Title: Should ecological interactions influence diversification rates in ecological networks?

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24 Abstract

Introduction

Competitive interactions are widely considered to be dominant in governing the ecological and evolutionary dynamics of biodiversity on earth. Extensive empirical evidence demonstrates that competitive interactions govern the use of resources by species in communities (e.g., Lotka-Volterra, Tilman 1982; Diamond and Case 1986), the mechanism of natural selection (e.g., Darwin 1859; Simpson 1953), character displacement and adaptive radiation (Brown and Wilson 1956; Schluter 2000a,b; Losos 2009). In evolutionary biology, competition has been widely invoked to explain species richness across time and space (see review in Rabosky 2013). Competition among species and clades for finite resources (e.g., "ecological limits") is thought to impose carrying capacities on species diversity, and thus diversity-dependent diversification (Rabosky 2013). Compelling evidence exists that supports the view that diversity- dependent processes operate to regulate patterns of biodiversity at local, regional, and continental scales. This includes lack of a correlation between clade age and species richness (Ricklefs and Renner 1994; Rabosky 2012; Rabosky et al. 2012); evidence from the fossil record of stable diversity through time at local (Knoll 1986; Wing and DiMichele 1995; DiMichele et al. 2004; Cleal et al. 2012) and global scales (Spekoski 1978, 1984; Alroy 2010a,b; Smith et al. 2012; but see Benton and Emerson 2007; Friedman and Sallan 2012; Lloyd and Friedman 2012); and, most controversially, some evidence from the branching patterns of molecular phylogenies (see discussion and references in Rabosky 2013).

Substantial evidence indicates that diversity-dependence of diversification rates are likely real in many cases, but substantial evidence questioning its primacy exists as well. Not all studies examining diversity through time find support for this view in molecular phylogenies, with some studies arguing that such data are consistent with or mask continuously increasing (Morlon et al. 2010; Manceau et al. 2015) or declining diversity trajectories (Quental and Marshall 2010; Morlon et al. 2011). Furthermore, molecular

phylogenetic studies apparently consistent with density-dependence might alternately reflect a pattern of some clades undergoing increases in diversity and others decreases at any given point in time (Pyron and Burbrink 2012; Rabosky et al. 2012). The same is true for the fossil record, where there is substantial disagreement over whether patterns of standing diversity through time are consistent with ecological limits; certainly, over deep time, global patterns of diversity (e.g., Sepkoski 1978, 1984) are variously described as consistent with nonequilibrial fluctuations in diversity or a "stepped logistic" increase (see review in Harmon and Harrison 2015). It is possible that some of these examples simply represent exceptional cases — such as the subset of clades that have recently diversified into new adaptive zones (Simpson 1953; Rabosky and Hurlbert 2015). Furthermore, the boundary between the sets of conditions under which competition promotes diversity (e.g., through character displacement, or the ecological theory of adaptive radiation; Lack 1947; Simpson 1953; Brown and Wilson 1956; Schluter 200a,b) and constrains diversity (e.g., clade competition, ecological limits over macroevolutionary timescales; Simpson 1953; Jablonski 2008; Rabosky and Glor 2010; Pires et al. 2015) are not well- understood (Hembry et al. 2014; but see Bailey et al. 2013).

More importantly, in our view, the investigation of whether macroevolutionary dynamics are consistent with density-dependence and/or ecological limits on diversity have overlooked the fact that not all ecological interactions among species are competitive. Antagonistic interactions — particularly predator- pre y— have attracted substantial attention from paleobiologists, some of whom have emphasized the difficulty of distinguishing the effects of competition from those of predation (Dietl and Kelly 2002; Stanley 2008). In some evolutionary radiations, the two are likely intermixed (REF). Integrating mutualism into this macro-evolutionary theory has been more challenging, although a number of authors have argued that mutualism provides novel resources to interacting clades, thus providing ecological opportunity and spurring diversification (Lengyel et al.

2009; Gómez and Verdú 2012; Litsios et al. 2012; Joy 2013). It is certainly conceivable that competition trumps all other interactions, both because of global resource limitation and because mutualistic and antagonistic interactions often contain a component of interspecific competition within trophic levels for prey or mutualistic partners (Ehrlich and Raven 1964; Schluter 2000; Armbruster and Muchhala 2007). However, it is also possible that the effects of competition on diversity dynamics are substantially modulated by other ecological interactions, such as mutualism and predation.

SOMETHING MISSING HERE TO MOTIVATE A NETWORK APPROACH TO MACRO-EVOLUTION

Here, we introduce a simple model of competitive interactions in a natural community can, and through extensions to mutualistic and antagonistic predator-prey interactions, can generate easily interpretable predictions as to the effects of different types of interactions on mecroevolutionary diversity dynamics. In some cases, these predicted dynamics differ between competition and other types of ecological interactions, suggesting that mixed empirical evidence for diversity-dependence and ecological limits on diversity over evolutionary time may be due in part to the effects of antagonism and mutualism on diversity.

Graphical model of diversification dynamics

We start with a graphical model of speciation-extinction dynamics inspired by the theory of island biogeography and its recent extensions to include trophic interactions and other types of ecological networks (Gravel2011; Cazelles2015; Massol2017). The model allows to derive some basic predictions about the imapct of different types of interactions on diversification rates. Its simplicity however prevents the investigation of the macroevolution of network structure, and we thus relax some assumptions and perform numerical

simulations below.

Description

The rate of change in species richness R is a dynamic balance between speciation events and extinction events, represent as follows:

$$\frac{dR}{dt}\frac{1}{R} = S(R) - E(R) \tag{1}$$

where $S(R)$ is the function describing the speciation rate as a function of species richness, and $E(R)$ the extinction rate. The equilibrium species richness is found when $S(R) = E(R)$. A minimal birth-death model of macro- evolution is species-richness independent, such that S and E are constant rates s and e. We observe exponential diversification provided that $s > e$. More recent models use phenenological representation of the diversification dynamics, such as:

$$\frac{dR}{dt}\frac{1}{R} = (s - e)(1 - \frac{R}{K}) \tag{2}$$

where s and e are baseline speciation and extinction rates, and K is the maximal species richness the system can support. This approach could be sufficient to describe the dynamics of the system and test hypotheses, but it does not allow to understand the underlying ecological mechanisms fixing carrying capacity. It could not discriminate for instance the effect of various types of interactions, or if the constraints are imposed by coexistence or decreasing population size. Here we propose a general model with simple functions describing how ecological interactions could modify the speciation and extinction rates under different scenarios of ecological interactions.

Our derivation is inspired by the trophic theory of island biogeography (Gravel2011), which add redator-prey interactions to the MacArthur & Wilson model of colonization

and extinction dynamics without the addition of extra parameters. Ecological interactions are introduced with a simple assumption: predators require a prey to colonize islands and persist. If the last prey goes extinct, then there is secondary extinction of the predator (Dunne2002). The derivation is based on the computation of the expected number of preys a predator has on the island. As a first approximation, if the island holds R species and the connectance of the ecological network is C, then the expected number of interacting species is simply $I = CR$. Our subsequent derivation is based on this expected number of interacting species with the resident and newly speciated species. The exact formulation requires knowledge of interactions and species co-occurrence (see Cazelles2015), but the approximation holds for general predictions as we will see below with numerical simulations.

The key to develop the model further and investigate different types of interactions is to define the functions $S(R)$ and $E(R)$ appropriately. We consider a successful speciation event to be the combination of a mutation leading to speciation and the acquisition of traits that are ecological suitables (i.-e. they provide preys, mutualists or minimize competition). In what follows we use exponential equations for these functions, but other functional forms could be considered as well, depending on the assumptions considered. Thus, we define:

$$S(R) = u_{max}(u_0 + u_1 e^{-\alpha I}) \tag{3}$$

and

$$E(R) = e_{max}(e_0 + e_1 e^{-\alpha I}) \tag{4}$$

where u_{max} and e_{max} are the asymptotic speciation and extinction rates respectively, and $u_1 - u_0$ and $e_1 - e_0$ are the speciation and extinction rates in absence of interactions.

There are multiple ways to parameterize those functions, for different types of interactions. These are summarized at Table 1 and the functions are illustrated at Fig. 1-3. In short, interactions are modifiers of the u_{max} and e_{max} and the shape of the function depends on the type of interactions. Maximal speciation rate could happen either at null diversity (e.g. in absence of interactions) or at infinite interactions (e.g. with mutualism).

Competition

Competition could impact both speciation rate, because it could limit the establishment of mutants, and extinction rate because it decreases population size and therefore promotes stochastic extinction. We consider that a successful speciation event is limited by the availability of ecological niches (i.-e. there is a limiting similarity setting a cap to species richness - MacArthur1967). At this stage we do not represent niches explicitly, but simply assume that niche space is filled asymptotically with increasing species richness. Therefore, the speciation rate is maximal at $I = 0$, which means that $u_1 - u_0 = u_{max}$ and it decreases progressively as the number of competitors increase. We consider that it tends asymptotically to 0 with species richness approxing very large numbers (i.e. $u_0 = 0$). Alternatively, intense competition could also result in exclusion of already established species, either because mutants are more performant or because of reduced population size. We consequently consider that the extinction probability is minimal at $I = 0$ and increases asymtotatically with I to a maximal extinction probability $e_{\infty} = e_{max}$.

Mutualism

Mutualism could impact the speciation rate because newly speciated species require partners to establish their mutualism. The probability of finding at least one partner already present in the community, and the total benefit from all partners, should increase with the expected number of interactions. We consequently consider that the speciation rate

₁₆₆ is minimal at $I = 0$, with the extreme case of obligate mutualism where $u_1 - u_0 = 0$, and

₁₆₇ it saturates at the maximal speciation rate $u_0 = u_{max}$. At the opposite of competition,

₁₆₈ mutualism increases population size and fitness, such that the extinction rate is expected

₁₆₉ to decrease asymptotatically with the number of interactions. We consequently set the

₁₇₀ extinction probability in absence of interactions at the max $e_1 - e_0 = e_{max}$, with the

₁₇₁ extreme case of obligate mutualism where $e_{max} = 1$, and the asymptote to $e_0 = e_{min}$.

₁₇₂ This last probability is larger than 0 because extinctions independent of interactions

₁₇₃ could nonetheless occur. Note this model applies to mutualistic interactions as well as

₁₇₄ ammensalism (+,0).

Predator-prey interactions

₁₇₆ Predator-prey interactions combine the negative effect of interactions on extinction de-

₁₇₇ scribed for competition with the positive effect of mutualists on colonization described for

₁₇₈ mutualism. We consider that successful speciation of a predator require to find at least

₁₇₉ one prey to establish. The speciation function should thus be increasing and saturating

₁₈₀ with species richness, as it is for mutualism. The extinction function is however more

₁₈₁ complicated, as it combines two different constraints. First, there increasing benefit of

₁₈₂ having multiple preys since the likelihood of all preys going extinct should decrease with

₁₈₃ species richness. Second, predatory interactions could have a negative impact on the prey,

₁₈₄ reducing there density and potentially leading to extinctions. Depending on the relative

₁₈₅ importance of these two functions, the final extinction probability could be a monotonic

₁₈₆ decreasing and asymptotic function of the expected number of interactions, or alterna-

₁₈₇ tivel it could have a fast decrease followed by an increase of the extinction rate (such as

₁₈₈ illustrated at Fig. X). In this last situation, there is an initial reduction of extinction

₁₈₉ probability because of beneficial preys, followed by an increase because of harmful effects

₁₉₀ of predators.

Results

A graphical representation of the speciation and extinction curves allow one to understand the impact of different types of interactions on diversification dynamics. An equilibrium $\hat{R}$ exists at the location where the $S(R)$ and the $E(R)$ curves cross each other (Fig. 1A). The shape of the curves tells us about the stability of the equilibrium and the diversification dynamics, which could be stable or not. Species richness will increase when $S(R) > E(R)$ and conversely, it will decrease when $S(R) > E(R)$. Diversification dynamics will be stabilizing if $S(R) < E(R)$ when species richness is larger than the equilibrium $\hat{R}$ (species richness decreases) and $S(R) > E(R)$ when species richness is smaller than the equilibrum. The opposite leads to exponential diversification dynamics.

The simple analysis of this graphical model reveals that competitive interactions will limit species diversification if the speciation and extinction curves cross each other (Fig. 1). Given the above described assumptions for the shape of the speciation and extinction functions, we find there is only one equilibrum and it will always be stable. The consequent per species diversification rate will be a monotonic negative relationship with species richness, which shape will depend on the assumptions underlying the $S(R)$ and $E(R)$ functions.

Mutualistic interactions on the other hand are susceptible to unbounded diversification (Fig. 2). In contrast with competitive interactions, the speciation and the extinction curves could cross but the equilibrium species richness will be unstable and per species diversification rate will accelerate with increasing species richness. In this situation, an increase of species richness above the equilibrium will result in a speciation rate higher than the extinction rate, and so diversity will increase without boundaries. The per species net diversification rate will consequently be a positive monotonic function of species richness. Alternatively, insufficient initial species richness could lead to a collapse of the system.

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²¹⁷ Predator-prey interactions combine the findings of both competitive and mutualistic

²¹⁸ interactions. The speciation function follows the same shape to the mutualistic function.

²¹⁹ The extinction function on the other hand could take various forms, with various out-

²²⁰ comes. The most interesting case is a hump- shape relationship, susceptible to cross the

²²¹ speciation curves twice, generating potentially two equilibrium points (Fig. 3). The first

²²² equilibrium $\hat{R}_1$ is unstable. In this case, if species richness is below the equilibrium, speci-

²²³ ation will be insufficient to balance extinctions and the system will collapse. If the initial

²²⁴ species richness is larger than this point, then species richness will increase and reach

²²⁵ the second equilibrium, which is stable. Species richness will decrease if starting from

²²⁶ higher species richness than the second equilibrium. The shape of the extinction curve

²²⁷ will determine wether only one or two equilibrium will be found. The shape depends on

²²⁸ the relative rates of change of the extinction functions for the effects of prey (more preys

²²⁹ decrease extinctions) and predators (more predators increase extinctions). If the decay

²³⁰ parameters α are similar, then the function will be a negative exponential and there will

²³¹ be a single stable equilibrium. Two equilibrium will be found when the positive effect of

²³² preys saturates much faster than the negative effect of predators.

Simulation of network macro-evolution

Description

²³⁵ The graphical model yields very general conclusions about the impact of different types of

²³⁶ interactions on diversification dynamics, but it does not allow the investigation of network

²³⁷ macro-evolution, thereby neglecting any impact of network topology on its development.

²³⁸ Therefore, in addition to the simple analytical model, we run stochastic simulation with

²³⁹ a more explicit representation of ecological interactions. The analytical model considers

²⁴⁰ that all species interact similarly (they have on average the same number of interactions)

and that the role of the species in the network (Stouffer2012) does not influence diversification dynamics. Previous work on the TTIB shown this approximation to be valid to understand the broad principles of spatial food web dynamics, but that a more realistic representation of trophic position and species role does influence occupancy (Gravel2011; Massol2017). In addition to these limitations, the inheritance of traits and the consequently progressive building of the network is susceptible to impact diversification rate (Romanuk2017). For instance, in a predator-prey system, a top carnivore with trophic level 4 requires at least the presence of herbivores and inferior carnivores to establish. The probability of a successful speciation event toward a top predator will therefore increase with species richness, much later than for herbivores.

Speciation and extinction probabilities are computed exactly as described above for the analytical model, except that I is extracted from the knowledge of the interaction network. We therefore need to model the macro- evolution of this network and the role of each species in it. We couple the speciation-extinction model described above with a network model describing interactions as a function of a set of evolving traits for each species. We adopt the formalism of the niche model of food web interactions (Williams2000), extended to represent as well competitive and mutualistic interactions.

Each species is characterized by a set of traits defining their niche. Competition, mutualistic and predator-prey interactions differ by the rules that are set to relate the optimum and the range to the niche position. For simplicity, we consider univariate competition networks and bipartite mutualistic networks. In both cases, species have a niche position n_i and a niche range r_i. A species i interact with other species j whose niche position falls within the range $[n_i - r_i, n_i + r_i]$. In addition for predator-prey interactions, because the interactions are directed, each species has a niche position n_i and an optimum o_i. A predator with niche position n_i feeds on preys whose niche position n_j falls within the range $[o_i - r_i, o_i + r_i]$.

Different rules determine sampling of traits for initial ancestral species and their mutants m. At the start of a simulation, for all three types of interactions, niche position is drawn at random from a uniform distribution bounded between 0 and 1. For simplicity and to avoid the evolution of super generalists (there are no explicit trade-offs giving costs to generality), the range is drawn from a beta distribution with an average $E[r] = 0.2$ and a shape parameter β_r. The optimum is drawn from a beta distribution with mean $E[o] = \gamma_0 + \gamma_1 n$ and shape parameter β_o. This constraint imposes a relationship between niche position, range and optimum inspired by the relationship between predator and prey body size (Gravel2013).

Mutants inherit traits from their ancestors. The niche position is drawn from the beta distribution with an average $E[n]_i$ and a shape parameter β_n. The shape parameter determines the spreading around the average trait value and thus controls the innovation at each mutation event. This trait is the only one to evolve. The range is fixed for all three scenarios. The optimum is deterministically determined from the new niche position. The difference between the expected niche optimum given the niche position is transposed to the new niche optimum. In other words, the niche optimum of the mutant is given by the equation $o_M = E[o_M] + (E[o_A] - o_A)$, where $E[o_i]$ is the expected optimum given the niche position, as described above.

Results

Discussion

- summary of the main conclusions

- the reality can't be any of these extreme cases

- is there any partial support for any of these interpretations ? Can we use the

predictions to revisit some classical studies ?

- what are the additional predictions to test ?

Conclusion

Acknowledgements

Table 1: Summary of model parameters and values used for figures 1-3

. The (-) sign for the extinction function indicates the negative Extinction-Richness relationship and the (+) sign indicates the positive relationship. Connectance was set at 0.1 for all figures.

Variable	Name	Competition	Mutalism	Predation
u_{max}	Maximal speciation rate	0.5		
u_0	Asympotic speciation rate	0		
u_1	Speciation rate at null richness	0.5		
e_{max}	Maximal extinction rate	1		
e_{0-}	Asymptotic extinction rate (-)	0.2		
e_{1-}	Extinction rate at null richness (-)	0.1		
e_{0+}	Maximal speciation rate (+)	NA		
e_{1+}	Maximal speciation rate (+)	NA		
α_u	Decay of $S(R)$ function	0.1		
α_{e-}	Decay of $E(R)$ function for -	0.1		
α_{e+}	Decay of $E(R)$ function for +	NA		

Figure legends

Figure 1

Graphical interpretation of the diversification dynamics with competitive interactions. The vertical dotted line indicate the equilibrium species richness. Arrows points in the direction of the dynamics when the system is out of equilibrium species richness. All parameters are provided at Table 1.
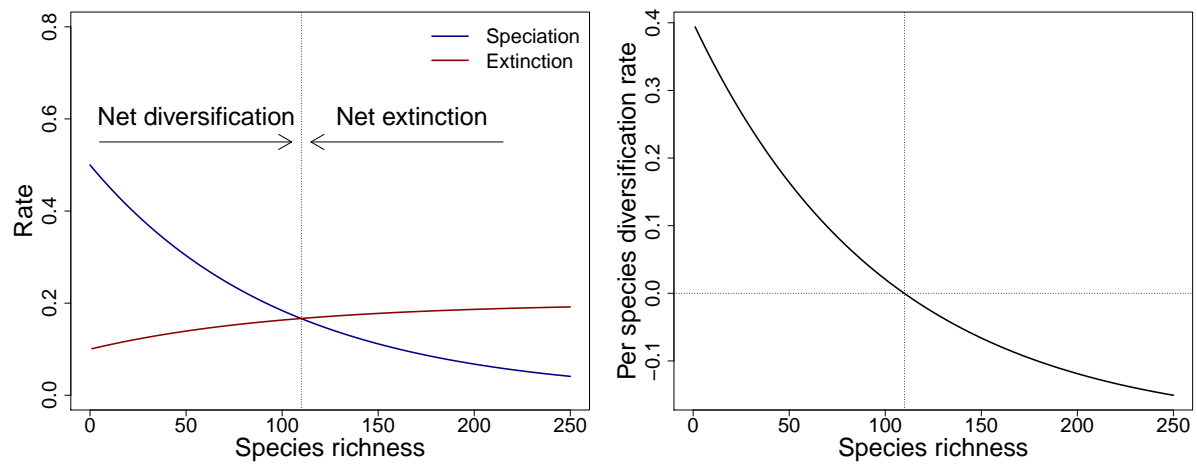
Figure 2

Graphical interpretation of the diversification dynamics with mutualistic interactions. All parameters are provided at Table 1.
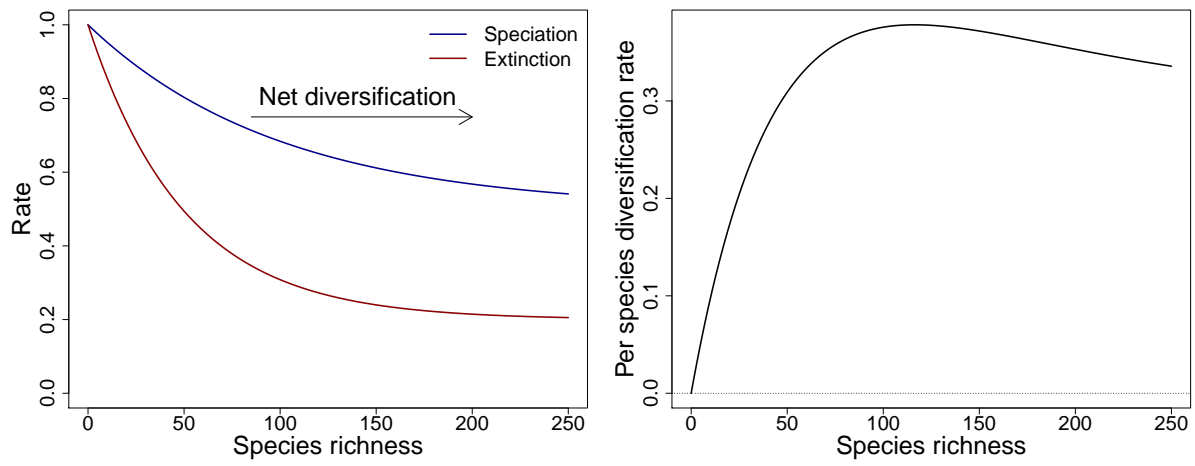
Figure 3

Graphical interpretation of the diversification dynamics with predator-prey interactions. All parameters are provided at Table 1.

Figure 4
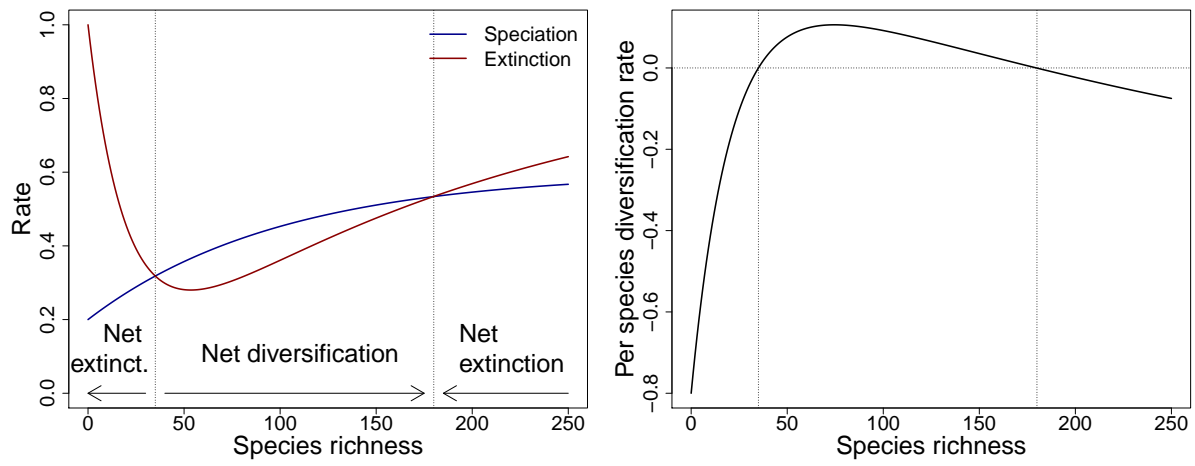
Figure 1

Figure 2

Figure 3

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