

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

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25 Introduction

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

45 Substantial evidence indicates that diversity-dependence of diversification rates are
46 likely real in many cases, but substantial evidence questioning its primacy exists as well.
47 Not all studies examining diversity through time find support for this view in molecu-
48 lar phylogenies, with some studies arguing that such data are consistent with or mask
49 continuously increasing (Morlon et al. 2010; Manceau et al. 2015) or declining diversity
50 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 nonequilibrium 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-prey — 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.

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2009; Gómez and Verdú 2012; Litsios et al. 2012; Joy 2013).  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 in-

terspecific competition within trophic levels for prey or mutualistic partners (Ehrlich and

Raven 1964; Schluter 2000; Armbruster and Muchhala 2007).  ever, it is also possi-

ble 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 interac-

tions 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 macroevo-

lution of network structure, and we thus relax some assumptions and perform numerical

101 simulations below.

102 **Description**

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

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

105 where $S(R)$ is the function describing the speciation rate as a function of species
106 richness, and $E(R)$ the extinction rate. The equilibrium species richness is found when
107 $S(R) = E(R)$. A minimal birth-death model of macro- evolution is species-richness
108 independent, such that S and E are constant rates s and e . We observe exponential
109 diversification provided that $s > e$. More recent models use phenenological representation
110 of the diversification dynamics, such as:

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

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

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

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

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

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


139 and

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


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

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

147 Competition

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

161 Mutualism


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

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is minimal at $I = 0$, with the extreme case of obligate mutualism where $u_1 - u_0 = 0$, and it saturates at the maximal speciation rate $u_0 = u_{max}$.  the opposite of competition, mutualism increases population size and fitness, such that the extinction rate is expected to decrease asymptotically with the number of interactions. We consequently set the extinction probability in absence of interactions at the max $e_1 - e_0 = e_{max}$, with the extreme case of obligate mutualism where $e_{max} = 1$, and the asymptote to $e_0 = e_{min}$. This last probability is larger than 0 because extinctions independent of interactions could nonetheless occur. Note this model applies to mutualistic interactions as well as ammensalism (+,0).

Predator-prey interactions

Predator-prey interactions combine the negative effect of interactions on extinction described for competition with the positive effect of mutualists on colonization described for mutualism.  consider that successful speciation of a predator require to find at least one prey to establish. The speciation function should thus be increasing and saturating with species richness, as it is for mutualism. The extinction function is however more complicated, as it combines two different constraints. First, there increasing benefit of having multiple preys since the likelihood of all preys going extinct should decrease with species richness. Second, predatory interactions could have a negative impact on the prey, reducing there density and potentially leading to extinctions. Depending on the relative importance of these two functions, the final extinction probability could be a monotonic decreasing and asymptotic function of the expected number of interactions, or alternatively it could have a fast decrease followed by an increase of the extinction rate (such as illustrated at Fig. X). In this last situation, there is an initial reduction of extinction probability because of beneficial preys, followed by an increase because of harmful effects 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 equilibrium. 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 equilibrium 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.

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 whether 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.

233 Simulation of network macro-evolution

234 Description

235 The  **topological 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,  by 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)

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2 notes:

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 $[o_i - r_i, o_i + r_i]$.

267 Different rules determine sampling of traits for initial ancestral species and their mu-
 268 tants m . At the start of a simulation, for all three types of interactions, niche position is
 269 drawn at random from a uniform distribution bounded between 0 and 1. For simplicity
 270 and to avoid the evolution of super generalists (there are no explicit trade-offs giving costs
 271 to generality), the range is drawn from a beta distribution with an average $E[r] = 0.2$
 272 and a shape parameter β_r . The optimum is drawn from a beta distribution with mean
 273 $E[o] = \gamma_0 + \gamma_1 n$ and shape parameter β_o . This constraint imposes a relationship between
 274 niche position, range and optimum inspired by the relationship between predator and
 275 prey body size (Gravel2013).

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

285 Results

286 Discussion

- 287 • summary of the main conclusions
- 288 • the reality can't be any of these extreme cases
- 289 • is there any partial support for any of these interpretations ? Can we use the

290 predictions to revisit some classical studies ?

291 • what are the additional predictions to test ?

292 **Conclusion**

293 **Acknowledgements**

294 This is a contribution to the working group Space and time variation of ecological net-
295 works, support by the NIMBIOS.

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	Mutualism	Predation
u_{max}	Maximal speciation rate	0.5		
u_0	Asymptotic 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

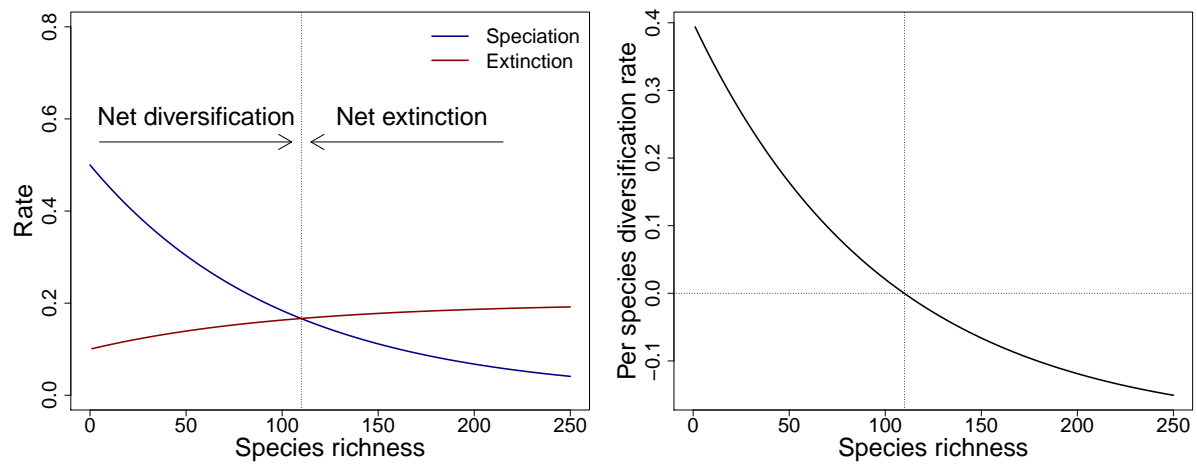
Graphical interpretation of the diversification dynamics with mutualistic interactions. All parameters are provided at Table 1.

Figure 3

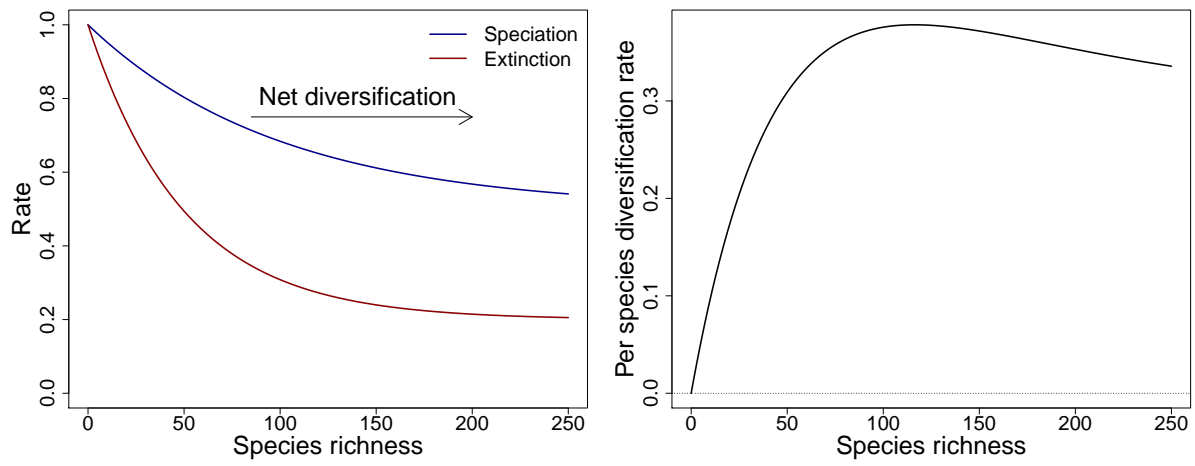
Graphical interpretation of the diversification dynamics with predator-prey interactions. All parameters are provided at Table 1.

308 **Figure 4**

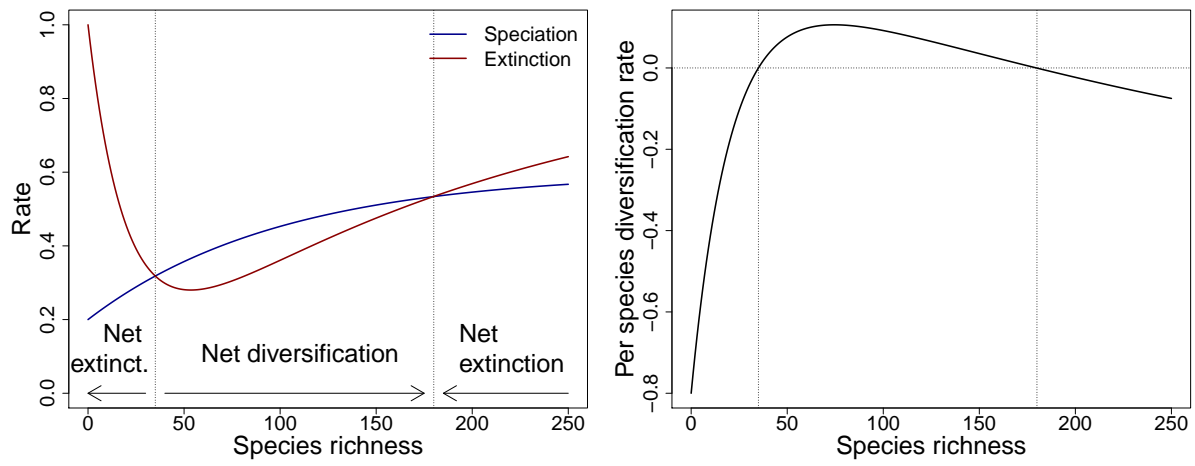
309 **Figure 1**



310 **Figure 2**



311 **Figure 3**



312 **Figure 4**

Should ecological interactions influence diversification rates in ecological networks?

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