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The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity

Pontarp, Mikael ; Wiens, John J

Abstract: Aims: Patterns of species richness, such as the remarkable biodiversity of tropical regions, have been documented and studied for centuries. However, their underlying evolutionary and ecological causes are still incompletely understood. A commonly stated paradigm in the literature is that high richness in some habitats is directly caused by one of three competing explanations: (1) greater time-for-speciation (earlier colonization), (2) more rapid diversification rates (faster speciation relative to extinction) or (3) higher carrying capacity. However, these three explanations have been relatively little studied using theoretical approaches (especially in terms of comparing all three). Furthermore, empirical studies give conflicting results about their relative importance. Here, we use simulations to study the processes that drive richness patterns along environmental gradients. Location: Globally applicable. Methods: We use individual-based and trait-based modelling of eco-evolutionary dynamics to simulate the evolutionary radiation of a clade across five habitats with differing ecological conditions, and track patterns of species richness within and between habitats over time. We specifically address the roles of time and diversification rates in explaining richness patterns and the potential impact of carrying capacity. Main results and conclusions: Contrary to the widespread paradigm, we find that variation in carrying capacity can underlie differences in diversification rates and time-for-speciation among habitats. Therefore, carrying capacity is not a competing, alternative explanation for richness patterns. We also find that the time-for-speciation effect dominates richness patterns over short time-scales, whereas diversification rates dominate over longer time-scales. These latter observations can help reconcile the seemingly conflicting results of many empirical studies, which find that some patterns are explained by time and others by differences in diversification rates.

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25 **ABSTRACT**

26 **Aims** Patterns of species richness, such as the remarkable biodiversity of tropical regions,
27 have been documented and studied for centuries. However, their underlying evolutionary
28 and ecological causes are still incompletely understood. A commonly stated paradigm in
29 the literature is that high richness in some habitats is directly caused by one of three
30 competing explanations: higher richness is caused by either (i) higher carrying capacity,
31 (ii) greater time for speciation (earlier colonization), or (iii) more rapid diversification
32 rates (faster speciation relative to extinction). However, these three explanations have
33 been relatively unstudied theoretically using theoretical approaches (especially in terms
34 of comparing all three). Furthermore, empirical studies give conflicting results about their
35 relative importance. Here, we use simulations to study the processes that drive richness
36 patterns along environmental gradients.

37 **Location** Globally applicable.

38 **Methods** We use individual-based and trait-based modelling of eco-evolutionary
39 dynamics to simulate the evolutionary radiation of a clade across five habitats with
40 differing ecological conditions, and track patterns of species richness within and between
41 habitats over time. We specifically address the roles of time and diversification rates in
42 explaining richness patterns and the potential impact of carrying capacity.

43 **Main results and conclusions** Contrary to the widespread paradigm, we find that
44 variation in carrying capacity can underlie differences in diversification rates and time-
45 for-speciation among habitats. Therefore, carrying capacity is not a competing,
46 alternative explanation for richness patterns. We also find that the time-for-speciation
47 effect dominates richness patterns over short time scales, whereas diversification rates

48 dominate over longer time scales. These latter observations can help reconcile the
49 seemingly conflicting results of many empirical studies, which find that some patterns are
50 explained by time and others by differences in diversification rates.

51

52 INTRODUCTION

53 Explaining patterns of species richness is a fundamental goal of biogeography, ecology,
54 and evolutionary biology. Species richness often varies along environmental gradients,
55 and at many different spatial scales. For example, many clades have more species in
56 tropical than temperate regions (e.g. Pianka, 1966; Rohde, 1992; Hillebrand, 2004). Yet,
57 richness can also vary among habitats within a region, such as at different elevations (e.g.
58 Rahbek, 1995).

59 There has been growing appreciation for the idea that these diverse species
60 richness patterns originate through a combination of both ecological and evolutionary
61 processes (e.g. Ricklefs, 1987; Wiens & Donoghue, 2004; Mittelbach *et al.*, 2007).
62 Richness patterns arise through the processes of speciation, extinction, and dispersal,
63 where dispersal refers to successful establishment of a lineage in a new region or habitat.
64 These are the processes that directly change the number of species in a given location,
65 even if there is a perfect relationship between richness and one or more environmental
66 variables (i.e. correlations with ecological variables do not negate the importance of these
67 evolutionary and biogeographic processes). Therefore, in order to understand how
68 richness patterns originate along environmental gradients, we need to understand how
69 environmental variables influence these three processes (e.g. Ricklefs, 1987; Wiens &
70 Donoghue, 2004; Mittelbach *et al.*, 2007).

71 Given this perspective, a widespread paradigm in the literature is that there are
72 three main explanations for why species richness patterns vary along environmental
73 gradients. These explanations involve variation in diversification rates, time, and carrying
74 capacity (review in Mittelbach *et al.*, 2007; see also Rabosky, 2009). Many prominent

75 studies have specifically emphasized the idea that these are three competing explanations
76 (e.g. Rabosky & Glor, 2010), especially diversification rates and carrying capacity (e.g.
77 Rabosky, 2009).

78 First, local environmental conditions at one end of the gradient may increase
79 diversification rates there (diversification is the balance of speciation and extinction over
80 time). Various ecological factors may act to modify these rates and patterns of speciation
81 and extinction (review in Mittelbach *et al.*, 2007). For example, the latitudinal diversity
82 gradient may arise due to higher tropical speciation rates (possibly related to narrower
83 ecological niches in the tropics) and higher temperate extinction rates (potentially caused
84 by climatic changes associated with glacial cycles).

85 Second, patterns of richness may be explained by the time-for-speciation effect
86 (*sensu* Stephens & Wiens, 2003). Specifically, if one part of the gradient is colonized
87 first, then these habitats may have higher richness simply because there is more time for
88 speciation to occur and for species to accumulate in these habitats. Limited dispersal
89 between habitats is a key component of this hypothesis, and may be related to strong
90 ecological differences between habitats and the limited ability of species to adapt to these
91 differences (e.g. niche conservatism; review in Wiens *et al.*, 2010).

92 Empirical studies have found mixed support for these first two hypotheses, with
93 many studies within regions supporting the time effect (e.g. Brown *et al.*, 2000; Rangel *et*
94 *al.*, 2007; Wiens *et al.*, 2007; Kozak & Wiens, 2010; Hutter *et al.*, 2013), many larger-
95 scale studies supporting the diversification rate hypothesis (e.g. Jansson & Davies, 2008;
96 Condamine *et al.*, 2012; Pyron & Wiens, 2013; Rolland *et al.*, 2014), and some global-
97 scale studies supporting the time hypothesis within smaller clades (e.g. families: Stephens

98 & Wiens, 2003; Stevens, 2006; Wiens *et al.*, 2006; Wiens *et al.*, 2009; Wiens *et al.*, 2011;
99 Kozak & Wiens, 2012). The explanation for these conflicting results remains unclear.

100 A third explanation is based on carrying capacity or “ecological limits” related to
101 finite resources (e.g. Mittelbach *et al.*, 2007; Rabosky, 2009; but with many earlier
102 antecedents in the ecological and paleontological literatures; e.g. MacArthur & Wilson,
103 1967; Raup, 1972). This hypothesis is based on the idea that competition for limited
104 resources will constrain the number of species that can occur together in a given location
105 or habitat. However, the specific mechanisms that relate this hypothesis to richness
106 patterns along environmental gradients are still not fully understood. Furthermore,
107 carrying capacity might instead be seen as another ecological factor that influences
108 speciation, extinction, and colonization of new habitats over time (Wiens, 2011). Thus,
109 carrying capacity might influence both diversification and time-for-speciation rather than
110 being a third, separate explanation (Wiens, 2011). This makes it difficult to assess the
111 extent to which empirical studies have (or have not) supported this hypothesis.

112 Despite many empirical studies, the evolutionary and ecological processes that
113 generate richness patterns along environmental gradients remain incompletely understood
114 from a theoretical perspective (i.e. including analytical, modelling, and simulation
115 studies). For example, no theoretical studies have addressed under what conditions the
116 time-for-speciation effect might explain richness patterns instead of diversification rates
117 (and thus the reasons for the conflicting results of empirical studies over these two
118 hypotheses are uncertain). Similarly, despite interest in the idea of ecological limits on
119 richness (e.g. Mittelbach *et al.*, 2007; Rabosky, 2009; Rabosky & Glor, 2010), the
120 mechanisms underlying this hypothesis are also unclear (but see Hurlbert & Stegen,

121 2014). Nevertheless, some theoretical papers have addressed related issues. Goldberg *et*
122 *al.* (2005) studied how differences in richness develop between two regions, and Roy &
123 Goldberg (2007) examined modelling methods to explain differences in richness between
124 habitats. However, these two studies did not explicitly address the processes underlying
125 richness differences. McPeck (2008) analysed diversification and community assembly
126 along an environmental gradient, but focused on declining diversification rates over time,
127 rather than richness patterns. Birand *et al.* (2012) examined speciation, extinction, and
128 range sizes, but not species richness. Stegen *et al.* (2009; 2012a,b) examined how
129 diversity evolves along a temperature gradient, focusing on how temperature impacts
130 diversification and the metabolic theory of ecology (see also Allen *et al.*, 2002).
131 Rosindell & Phillimore (2011) examined the processes underlying richness patterns on
132 islands, but without including ecological differences among islands or species. Rabosky
133 (2012) simulated the time-for-speciation effect, primarily to test the effectiveness of
134 methods for detecting this pattern. Hurlbert & Stegen (2014) examined the possible role
135 of energetic constraints in generating richness patterns, focusing mostly on how the
136 presence of ecological limits influenced patterns of species richness (rather than on the
137 processes by which this occurred). An important set of studies has also used simulations
138 to help address the origins of specific observed richness patterns (review in Gotelli *et al.*,
139 2009), but have not focused on the three hypotheses described above. In general, there is
140 an extensive literature on richness patterns (much of which is theoretical; e.g. Hubbell,
141 2001) but which has not focused on comparing the relative importance of time,
142 diversification rates, and carrying capacity. Thus, despite these important contributions,
143 many questions remain unexplored.

144 Here, we focus on the question of how patterns of species richness arise along
145 environmental gradients. We use individual-based modelling of eco-evolutionary
146 dynamics to simulate the evolutionary radiation of a clade across five habitats with
147 differing ecological conditions (in terms of both abiotic environment and biotic
148 resources), and track patterns of species richness within and between habitats over time.
149 We specifically address the roles of time and diversification rates in explaining richness
150 patterns and the potential impact of carrying capacity. We explore how relevant
151 parameters (e.g. biotic and abiotic niche widths of species, carrying capacity, abiotic and
152 biotic differences among habitats) are related to the processes that directly control
153 richness (speciation, extinction, colonization) and to the buildup of richness among
154 habitats over time. Although simulations cannot match the complexity of real systems,
155 they can offer mechanistic insights that would be difficult to obtain with empirical data
156 alone (e.g. how processes underlie patterns).

157 We test the following predictions. (i) Following from the carrying capacity
158 hypothesis, overall richness will be positively related to ecological variables increasing
159 resource availability (i.e. narrower resource specialization and higher environmental
160 carrying capacity in some habitats). But this increased richness will be directly caused by
161 influencing diversification rates or the timing of colonization of different habitats. (ii)
162 Strong richness gradients will develop rapidly when the first habitat colonized has
163 conditions that potentially promote diversification, such that the effects of time and
164 diversification rates on richness are concordant. (iii) In contrast, the differing impacts of
165 diversification rates and time will be most evident when a clade initially colonizes
166 habitats that yield low diversification rates. Under these conditions, species richness

167 should initially be highest in the habitats colonized first (supporting time) but should
168 eventually become highest in habitats that promote diversification (supporting the
169 diversification rates hypothesis). This latter prediction (if supported) might explain why
170 many studies at smaller and shorter spatial and temporal scales support the importance of
171 time (e.g. younger clades), whereas larger-scale studies support diversification rates
172 instead.

173 In the methods section, we describe the details of our model and simulations. We
174 give a brief outline here (Fig. 1). We expand the model by Pontarp *et al.* (2015) to
175 multiple traits and we simulate the evolutionary radiation of a clade over time (starting
176 from a single species) across five habitats that potentially differ in abiotic environments
177 and biotic resources. There is spatial structure among the five habitats but not within
178 them (i.e. all individuals in a habitat can compete). Habitats can be inhabited only by
179 individuals having certain abiotic tolerances and certain values for a trait that allows them
180 to utilize the biotic resources present in that habitat. These abiotic tolerances and resource
181 utilization traits can evolve over time (e.g. due to mutation, changes in fitness, and
182 selection). Speciation occurs largely through ecological divergence among individuals
183 (Fig. 2), both within and between habitats, and trait-based competition for finite biotic
184 resources is one of the potential drivers of speciation. We also explore the impacts of
185 incorporating non-ecological speciation. Species richness builds up in local habitats over
186 time both through speciation and dispersal among habitats. We explore how overall
187 richness across all five habitats is influenced by changing relevant parameters (e.g. biotic
188 and abiotic niche widths of species, carrying capacity, abiotic and biotic differences
189 among habitats). We then explore how these parameters are related to processes that

190 directly control richness (speciation, extinction, diversification, colonization, and
191 colonization times). Finally, and most importantly, we explore how varying key
192 parameters across habitats influences the buildup of richness among habitats over time.

193

194 **METHODS**

195 **Model outline and general assumptions**

196 We model five discrete habitats along an environmental gradient, each having a specific
197 biotic resource distribution (e.g. seeds of different size for a granivorous bird) and values
198 for an abiotic environmental variable (e.g. temperature). Individuals are defined by their
199 resource utilization trait and an abiotic tolerance trait. Resources in each habitat are
200 modeled as a Gaussian resource distribution (see eq. 2 below) in trait dimension (z) and a
201 population of identical individuals will have a local carrying capacity based on its
202 utilization trait (also in trait dimension z) (Fig. 2). Sticking to the seed/bird analogy, a
203 habitat with relatively few small and large seeds but many intermediate-sized seeds, and a
204 bird population with intermediate-sized beaks will therefore have a larger carrying
205 capacity in that habitat than birds with small and large beaks. Individuals can disperse
206 between habitats and mutate in their traits. We assume that local competition between
207 individuals for common resources is a function of the distance in trait space between
208 them (e.g. individual birds with similar-sized beaks compete more with each other than
209 dissimilar ones as they utilize similar resources). Finally, we assume that the reproductive
210 output of individuals is influenced by their abiotic environment and the match between
211 the environment and their abiotic tolerance trait (u).

212 Given these general assumptions, the fitness of a focal individual in a given
 213 habitat is modeled as a function of its resource utilization trait (z ; e.g. beak size), abiotic
 214 tolerance trait (u ; e.g. physiological tolerance to temperature, influencing reproduction
 215 and survival), the z trait of all other individuals competing for the same resources locally,
 216 the local resource distribution, and local abiotic environmental conditions. These
 217 assumptions follow well-established precedents in classic studies (e.g. Christensen &
 218 Loeschke, 1980; Brown & Vincent, 1987; Dieckmann & Doebeli, 1999).

219 We implement these assumptions in simulations that track the diversification of
 220 lineages in geographical space (habitats) and trait space. Below we specify the basic
 221 ecological model and describe our simulation algorithm. We then describe how
 222 speciation occurred, the species definition, the parameters examined, and our methods for
 223 evaluating the link between parameters, processes, and richness patterns. Additional
 224 details of the model, model parameters, simulation methods, and data analysis are
 225 provided in Appendix S1.

226

227 **Ecological model**

228 Under this model (and ignoring abiotic tolerances for now), the potential reproductive
 229 output (R) of a focal individual will be:

$$230 \quad R(z, \mathbf{z}, z_{opt}) = 1 + r \left(1 - \frac{\sum_j \alpha(z, z_j)}{K(z, z_{opt})} \right) \quad (1)$$

231 where

$$232 \quad K(z, z_{opt}) = K_0 e^{-\frac{(z_{opt}-z)^2}{2\sigma_K^2}} \quad (2)$$

233 and

234
$$\alpha(z, z_j) = e^{-\frac{(z-z_j)^2}{2\sigma_a^2}} \quad (3).$$

235 $K(z, z_{opt})$ represents the carrying capacity for a monomorphic population of
 236 individuals with trait value z in a habitat characterized by the point z_{opt} (Fig. 2). K_0
 237 denotes the maximal carrying capacity (at $z = z_{opt}$), and the resource availability declines
 238 symmetrically as z deviates from z_{opt} according to the width of the resource distribution
 239 (σ_K). Note that this way of modelling carrying capacity is conceptually similar to a Lotka-
 240 Volterra population model. However, we utilize an individual-based approach and
 241 formulate reproductive output for a focal individual (i) as a function of the sum of its
 242 individual competitors (j), weighted by their interaction coefficient α_{ij} , and divided by
 243 carrying capacity. Equation 3 models the interaction coefficient, $\alpha(z, z_j)$, between the focal
 244 individual (defined by its trait z) and its competitors (defined by their traits z_j). Here, we
 245 standardize the competition coefficients so that, for a focal individual i , $\alpha_{ii} = 1$ and $0 <$
 246 $\alpha_{ij} < 1$ ($z_i \neq z_j$). σ_a determines the degree of competition between individuals given certain
 247 utilization traits and r denotes the intrinsic growth rate (equal for all individuals).

248 Including the abiotic variable as an effect on fitness, we define the realized
 249 reproductive output (fitness) of a focal individual as a fitness generating function
 250 (Dieckmann & Doebeli, 1999):

251
$$G(z, u, \mathbf{z}, z_{opt}, u_{opt}) = E(u, u_{opt}) * R(z, \mathbf{z}, z_{opt}) \quad (4)$$

252 where

253
$$E(u, u_{opt}) = e^{-\frac{(u_{opt}-u)^2}{2\sigma_u^2}} \quad (5).$$

254 $E(u, u_{opt})$ represents the effect of the abiotic environment as experienced by an
 255 individual with an abiotic trait value u in an environment characterized by u_{opt} (Fig. 2).

256 Equation 5 equals one at $u = u_{opt}$ leading to the realized reproductive output (eq. 4) being
257 equal to the potential reproductive output (eq. 1). However, realized reproduction
258 declines symmetrically as u deviates from u_{opt} according to σ_u and σ_u can thus be viewed
259 as the abiotic environmental niche width.

260

261 **Simulations**

262 For each set of simulations (defined as a combination of biotic and abiotic conditions,
263 specified below), we simulated alternating phases of reproduction and dispersal for
264 100,000 generations (time-step) and each simulation was replicated a total of 10 times
265 (following Pontarp *et al.*, 2012, 2015). At the beginning of each simulation replicate, a
266 habitat at the extreme end of the gradient was seeded with 10 monomorphic individuals.
267 During reproduction each individual reproduced according to its fitness and each
268 offspring inherited the same trait values as their parent (asexual reproduction) unless the
269 offspring mutated (see below). All offspring were born into the habitat of their parent, but
270 dispersed with a probability (d) during the dispersal phase to one of the neighbouring
271 habitats according to a stepping-stone dispersal algorithm (Pontarp *et al.*, 2012, 2015).

272 We followed all individuals, calculated their fitness, and allowed them to
273 reproduce and disperse. As a result, the simulation output is a distribution of individuals
274 in trait space and geographical space for each time step (Fig. 2). The mutation process
275 (with offspring values close to parental values), together with the evolutionary process
276 (driven by the fitness generating function), generates a clustered distribution of trait
277 values along the trait axes (Fig. 2). We treat these clusters of similar individuals as
278 species (Pontarp *et al.*, 2012, 2015). See Appendix S1 for details.

279 Results were very similar among replicates, strongly suggesting that 10 replicates
280 were adequate. In our main analysis we assumed that speciation is driven by local
281 adaptation and disruptive selection (e.g. ecological speciation; Schluter, 2009; Nosil,
282 2012). We also performed a set of simulations incorporating non-ecological speciation,
283 which gave similar results (see Appendix S2 in Supporting Information).

284

285 **Speciation**

286 Speciation occurred both within and between habitats (see Appendix S1 for detailed
287 description). At the local scale (within habitats), clusters of individuals (species) with
288 similar phenotype branched into distinct clusters in trait space (Fig. 2), representing
289 speciation (e.g. Geritz *et al.*, 1998; Dieckmann & Doebeli, 1999; Pontarp *et al.*, 2012,
290 2015). The diversification process continued until new species were prone to stochastic
291 extinctions due to decreased population sizes and weak disruptive selection (e.g.
292 Johansson & Ripa, 2006; Claessen *et al.*, 2007; Johansson *et al.*, 2010).

293 Speciation also occurred between habitats. Given that individuals disperse
294 between habitats, individuals from a particular species could establish in several habitats
295 if they had positive fitness after colonization of each habitat. Differences between
296 habitats in abiotic conditions (Δu_{opt} ; temperature hereafter) and/or resource types (Δz_{opt})
297 could then lead to disruptive selection and allopatric speciation. Here, dispersal is defined
298 as the probability that each offspring disperses from the parental habitat to a
299 neighbouring habitat. Note that dispersal is a parameter of the model, whereas
300 establishment of dispersing individuals is part of our results (see below).

301 Species were defined as groups of individuals having common descent and a
302 continuous distribution of traits (no gaps in the trait distribution >0.1) in both trait
303 dimensions (resource utilization, abiotic tolerance). This definition was independent of
304 which habitat individuals occurred in, such that a single species could occur in multiple
305 habitats. When a gap >0.1 was detected in either trait dimension within an existing
306 species, it was considered a speciation event (i.e. one species branching into two). These
307 clusters of similar individuals (species) appeared to be distinct and stable over time.

308 The specific value of 0.1 was chosen following Pontarp *et al.* (2015). Smaller
309 thresholds would lead to more speciation events but with species that were non-viable. A
310 larger limit would lead to discrepancies between registered speciation events and the
311 clustering that were obvious from visual inspection of the simulation outputs. A limit of
312 0.1 also makes biological sense in the context of our simulations as it is large enough to
313 prevent speciation by only a few mutations. Furthermore, the smallest niche width we
314 used in our simulations was also 0.1. Thus, we required a separation of not more than one
315 niche width to count a cluster as a species.

316

317 **Simulation design and data analysis**

318 Based on preliminary simulations that extensively varied many parameters, we identified
319 several key parameters that most strongly influenced richness patterns among habitats.

320 These parameters were: abiotic differences between habitats (Δu_{opt}), biotic resource
321 differences between habitats (Δz_{opt}), biotic niche widths (σ_a), abiotic niche widths (σ_u),
322 carrying capacity (K_0) and dispersal probability (d). See Appendix S1 and Table 1 for
323 default values and for parameter space justification.

324 We first explored the impact of different parameter values on richness patterns
325 and the underlying processes (specific values in Table 1). Although the specific values
326 examined are somewhat arbitrary, they nevertheless provide insights on how changing
327 the values influences the direction of changes in richness (Fig. 3) and the mechanisms by
328 which these changes occur (Fig. 4). More specifically, to understand how ecological
329 variables influenced the processes that directly influenced richness, we estimated the time
330 (in generations) until all habitats were colonized and also the rates of speciation,
331 extinction, and colonization of habitats (as events per unit time, over the time course of
332 the simulation). We then analysed richness patterns when all five habitats had the same
333 conditions for high, intermediate, and large values of each parameter separately
334 (symmetric case; Table 1). We refer to this as the symmetric case.

335 We also analysed cases in which three key variables differed among habitats
336 (mean biotic niche width, abiotic niche width, and carrying capacity) and tracked the
337 species richness in habitats over time. We refer to this as the asymmetric case. Each of
338 these three variables varied across habitats, and all other parameters were held constant
339 (see Table 1). For each variable, a set of simulations was run with the variable forming a
340 gradient in a different direction among habitats (e.g. the seeded habitat, habitat 1, had the
341 lowest carrying capacity versus the highest carrying capacity). These analyses were used
342 to compare the relative impact of time and diversification rates on richness patterns
343 among habitats. Specifically, under the time hypothesis, the seeded habitat should have
344 the highest richness (regardless of variable values), whereas under the diversification rate
345 hypothesis, the habitat with variable values that increased diversification should have the
346 highest richness (regardless of which was the seeded habitat).

347 We tested whether net diversification rates (rates of speciation – extinction) were
348 correlated with the final, local species richness of each habitat in the asymmetric case,
349 and with values of the three variables varied among habitat (biotic niche width, abiotic
350 niche width, and carrying capacity). Rates for each habitat were estimated as the number
351 of events (speciation, extinction, diversification [speciation – extinction]) divided by the
352 time of colonization of that habitat. A separate correlation analysis was conducted in each
353 of the six asymmetric cases examined here, with habitats as the units of analyses (based
354 on mean values for each habitat from all 10 replicates).

355 We also examined patterns of speciation and extinction in these habitats over time
356 in the asymmetric case (Fig. S5 in Appendix S3). However, given space limitations, we
357 do not discuss these results in detail.

358 Sample simulation results (richness in each habitat over time) are illustrated in
359 Figs. S1–S3 in Appendix S3. These are each based on a single replicate (for ease of
360 visualization), but results are similar when including all 10 replicates (Figs. 3–5).

361

362 **RESULTS**

363 We first analysed how different parameters influenced overall richness (total number of
364 species across all habitats), with parameter values equal across the five habitats (Table 1).

365 Additional theoretical background and discussion of mechanisms is provided in
366 Appendix S1.

367 Biotic niche width (σ_a) strongly influenced overall richness patterns, with
368 narrower niche specialization driving higher richness (Fig. 3b). High local carrying
369 capacity (K_0) also promoted higher overall species richness (Fig. 3b). Small temperature

370 differences between habitats (Δu_{opt}), wide abiotic niche width (σ_u), and high dispersal
371 probability (d) all reduced richness (Fig. 3c,e), presumably by facilitating movement
372 between habitats and thereby disrupting speciation (e.g. Brown & Pavlovic, 1992; Mizera
373 & Meszema, 2003; Parvinen & Egas, 2004). Variation in resource differences among
374 habitats (Δz_{opt}) had little effect on richness (Fig. 3f), although smaller resource
375 differences led to slightly higher richness.

376 Additional analyses (Fig. 4) revealed how these parameters were related to the
377 processes that directly control species richness (speciation, extinction, dispersal; see also
378 Appendix S1). The biotic (resource) niche width (σ_a) influenced both speciation and
379 extinction rates (events per generation), with narrower niche widths increasing both
380 speciation and extinction (Fig. 4a,b). Low carrying capacity decreased both speciation
381 and extinction rates. Other variables had lesser impact on speciation and extinction rates.
382 Diversification rates (speciation – extinction rates) were higher with narrow biotic niche
383 widths and lower with low carrying capacity and small temperature differences among
384 habitats (Fig. 4e). The number of generations until all habitats were colonized was
385 strongly and positively related to differences in temperature among habitats (Δu_{opt}), with
386 small differences between habitats decreasing the time until all habitats were colonized
387 (Fig. 4c). Resource differences among habitats also had a positive relationship with
388 colonization time (albeit a weaker one). Carrying capacity, abiotic niche width, and
389 dispersal probability all showed negative relationships with colonization time (Fig. 4c).
390 We found a strong positive relationship between colonization rate and abiotic niche width
391 (Fig. 4d). Most other parameters were weakly and negatively related to colonization rate

392 (e.g. biotic niche width, carrying capacity). Surprisingly, low dispersal probability (set by
393 parameter d) was strongly related to high rates of colonization.

394 Most importantly, we examined patterns of species richness in the five habitats
395 over time when ecological parameters varied across habitats (Fig. 5). Note that habitat 1
396 (seeded habitat) was always colonized first. Biotic niche width had a dramatic impact on
397 patterns of richness in habitats over time (Fig. 5a,b), seemingly through the impacts of
398 niche width on speciation, with narrower niches increasing speciation and diversification
399 rates (Fig. 4). Nevertheless, these results showed that the time-for-speciation effect
400 determined patterns of species richness over short time scales, even under conditions
401 where variation in diversification rates eventually dominated richness patterns.
402 Specifically, when biotic niche widths were wider in habitat 1 (conditions that reduce
403 speciation), habitat 1 and the adjacent habitat 2 initially had the highest richness. Habitat
404 5 was not colonized until ~40,000 generations. However, after that point, habitats 4 and 5
405 quickly increased in richness until they had the highest richness. In other words, the
406 richness gradient “flipped” over the course of the simulation, showing a strong time-for-
407 speciation effect initially but the impact of diversification rates later.

408 In contrast, when biotic niche widths were narrower in habitat 1, then habitats 1
409 and 2 quickly developed the highest richness and maintained the highest richness
410 throughout the simulation. Interestingly, richness increased slowly over time in habitats
411 3, 4, and 5. Habitat 5 was not colonized until 30,000 generations had been reached.
412 Overall, we found the consistently strongest species richness gradient (greatest
413 differences between the most species-rich and species-poor habitats over time) under

414 these conditions, when the time-for-speciation effect and environmental impacts on
415 diversification favored higher species richness in the same habitats.

416 The results in which carrying capacity varied among habitats showed strong
417 parallels to those for biotic niche width (Fig. 5c,d). First, when carrying capacity was
418 lowest in habitat 1, the gradient in richness again “flipped” over the course of the
419 simulation, with higher richness in habitats 1 and 2 until ~30,000 generations were
420 reached, and higher richness in habitats 3, 4, and 5 after 50,000 (although habitat 5 never
421 had the highest richness). Second, when the carrying capacity was highest in habitat 1,
422 this habitat had relatively high richness throughout the simulation. Third, regardless of
423 whether the carrying capacity was low or high in habitat 5, this habitat was not colonized
424 until after 30,000 generations.

425 This latter pattern (late colonization of habitat 5) may seem surprising given that
426 habitat 5 has many resources (high carrying capacity) and no species occupying it.
427 However, these results show that colonization of a new habitat requires many individuals
428 (or species) in the adjacent habitat (i.e. more potential dispersers). For example,
429 regardless of whether carrying capacities were high or low in habitats 4 and 5, habitat 4
430 was only colonized when there were ~10 species in habitat 3, and habitat 5 was only
431 colonized when there were ~10 species in habitat 4 (Fig. 5). Thus, carrying capacity
432 impacted the colonization of habitats through the number of dispersers available in
433 adjacent habitats.

434 Variation in abiotic niche width across habitats generally had little effect on
435 richness patterns over time (Fig. 5e,f). Nevertheless, there was a greater time-for-

436 speciation effect as niche width decreased from habitat 1 to 5 (Fig. 5f), such that more
437 time was required to colonize habitats with narrower niche widths (as in Figure 3c).

438 To test the robustness of the results on richness in habitats over time (Fig. 5), we
439 repeated these analyses after incorporating non-ecological speciation. Richness patterns
440 were very similar (Table S1 and Fig. S4 in Appendix S3). Most importantly, our
441 conclusions were upheld about the initial importance of the time-for-speciation effect and
442 later importance of diversification rates.

443 We also examined the relationships between net diversification rates, values for
444 the three ecological variables among habitats (abiotic and biotic niche widths, carrying
445 capacity), and the final local richness of each habitat. Correlation coefficients (rc) and p -
446 values (P) presented below are associated with our two asymmetric cases (hence two rc
447 and P values for each relationship presented) with decreasing and increasing ecological
448 variables across habitats (see also Table S2 in Appendix S3). Net diversification rates
449 were strongly related to local richness when carrying capacity varied among habitats (rc
450 = 0.94, 0.89; P = 0.02, 0.04), and the relationship between carrying capacity and
451 diversification rate (rc = 0.68, 0.91; P = 0.21, 0.03) could be stronger than the
452 relationship between carrying capacity and local richness (rc = 0.73, 0.70; P = 0.16,
453 0.19). When biotic niche width varied among habitats, biotic niche width was strongly
454 related to both local richness (rc = 0.93, 0.91; P = 0.02, 0.03) and diversification rate (rc
455 = 0.89, 0.92; P = 0.04, 0.03). The relationship between diversification rate and local
456 richness under these conditions was similar, but only marginally significant (rc = 0.84,
457 0.85; P = 0.08, 0.07). Relationships between abiotic niche width, net diversification, and
458 local richness were weak and non-significant (Table S2 in Appendix S3). Overall, these

459 results demonstrate that finite carrying capacities do not make net diversification rates
460 meaningless or misleading (contra Rabosky 2009). Instead, more limited carrying
461 capacities in some habitats can influence overall richness patterns among habitats through
462 their impacts on net diversification rates in each habitat.

463

464 **DISCUSSION**

465 **Overview**

466 Relatively few studies have used simulations to elucidate the interplay of evolutionary
467 and ecological processes that drive species richness patterns among habitats, especially
468 the relative importance of time, diversification rates, and carrying capacity. Our study
469 offers three general insights.

470 First, our results provide an explanation for why some empirical studies support
471 the time-for-speciation effect as a cause of richness patterns whereas others support
472 diversification rates instead. We find that the time-for-speciation effect can have a strong
473 influence on patterns of species richness among habitats over shorter time scales. This is
474 most apparent in our simulations (Fig. 5) in which the clade originates in habitats that
475 have wide biotic niche widths or low carrying capacities (conditions which lower rates of
476 speciation). There is initially higher species richness in habitats colonized first (relative to
477 habitats colonized later), but when all habitats are colonized the habitats with conditions
478 that promote diversification “catch up” and eventually have the highest richness. Thus,
479 we show that diversification rates and the time-for-speciation effect could explain
480 contrasting richness patterns along the same ecological gradient, but at different points in
481 time.

482 This set of results provides theoretical support for the idea that the time-for-
483 speciation effect may be most important for explaining richness patterns over shorter
484 spatial and temporal scales (e.g. within regions, in smaller clades), and diversification
485 rates over larger spatial and temporal scales (e.g. the latitudinal diversity gradient;
486 Rabosky, 2009; Wiens, 2011). Our results may also help explain why studies of younger
487 clades often fail to find a latitudinal gradient in diversification rates, whereas analyses of
488 older clades often do (e.g. studies within frog families versus across amphibians: Wiens
489 *et al.*, 2006; Wiens *et al.*, 2009 versus Pyron & Wiens, 2013; studies within mammal
490 genera versus across mammals: Soria-Carrasco & Castresana, 2012 versus Rolland *et al.*,
491 2014). These results might also help explain the reverse latitudinal richness gradient in
492 some young subclades (i.e. higher temperate diversity) within older groups that show
493 high tropical richness overall (e.g. mammals: Buckley *et al.*, 2010). Some of these results
494 also have precedents in the simulation results of Hurlbert & Stegen (2014) who showed
495 an inverse latitudinal gradient arising before equilibrium richness was reached, even
496 though a latitudinal gradient arose eventually after equilibrium (their Fig. 2b), given a
497 temperate origin and strong ecological limits.

498 Second, our results call into question the idea that carrying capacity, time, and
499 diversification rates represent three competing explanations for richness patterns (as in
500 Fig. 1 of Mittelbach *et al.*, 2007). Our results suggest that carrying capacity should
501 instead be viewed as an ecological factor that can influence both diversification rates and
502 time, rather than a direct explanation for richness patterns (just as climate is not itself a
503 direct explanation for richness patterns). We found that low carrying capacities and wide
504 resource niche widths lead to reduced rates of speciation and diversification (Fig. 4) and

505 lower overall richness (Fig. 3). Hence, carrying capacities and ecological limits are not
506 alternative paradigms relative to diversification rates. Instead, they are important
507 ecological factors that can potentially influence net speciation and extinction over time
508 (along with many other factors).

509 Similarly, we found that explanations for richness patterns based on the time-for-
510 speciation effect and carrying capacity of habitats can also be linked rather than
511 competing. We found that limited carrying capacities in some habitats may increase the
512 time until they are colonized (Fig. 4) and thereby underlie the time-for-speciation effect.
513 We also found strong richness gradients caused by differences in the timing of
514 colonization when carrying capacity varied across habitats (Fig. 5), regardless of whether
515 the seeded habitat had high or low carrying capacity. These results also suggest how
516 factors related to species interactions (e.g. limited carrying capacity, wide biotic niche
517 widths) could influence dispersal between habitats over time and act as an underlying
518 cause of niche conservatism (i.e. Wiens *et al.*, 2010).

519 In summary, these latter results suggest that carrying capacity, time-for-
520 speciation, and diversification rates are not competing explanations or alternative
521 paradigms. Instead, we found that carrying capacity is an important ecological factor that
522 can influence both diversification rates (by impacting speciation) and time-for-speciation
523 (by impacting when habitats are colonized). But carrying capacity itself is not a direct
524 explanation for richness patterns, and like other ecological factors (e.g. climate), it can
525 only impact richness by influencing rates and patterns of speciation, extinction, and
526 dispersal.

527 Third, our results raise the possibility that biotic (resource-based) niche width
528 may be more important for driving species richness patterns than carrying capacity itself
529 (Fig. 2, 3). For example, simply increasing a limiting resource may increase the number
530 of individuals of a given species in a given habitat, but need not increase the number of
531 species. Instead, it is a narrow biotic niche width that may be particularly important for
532 allowing species to partition resources, diverge, speciate, and co-exist.

533

534 **Assumptions and limitations**

535 In this study, we used a generalized, individual-based model that minimized a priori
536 assumptions about the evolutionary and ecological processes that generate species
537 richness patterns. However, as in any simulation study, we still made several assumptions
538 that may or may not impact our conclusions. First, our main results (Figs. 3–5) are based
539 on simulated speciation that occurs through ecological divergence. There is growing
540 evidence that ecological divergence is important in speciation (reviews in Schluter, 2009;
541 Nosil, 2012), but there is also evidence that ecological similarity over time (niche
542 conservatism) can drive allopatric speciation initially (e.g. Kozak & Wiens, 2006; Hua &
543 Wiens, 2013). However, we also show that our main conclusions are robust to including
544 non-ecological speciation (see Fig. S4 in Appendix S3).

545 We assume that environments have finite carrying capacities that limit their
546 richness over long time scales. It is unclear if this is generally a realistic model (e.g.
547 Wiens, 2011). For example, species can potentially evolve to utilize new resources, thus
548 launching clades into new “adaptive zones” and driving new radiations with minimal
549 competition with existing radiations (e.g. Schluter, 2000). Regardless, patterns that occur

550 before these limits are reached can be readily observed in our simulations (Fig. 5).
551 Furthermore, a major goal of our study was to evaluate the implications of finite carrying
552 capacity for the origin of richness patterns.

553 A major assumption of our study is that we model asexual organisms. However, it
554 seems that our major results should be robust to this assumption. We think that the only
555 practical implication of this assumption is that we do not explicitly model speciation as
556 the evolution of intrinsic reproductive isolating mechanisms (e.g. Coyne & Orr, 2004).
557 Instead, we assume that speciation occurs largely through ecological divergence (a
558 process known to be widely important in speciation in sexual organisms; Schluter, 2009;
559 Nosil, 2012). It would be interesting to model the evolution of isolating mechanisms in
560 sexual organisms and relevant approaches already exist (e.g. Dieckmann & Doebeli,
561 1999; Doebeli & Dieckmann, 2003; Heinz *et al.*, 2009; Gilman & Behm, 2011).
562 However, this would be difficult to apply to our simulations of hundreds of species, due
563 to the computational cost of the increased model complexity. Most importantly, it is
564 unclear if this would impact our results at all, given the demonstrated robustness of our
565 main results to incorporating non-ecological speciation (Fig. S4 in Appendix S3).

566 Furthermore, the linear arrangement of habitats we assumed here may not apply
567 universally, and in some cases influenced our results. For example, we sometimes
568 observed the highest richness in habitats 2 or 4, even when conditions favoring speciation
569 were higher in habitats 1 or 5 (Fig. 5). This occurred because “middle” habitats can share
570 species with habitats on either side, whereas “end” habitats only share species with one
571 adjacent habitat. Nevertheless, this linear arrangement of habitats may apply to many
572 empirical systems such as elevational and latitudinal gradients.

573 Finally, we note that there are several other assumptions in our simulations (e.g.
574 non-overlapping generations, temporally stable environments). For many of these
575 assumptions, we can see no plausible mechanism by which they would overturn our
576 conclusions about the origin of richness patterns. For others, violating these assumptions
577 might influence our results (e.g. mass extinction events in some habitats). However,
578 trying to include every potentially realistic detail is not practical and would detract from
579 our goal of understanding how the focal processes of our study generate richness patterns.
580 Moreover, our results are broadly consistent with many empirical studies and should thus
581 provide insights into the general processes that underlie diversity patterns, even if they do
582 not perfectly mimic the details of any particular empirical system.

583

584 **Conclusions**

585 We explore the origins of richness patterns along environmental gradients, and the
586 widespread paradigm that time, diversification rates, and carrying capacities are
587 competing explanations for species richness patterns. We find that these explanations can
588 be intertwined rather than competing. Specifically, we find that carrying capacity can
589 influence both diversification rates and the time-for-speciation effect but may not itself be
590 a direct explanation for richness patterns (like climate).

591 We also illuminate why some richness gradients are explained by diversification
592 rates and others by time. We show that “young” gradients (i.e. in young clades or sub-
593 clades) seem most likely to be explained by time and “old” gradients by differences in
594 diversification rates across the gradient. Thus, our results may help reconcile the

595 seemingly conflicting results of many empirical studies of the evolutionary and
596 ecological origins of richness gradients.

597

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604

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761

762 **SUPPORTING INFORMATION**

763 Additional Supporting Information may be found in the online version of this article:

764 **Appendix S1:**

765 Details of model parameters, biotic and abiotic conditions, and eco-evolutionary
766 processes

767 **Appendix S2:**

768 Simulating non-ecological and testing the impacts of different mutation rates.

769 **Appendix S3:**

770 Supplementary tables and figures

771 **Table S1.** Comparison of results with and without non-ecological speciation

772 **Table S2.** Results of correlation analyses between net diversification rates, final local
773 richness, and values of three ecological variables across habitats.

774

775 **Figure S1.** Sample simulation results (richness in each habitat over time) when parameter
776 values are the same across habitats (symmetric) but different ecological variables differ
777 between simulations, including: (a) biotic (resource) variation across habitats, (b) abiotic
778 (temperature) variation across habitats, (c) dispersal rates between habitats, and (d)
779 carrying capacity.

780 **Figure S2.** Sample simulation results (richness in each habitat over time) when parameter
781 values are the same across habitats (symmetric) but different ecological variables differ
782 between simulations, including: (a) biotic (resource) variation across habitats, (b) abiotic
783 (temperature) variation across habitats, (c) dispersal rates between habitats, and (d)
784 carrying capacity.

785 **Figure S3.** Sample simulation results (richness in each habitat over time) when parameter
786 values differ across habitats (asymmetric).

787 **Figure S4.** Sample simulation results (richness in each habitat over time) when including
788 non-ecological speciation.

789 **Figure S5.** Mean number of speciation events, extinction events and colonization events
790 events over time in the asymmetric case.

791 **Figure S6.** Accumulation of local richness over time in five habitats, testing the effects of
792 increasing the mutation rate by 50%.

793 **Figure S7.** Accumulation of local richness over time in five habitats, testing the effects of
794 decreasing the mutation rate by 50%.

795

796 BIOSKETCHES

797 **Mikael Pontarp** is a postdoctoral fellow at the Institute of Evolutionary Biology and
798 Environmental Studies at the University of Zurich. He studies the link between
799 fundamental ecological, evolutionary, and biogeographical assembly processes and
800 community patterns such as diversity, trait distribution, and phylogenetic structure. To
801 this end, Mikael use a wide variety of eco-evolutionary modelling and simulation
802 approaches.

803

804 **John J. Wiens** is a professor in the Department of Ecology and Evolutionary Biology at
805 the University of Arizona. His main interest is in using integrative phylogenetic
806 approaches to address conceptual questions at the interface of ecology and evolutionary
807 biology, including species richness, speciation, niche evolution, and species responses to
808 climate change.

809

810 **Editor:** Holger Kreft

811 **Table 1.** Parameter values used in the simulations, with values either the same
 812 (symmetric) or different (asymmetric) across habitats. First, richness patterns were
 813 analysed for small, intermediate, and large values (evenly distributed throughout
 814 parameter space) for six of the model parameters separately. Local conditions were
 815 identical among habitats (symmetric case) and defined by default parameter values
 816 (underlined). Second, patterns were analysed in simulations when biotic and abiotic niche
 817 width and carrying capacity differed (asymmetric case) among habitats. Note that the
 818 specific units for many of these variables are not intuitive; see Methods and Appendix S1
 819 for explanation.
 820

Symmetric			
Parameters	Small	Intermedi ate	Large
Abiotic differences between habitats (Δu_{opt})	0.1	<u>0.5</u>	1.0
Resource differences between habitats (Δz_{opt})	0.1	<u>0.5</u>	1.0
Biotic niche widths (σ_a)	0.1	<u>0.2</u>	0.3
Abiotic niche widths (σ_u)	0.5	<u>1.0</u>	1.75
Carrying capacity (K_0)	500	<u>1500</u>	2500
Dispersal probability (d)	0.001	<u>0.01</u>	0.1
Resource distribution width (σ_K)	1.0	<u>1.0</u>	1.0
Asymmetric			
Habitat			

821

Parameters	1	2	3	4	5
Abiotic differences between habitats (Δu_{opt})	0.5	0.5	0.5	0.5	0.5
Resource differences between habitats (Δz_{opt})	0.5	0.5	0.5	0.5	0.5
Biotic niche widths (σ_a)	0.1	0.2	0.3	0.4	0.5
Abiotic niche widths (σ_u)	1.5	1.25	1.0	0.75	0.5
Carrying capacity (K_0)	500	1000	1500	2000	2500
Dispersal probability (d)	0.01	0.01	0.01	0.01	0.01
Resource distribution width (σ_K)	1.0	1.0	1.0	1.0	1.0

823 **FIGURE LEGENDS**

824

825 **Figure 1.** Diagrams illustrating the basic simulation model and the overall simulation
826 design. The basic simulation model is to simulate the reproduction, mutation, adaptation,
827 and speciation of individuals within habitats over time (circles indicate each habitat).
828 Individuals can also disperse between habitats (indicated with arrows between circles),
829 based on their dispersal rate, their tolerance to abiotic conditions there, the fit of their
830 biotic resource trait to local biotic resources, and competition. Individuals that disperse
831 may then speciate or remain as conspecific individuals distributed across multiple
832 habitats. Speciation is determined by branching along trait axes (see Fig. 2). The overall
833 simulation design involves a symmetric case (conditions identical across habitats, testing
834 the impact of different variables on rates of speciation, extinction, diversification, and
835 colonization, and time until all habitats are colonized) and an asymmetric case
836 (conditions differ across habitats, tracking richness in habitats over time).

837

838 **Figure 2.** Illustrations of the model used. (a) An example of the fitness landscape in two
839 dimensional trait space as a function of resource distribution and abiotic conditions in
840 three habitats (red, black, blue curves). Resource distribution and abiotic conditions are
841 modeled as Gaussian functions of a biotic trait (z) and abiotic trait (u). Resource
842 differences among habitats are denoted by Δz_{opt} and fitness in each habitat decreases as
843 the resource trait z deviates from z_{opt} . Similarly, differences in abiotic conditions are
844 denoted by Δu_{opt} . with decreasing fitness as individuals deviate from u_{opt} . (b) An
845 example of adaptive radiation in two-dimensional trait space among three habitats. Each

846 individuals trait combination is plotted over time. Each line represents one species. Color
847 denotes different habitats. Speciation can occur through: colonization of novel habitats
848 (denoted by 1), colonization of an occupied habitat (2), and local speciation within a
849 habitat (3).

850

851 **Figure 3.** Accumulation of regional richness over time (total number of unique species,
852 summed across all habitats) calculated as the mean (lines) and standard deviation (error
853 bars) of 10 replicated simulations. Note the substantially higher richness values in (a): all
854 other y-axes are identical. Simulations were run for small, large, and intermediate values
855 of six model parameters (see title of each panel): note that these different values are
856 evenly distributed within a variable but are not necessarily equivalent between variables
857 (see Table 1). All other parameters were set to default values (Table 1). Local conditions
858 such as niche widths and resource amounts were equal among habitats.

859

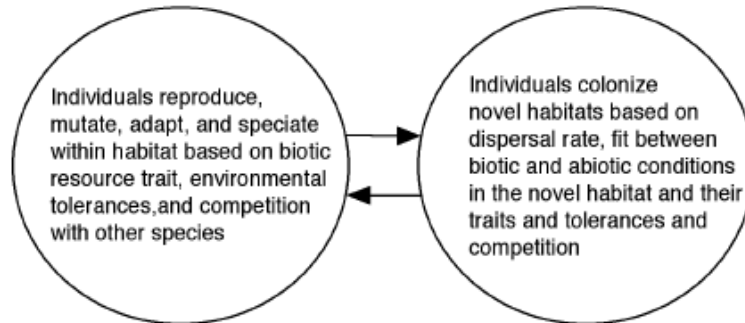
860 **Figure 4.** The impact of six model parameters on relevant processes, including
861 speciation rate (a), extinction rate (b), time until all habitats were colonized (c),
862 colonization rate (d) and diversification rate (e) that drive richness patterns among
863 habitats. Note that small, medium, and large values are evenly distributed within a
864 variable but are not necessarily equivalent between variables (see Table 1). All other
865 parameters were set to default values (Table 1). Local conditions such as niche widths
866 and resource amounts were equal among habitats. The results show the mean (point
867 symbols) and standard deviation (error bars) for 10 replicated simulations.

868

869 **Figure 5.** Accumulation of local richness over time in each of the five habitats calculated
870 as the mean (lines) and standard deviation (error bars) of 10 replicated simulations. Local
871 ecological conditions (see title of each panel) differed among habitats along the
872 environmental gradient. All other parameters were set to default values (Table 1).
873

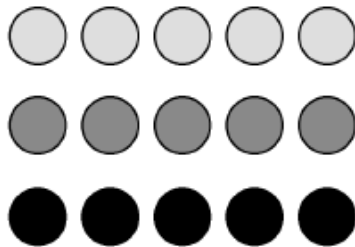
874 **Figure 1**

Basic simulation model



Overall simulation design

symmetric case



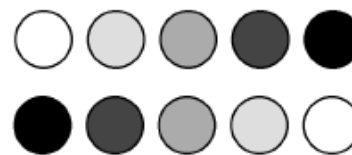
Separate simulations, each with 3 different values (low, intermediate, high) across all 5 habitats for

- biotic niche width
- carrying capacity
- temperature differences among habitats
- abiotic niche width
- dispersal
- resource differences among habitats

How do different values influence:

- speciation rate
- extinction rate
- diversification rate
- invasion rate
- time until all habitats colonized

asymmetric case



Separate simulations in which there is an environmental gradient among habitats in one of three variables

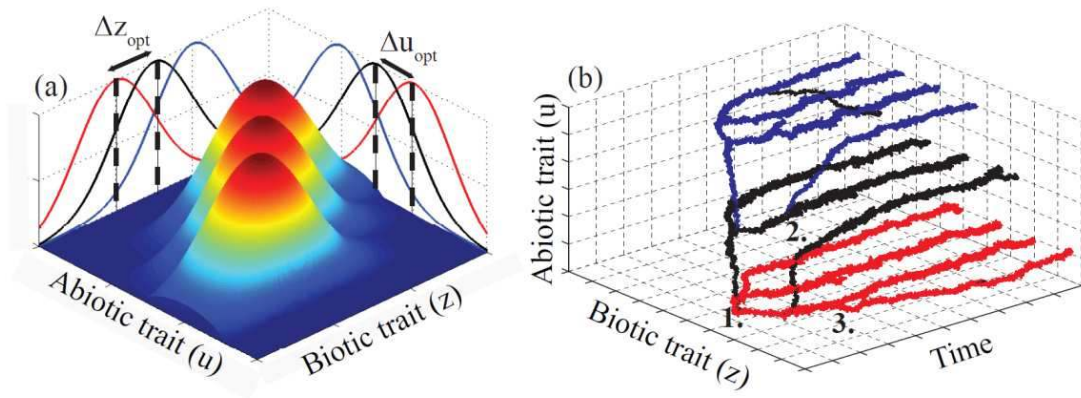
- biotic niche width
- carrying capacity
- abiotic niche width

First habitat colonized has either highest or lowest value for the variable

Track changes in species richness in each habitat over time

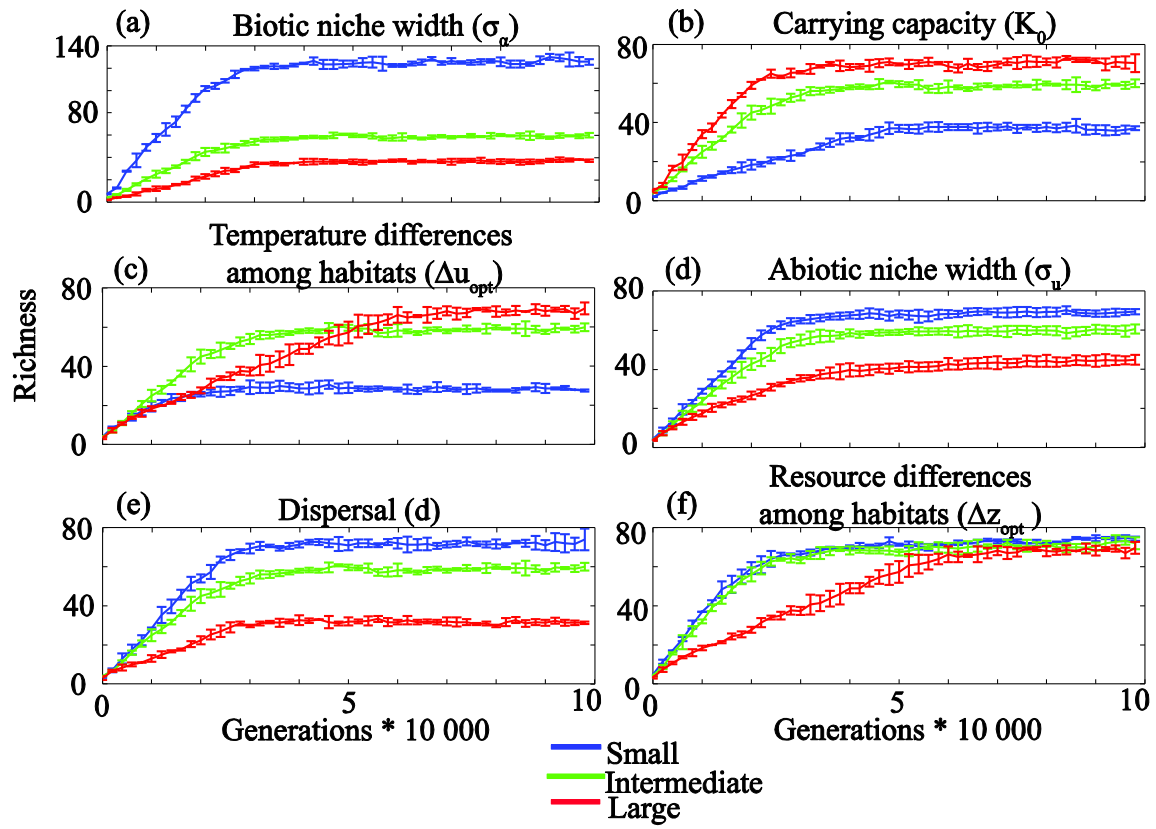
Is richness determined by time of colonization or conditions promoting diversification in different habitats?

876 **Figure 2**



877
878

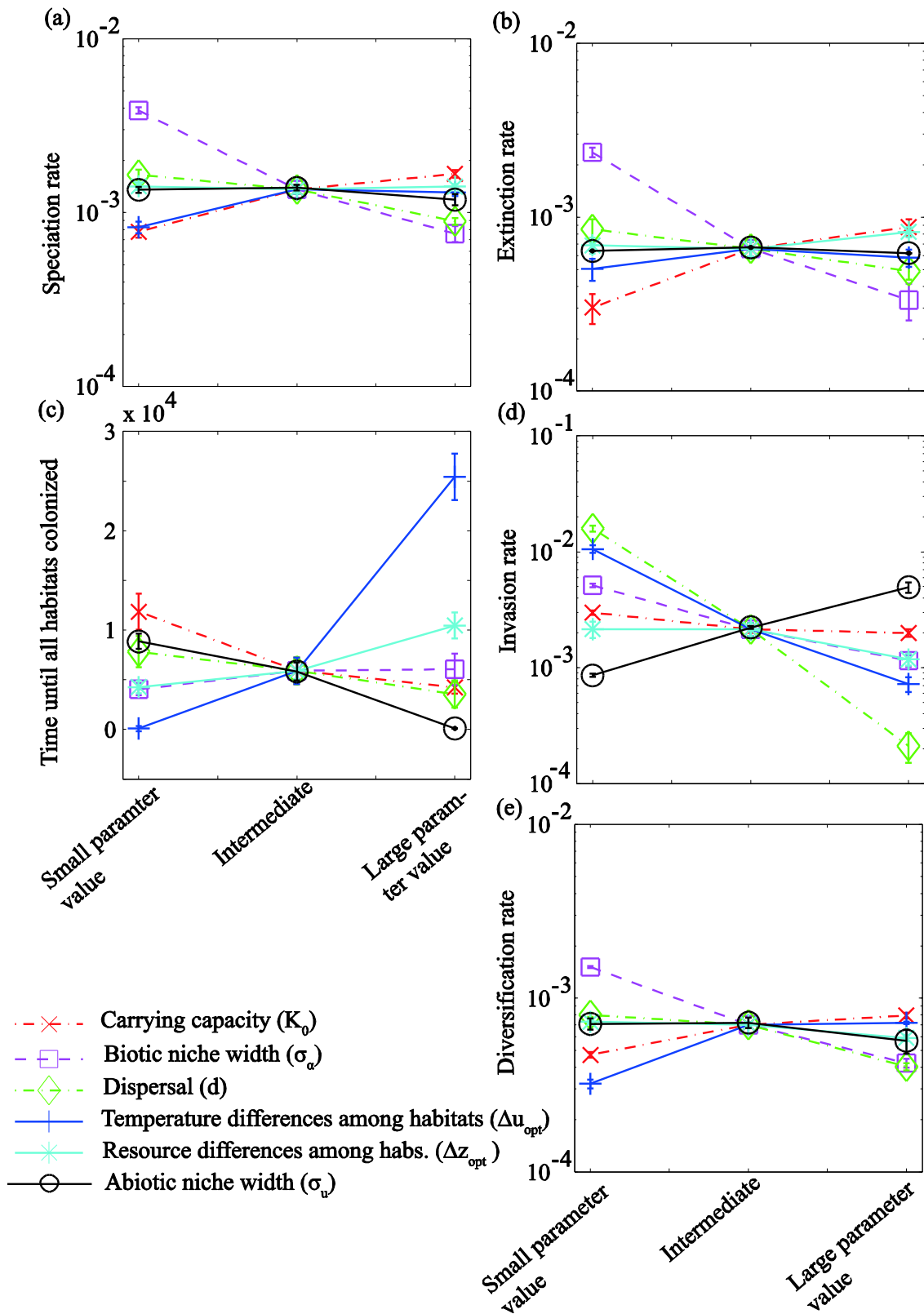
879 **Figure 3**



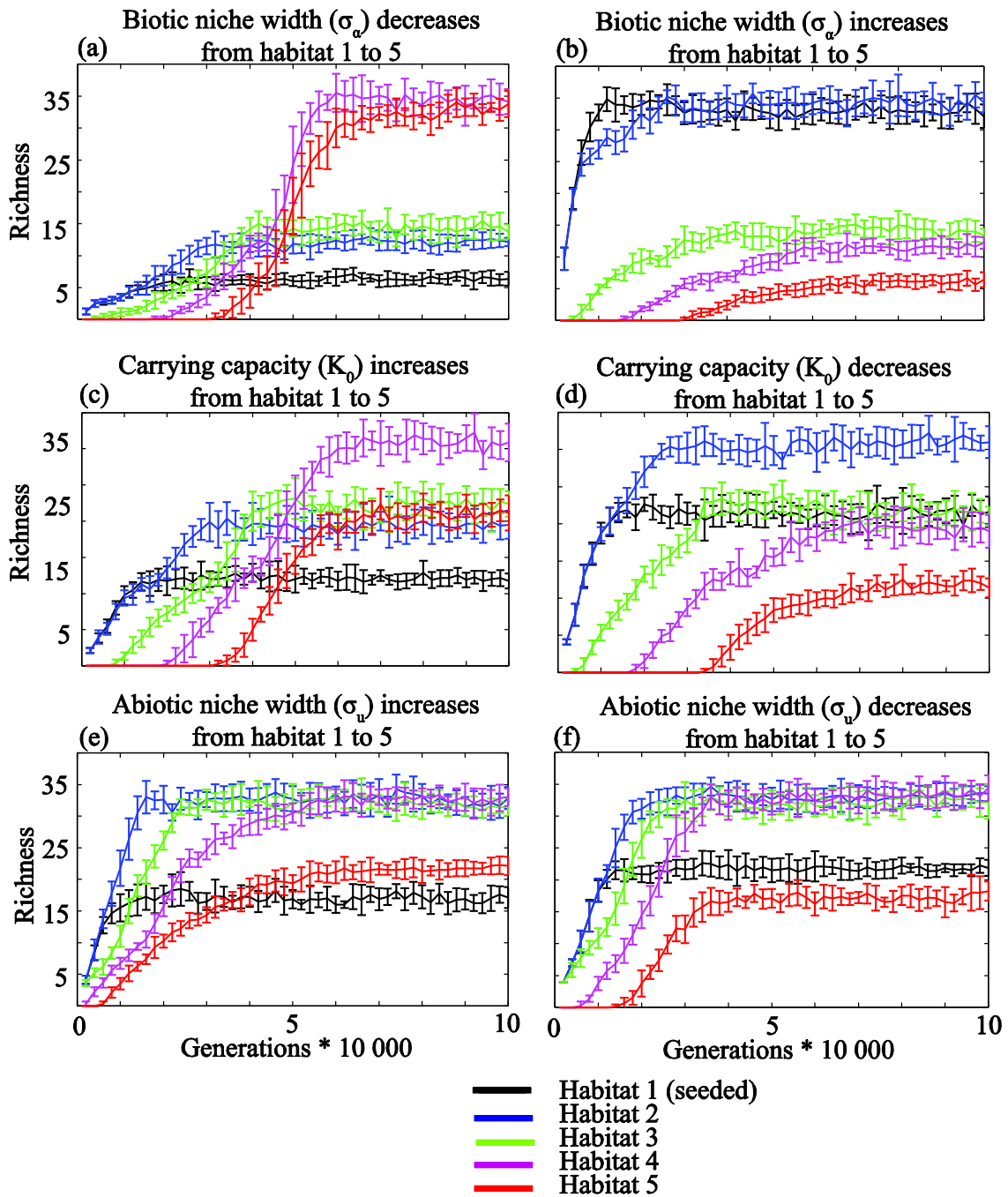
880

881

882 **Figure 4**



884 **Figure 5**



885

886