show high interaction rates. Biologically this occurs because genetic drift, on average, increases the phenotypic distance between any two species over evolutionary time which, for interactions mediated by phenotype matching, reduces the overall rate of interaction. Thus, if most species have originated recently, their phenotypes will be similar to one another having not yet diverged because of genetic drift. In addition, eqn 7 reveals an interaction between the relative abundance of species and the time since speciation. Specifically, overall rates of interaction within a community will be greatest when pairs of the most numerically abundant species (i.e. those with a high frequency f_i and f_j) are closely related (small $\tau - t_{ij}$).

Evolution by genetic drift and stabilising selection (Ornstein–Uhlenbeck)

We next consider predictions for species interactions when the trait mediating interactions within the community evolves in response to random genetic drift and stabilising selection (e.g.

following an OU model). We can again use expressions (4) to predict the expected rate of interaction between any pair of species i and j . For the model of phenotype matching, the predicted rate of interaction is as follows:

$$\hat{P} = f_i f_j \left(1 - \alpha G \left(\frac{(1 - \text{Exp}[-2\psi(\tau - t_{ij})])}{N\psi} \right) - \alpha (\sigma_{z_i}^2 + \sigma_{z_j}^2) \right) \quad (8a)$$

and for the model of phenotype differences it is as follows:

$$\hat{P} = \frac{f_i f_j}{2} \quad (8b)$$

where $\psi = 2\gamma G$ and measures the strength of stabilising evolution (see supporting online material for full derivation). Although significantly more complex than the expressions we derived for random genetic drift alone, eqns 9 tell a similar story about the interaction between phylogeny and interaction rates: phylogeny has predictive power for only those communities where a mechanism of phenotype matching predominates. In these cases, interaction rates are again expected to be highest for pairs of species that have recently diverged (Fig. 1). This result can be easily seen by noting that (8a) is maximised when the quantity $(\tau - t_{ij}) = 0$ and declines as this quantity increases.

As stated earlier, we can also study how the overall rate of interaction within a community dominated by phenotype matching is influenced by the phylogenetic relationships

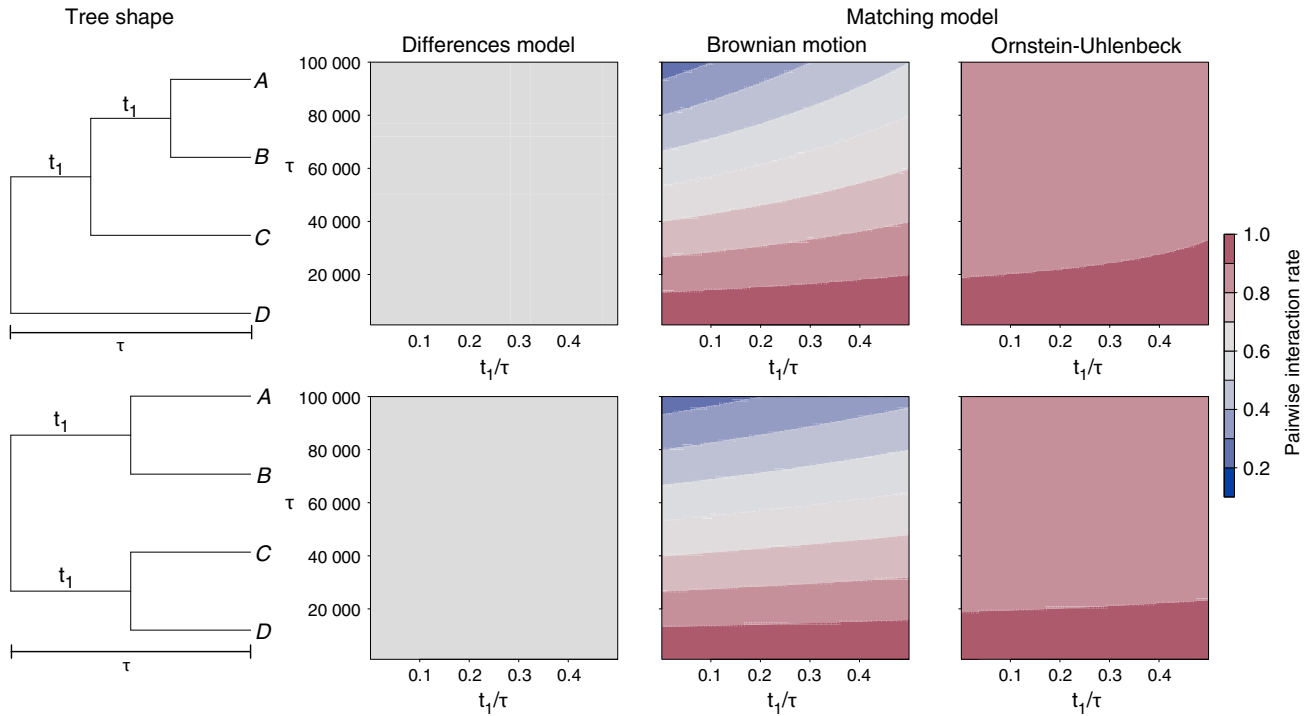


Figure 2 Average interaction rate within a four species community for two alternative phylogenetic trees (top row = pectinate, bottom row = balanced), two mechanisms of species interaction (Differences vs. Matching) and two models of evolution (Brownian motion vs. Ornstein–Uhlenbeck). We varied tree branch length to explore the effect of both τ (y-axis) and the ratio t_{ij}/τ (x-axis). All evolutionary/coevolutionary models used the following parameters: $G = 1$, $N = 1000$, $\sigma_{z_i}^2 = \sigma_{z_j}^2 = 1$, $\alpha = 0.0005$, and $z_0 = 10$. For the Ornstein–Uhlenbeck model, $\gamma = 0.000001$ and $\theta = 10$. In each case, we plot interaction rates under two types of models (phenotypic differences and phenotypic matching; for the differences model, both of these trait evolution models make the same predictions).

among component species. Specifically, the overall rate of interaction is given in the following equation:

$$\bar{P} = \sum_{i=1}^n \sum_{j=1}^n \left(f_i f_j \left(1 - \alpha G \left(\frac{(1 - \text{Exp}[-2\psi(\tau - t_{ij})])}{N\psi} \right) - \alpha \left(\sigma_{z_i}^2 + \sigma_{z_j}^2 \right) \right) \right) \quad (9)$$

(see supporting online material for full derivation). Consistent with the pure drift model considered in the previous section, communities where most species have originated recently will have higher rates of interaction than those where most species originated long ago (Fig. 2). A key difference, however, between evolution driven by drift alone and evolution driven by both drift and stabilising selection is that the influence of evolutionary history decays rapidly in the presence of stabilising selection (Fig. 2). As a consequence, rates of interaction are generally less influenced by evolutionary history when stabilising selection has been important in the past (Fig. 2). Finally, eqn 9 supports our earlier conclusion that overall rates of interaction within a community will be greatest when pairs of the most numerically abundant species (i.e. those with a high frequency f_i and f_j) are closely related (small $\tau - t_{ij}$).

Evolution by genetic drift, stabilising selection and species interactions

There is a logical inconsistency in arguing that species interactions play an important contemporary role in ecological communities using models where those interactions have had no impact on trait evolution of the interacting species over evolutionary history. Yet, this is exactly what we have done in the previous two sections by assuming phenotypic evolution follows a Brownian Motion or Ornstein–Uhlenbeck model. In these models evolutionary change along each branch of the phylogenetic tree is independent of evolution along every other branch in the tree, and this key assumption is shared by many previous approaches evaluating the importance of phylogeny for patterns of species interaction (Ives & Godfray 2006; Rezende *et al.* 2007; Rafferty & Ives 2013; Hadfield *et al.* 2014), and, for that matter, all current tractable models of evolution that can be fit to traits on phylogenetic trees (but see Rabosky & Glor 2010). In this section, we fill this gap by developing simple models of coevolution among interacting lineages. These models allow us to predict how traits will evolve in response to coevolution when the phylogenetic relationships among the interacting species are known. In turn, this information on trait evolution can be used to predict contemporary rates of interaction between pairs of species and among all species within a community, and to further evaluate when the structure of a phylogenetic tree might be predictive of patterns of species interactions.

Our basic approach to modelling coevolution builds on our earlier models by adding the potential for trait coevolution driven by interactions between species. The key assumptions we will make include those used previously, such as weak selection, fixed additive genetic variance, G and population size, N . We again assume that individuals encounter one another at random over evolutionary time. This effectively assumes the clade we study has evolved in sympatry with

ample opportunity for interaction among community members. With these assumptions, when species interactions depend on phenotype matching, trait evolution is described by the following system of differential equations:

$$\frac{d\mu_i}{dt} = \psi(\theta - \mu_i) \quad (10a)$$

$$\frac{d\sigma_{z_i}^2}{dt} = -\left(\frac{2(n-1)}{n}S + 2\psi\right)\sigma_{z_i}^2 + \frac{2S}{n}\left(\sum_{(j \neq i)}^n \sigma_{z_i, z_j}\right) + \frac{G_i}{N} \quad (10b)$$

$$\begin{aligned} \frac{d\sigma_{z_i, z_j}}{dt} = & -\left(\frac{2(n-1)}{n}S + 2\psi\right)\sigma_{z_i, z_j} \\ & + \frac{S}{n}\left(\sum_{k \neq j}^n \sigma_{z_i, z_k} + \sum_{l \neq i}^n \sigma_{z_l, z_i}\right) \end{aligned} \quad (10c)$$

where $\psi_i = 2\gamma G_i$ and $S_i = \frac{2\alpha\xi_i G_i}{(1+\xi_i)}$ (see supporting online material for full derivation). For communities where interactions are instead mediated by a mechanism of phenotype differences, trait evolution is described by the following system of equations:

$$\frac{d\mu_i}{dt} = \psi(\theta - \mu_i) + S \quad (11a)$$

$$\frac{d\sigma_{z_i}^2}{dt} = -2\psi\sigma_{z_i}^2 + \frac{G_i}{N} \quad (11b)$$

$$\frac{d\sigma_{z_i, z_j}}{dt} = -2\psi\sigma_{z_i, z_j} \quad (11c)$$

where $\psi_i = 2\gamma G_i$ and $S_i = \frac{\alpha\xi_i G_i}{2(2+\xi_i)}$ (see supporting online material for a full derivation).

Although significantly more complex than the previous models of evolution we have considered, eqns 10–11 provide two immediate and important insights into the consequences of different forms of coevolution for the evolution of traits on phylogenetic trees. First, coevolution mediated by a mechanism of phenotype differences generates evolutionary dynamics that are essentially indistinguishable from those of random genetic drift and stabilising selection. Put differently, coevolution mediated by weak phenotype differences is for all intents and purposes an Ornstein–Uhlenbeck process. Second, and in stark contrast, coevolution mediated by a mechanism of phenotype matching generates evolutionary dynamics of trait evolution that is completely unlike those predicted by Brownian motion or Ornstein–Uhlenbeck processes (Figs 1 and 4).

Solving eqns (11) for specified phylogenetic tree topologies and branch lengths allows us to gain two additional insights into the role evolutionary history plays in defining contemporary rates of interaction and ecosystem function under our model (Figs 1, 3, and 4; also see supporting online material for details). First, as was the case for evolution driven by genetic drift or genetic drift and stabilising selection, when interactions coevolve through a mechanism of phenotype matching, rates of interaction are greatest for species which have diverged most recently (Fig. 1). This result holds irrespective of whether the evolutionary history of the group has been dominated by mutualism or competition. What our analytical results also show, however, is that the rate at which interaction rates change as a function of divergence time is, in general, much more rapid when evolution is driven by competitive than mutualistic coevolution (Fig. 1). Thus, all else

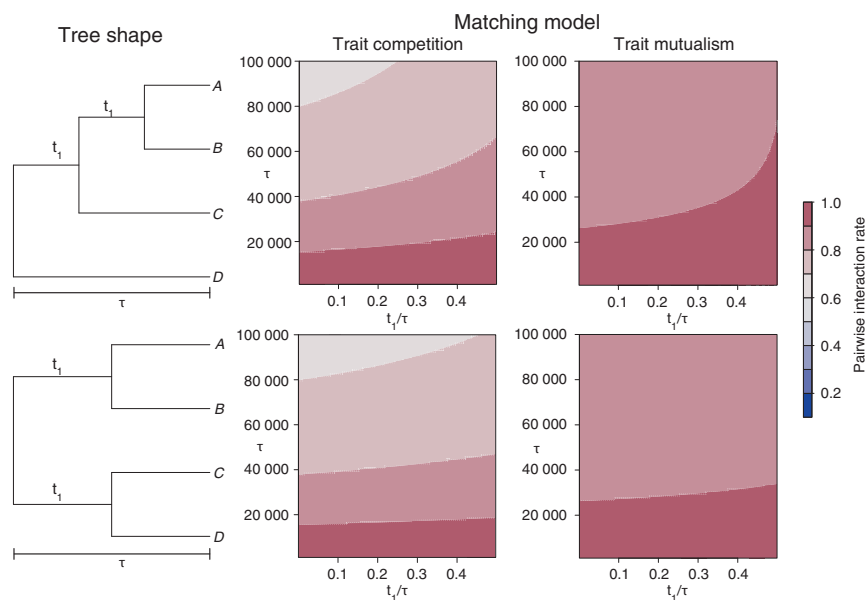


Figure 3 Average interaction rates within a four species community for two alternative phylogenetic trees (top row = pectinate, bottom row = balanced) and two different models of coevolution (columns). We varied tree branch length to explore the effect of both τ (y-axis) and the ratio t_{ij}/τ (x-axis). All coevolutionary models used the following parameters: $G = 1$, $N = 1000$, $\sigma_{z_i}^2 = \sigma_{z_j}^2 = 1$, $\alpha = 0.0005$, $\gamma = 0.000001$, $\theta = 10$ and $z_0 = 10$. For the case of competitive coevolution shown in the first column, $S = -0.000001$; for the case of mutualistic coevolution shown in the second column $S = 0.000001$.

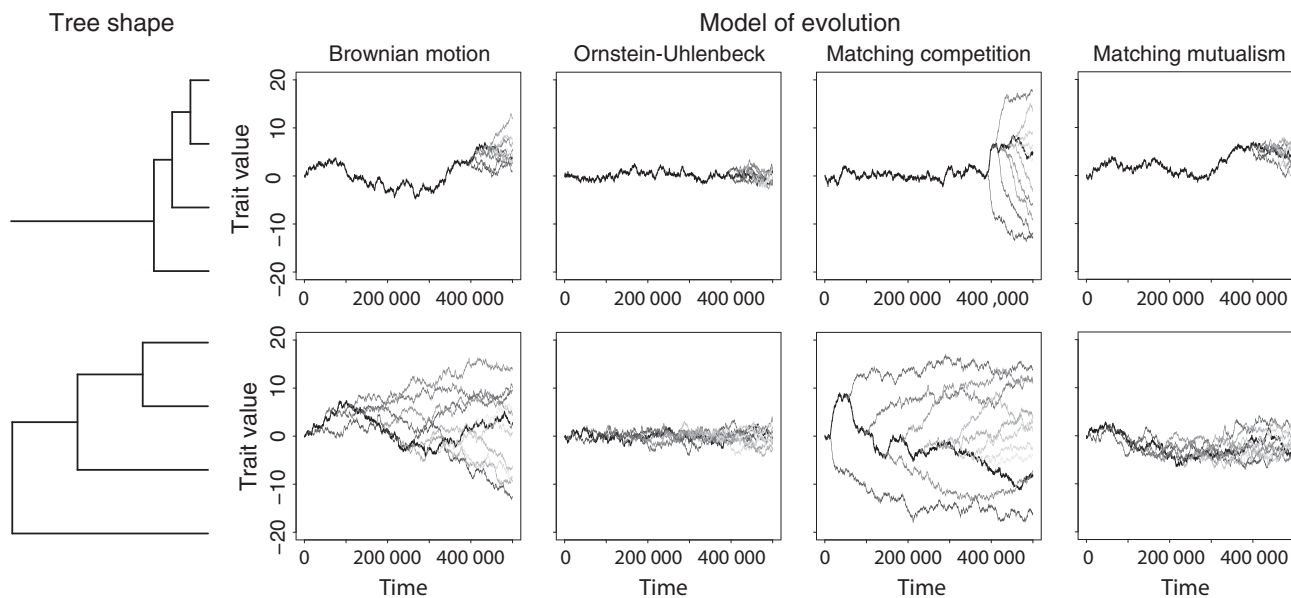


Figure 4 The evolution and coevolution of species mean phenotypes over time for four different models of evolution/coevolution and two different sets of pectinate phylogenetic relationships among species. Each panel shows the evolution/coevolution of mean phenotypes within a twelve species community, with each species represented by a line of different colour. In all cases, simulations were run for 500 000 generations. In the first row, diversification occurs rapidly and recently with species forming every 5000 generations starting in generation 445 000. In the second row, diversification occurs slowly and steadily with species forming every 45 000 generations starting in generation 5000. Parameters for these simulations were $N = 2000$, $\sigma_S^2 = 0.1$, and $\alpha = 0.01$ in all cases. For the Ornstein–Uhlenbeck, Mutualism and Competition models, $\gamma = 0.0001$ and $\theta = 0$. For the Mutualism model $\xi = 0.01$ and for the Competition model $\xi = -0.01$.

being equal, the importance of phylogeny and evolutionary history in determining pairwise rates of interaction is much greater for competitive than mutualistic interactions (Fig. 1).

Second, our analytical results show that overall rates of interaction within the community are, as we saw previously,

much greater when community members have arisen through a rapid radiation rather than a slow and steady process of occasional speciation (Fig. 3). However, when trait evolution is driven by coevolution, the ecological form of the interaction matters a great deal. Specifically, when evolution has been

dominated by mutualistic coevolution, the influence of phylogeny is quite weak, on par with the influence of phylogeny when evolution has been driven by stabilising selection and drift (Fig. 3). In contrast, when evolution has been dominated by competitive coevolution, the influence of phylogeny can be very strong (Fig. 3). The reason for this fundamental difference in the importance of phylogeny across different ecological forms of interaction is that mutualistic coevolution tends to retard the diversification of traits mediating interactions whereas competitive coevolution tends to accelerate trait diversification (Fig. 4).

The difference in rate of trait diversification we observe as a function of the ecological form of interactions has interesting consequences for the interplay between phylogeny and overall rates of interactions within a community, which one might relate to ecosystem function. Specifically, we find that overall interaction rates are generally greater for communities that have radiated very recently. For mutualistic communities, where such interactions are positive, one might then expect greater ecosystem functioning in such young communities; in contrast, competitive communities that have radiated very recently might suffer from intense competition and thus exhibit reduced ecosystem functioning. The reason for this result is simply that the exchange of mutualistic benefits under a model of phenotype matching is maximised when the traits of the interacting species are similar, which is most likely to occur when species share recent common ancestry. In contrast, competition for shared resources is minimised for a model of phenotype matching when the traits of the interacting species are very dissimilar, which is most likely to occur when species have long been free from the constraints of common ancestry.

INDIVIDUAL-BASED SIMULATIONS

The analytical results described above rest upon a number of important assumptions including interaction rates that depend only weakly on traits, weak selection and fixed additive genetic variance. Because these assumptions are likely to be violated to some extent in all biological communities we developed and analysed individual-based simulations that relax these key assumptions. Simulations studied communities of n interacting species where each species is composed of N_i individuals, each with a particular value of the continuous phenotype z_{ik} . Each simulation begins with a single ancestral species. Over evolutionary time, the number of species in this community grows as speciation occurs. Within each generation, individuals follow a life cycle consisting of stabilising selection, species interactions, selective mortality and finally, reproduction.

Speciation is integrated into simulations according to a pre-determined phylogeny. When the simulation reaches a bifurcation within the phylogeny, the appropriate existing species gives rise to a daughter species. This new species is created by sampling a number, N_i , of individuals at random from the ancestral species. Thus, the population mean phenotype of the new species is, on average, equal to that of its progenitor. However, because the individuals of the new species are selected at random, the population mean phenotype of the

new species is stochastic, with some amount of variance caused by random genetic drift.

Extensive analyses of simulated communities provide broad support for the conclusions we derived from our analytical model. Specifically, our simulation results confirm that phylogeny matters for contemporary rates of interaction and ecosystem function only when interactions among community members are currently being mediated by a mechanism of phenotype matching. If interactions are currently mediated by a mechanism of phenotype differences, phylogeny is irrelevant. When contemporary interactions are mediated by phenotype matching, our individual-based simulations confirm that the impact of phylogeny and evolutionary history is maximised when evolution has been driven by random genetic drift acting in isolation or by competitive coevolution (Figs 5 and 6). Evolution driven by stabilising selection and/or mutualistic coevolution minimises the impact of phylogeny on contemporary rates of interaction and ecosystem function (Figs 5 and 6). In addition to providing support for these large scale, qualitative results, our simulations supported the quantitative predictions of our analytical model when, as expected, traits of interacting species only weakly influence rates of interaction.

RESULTS AND DISCUSSION

We have used simple models of species interactions and coevolution to explore the potential utility of phylogenetic information for predicting rates of pairwise interactions among species and overall rates of interaction within communities. Our mathematical and computational analyses of these models reveal that phylogenetic relationships among community members can play an important role, but only for specific types of species interactions and modes of evolution. Whether phylogenetic information is useful for predicting the ecological properties of a community depends primarily on the mechanistic underpinnings of species interactions. In particular, if the outcome of encounters between species depends on the degree to which traits of the interacting individuals match, phylogenetic information can have substantial predictive power. In contrast, if the outcome of encounters between species depends only on which individual has the larger trait value, phylogenetic information is of limited or no utility in predicting interaction rates.

In cases where phylogenetic information has predictive power, our results show that the critical piece of information is phylogenetic diversity (PD). Recently diverged species are more likely to interact than those that diverged long ago. As a direct result, overall rates of interaction within communities are predicted to be maximised in young explosive radiations with low phylogenetic diversity. In contrast, communities that include sets of deeply divergent species are predicted to have lower interaction rates. This prediction holds qualitatively regardless of the model under which traits evolve, but quantitative predictions do differ depending on the details of the trait evolutionary model. These predictions for overall rates of interaction within communities of interacting species have potentially interesting consequences for ecosystem function. For instance, in communities where interactions are generally

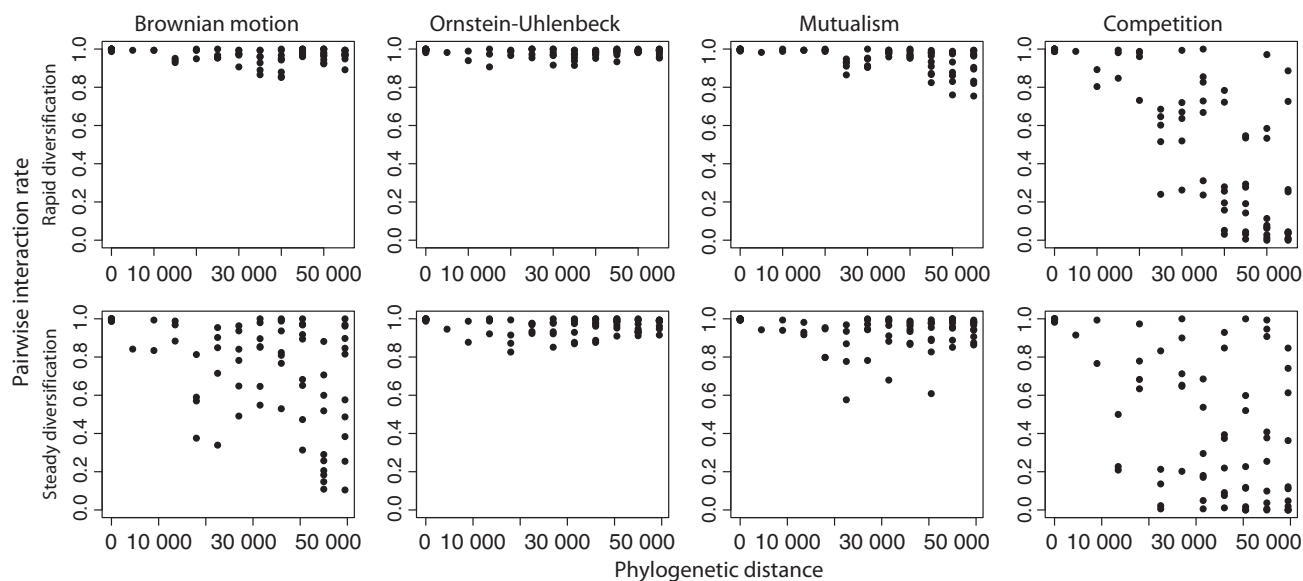


Figure 5 Interaction rates between all possible pairs of species within a twelve species community for four different models of evolution/coevolution and two different sets of pectinate phylogenetic relationships among species. In all cases, simulations were run for 500 000 generations. In the first row, diversification occurs rapidly and recently with species forming every 5000 generations starting in generation 445 000. In the second row, diversification occurs slowly and steadily with species forming every 45 000 generations starting in generation 5000. Parameters for these simulations were $N = 2000$, $\sigma_S^2 = 0.1$, and $\alpha = 0.01$ in all cases. For the Ornstein–Uhlenbeck, Mutualism and Competition models, $\gamma = 0.0001$ and $\theta = 0$. For the Mutualism model $\xi = 0.01$ and for the Competition model $\xi = -0.01$.

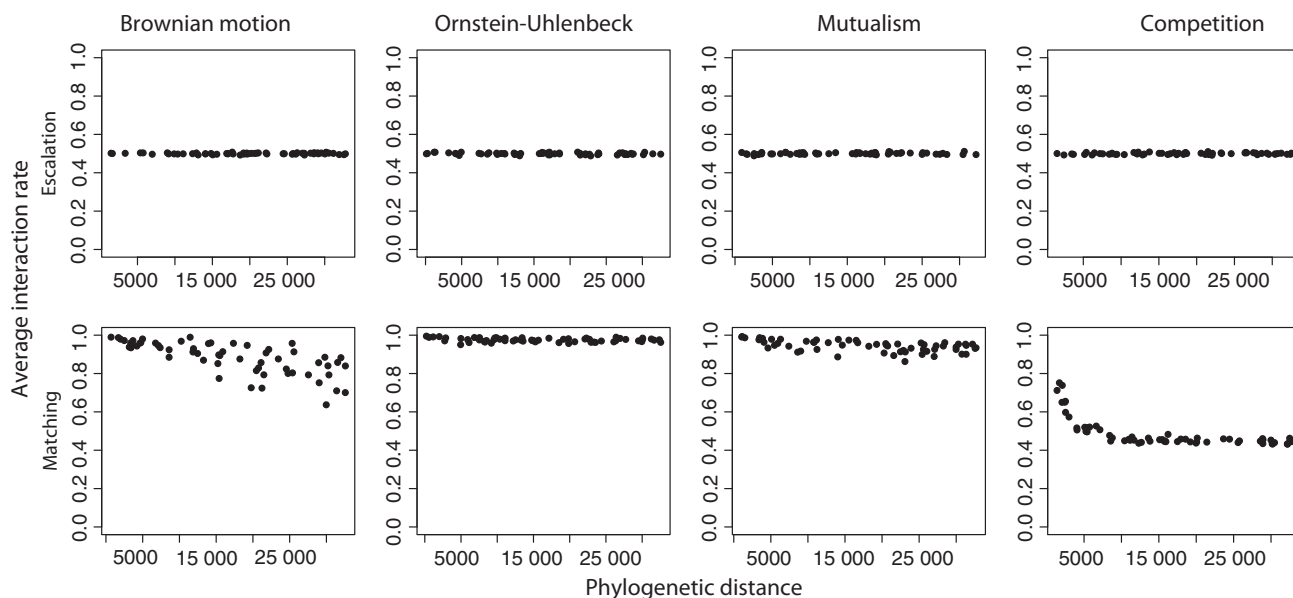


Figure 6 The average rate of interaction among members of an eight species community for four different models of evolution/coevolution and two different models of species interaction as a function of the rate of diversification. In all cases, simulations were run for 400 000 generations. The parameter, b , on the x -axis is the interval between speciation events such that small values of b indicate rapid, recent diversification and large values of b indicate slow and steady diversification. Parameters for these simulations were $N = 2000$, $\sigma_S^2 = 0.1$, and $\alpha = 0.01$ in all cases. For the Ornstein–Uhlenbeck, Mutualism and Competition models, $\gamma = 0.0001$ and $\theta = 0$. For the Mutualism model $\xi = 0.01$ and for the Competition model $\xi = -0.01$.

mutualistic or facilitative, the rate at which benefits are exchanged among community members – and thus presumably ecosystem function – is maximised when species are all closely related (low PD). In contrast, for communities where interactions are primarily competitive, competition is reduced

and ecosystem function presumably enhanced, when communities contain sets of deeply divergent species (high PD). The idea that PD should be related to ecosystem function has some support from recent empirical studies (e.g. Gravel *et al.* 2012; Srivastava *et al.* 2012).

Although evolutionary relationships generally influence rates of interaction in communities where phenotype matching predominates, the strength of this effect depends on the historical forces driving trait evolution. For instance, phylogenetic relationships have a stronger effect on contemporary rates of interaction when traits have evolved in response to genetic drift or competitive coevolution than when trait evolution has been driven by stabilising mutualistic coevolution. This difference arises because genetic drift and competitive coevolution promote phenotypic diversification whereas stabilising selection and mutualistic coevolution inhibit diversification and erode the covariance among traits of related species. In other words, under stabilising mutualistic coevolution, close relatives are not any more similar than distant relatives, so phylogenetic trees have little predictive power. Although this key difference has been described for drift (BM) and stabilising selection and drift (OU; e.g. Hansen & Martins 1996), the difference between competitive and mutualistic coevolution was previously unknown.

Our demonstration that contemporary ecological patterns depend on the ecological forces driving trait evolution over historical time is intuitive, yet quite different from standard assumptions of comparative studies. Specifically, the majority of studies exploring how phylogeny influences species interactions assume that historical patterns of trait evolution are accurately captured by BM or OU models (e.g. Ives & Godfray 2006; Rezende *et al.* 2007; Rafferty & Ives 2013; Hadfield *et al.* 2014). Although our results show that this assumption holds when interactions depend on a mechanism of phenotype differences, it breaks down when interactions depend on phenotype matching. Specifically, when traits have evolved in response to coevolutionary selection mediated by a mechanism of phenotype matching, the covariance structure describing contemporary traits may no longer be well described by a BM or OU process. As a consequence, both species' traits and their contemporary rates of ecological interaction differ significantly when coevolution has played an important historical role (Fig. 1).

An important caveat to our conclusions is that we have focused our ecological predictions on rates of interaction between pairs of species and among all species within a community. Our choice of metrics was driven by the important role interaction rates play in ecology and evolution, the frequency with which these quantities are measured in empirical studies, and their central role in previous theoretical investigations. There are, of course, other metrics that could be of interest when studying species interactions and community ecology. For instance, the degree to which interactions are asymmetrical could have important ecological consequences (Bascompte *et al.* 2006; Guimaraes *et al.* 2006; Vazquez *et al.* 2007; Godoy *et al.* 2014). If our focus were on the expected asymmetry of interactions between pairs of species rather than on their expected rate of interaction, our results and predictions could be quite different for the phenotype differences model (the phenotype matching model is symmetric by definition). Specifically, because we would expect average trait values to be more similar for closely related pairs of species than distantly related pairs of species, interaction

asymmetry would be greater for distantly related species. Thus, we might predict that pairs of species with strong asymmetries (e.g. a competitively superior species and a competitively inferior species) would tend to be comprised of more distantly related species (as observed empirically by Godoy *et al.* 2014). This observation emphasises one of our central conclusions: the importance of phylogenetic patterns depends very much on the ecological quantities we wish to predict.

The results we report here generate interesting predictions that may be testable in a wide range of natural communities. For instance, our models suggest that mutualistic communities should show significantly less phylogenetic signal in rates of interaction than competitive communities. Our results also predict that communities where interactions are mediated by a mechanism of phenotype differences or trait escalation should show little or no phylogenetic signal in interaction rates compared to communities where phenotype matching predominates. However, there are also significant limitations on the applicability of our results. Chief among these is our assumption that a single group of competitors or mutualists has radiated *in situ*. Although there are well-studied systems where this appears to be a reasonably accurate description of evolutionary history (Gillespie 2004; Joyce *et al.* 2005), there are many cases where it does not. Extending the techniques we have developed here to cases where speciation is allopatric and communities have assembled rather than radiated in place will be an important goal for future research. Another important avenue for future work will be to broaden our approach so that we can accommodate interacting guilds of species, such as parasites and their hosts, each of which is represented by an independent phylogeny.

ACKNOWLEDGEMENTS

We thank Matt Pennell, Blake Matthews, Catherine Wagner and Mike Alfaro for helpful comments and NSF grants DMS 0540392 and DEB 1118947 (SLN) and DEB 0919499 and DEB 1208912 (LJH) for funding.

AUTHORSHIP

SLN and LJH conceived of the study. SLN performed the mathematical and simulation analyses. SLN and LJH wrote the paper. LJH prepared the figures.

REFERENCES

- Abrams, P.A. (2000). The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.*, 31, 79–105.
- Agrawal, A.A. & Fishbein, M. (2008). Phylogenetic escalation and decline of plant defense strategies. *Proc. Natl Acad. Sci. USA*, 105, 10057–10060.
- Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312, 431–433.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.

- Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, 4, e5695. DOI: 10.1371/journal.pone.0005695.
- Cadotte, M., Albert, C.H. & Walker, S.C. (2013). The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecol. Lett.*, 16, 1234–1244.
- Felsenstein, J. (1973). Maximum-likelihood estimation of evolutionary trees from continuous characters. *Am. J. Hum. Genet.*, 25, 471–492.
- Friman, V.P., Jousset, A. & Buckling, A. (2014). Rapid prey evolution can alter the structure of predator-prey communities. *J. Evol. Biol.*, 27, 374–380.
- Gavrilets, S. (1997). Coevolutionary chase in exploiter-victim systems with polygenic characters. *J. Theor. Biol.*, 186, 527–534.
- Gillespie, R. (2004). Community assembly through adaptive radiation in Hawaiian spiders. *Science*, 303, 356–359.
- Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.*, 17, 836–844.
- Gravel, D., Bell, T., Barbera, C., Combe, M., Pommier, T. & Mouquet, N. (2012). Phylogenetic constraints on ecosystem functioning. *Nat. Commun.*, 3, DOI: 10.1038/ncomms2123.
- Guimaraes, P.R. Jr, Rico-Gray, V., dos Reis, S.F. & Thompson, J.N. (2006). Asymmetries in specialization in ant-plant mutualistic networks. *Proc. Biol. Sci.*, 273, 2041–2047.
- Hadfield, J.D., Krasnov, B.R., Poulin, R. & Nakagawa, S. (2014). A tale of two phylogenies: comparative analyses of ecological interactions. *Am. Nat.*, 183, 174–187.
- Hairston, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.*, 8, 1114–1127.
- Hansen, T.F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, 51, 1341–1351.
- Hansen, T.F. & Martins, E.P. (1996). Translating between microevolutionary process and macroevolutionary patterns: the correlation structure of interspecific data. *Evolution*, 50, 1404–1417.
- Harmon, L.J., Losos, J.B., Davies, T.J., Gillespie, R.G., Gittleman, J.L., Jennings, W.B. *et al.* (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, 64, 2385–2396.
- Ives, A.R. & Godfray, H.C.J. (2006). Phylogenetic analysis of trophic associations. *Am. Nat.*, 168, E1–E14.
- Ives, A.R. & Helmus, M.R. (2011). Phylogenetic metrics of community similarity (vol 176, pg E128, 2011). *Am. Nat.*, 178, 559–559.
- Joyce, D.A., Lunt, D.H., Bills, R., Turner, G.F., Katongo, C., Duftner, N. *et al.* (2005). An extant cichlid fish radiation emerged in an extinct Pleistocene lake. *Nature*, 435, 90–95.
- Kembel, S.W. (2009). Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecol. Lett.*, 12, 949–960.
- Koricheva, J., Nykanen, H. & Gianoli, E. (2004). Meta-analysis of trade-offs among plant antiherbivore defenses: are plants jacks-of-all-trades, masters of all? *Am. Nat.*, 163, E64–E75.
- Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30, 314–334.
- Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, 11, 995–1003.
- Losos, J.B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, Berkeley, CA.
- Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. (2010). Ecological opportunity and the rate of morphological evolution in the diversification of greater antillean anoles. *Evolution*, 64, 2731–2745.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.
- Moore, J.C., Obbard, D.J., Reuter, C., West, S.A. & Cook, J.M. (2008). Fighting strategies in two species of fig wasp. *Anim. Behav.*, 76, 315–322.
- Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J. *et al.* (2012). Ecophylogenetics: advances and perspectives. *Biol. Rev.*, 87, 769–785.
- Nuismer, S.L., Jordano, P. & Bascompte, J. (2013). Coevolution and the architecture of mutualistic networks. *Evolution*, 67, 338–354.
- Pillar, V.D., Blanco, C.C., Mueller, S.C., Sosinski, E.E., Joner, F. & Duarte, L.D.S. (2013). Functional redundancy and stability in plant communities. *J. Veg. Sci.*, 24, 963–974.
- Rabosky, D.L. & Glor, R.E. (2010). Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *Proc. Natl Acad. Sci. USA*, 107, 22178–22183.
- Rafferty, N.E. & Ives, A.R. (2013). Phylogenetic trait-based analyses of ecological networks. *Ecology*, 94, 2321–2333.
- Revell, L.J., Harmon, L.J. & Collar, D.C. (2008). Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.*, 57, 591–601.
- Rezende, E.L., Jordano, P. & Bascompte, J. (2007). Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos*, 116, 1919–1929.
- Roughgarden, J. (1996). *Theory of Population Genetics and Evolutionary Ecology*. Prentice-Hall, Upper Saddle River, NJ.
- Schoener, T.W. (2011). The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science*, 331, 426–429.
- Srivastava, D.S., Cadotte, M.W., MacDonald, A.A.M., Marushia, R.G. & Mirotchnick, N. (2012). Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.*, 15, 637–648.
- Vazquez, D.P., Melian, C.J., Williams, N.M., Bluethgen, N., Krasnov, B.R. & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116, 1120–1127.
- Verdu, M. & Valiente-Banuet, A. (2011). The relative contribution of abundance and phylogeny to the structure of plant facilitation networks. *Oikos*, 120, 1351–1356.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.
- Williams, E.E. (1972). The origin of faunas evolution of lizard congeners in a complex island fauna a trial analysis. *J. Evol. Biol.*, 6, 47–89.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G. Jr (2003). Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, 424, 303–306.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Editor, Jerome Chave

Manuscript received 5 May 2014

First decision made 10 June 2014

Second decision made 27 July 2014

Manuscript accepted 17 September 2014