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ECOLOGY LETTERS

Understanding the effect of competition during evolutionary radiations: an integrated model of phenotypic and species diversification

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Aristide & Morlon - Files.zip	

TITLE:

UNDERSTANDING THE EFFECT OF COMPETITION DURING EVOLUTIONARY
RADIATIONS: AN INTEGRATED MODEL OF PHENOTYPIC AND SPECIES
DIVERSIFICATION

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STATEMENT OF AUTHORSHIP: LA & HM designed the study. LA performed analyses. LA
& HM wrote the manuscript.

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available at the RPANDA GitHub repository (<https://github.com/hmorlon/PANDA>).

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For Review Only

INTRODUCTION

A long-standing goal in ecology and evolutionary biology is to understand how competition among species modulates the origination and extinction of lineages, and the evolution of phenotypic differences among them (Sepkoski 1996; Doebeli & Dieckmann 2000; Rundle & Nosil 2005; Pfennig & Pfennig 2009; Rabosky 2013; Vermeij 2013; Liow *et al.* 2015; Silvestro *et al.* 2015). Competition is in particular thought to play a key role during adaptive radiations — monophyletic lineages diversifying into several adaptive forms, where each occupies a portion of available ecological space through changes in relevant phenotypic traits (Simpson 1953; Futuyma 1998; Schluter 2000). Adaptive radiation theories have postulated that a lineage can diversify rapidly driven by competition and natural selection in face of an ecological opportunity, and that species and trait diversification rates should slowdown progressively as the available ecological space becomes more densely occupied (Gavrilets & Losos 2009; Harmon *et al.* 2010; Rabosky 2013).

A large number of recent studies have looked for adaptive radiation signatures in comparative datasets (i.e. a phylogeny and associated trait data; Soulebeau *et al.* 2015). As phylogenetic methods that explicitly encapsulate ecological mechanisms are generally lacking (Pennell & Harmon 2013; but see Drury *et al.* 2016; Clarke *et al.* 2017; Manceau *et al.* 2017), most researchers resort to pattern-based tests (e.g. γ statistic for trees, Pybus & Harvey 2000; Phillimore & Price 2008; K statistics for traits, Blomberg *et al.* 2003) or phenomenological models (e.g. “early-burst” for traits, Harmon *et al.* 2010) built upon the general prediction for adaptive radiations of declining macroevolutionary rates. The most mechanistic studies have considered diversity-dependent models built upon the prediction that rates decline as species accumulate (Rabosky & Lovette 2008; Mahler *et al.* 2010; Etienne *et al.* 2012; Weir & Mursleen 2013), or competition models where species phenotypes tend to evolve in unoccupied parts of phenotypic space (Drury *et al.* 2016; Clarke *et al.* 2017; Manceau *et al.* 2017). Using these tools, success or failure in finding the expected signatures is interpreted in terms of the mechanisms generating diversity in the studied clade.

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Despite a substantial research effort, the role and the effect of competition on diversification during evolutionary radiations remain controversial. Several studies indicate that competition within species can promote lineage splitting through disruptive selection on traits (i.e. ecological speciation; Dieckmann & Doebeli 1999; Schluter 2001), but competition can also prevent diversification by reducing ecological opportunity and by driving species to extinction (Bailey *et al.* 2013; Rabosky 2013). How these contrasting effects of competition interact to shape traits and lineages macroevolutionary dynamics and the patterns observed in comparative datasets remains unclear (Meyer & Kassen 2007; McPeck 2008; Bailey *et al.* 2013; Clarke *et al.* 2017). Intriguingly, while competition mechanistically links phenotypic evolution with speciation (*via* ecological character displacement, Doebeli & Dieckmann 2000; Schluter 2001; Rundle & Nosil 2005) and extinction (*via* competitive exclusion of phenotypically similar species, Sepkoski 1978), these processes have not been integrated in a unified macroevolutionary model (Weber *et al.* 2017).

In order to clarify the effect of competition on diversification dynamics and the patterns left on comparative data, we begin by developing an integrated lineage-based model, the Matching Competition Birth-Death model (MCBD), where traits evolve according to a matching competition process (Nuismer & Harmon 2015; Drury *et al.* 2016) and influence speciation-extinction dynamics in a protracted birth-death process (Etienne & Rosindell 2012). Next, we examine the effect of competition by simulating the MCBD model. Particularly, we investigate the conditions under which competition spurs species and phenotypic diversity, and generates the evolutionary rate declines expected from verbal adaptive radiation theory. Finally, we investigate the signatures left on comparative data and discuss our results.

METHODS

The Model

We model lineage diversification using a protracted speciation-extinction process (PBD, Etienne & Rosindell 2012), an extension of the classical birth-death

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3 process (BD; Nee *et al.* 1994) that accounts for the fact that speciation takes time to
4 complete (Etienne & Rosindell 2012). Under the PBD, species produce “incipient
5 species” at a rate λ_1 (speciation initiation) that become “good species” at a rate λ_2
6 (speciation completion). This modeling approach provides a convenient intermediate
7 between simpler lineage-based BD models that cannot incorporate intra-specific
8 processes such as competition-driven population divergence, and more mechanistic
9 models from populations genetics (e.g. Slatkin, 1980) or adaptive dynamics (e.g.
10 Doebeli & Ispolatov 2017), which have the advantage of being based on first principles
11 of drift, fitness, and response to selection, but generally do not make predictions that
12 can be confronted to comparative phylogenetic data (but see Aguilée *et al.* 2018).

23 We consider two versions of the model: one with “asymmetric” speciation
24 initiation (main text), where the ancestral good species persists as a good species and
25 produces one daughter incipient species, and one with “symmetric” speciation
26 initiation (Supplement Information), where the ancestral good species gives rise to two
27 incipient lineages. Incipient lineages inherit trait values from their parent species, and
28 do not give rise to new incipient species. Speciation completion is contingent upon the
29 accumulation of phenotypic differences (Fig. 1a): the speciation completion rate of
30 incipient species i at time t increases with the phenotypic distance with its parent good
31 species (or sister incipient species) j at this time:

$$\lambda_{2i}(t) = \tau_0 e^{\beta(x_i(t)-x_j(t))^2} \quad (1)$$

32 where τ_0 is the basal speciation completion rate, $x_i(t)$ and $x_j(t)$ are the trait values of
33 lineages i and j at time t , and β expresses the extent of the effect of trait differences on
34 the speciation completion rate.

35 Lineages are driven to extinction if they fail to become sufficiently different
36 from other competing lineages, according to the principles of limiting similarity and
37 competitive exclusion (Fig. 1b). The extinction rate μ_i of a lineage i (incipient or good)
38 is a decaying function of the phenotypic distance with all other lineages at time t :

$$\mu_i = \alpha_1 \mu_0 e^{-\alpha_1 (\sum_{j \neq i} (x_i(t)-x_j(t))^2)} + \mu_{bg} \quad (2)$$

where μ_{bg} is a background extinction rate, μ modulates the relative contribution of competition-related extinction with respect to μ_{bg} , and α_1 modulates the effect of trait differences on the extinction rate. μ_{bg} and μ can take distinct values for good and incipient species.

We model trait evolution using a modified version of the “matching competition” (MC) process described in Drury *et al.* (2018), which is based on a model derived by Nuismer & Harmon (2015) from quantitative genetics first principles. The MC model represents character displacement, with competition between co-existing lineages driving phenotypic divergence (Fig. 1c). Competition-driven trait divergence facilitates speciation completion following Eq. 1, and reduces extinction following Eq. 2. We express the change of trait value x on lineage i after an infinitesimally small timestep dt as:

$$x_i(t + dt) = x_i(t) + m\alpha_2 \left[\sum_{j \neq i}^n \text{sign}(x_i(t) - x_j(t)) \times e^{-\alpha_2(x_i(t) - x_j(t))^2} \right] dt + \delta \quad (3)$$

where δ , the Brownian Motion (BM), is a normally distributed random variable with mean 0 and variance $\sigma^2 dt$, and m is a scaling parameter modulating the contribution of the deterministic competition component with respect to the BM. The “sign” term determines the direction of the repulsion in trait space (i.e. species i evolves towards higher trait values if $x_i > x_j$, and lower trait values if $x_i < x_j$), and n is the number of lineages at time t . Finally, α_2 modulates the effect of trait differences on trait evolution. When $\alpha_2=0$, trait evolution is purely neutral (i.e. following BM). Eq. 3 is equivalent to Eq. 1 from Drury *et al.* (2018), without the Ornstein-Uhlenbeck attraction to an optimum, and the m parameter here equals $\frac{m_D}{\alpha_2}$ where m_D is the m parameter in Eq. 1 from Drury *et al.* (2018). This alternative parametrization allows us to evaluate the effect of competition on trait evolution by varying only the parameter α_2 . We consider two versions of the model: one with an unbounded trait space, and one with hard limits on trait space beyond which lineages cannot evolve (Clarke *et al.* 2017). Such hard limits can arise from physiological or genetic constraints. They also represent the

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3 idea of “ecological limits”, that is the existence of a limited breadth of resources that
4 puts a hard limit on the number of species a system can sustain (Rabosky 2009). Note
5 that hard ecological limits are not required to produce ecological constraints: as soon
6 as clades diversify and species start occupying niches, this imposes constraints on the
7 trait values that emerging species can take.
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13 Eqs. 2-3 implement a Gaussian functional form, a convenient and realistic
14 approximation to model the effect of phenotypic distance in trait-driven models of
15 competitive interactions (MacArthur & Levins 1967; Dieckman & Doebeli 1999). We
16 kept a similar functional form (i.e. exponential) in Eq. 1 for consistency, but with the
17 speciation completion rate increasing with phenotypic distance, ensuring that
18 speciation occurs when large phenotypic differences are attained.
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25 Finally, we allow all lineages to interact with one another, implying that they
26 evolve in the same geographic area, a simplifying assumption but an arguably
27 common feature of adaptive radiations (Stroud & Losos 2016). We consider the case of
28 a univariate trait, although it would be straightforward to extend Eqs. 1-3 to consider
29 a multidimensional trait. The univariate case is the simplest, and could be a common
30 scenario if radiations unfold along single, highly integrated phenotypic axes (e.g. lines
31 of least evolutionary resistance; Schluter 1996).
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41 **Simulations**

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43 We implemented a time-discretization of the model in which we sequentially
44 computed trait values and lineage speciation-extinction over many small time-steps.
45 In order to control the crown age of the process, we started each simulation with one
46 good and one incipient species (attributed equal trait values). We ran the simulations
47 for 50 Ma, with time steps of 0.01 Ma. Each simulation produced a diversifying
48 trajectory of lineages and traits through time (Fig. 1d,e). We followed these radiations
49 by registering the traits’ evolutionary history and time of all speciation/extinction
50 events, which we used to build a phylogenetic tree of each process. This tree consisted
51 of extinct lineages, and living good and incipient species (Fig. 1f). By pruning the latter
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3 and extinct lineages, we obtained a reconstructed tree and a vector of present-day trait
4 values (Fig. 1f). Codes for running the simulations are available in RPANDA (function
5 `sim.MCBD`; Morlon *et al.* 2016). We simulated 100 processes for each different
6 parameter setting, discarding simulations that produced reconstructed trees with less
7 than 5 tips or extinct radiations (although these rarely occurred).
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13 In order to easily explore the effects of changing competition strength on
14 diversification, we ran all our simulations with the same values for the effect of trait-
15 driven competition on extinction (α_1) and trait evolution (α_2). We expect α_1 and α_2 to
16 co-vary, as extinction and trait evolution are both driven by the same individual-level
17 process, namely reduced survival of individuals experiencing strong competition
18 (Dieckman & Doebeli 1999). Thereafter we note $\alpha = \alpha_1 = \alpha_2$, and refer to α as the
19 competition strength. We ran a first set of simulations with no bounds in trait space.
20 We set $\beta = 0.6$, $m = 0.2$ and varied competition strength ($\alpha = 0-0.1$). We ran simulations
21 without and with extinction. For those with extinction, we set good and incipient
22 species background extinction rates to $\mu_{bg1} = 0.01$ and $\mu_{bg2} = 0.016$, allowing for trait-
23 dependent extinction rates (competitive exclusion) by setting μ_0 to 50 times μ_{bg1} and μ_{bg2}
24 values, respectively. We set higher incipient extinction rates to account for potentially
25 lower population sizes in incipient lineages. Population size will affect the background
26 extinction rate through both stochastic demographic fluctuations (Lande, 1993) and
27 genetic factors such as inbreeding depression (Frankham, 2005). It will also affect the
28 competition-driven extinction rate as the response to directional selection (and the
29 resulting effect on individuals' fitness if adaptation is too slow) depends on effective
30 population size (Wright, 1931).
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49 We fixed $\sigma^2 = 0.5$ to achieve a good balance between the stochastic and deterministic
50 components of trait evolution. We then ran a second set of simulations with
51 increasingly larger symmetric hard bounds on trait space around the root value and
52 with extinction; fixing competition strength ($\alpha = 0.04$). All other parameter values were
53 the same as in the unbounded simulations. These values were selected through
54 preliminary exploration of the behavior of the model as to obtain biological realism.
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3 For example, ensuring trees of reasonable size for adaptive radiations (i.e. < 30 tips
4 when possible; Harmon et al. 2010) and extinction rates that were not too high (e.g. a
5 maximum turnover rate of 0.4 in the most strongly competitive case).
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10 11 **Model output**

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13 To assess the effect of competition on species richness, trait diversity, and the
14 dynamics of macroevolutionary rates under the MCBBD model, we recorded for each
15 radiation and at each time step species richness, phenotypic disparity, realized
16 speciation, extinction and net diversification rates, speciation duration, and trait
17 evolution rates (Appendix S1).
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23 To investigate the footprint that competition leaves on phylogenetic trait data
24 under the MCBBD model, we applied a set of comparative tools commonly used for
25 detecting adaptive radiations. For each reconstructed tree we computed the γ statistic
26 (Pybus & Harvey 2000), a metric used to test for declines in diversification rates
27 through time. Negative γ values indicate a slowdown in speciation rate towards the
28 present. We also compared the fit (using the AICc; Burnham & Anderson 2004) of
29 different models of diversification, representing: i) constant rates of
30 speciation/extinction (with and without extinction), ii) time-dependent rates with
31 linear/exponential dependences, or iii) diversity-dependent rates with linear
32 dependency on speciation and constant or not extinction (Appendix S2). For each
33 reconstructed tree and associated trait data, we estimated a measure of the
34 phylogenetic signal (K ; Blomberg *et al.* 2003). $K = 1$ is expected under BM and which K
35 values to expect under competition-driven radiations is not entirely clear (Appendix
36 S2). We also compared the fit of commonly used models of phenotypic evolution
37 representing: random (BM; Felsenstein 1985) or constrained (OU; Hansen 1997)
38 evolution, exponentially-changing rates through time (ACDC; Blomberg *et al.* 2003),
39 diversity-dependent rates (DD; Weir & Mursleen 2013), and a model incorporating
40 competitive interactions (MC; Drury *et al.* 2016). We also obtained reconstructed trees
41 and associated γ and K values along the simulations.
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3 Comparative analyses were performed with the R packages RPANDA, geiger
4 (Pennell *et al.* 2014), DDD (Etienne *et al.* 2012), and phytools (Revell 2012).
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8 9 **RESULTS**

10 11 12 *Dynamics of speciation, extinction and species richness*

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15 There were only few conditions under which competition increased the number of
16 species in a clade (Fig. 2a,b & Fig. 3a,b). Even in the absence of both trait limits and
17 extinction, species richness was highest at intermediate (not at highest) competition
18 strength (Fig. 2a,b). As expected from adaptive radiation theory, competition spurred
19 diversification early in the radiation, but then generated fast declines in speciation
20 rates (Fig. 2c). Indeed, competition accelerated speciation completion at the beginning
21 of the radiation and then slowed it down toward the present (Fig. 2d). Hard trait limits
22 were not required to obtain such patterns, as incipient species experienced the
23 constraints imposed by coexisting species (Fig. S1a), which was sufficient to slow
24 down speciation completion and limit species richness.
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35 Competition had a strong effect on the intensity and temporal dynamics of
36 extinction (Fig. 3c), which had cascading effects on other aspects of the radiation
37 (compare Fig. 3 with Fig. 2). Extinction rates of good species were overall higher for
38 stronger competition and increased nearly linearly with time as trait space became
39 more packed (Fig. 3c). Extinction rates of incipient species were also higher for
40 stronger competition. This erased the negative effect of competition on the time to
41 complete speciation towards the present (compare Fig. 3d with Fig. 2d), as only fast
42 diverging incipient lineages escaped extinction and became good species. Speciation
43 rates therefore remained higher under strong competition throughout the radiation
44 (Fig. 3c), even if they declined slightly through time as a result of frequent incipient
45 species extinction (Fig. 3c). The combined effect of competition on extinction and
46 speciation rates led to net diversification rates that were higher early in the radiation
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3 and declined faster later on (Fig. 3c). This resulted in a lower species richness (Fig.
4 3a,b).
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7 Finally, limiting trait space led to markedly fewer species compared to the
8 unbounded case (Fig. 4a,b). This resulted from overall lower speciation rates caused
9 by increasing failed speciation in narrower trait spaces, as there was almost no effect
10 on speciation duration or extinction rates (Fig. 4c-d). Limiting trait space did not have
11 a marked effect on temporal diversification dynamics: as in the unbounded case,
12 speciation slowed down and extinction increased strongly, resulting in a net
13 diversification rate slow down (Fig. 4c-d).
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23 *Dynamics of trait disparity and evolution rates*

24 While competition did not necessarily increase clade size, it generated clades with
25 high trait disparity (Fig. 2e & 3e), unless this disparity was limited by hard trait bounds
26 (Fig. 4e). Even low levels of competition lead to an exponential increase in trait
27 disparity through time, compared to a linear increase in the absence of competition
28 (Fig. 2e & 3e). In unbounded trait spaces, even though competition generated all the
29 ecological constraints on evolution mentioned above, this did not result in a slowdown
30 in the accumulation of trait disparity. The accumulation of trait disparity only
31 progressively slowed down in bounded trait spaces, and only once bounds were hit
32 (which occurred increasingly late as boundaries got wider, Fig. 4e).
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44 Contrary to what happened for species diversification dynamics, we rarely
45 observed slowdowns in mean trait evolution rates (Fig. 2f, 3f and 4f). There was an
46 initial drop down very early in the radiation, in the period preceding the first
47 speciation event, when trait space was empty and the only two existing lineages could
48 freely evolve away from each other. After this short period, mean trait evolution rates
49 were either slightly increasing (in unbounded radiations without extinction, Fig. 2f) or
50 constant (in bounded and unbounded radiations with extinction, Fig. 3f & 4f). These
51 average rate patterns hide a strong heterogeneity across lineages (Fig. S2). Coherent
52 with ideas of ecological opportunity and ecological limits, directional evolution in
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3 competition-driven radiations was faster in lineages near empty zones of trait space
4 (i.e. edges in unbounded radiations), with near-stasis in the crowded, constrained
5 middle (Fig. S2a,b). In the absence of extinction, this increase in evolutionary rate at
6 edges overcompensated the decrease towards the middle, leading to the observed
7 slight increase in mean rates (Fig. 2f & S2a). Extinction erased this increase by
8 moderating the competitive pressure experienced by lineages (Fig. 3f and S2b). Even
9 in the presence of hard trait limits, when bounds were reached and diversity
10 approximated equilibrium, mean rates did not decline (Fig. 4f & S2c). Lineages near
11 the bounds experienced slow rates as they could not evolve further, but intense
12 competition drove many species extinct, constantly freeing up trait space. Overall,
13 these cycles of extinction, branching and reoccupation of trait space leveled off
14 evolutionary rate declines imposed by bounds.
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30 *Patterns left in contemporary data*

31 γ did not appear as a robust signal of competition (Fig. 5, first column). Without
32 extinction, reconstructed trees showed increasingly negative γ values with increasing
33 competition strength (Fig. 5a), but neutral radiations also exhibited negative γ values,
34 indicating that at least part of this signal stemmed from the protracted nature of the
35 speciation process. Moreover, γ values between competitive and neutral radiations
36 only began to diverge late in time (Fig. S3a). In the presence of extinction, γ values
37 increased rather than decreased with competition strength, as radiations with more
38 intense competition experienced more extinctions (Fig. 5b). Finally, trees from
39 bounded competition-driven radiations had γ values that became less negative as trait
40 space became narrower (Fig. 5c).
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51 Diversification models were not particularly useful either for detecting
52 competition-driven radiations (Fig. 5, second column). Without extinction, both
53 neutral and competition-driven radiations produced an important proportion of
54 reconstructed trees that best supported models with declining (mostly linearly)
55 speciation rates. Extinction progressively erased the signal of diversification rate
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3 decline as competition increased: trees from neutral radiations indicated support for
4 models of declining speciation and increasing extinction rates, while for competition-
5 driven radiations support increased toward models of constant speciation-extinction
6 (Fig. 5b). Support for models with declining speciation and increasing extinction
7 decreased further in the presence of bounds and as bounds got narrower (Fig. 5c).
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13 Phylogenetic signal (K) in tip trait data provided a more consistent signature of
14 competition (Fig. 5, third column). K values were higher for competition-driven than
15 for neutral radiations, indicating that as morphospace is progressively occupied,
16 competition constrains closely related species to a limited portion of this space (Fig.
17 S2). In the absence of bounds, the signature of competition provided by K became
18 stronger as the radiation proceeded (Fig. S3a,b). In bounded radiations, K was highest
19 at the time when the bounds were hit, and then remained stable or slowly decreasing
20 (Fig. S3c). K therefore decreased with increasingly tight trait spaces, but remained
21 generally higher than under neutral radiations (Fig. 5c, the only exception occurred in
22 the most constrained trait space).
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33 The other consistent signature of competition was the statistical support for the MC
34 model (Fig. 5, last column), which is noteworthy as it is different in several aspects
35 from the generating model (Appendix S2). Trait model fitting generally recovered the
36 MC model as the best for all competition-driven radiations, while the BM model was
37 recovered for most neutral radiations (Fig. 5a,b). Support for the MC model was
38 however progressively lost as bounds got tighter (Fig. 5c). Models with decreasing
39 rates of evolution (e.g. diversity or time dependent rates) were never selected over MC.
40 When we nevertheless examined the recovered rate change parameter for the ACDC
41 model in competition-driven radiations, we found that it was generally negative
42 (representing a model with declining rates), the only exception being tightly bounded
43 radiations where this parameter was positive (Fig. S4).
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58 DISCUSSION

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3 We investigated the macroevolutionary consequences of interspecific
4 competition during radiations, and the signal left on contemporary data under several
5 scenarios. We found four main results: first, competition-driven radiations promote
6 trait diversity, but not necessarily species richness; second, competition-driven
7 radiations show declines in speciation and net diversification rates, even in
8 unbounded trait spaces, but not in trait evolution rates, even in bounded trait spaces;
9 third, testing for early burst patterns of species and/or trait diversification in
10 comparative data does not provide a good test of adaptive radiations; fourth,
11 phylogenetic signal in trait data and support for matching competition models may
12 provide promising alternatives for detecting adaptive radiations.
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15 It has been suggested that much of life's diversity, both in terms of species
16 number and body form, originated as adaptive radiations (Simpson 1953). Whether
17 this is the case or not, here we find that competition-driven radiations tend to generate
18 phenotypic diversity, but not higher species richness than neutral radiations. While
19 competition-driven character displacement increases speciation rates at the beginning
20 of clades' history, either the ecological constraints in trait space imposed by competing
21 species or competitive exclusion ("Darwinian extinction", Sepkoski 1978; Webb 2003;
22 Pfennig & Pfennig 2005) limit this diversity-generating process once trait space is
23 packed.
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26 Another general expectation of verbal theories of adaptive radiation is that there
27 are "early bursts" of both speciation and trait evolution, with rates that are highest at
28 early stages of diversification, declining later as competition for ecological space
29 increases (Simpson 1953; Schluter 2000). We did observe early burst patterns of
30 speciation: rates are initially high as fast trait divergence in an empty ecological space
31 leads to fast speciation, declining afterwards. In the absence of extinction, the decline
32 is driven by a "duration" control of speciation (Dynesius & Jansson 2014): speciation
33 takes more time to complete as incipient lineages have more difficulty diverging
34 ecologically from their parent species in an increasingly packed morphological space.
35 In the presence of extinction, the decline is instead driven by increasing extinction of
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3 incipient lineages, as in “ephemeral speciation” models (Stanley 1979; Futuyma 2010;
4 Rosenblum *et al.* 2012). Bounds in trait space and saturation of ecological space
5 exacerbate competition-driven declines in diversification rates, but are not required:
6 the constraints in phenotypic space imposed by competing lineages is sufficient by
7 itself to slow down diversification as radiations proceed. Although radiating in
8 multidimensional trait spaces might alleviate these constraints (Doebeli & Ispolatov
9 2017), if species mostly diversify along single or a few phenotypic axes (e.g. lines of
10 least evolutionary resistance; Schluter 1996), the described scenario might be common
11 and invocation of contentious hard ecological limits to diversity not needed, favoring
12 “damped” diversification explanations instead (Cornell 2013, Harmon & Harrison
13 2015).

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Conversely, we did not observe early burst patterns of trait evolution in
competitive radiations, even in bounded trait spaces. Mean rates tended to remain
constant or even slightly increased. As lineages diversify trait space becomes more
packed and competitive pressure increases (this occurs even in multidimensional
phenotypic spaces; Doebeli & Ispolatov 2017). In radiations far from (or without)
ecological limits and with no extinction, fast competition-driven evolution at edges of
occupied trait space overcompensates the effect of the constraints imposed by trait
space packing in its central region; this even results in slight increases in mean trait
evolution rates. Some empirical studies have indeed found evidence for higher rates
at extremes of occupied morphospace (e.g. Cooper & Purvis 2009) or increasing
evolutionary rates towards the present in adaptive traits (e.g. Venditti *et al.* 2011;
Hopkins & Smith 2015). When increased competition leads to frequent extinctions,
these open up trait/niche space, which reduces the competitive pressure to evolve at
edges and the constraints imposed by trait space packing in its central region, resulting
in nearly constant mean trait evolution rates. These results are consistent with recent
paleontological studies that did not find evidence for trait evolution rate declines in
adaptive macroevolutionary diversification (Hopkins & Smith 2015). Hence, the idea
that mean trait evolution rates will decline during adaptive radiations because of

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3 increased competitive constraints on morphospace occupation might not necessarily
4 hold; instead, we suggest that under some conditions character displacement and high
5 lineage turnover fostered by increased competitive pressure may balance the effect of
6 niche packing. Empirical studies are needed to clarify the potential generality of this
7 process.
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13 As expected (even for constant-rate neutral evolution; Foote 1996), in bounded trait
14 spaces trait disparity reaches its maximum when boundaries are reached. However,
15 competition does not necessarily lead lineages to trait boundaries early in a radiation
16 unless the bounds are small compared to niche width: character displacement pushes
17 species away in trait space, but it does so just enough to escape competition, so that it
18 takes time before lineages reach the boundaries of trait space. Thus, our model predicts
19 that relatively early disparity peaks may only be observed in adaptive radiations that
20 are either very old compared to the moment where they hit bounds, or characterized
21 by a tightly constrained trait space where significant species diversification would be
22 difficult. Hence, if early disparity peaks are repetitively observed across species-rich
23 clades irrespective of their age, as has been observed in the fossil record (Hughes *et al.*
24 2013), this suggests that the traits considered evolve in such constrained
25 morphological spaces (Foote 1996; Gavrillets 1999), but that these traits are not the ones
26 that are involved in competitive interactions and niche partitioning (if such
27 interactions and partitioning occur).
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44 Taken together, our results show a decoupling between rates that are often thought
45 to be coupled. In particular, rates of trait evolution can remain constant (or even
46 increase) despite decreasing diversification rates. And in adaptive radiations that
47 reached ecomorphological limits, rates of trait evolution can remain constant despite
48 disparity reaching a plateau, similarly to the “fly in a tube” effect (Felice *et al.* 2018).
49 These two decoupling are both linked to the continuous reoccupation of vacated trait
50 space after extinctions.
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57 Biologists have searched for early burst patterns in comparative data as a signal of
58 adaptive radiations (Harmon *et al.* 2003, 2010; Moen & Morlon 2014). Paradoxically,
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3 despite not producing declines in trait evolution rates, fits of the ACDC model to our
4 simulated competition-driven radiations infer a decelerating rate process, except in
5 tightly bounded trait spaces where an increasing rate process is inferred (Fig. S4).
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7 These later results add to a growing literature suggesting that temporal trends found
8 when fitting an ACDC model to extant trait data should not be used to draw
9 conclusions about the process itself (Revell *et al.* 2008; Uyeda *et al.* 2015). Our analyses
10 also confirm that early bursts of diversification may be difficult to discriminate from
11 an apparent decline stemming from the protracted nature of speciation (Etienne &
12 Rosindell 2012). Additionally, we corroborate that extinction erases the signature of
13 declining rates in reconstructed trees (Rabosky & Lovette 2008b; Liow *et al.* 2010). Thus,
14 commonly observed slowdowns in real phylogenies (McPeck 2008; Phillimore & Price
15 2008; Morlon *et al.* 2010) might not necessarily be indicative of ecological modes of
16 diversification but of other mechanisms (Moen & Morlon 2014). Our results suggest
17 that increasing extinction rate could be another mark of adaptive radiations (as
18 proposed in previous studies, e.g. McPeck 2008; Rabosky & Lovette 2008a; Aguilée *et*
19 *al.* 2018), but that this signal is not picked up by common likelihood-based models of
20 diversification.
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37 While searching for early bursts in comparative data does not seem the most
38 reliable way to detect competition-driven radiations, our results suggest that
39 alternative signals could be exploited. The two clear signatures are a strong
40 phylogenetic signal (as measured by Blomberg's K) and a greater likelihood of
41 phenotypic models incorporating competitive interactions (Drury *et al.* 2016). That
42 competition leads to high phylogenetic signal (indicating that closely related species
43 are more similar than expected) is perhaps unanticipated, as character displacement
44 will tend to increase differences between two competing species (Pfennig & Pfennig
45 2009). Conversely, here we show (similarly to Clarke *et al.* 2017) that tree wide
46 competition, while increasing overall disparity, tends to limit the morphospace
47 occupied by subclades, leading to a strongly structured trait distribution in which
48 species tend to occupy the same trait regions as their ancestors (e.g. niche
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3 conservatism; Harmon *et al.* 2003; Losos 2008). The only scenarios under which
4 competition-driven radiations do not generate a high phylogenetic signal are scenarios
5 with tight trait bounds (Fig. 5c; Revell *et al.* 2008) that produce low species diversity.
6 Those are also the only exceptions to the otherwise widespread support for matching
7 competition models (Drury *et al.* 2016). Support for models incorporating competitive
8 interactions is even more informative than phylogenetic signal alone. Indeed, while a
9 declining rate unrelated to competition would also generate phylogenetic signal
10 (Revell *et al.* 2008), trait evolution models can distinguish these two scenarios because
11 they induce a different morphospace occupation: gaps in trait space under declining
12 rates, and more even distribution under competition (Clarke *et al.* 2017). It would be
13 interesting to test if novel statistics that capture finer scale variation in a trait's
14 distribution than Blomberg's K (e.g. Lewitus *et al. in review*) are also able to distinguish
15 these two scenarios, as well as to check if phylogenetic signal remains a feature of
16 adaptive radiations in multidimensional trait space (Harvey & Rambaut 2007, Doebeli
17 & Ispolatov 2017). Likewise, it would be useful to assess the robustness of the support
18 for Drury *et al.*'s MC models (2016) with a variety of competition-driven radiation
19 scenarios, as it could be argued that our generating model resembles the MC inference
20 tool. In addition to a strong phylogenetic signal and support for the matching
21 competition model, competition-driven radiations can generate heterogeneous trait
22 evolution rates (and also most likely diversification rates), with higher rates for species
23 at the extremes of occupied morphospace. This pattern could potentially be exploited
24 with recent comparative methods that allow estimating branch-specific rates (Venditti
25 *et al.* 2011; Rabosky 2014; Maliet *et al.* 2019).

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As with any modelling approach, we made a series of simplifying assumptions that
may impact our results. In particular, population-level dynamics or landscape features
may affect macroevolutionary outcomes (Aguilée *et al.* 2018). Nonetheless, we were
able to investigate in a formal framework some fundamental ideas on adaptive
radiations that clarify the macroevolutionary consequences of competition and will
hopefully help design more precise and powerful tools to investigate them.

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26 27 28 29 30 31 SUPPORTING INFORMATION

32
33 Additional Supporting Information may be downloaded via the online version of this
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35 article at Wiley Online Library (www.ecologyletters.com).

36 37 38 39 40 FIGURE LEGENDS

41 42 43 **Figure 1 - An integrated phylogenetic model of traits and species diversification.**

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45 The speciation completion rate of a lineage depends on the distance with its parental
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47 species (A). The extinction rate (B) and the competition-driven component of trait
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49 evolution (C) are plotted as a function of the distance between two competing lineages.

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51 The α parameters control competition strength. Higher α values model a scenario
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53 where more similar phenotypes compete more strongly, implying a strong association
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55 between trait values and resource use. Conversely, a scenario where the evolving trait
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57 is less important for resource allocation is modeled by lower α values, as competition
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59 is less intense and less related to phenotypic differences among lineages. (D, E)

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3 Simulations produce a diversifying trajectory of species and traits through time, and
4 we study the effect of competition by varying α values. (D) shows an example
5 radiation under competitive evolution, and (E) under purely neutral evolution.
6 Lineages in orange are incipient species. (F) From a simulation we obtain a tree
7 describing the full diversification process (first panel), from which we derive the fossil
8 tree (second panel) and the reconstructed tree with trait values at tips (third panel).
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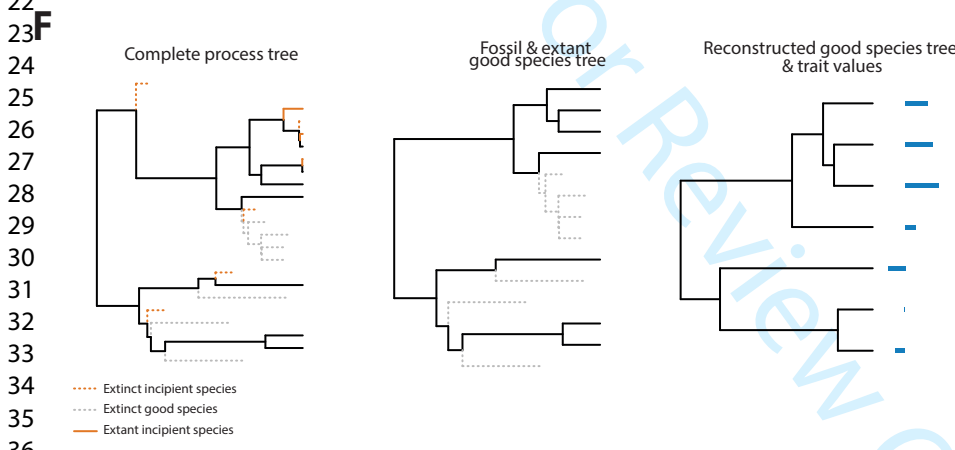
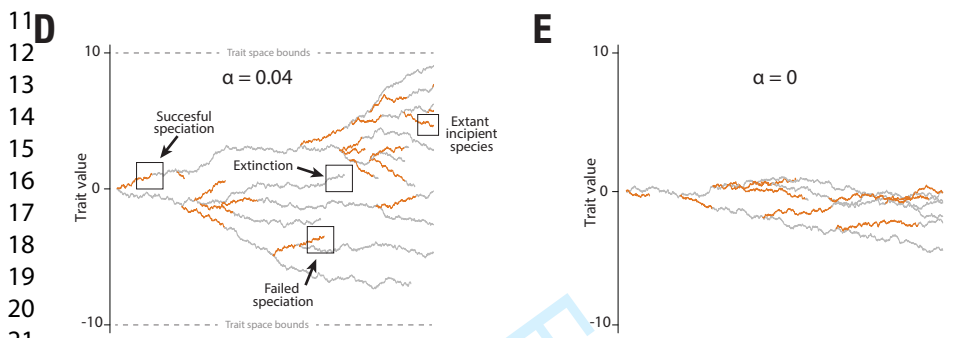
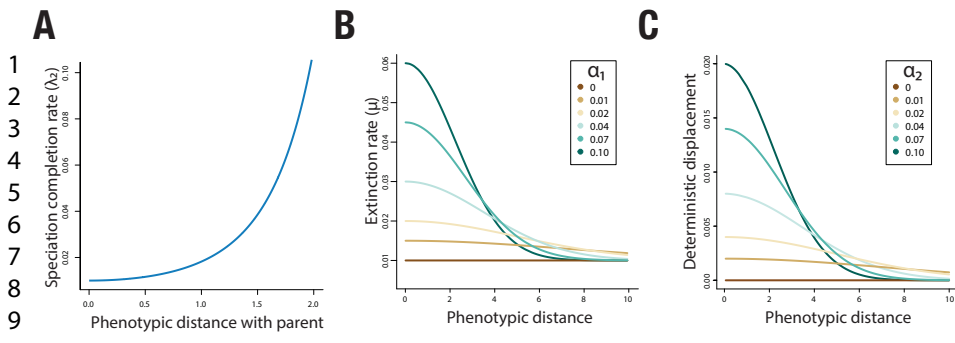
17 **Figure 2 – Effect of competition on diversification patterns in an unbounded trait**
18 **space and no extinction.** We performed 100 simulations for each α value. All other
19 parameters were fixed (see methods). (A) Mean species richness (log scale) through
20 time. (B) Final species richness (reconstructed tree size). (C, D) Realized mean
21 speciation rates and speciation duration through time. (E) Mean trait disparity. (F)
22 Mean trait evolution rate. Colored lines in (C,D,F) are a smoothed function fitted to
23 the colored dots (1 Ma bins) for clearer representation. Notice the higher stochasticity
24 at the beginning of the simulations given the fewer lineages present.
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35 **Figure 3 - Effect of competition on diversification patterns in an unbounded trait**
36 **space with competitive exclusion.** (A) Mean species richness (log scale) through time.
37 (B) Final species richness (reconstructed tree size). (C) Realized mean speciation rates,
38 good species extinction rates, and net diversification rates (speciation minus
39 extinction). (D) Speciation duration. (E) Mean trait disparity. (F) Mean trait evolution
40 rate.
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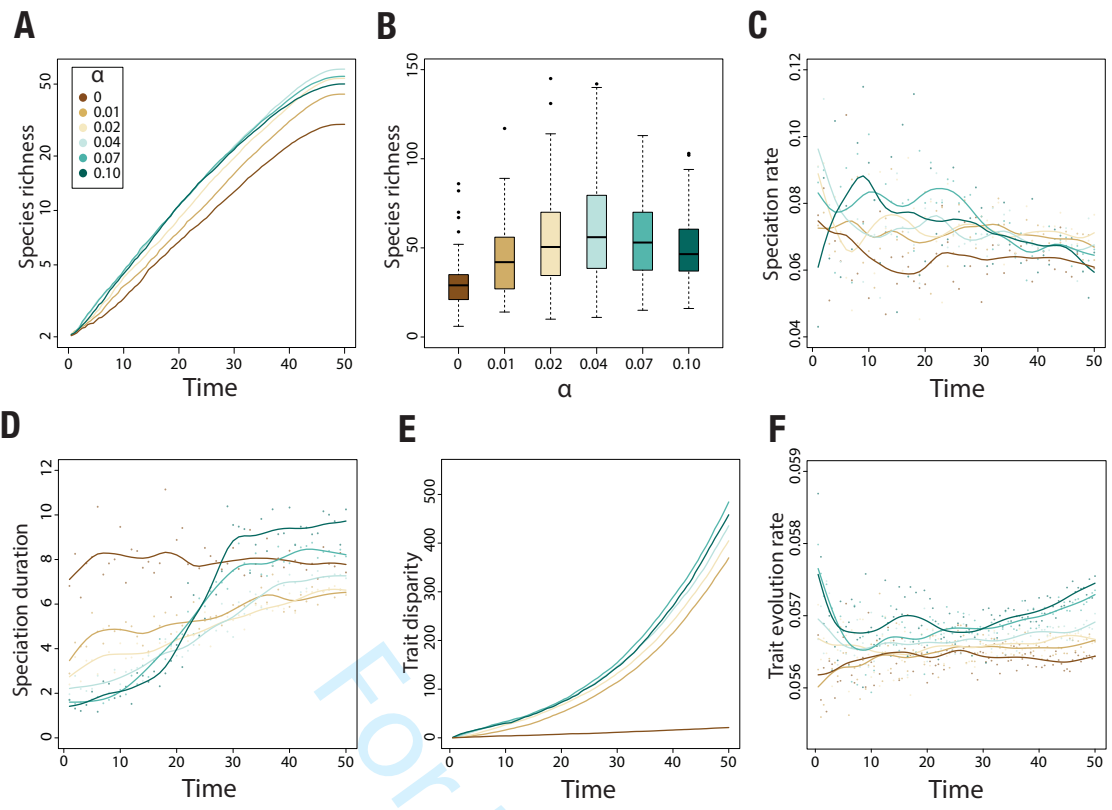
50 **Figure 4 - Effect of competition on diversification patterns with bounds on trait**
51 **space and competitive exclusion.** Competition strength was fixed at an intermediate
52 value ($\alpha = 0.04$). Trait/ecological space was increasingly larger (higher width). (A)
53 Mean species richness (log scale) through time. (B) Final species richness
54 (reconstructed tree size). (C) Realized mean speciation rates, good species extinction
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3 rates, and net diversification rates (speciation minus extinction). (D) Speciation
4 duration. (E) Mean trait disparity. (F) Mean trait evolution rate.
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9 **Figure 5 – Patterns recovered on reconstructed trees and trait tip data using**
10 **phylogenetic comparative methods.** Results for simulated radiations without (A) and
11 with competitive exclusion (B) and no bounds, and with competitive exclusion and
12 bounds (C). From left to right: γ statistic for tree shape; species diversification model
13 fit (proportion of trees showing support for a given birth-death model, where B/D
14 indicate speciation/extinction, and cst, lin and exp indicate constant, linearly or
15 exponentially time-changing rates); phylogenetic signal (K) in trait data; and
16 phenotypic evolution model fit (proportion of trees showing support for each of the
17 following models: Matching Competition (MC), single optimum Ornstein-Uhlenbeck
18 (OU), exponentially increasing or decreasing rates through time (ACDC), Brownian
19 motion (BM), and exponential (DDe) or linear (DDl) diversity-dependent rates). See
20 Appendix S2 for details.
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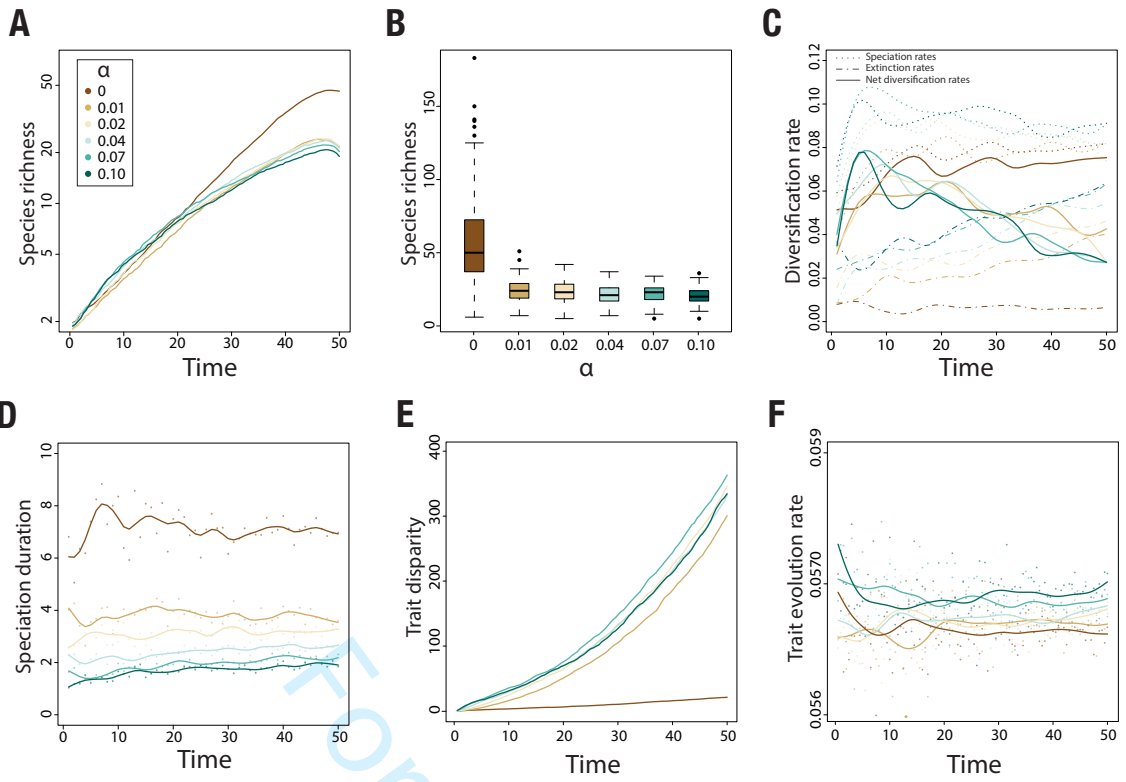


..... Extinct incipient species
..... Extinct good species
——— Extant incipient species



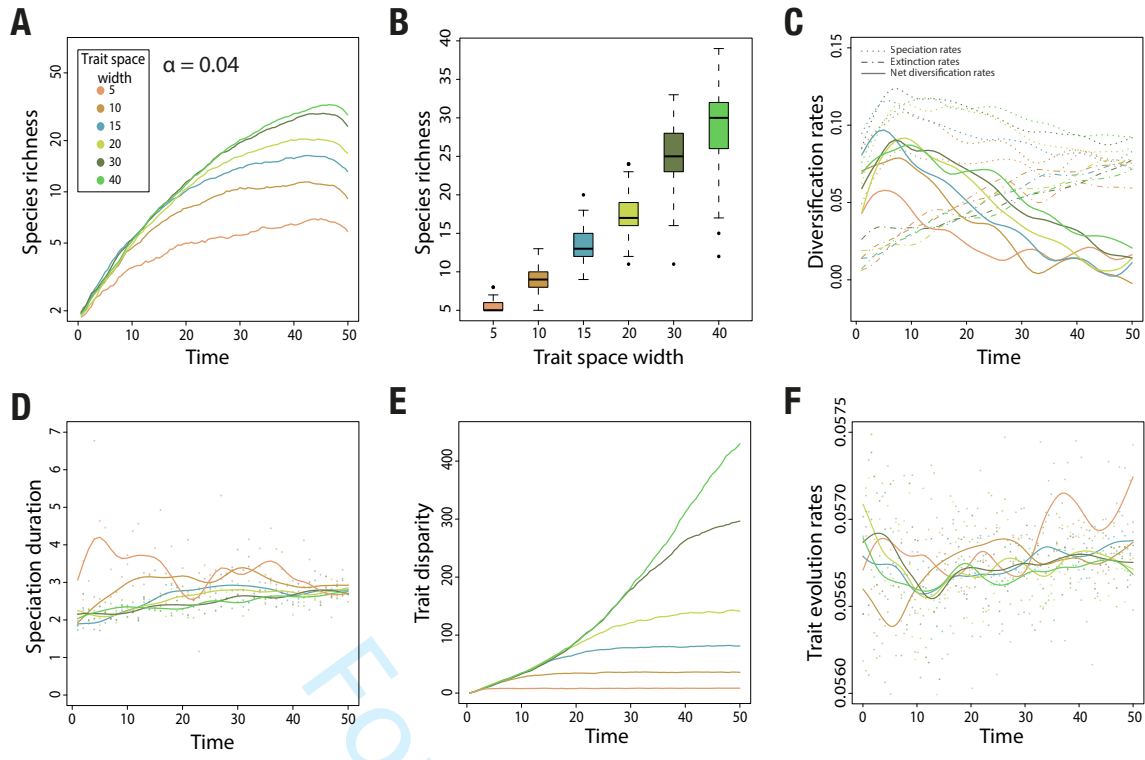
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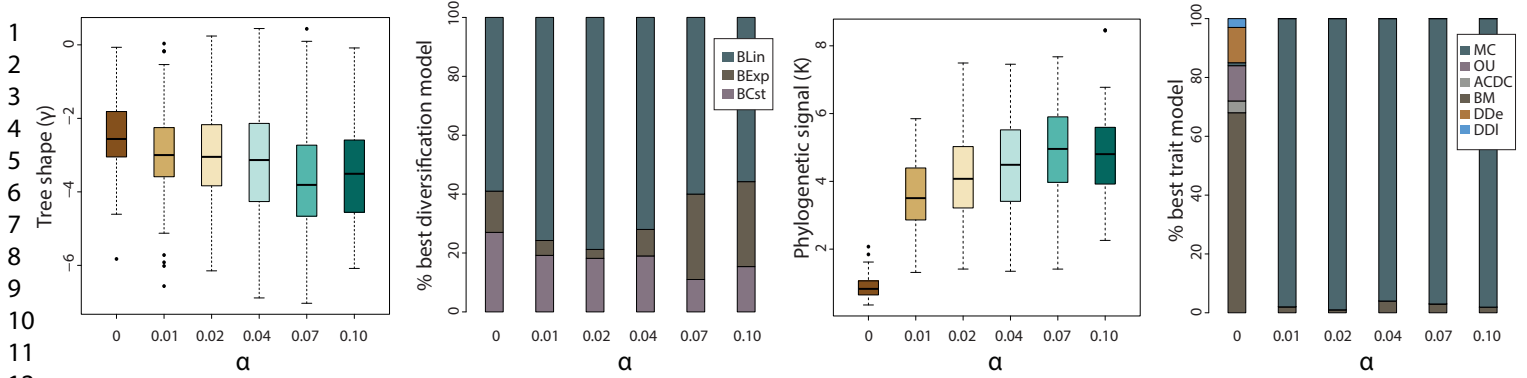
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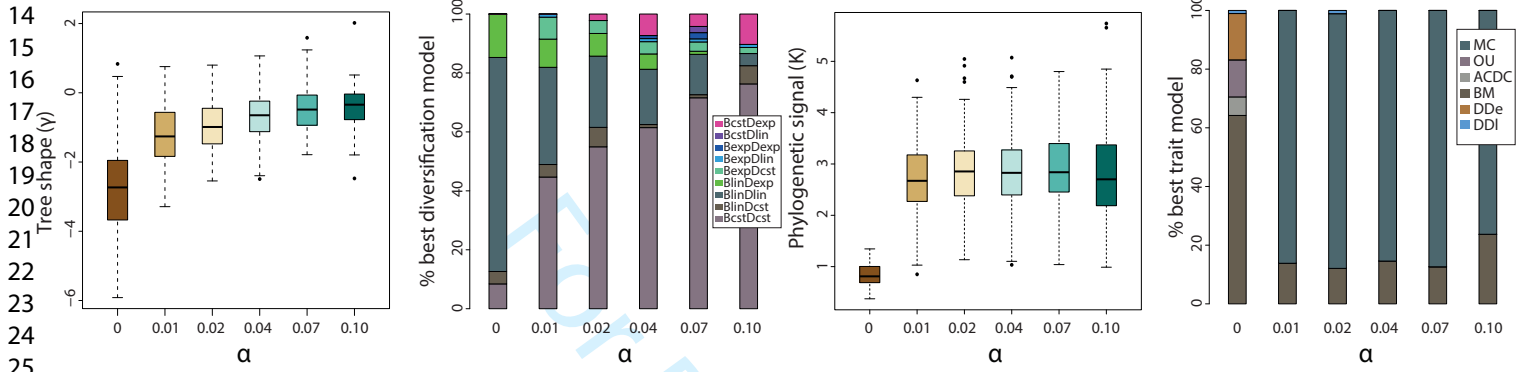
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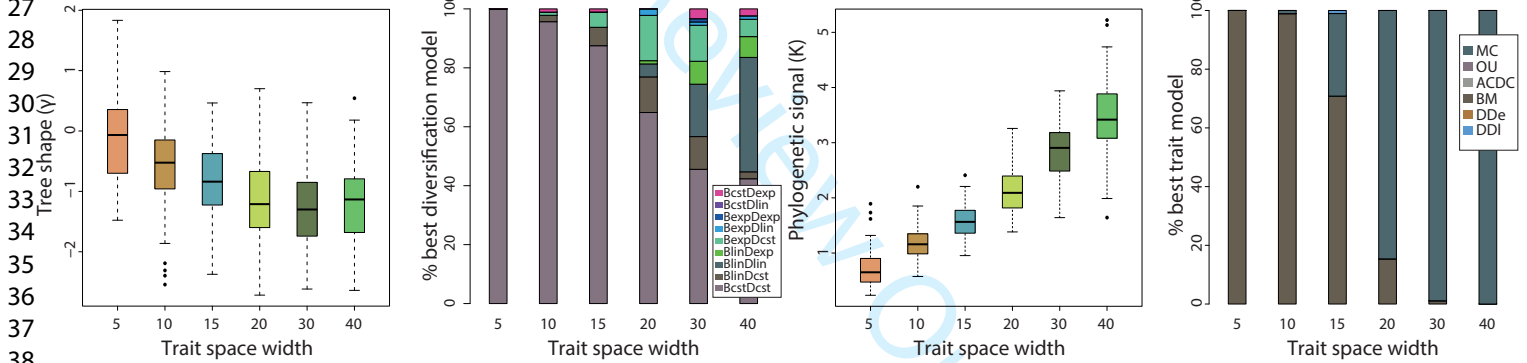
A No extinction, no bounds



B With extinction, no bounds



C Fixed α (0.04), with extinction and bounds



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