

1 **Title:** Ecological strategies in stable and disturbed environments depend on species
2 specialisation

3

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20 Dispersal, Generation overlap

21 **Abstract**

22 Ecological strategies are integral to understanding species survival in different environments.
23 However, how habitat specialisation is involved in such strategies is not fully understood,
24 particularly in heterogeneous and disturbed environments. Here, we studied the trait
25 associations between specialisation, dispersal ability, competitiveness, reproductive
26 investment and survival rate in a spatially explicit metacommunity model under various
27 disturbance rates. Though no unique trait values were associated with specialisation,
28 relationships were uncovered depending on environmental factors. We found strong trait
29 associations mainly for generalist species, while specialist species exhibited a larger range of
30 trait combinations. Trait associations were driven first by the disturbance rate and second by
31 species' dispersal ability and generation overlap. With disturbance, low dispersal ability was
32 strongly selected against, for specialists as well as for generalists. Our results demonstrate that
33 habitat specialisation is critical for the emergence of trait strategies in metacommunities and
34 that disturbance in interaction with dispersal ability limits not only the range of trait values
35 but also the type of possible trait associations.

36

37 **Introduction**

38 Characteristics such as size, dispersal ability, reproduction, or survival rate, vary drastically
39 among species. For example, the magnitude of divergence of seed size and mass among
40 flowering plants can reach 10^{11} and 10^5 , respectively (Westoby et al. 1992). Similarly,
41 flowering plants' longevity ranges from desert annuals, completing their life cycle in a few
42 weeks, to thousand-year-old trees such as the bristlecone pine *Pinus longaeva* (Borges 2009).
43 These variations in life history or functional trait values are shaped by the evolutionary
44 history of the species; for a given species, the association of particular trait values defines its
45 ecological strategy, or syndrome (Westoby 1998, Reich et al. 2003, Grime and Pierce 2012).
46 A strategy is the result of selection for trait values whose combination confers a higher fitness
47 in a given environment (Agrawal et al. 2010, Stevens et al. 2014). This selection can act on
48 independent traits, or on traits constrained by trade-offs, narrowing the range of possible trait
49 combinations.

50 Ecological strategies have been thoroughly studied and several frameworks focusing therein
51 have been developed, from the classical r/Kselection theory (MacArthur and Wilson 1967,
52 Pianka 1970) and Grime CSR classification for vascular plants (Grime 1977), to the more
53 recent leaf-height-seed strategy scheme and leaf economics spectrum (Westoby 1998,
54 Westoby et al. 2002, Wright et al. 2004, Adler et al. 2014, Reich 2014). The description of
55 species' ecological strategies is intimately linked to their environment, especially in terms of
56 the intensity of stress and disturbance experienced (Grime 1977, Southwood 1988, Grime and
57 Pierce 2012, Westoby 1998).

58 Habitat specialisation also varies among species: at one extreme, specialists exhibit a narrow
59 niche breadth and/or environmental tolerance while generalists have a larger breadth and/or
60 tolerance (Levins 1968, Futuyma and Moreno 1988, Poisot et al. 2011). This degree of
61 specialisation changes how species experience their environments; for example, a given

62 environment may be perceived as more homogeneous by a generalist species than by a
63 specialist one. As a consequence, specialisation may also influence the selection on trait
64 values underlying ecological strategies. Despite the likelihood of such influence, few studies
65 have investigated these links specifically. Most studies have focused on the relationship
66 between specialization and dispersal. Empirically, specialists generally have a low dispersal
67 rate (Fig. 1A) (Warren et al. 2001, Verberk et al. 2010). Large scale empirical studies in
68 European land snails (Dahirel et al. 2015) and in European birds (Reif et al. 2015) also tended
69 to associate specialist species with low dispersal. Despite this, specialisation has
70 paradoxically been associated with high dispersal abilities (Fig. 1B), particularly when
71 specialisation concerns sparse or ephemeral habitats (Levin and Muller-Landau 2000, Fridley
72 et al. 2007). Stevens et al. (2014) have also suggested that while a link between specialisation
73 and dispersal is expected, it is difficult to predict the direction of this correlation.
74 Theoretically, studies have generally shown that generalist species are commonly associated
75 with disturbed and heterogeneous environments, and specialist species with stable and
76 homogeneous habitats (Futuyma and Moreno 1988, Devictor et al. 2008). In parallel,
77 investigations about the coevolution of life history traits have suggested that low rates of
78 dispersal are required for specialisation to evolve (Brown and Pavlovic 1992, Kisdi 2002,
79 Ravigné et al. 2009, Débarre and Gandon 2010, Nurmi and Parvinen 2011). Other studies
80 have suggested that specialists could be favoured at intermediate dispersal rates (Fig. 1C)
81 (Ronce and Kirkpatrick 2001) or, inversely, that they can be advantaged by small or large
82 values (Fig. 1D) (Nurmi and Parvinen 2008). However, analysing the conditions required for
83 specialisation to evolve is not equivalent to investigating the traits leading to the most
84 efficient strategies, especially in changing environments. The lack of consensus on the
85 direction of covariation between dispersal ability and specialisation may well be due to the
86 multiple roles of dispersal seen in life-history strategies (Poisot et al. 2011, Stevens et al.

87 2014), as well as different dispersal attributes (rate, distance and temporality) and phases
88 (Bonte et al. 2012, Buoro et al. 2014).

89 Less evidence has been shown regarding the links between specialisation and other life
90 history traits. Reif et al. (2015) have revealed complex relationships between habitat
91 specialisation, diet and climatic niches and flight attributes. Specialists are also traditionally
92 associated with K-strategy characteristics (Southwood 1988), such as high competitive ability
93 (Fig. 1EF) (Marvier et al. 2004). Specialists may also have longer life spans than generalists
94 (Fridley et al. 2007). These examples demonstrate that there is little consensus on the
95 association between the degree of specialisation and other traits, and that these aspects
96 deserve further investigations.

97 Most of the theoretical studies investigating the coevolution of life history traits and
98 ecological strategies include few habitat types and few competing species, mainly due to
99 difficult analytical tractability. Moreover, important life history traits other than dispersal,
100 such as survival rate or competitiveness have seldom been considered. Understanding the
101 evolution of specialisation and related strategies therefore deserves investigation in wider
102 settings. A simulation approach considers the multiplicity and complexity of trait interactions
103 involved in building ecological strategies. In this study, we use simulation experiments within
104 spatially explicit environments to investigate the selection of strategies in metacommunities
105 under different disturbance regimes. The modelling approach mimics community assembly
106 processes. Each simulation starts with the creation of a large pool of species harbouring
107 different strategies, which are then selected by environmental and spatial processes. Strategies
108 combine different values of habitat specialisation and dispersal ability, competitiveness and
109 reproductive investment. We analyse the resulting trait value associations across different
110 values of generation overlap and disturbance. We expect that different degrees of
111 specialisation are associated with distinct strategies. In particular, we investigate the

112 relationship between specialisation and dispersal and whether generalist species show trait
113 attributes linked to opportunistic strategies such as low competitiveness (Figure 1). We
114 predict, by modifying the intensity of competition and the spatial distribution of available
115 habitats, that both disturbance rate and generation overlap impact the trait associations
116 observed.

117

118 **Methods**

119 *Model description*

120 We used a metacommunity simulation model in which trophically-equivalent species (e.g. all
121 plants) compete for space in a heterogeneous environment (Büchi et al. 2009, Büchi and
122 Vuilleumier 2014). This model simulates sessile species, in which only juveniles dispersed
123 prior to settlement. The environment is composed of 25 x 25 local communities, or cells, each
124 cell being characterized by a carrying capacity K of 100 individuals and an environmental
125 value E_i that determines species growth rate. E_i varies from cell to cell (heterogeneous
126 environment) and follows a normalized gaussian probability distribution (with mean = 0 and
127 standard deviation = 1, Büchi et al. 2009). Metacommunity dynamics proceed in four discrete
128 time steps: 1. reproduction, 2. adult mortality and disturbance, 3. juvenile dispersal and 4.
129 competition for space. Each species is characterized by six traits: niche optimum μ_s , niche
130 breadth σ_s , dispersal ability δ_s , competitiveness κ_s , reproductive investment ω_s and survival
131 rate ψ_s .

132 Species' habitat specialization impacts their fecundity, with specialist species having a higher
133 fecundity in their optimal habitat compared to generalist species. Species fecundity R_s in a
134 community (cell) of environmental value E_i is determined by the individual reproductive
135 investment ω_s , niche optimum μ_s , and niche breadth σ_s as follows:

$$136 \quad R_s(E_i) = h \cdot \frac{\omega_s}{\sigma_s \sqrt{2\pi}} \cdot \exp \left[-\frac{1}{2} \cdot \left(\frac{E_i - \mu_s}{\sigma_s} \right)^2 \right] \quad (1)$$

137 Here h is a scaling factor transforming the rate of increase into an effective fecundity (h is set
138 to 10 in this study). The effective per capita number of offspring in each cell is the rounded
139 value of $R_s(E_i)$.

140 Mortality occurs after reproduction and is determined by adult survival ψ_s and disturbance
141 rate T . Adult survival probability equals to ψ_s at each time step. Disturbance causes total
142 extinction in proportion T of randomly chosen local communities (cells).

143 Juvenile dispersal occurs according to a dispersal kernel $D_s(x)$ (probability density function of
144 dispersal distance) whose shape is defined by the mean species dispersal ability δ_s ,

$$145 \quad D_s(x) = \frac{1}{\delta_s} \cdot \exp \left[-\frac{x}{\delta_s} \right] \quad (2)$$

146 Each juvenile disperses independently at a distance that is determined by the dispersal kernel
147 associated with its species. Direction is drawn randomly from a uniform distribution. Periodic
148 boundary conditions are considered, such that individuals reaching the environment borders
149 re-enter the environments from the opposite side.

150 Preemptive competition is assumed (i.e., adult individuals already settled cannot be displaced
151 by juveniles). Therefore, only juveniles compete for settlement in each local community;
152 successful juveniles are drawn randomly among the pool of competing juveniles, with a
153 weighting determined by their competitiveness κ_s . If there are fewer competing juveniles than
154 the number of places available, all juveniles can settle.

155 We further assume that competitiveness κ_s and reproductive investment ω_s are constrained by
156 the following trade-off (Levine and Rees 2002):

157 $\kappa_s \cdot \omega_s = 1$ (3)

158 This trade-off is inspired by the classic, well-documented trade-off between seed size and
159 seed number (Jakobsson and Eriksson 2000, Leishman 2001).

160 In this model, traits are randomly associated in species and advantageous strategies are
161 selected when providing a fitness advantage to species. During this process, trait values
162 remain constant. We thus assume that the time scale of the processes studied does not allow
163 for the evolution of traits, and only community dynamics are considered.

164 This model is an object-oriented model implemented in Borland Delphi, and code is available
165 upon request.

166

167 *Simulations*

168 For each simulation, we generated an initial metacommunity composed of species to which
169 we assigned trait values as described in Table 1. Three distinct scenarios were built in order to
170 address the influence of the different species traits sequentially. In the first scenario, all
171 species had competitiveness κ_s and reproductive investment ω_s set to 1 and had variable
172 dispersal ability δ_s drawn randomly between 0 and 1. In the second scenario, all species had
173 variable competitiveness κ_s and reproductive investment ω_s , which were randomly drawn for
174 each species following the trade-off presented in equation 3 (uniform distribution of their
175 logarithms), and had an identical and limited dispersal ability δ_s set to 0.1. In the third
176 scenario, all species had variable dispersal ability, competitiveness and reproductive
177 investment. In all scenarios, we varied for each species niche optimum μ_s (values between -
178 2.5 and 2.5) and niche breadth σ_s (values between 0.01 and 1). A value of 0.01 for σ_s
179 corresponded to very specialist species and a value of 1 corresponded to very generalist
180 species. Then, for each scenario, we investigated the influence of generation overlap (adult
181 annual survival) and disturbance as follows. Each scenario was run alternatively with adult

182 annual survival rate ψ_s set, to either 0 (no generation overlap) or to 0.95 (strong generation
183 overlap). Three rates of disturbance T were considered: $T = 0$, $T = 0.01$ and $T = 0.25$.
184 For each case studied, we considered pools of 100 different species to initiate the simulations.
185 Individuals of these species were randomly distributed in the landscape until carrying capacity
186 was reached in each cell. Metacommunity dynamics were simulated for 1000 time steps,
187 during which some species went extinct and others persisted. This duration is sufficient to
188 reach a steady state in terms of mean traits (weighted by species abundances) though the
189 species richness continued to decrease very slowly (Supplementary material Appendix 1). For
190 each of the simulation scenarios, 50 replicates were run, with a new species pool and
191 landscape for each replicate. At the end of each simulation, we recorded the characteristics
192 and abundance of the selected strategies in terms of niche breadth, dispersal ability,
193 competitiveness and reproductive investment. Mean trait values were computed for each
194 simulation considering the trait values of all the surviving individuals (mean species trait
195 value weighted by the abundance of each species). Results for trait associations given niche
196 breadth were analysed for five categories of niche breadth (from the most specialist to the
197 most generalist species): 0-0.1, 0.1-0.2, 0.2-0.4, 0.4-0.6, 0.6-1.
198 We also investigated the sensitivity of our results to the initial number of species (10 or 1000)
199 and to different environmental spatial autocorrelation. To generate autocorrelation between
200 the environmental values of two cells, we used the sequential Gaussian simulation algorithm
201 (Goovaerts 1998, see also figure 1 in Büchi et al. 2009). We considered moderate ($\alpha = 5$) and
202 strong ($\alpha = 10$) autocorrelation, where α represents the distance above which correlation falls
203 below 0.05 ($\alpha = 0$ in the other simulations). These results are presented in Supplementary
204 material Appendix 2 and 3.
205 Simulations results were analysed using R 3.0.2 (R Core Team 2013).

206

207 **Results**

208 *Associations between niche breadth and dispersal when competitiveness and reproductive*
209 *investment are fixed*

210 Metacommunities are mainly composed of species with low values of niche breadth, namely
211 specialist species (Fig. 2). Interestingly, a strong association between niche breadth and
212 dispersal abilities is observed (Fig. 2). In the absence of disturbance ($T = 0$), communities are
213 composed of a high number of specialist species with a large range of dispersal abilities, but
214 with very low abundances at the lowest dispersal values, while more generalist species have
215 lower dispersal abilities (Fig. 2). The presence of disturbance affects the association between
216 species niche breadth and dispersal abilities, such that specialist and generalist species with
217 limited dispersal values are progressively driven to extinction (Fig. 2). Generation overlap
218 changes this pattern only quantitatively, except at high disturbance rate where the pattern is
219 completely changed. In this situation, mean dispersal is higher than in any other situation, and
220 generalist species have higher dispersal abilities than specialist ones (Fig. 2).

221 The associations found between niche breadth and dispersal are quantitatively but not
222 qualitatively impacted by spatial autocorrelation (Supplementary Material Appendix 3). An
223 exception occurs when disturbance is high ($T = 0.25$) and generations overlap. In this case,
224 when spatial autocorrelation is low, dispersal was lower for all species, though this effect was
225 stronger for the most generalist species.

226 In the absence of disturbance, species can survive with a large range of niche optimum values,
227 whereas species with extreme niche optima (thus relying on rare habitats) disappear in the
228 presence of strong disturbance (Supplementary material Appendix 4).

229

230 *Associations between niche breadth and competitiveness/reproductive investment when*
231 *dispersal ability is limited*

232 In the absence of disturbance ($T = 0$), metacommunities are composed of species with a large
233 range of competitiveness and niche breadth, but with a higher proportion of species exhibiting
234 small niche breadth values (Fig. 3). With no generation overlap, generalist species show
235 reduced investment in competitiveness compared to specialist species with a large range of
236 possible competitiveness and a mean value similar to the initial state (Fig. 3). When
237 generations overlap, all categories of specialisation show both a mean and range of values
238 similar to the initial state, with no clear selection of a particular strategy.

239 Disturbance tends to decrease global investment in competitiveness in favour of reproduction.
240 When disturbance is moderate ($T = 0.1$), the association between competitiveness and niche
241 breadth is still negative, with competitiveness being globally lower with generation overlap.
242 In contrast, at high disturbance rate ($T = 0.25$), all categories of niche breadth show similarly
243 low investment in competition, with a reduced range of viable trait values (Fig. 3). This
244 pattern is particularly strong when generations overlap.

245 Here again, spatial autocorrelation has a slight quantitative influence on the relationship
246 between niche breadth and competitiveness (Supplementary Material Appendix 3). However,
247 when disturbance was high ($T = 0.25$), strong spatial autocorrelation allowed for a larger
248 range of competitiveness values for specialist species.

249 With limited dispersal ability, very generalist species can survive in the metacommunity.
250 They are however, in the absence of disturbance, restricted to extreme niche optima. In
251 contrast, very generalist species with intermediate niche optimum can survive in the presence
252 of disturbance (Supplementary material Appendix 4).

253

254 *Associations between niche breadth, dispersal and competitiveness/reproductive investment*

255 The change from fixed values of competitiveness and reproductive investment to variable
256 values has almost no influence on the association between dispersal ability and niche breadth
257 (Fig. 4 vs Fig. 2).

258 In contrast, the change from fixed values of dispersal ability to variable values has a clear
259 influence on the association between competitiveness and niche breadth (Fig. 5 vs Fig. 3).

260 First of all, dispersal limitation allows for the survival of a larger number of generalist species
261 than a variable dispersal ability. Then the decrease of competitiveness with increasing niche
262 breadth is clearly less pronounced when dispersal is variable (Fig. 5). The range of
263 competitiveness values observed in the presence of disturbance is also clearly higher,
264 especially at low niche breadth. So here, under disturbance and depending on dispersal
265 limitation, communities can be either composed by specialist species with a broad range of
266 competitiveness/reproductive investment values or by generalist and specialist species that
267 invest in reproduction and limit their investment in competitiveness.

268 Associations between dispersal and competitiveness/reproductive investment are visible when
269 taking into account the niche breadths of the surviving species, especially at high disturbance
270 rates (Fig. 6). When none or moderate disturbance occurs and there is no generation overlap,
271 generalists associate higher reproductive investment with lower dispersal ability compared to
272 specialists. When no disturbance occurs and generation overlap is high, generalists have lower
273 dispersal ability but with no clear selection on competitiveness values. The pattern changes
274 when disturbance rate is strong and generation overlap is high. In this case, generalist species
275 have higher dispersal ability with higher reproductive investment than specialist species (Fig.
276 6).

277

278 **Discussion**

279 In this study, we delineated ecological strategies by level of specialisation. We found larger
280 ranges and more numerous combinations of trait values for specialist species, but more
281 restricted trait combinations for the most generalist species. Additionally, our results show
282 that species specialisation and trait associations in metacommunities strongly depend on the
283 intensity of disturbance experienced by the species. Then, within a disturbance rate, species'
284 ability to disperse and generation overlap act in interaction on the trait associations observed.
285 Most of our results can be explained by the mechanisms that determine species' success in
286 settlement. In their optimal habitat, specialist species are dominant over generalists and tend
287 to exclude them, as they produce more juveniles. However, at the metacommunity scale,
288 specialist species, due to their specific habitat requirements, suffer from limited available
289 habitat with a scattered distribution. Their dispersal ability thus determines the amount of
290 suitable habitat accessible. Under disturbance, extinction-colonization dynamics favour
291 species that disperse (but see Ronce et al. 2000a); however, specialists succeed in settling in
292 their optimal habitat only when dispersal is very high. In contrast, generalist species, thanks to
293 their high environmental tolerance, benefit from a large number of suitable habitats,
294 accessible without large dispersal abilities. Generalists therefore have the advantage of easy
295 settlement over specialists when dispersal is limited. In contrast, while specialist species'
296 persistence is limited by their dispersal ability, generalist species' persistence is limited
297 instead by their low fecundity. Finally, the effective amount of habitat available for settlement
298 is regulated by adult survival (generation overlap) and disturbance (local community
299 extinction). Combinations of these processes drive the composition of metacommunities and
300 the surviving strategies observed in our study.

301

302 *Strategies involving specialisation and dispersal*

303 Strategies involving specialisation and dispersal abilities are dependent on the disturbance
304 rate. In the absence of disturbance, our results show that generalist species have limited
305 dispersal ability, while in contrast, specialist species are associated with a large range of
306 dispersal abilities. These results can be explained first by the cost of dispersal and second by
307 the amount of suitable habitat accessible. In the absence of disturbance, dispersal is costly
308 because the probability of a juvenile reaching an unsuitable habitat is high (Bonte et al. 2012),
309 and thus limited dispersal abilities develop (Hastings 1983). This result is observed here for
310 generalist species but not for specialist species. Indeed, specialist species produce more
311 juveniles than the number of local settlement opportunities; dispersal therefore favours their
312 persistence despite its inherent cost by allowing them to reach new habitats. In addition
313 limited dispersal ability drastically reduces specialist species' chances to settle in their
314 specific, rare and scattered suitable habitat. This result is reflected in the lower abundance
315 observed for the most specialist species at very low dispersal abilities. In contrast, generalist
316 species are less impacted by the distribution of their habitats, which tend to be widely
317 distributed and could be easily reached through dispersal from neighbouring habitats (Nilsson
318 et al. 1993, Dynesius and Jansson 2000).

319 The presence of disturbance strongly modifies the association between species niche breadth
320 and dispersal abilities. Under disturbance, specialist and generalist species with limited
321 dispersal abilities are excluded, as disturbance induces extinction-colonization dynamics
322 favouring species with high dispersal (Gandon and Michalakis 1999). Generalists face
323 additional barriers as well, such as their very low growth rate, which does not withstand
324 frequent disturbance (Parvinen and Egas 2004, Nurmi and Parvinen 2008). The coexistence of
325 specialist and generalist species is also driven by generation overlap. When adult survival is
326 null, recruitment to suitable habitat is high and specialist species dominate over generalist
327 species as they produce more juveniles. In contrast, when generations strongly overlap,

328 saturation of the metacommunity is very high. In such a saturated system, disturbance creates
329 gaps in adult density, and thus many spots are available locally for juveniles. In this case,
330 species with high dispersal ability have a strong advantage in finding these newly opened
331 positions. The production of numerous offspring can confer similar advantages, explaining
332 why very fecund specialists can perform well even when they have lower dispersal ability.
333 Some examples are tropical forests or coral reefs, where sudden gaps are often the only way
334 for new recruitment to occur (Connell 1978).

335 These results contrast the classical descriptions of specialists as having reduced dispersal
336 ability and generalists as being opportunistic species with high dispersal ability. This classic
337 view is supported by theoretical studies on the evolution of specialisation, or local adaptation,
338 in interaction with dispersal (Brown and Pavlovic 1992, Kisdi 2002, Ravigné et al. 2009).
339 Those studies demonstrate that reduced dispersal is required for specialisation, as dispersal
340 prevents adaptation to a local environment. As a corollary, high dispersal promotes generalist
341 species by increasing the variety of habitats a species experiences. The discrepancy between
342 these classic descriptions and the results seen here can be explained by differences in the
343 processes studied. Here, we investigated the dynamics and factors that drive specialist-
344 generalist coexistence in metacommunities and not how specialisation itself might evolve
345 (e.g. from an initial pool of generalist species). Although dispersal limitation favours
346 specialists, there is still a need to disperse in order to persist in dynamic and heterogeneous
347 environments. Interestingly, the diversity of trait associations observed in our study is
348 reflected by some empirical evidence. Both generalist and specialist species can have variable
349 dispersal abilities (e.g. Nilsson et al. 1993, Levin and Muller-Landau 2000, Warren et al.
350 2001, Verberk et al. 2010).

351

352 *Strategies involving specialisation and competitiveness/reproductive investment*

353 Strategies involving specialisation and competitiveness (or reproductive investment) are less
354 obvious than those involving dispersal, and are dependent on the disturbance rate in
355 interaction with generation overlap and dispersal ability. In the absence of disturbance and
356 when generation overlap is strong, recruitment is low and the coexistence of specialist and
357 generalist species is independent of their investment in competition or reproduction. Forests
358 are a typical example of a natural ecosystem with high generation overlap, as they are mainly
359 composed of long-lived species. In contrast, without generation overlap, recruitment is high
360 and generalists investing in competition rather than reproduction are excluded by specialist
361 species (Nurmi and Parvinen 2008). Specialist species, which produce many juveniles in their
362 given habitat, can afford to invest more in competitive ability, while generalist species are
363 strongly limited by their reduced fecundity (Nurmi and Parvinen 2008).

364 Disturbance has a drastic impact on the associations between niche breadth and
365 competitiveness or reproductive investment, but the patterns depend strongly on the dispersal
366 ability of the species. When dispersal is unconstrained, communities are composed of
367 specialist species, with generalists excluded. Disturbance creates extinction-colonization
368 dynamics that are known to favour dispersal, and provides empty habitat patches that are
369 efficiently colonized by specialist species due to two factors: their local fitness advantage and
370 the larger number of dispersing juveniles. Thus, disturbance favours species with high
371 dispersal and fecundity as they efficiently settle in empty habitat patches. Dispersal limitation,
372 however, completely shifts this pattern: though new habitat becomes available after
373 disturbance, the sparseness of suitable habitat for specialists and their limited ability to
374 disperse prevents occupation of these new areas, and thus prevents displacement of the (less
375 efficient) generalists. Communities are composed of species with a wide range of
376 specialisation but usually with all species investing in reproduction. Species with high
377 competitiveness go extinct due to their corresponding low colonization potential.

378 Our results show thus that specialist and generalist species can either invest in reproduction or
379 in competition, except in the condition of high disturbance rate with limited dispersal, where
380 investment in reproduction is critical for survival. Our results therefore contrast with the
381 common conclusion that specialist species benefit from "K-strategy" characteristics such as
382 high competitive ability, while generalists are more associated with "r-strategy"
383 characteristics such as low competitive ability (Southwood 1988). We also find that
384 competition and reproductive investment play less of an important role in specialist-generalist
385 coexistence and in the emergence of trait strategies, when compared to the fundamental role
386 of dispersal.

387

388 *Strategies involving specialisation, dispersal and competitiveness or reproductive investment*

389

390 In agreement with the results obtained by Ronce (2000b), no global association was observed
391 between dispersal and competitiveness/reproductive investment when dispersal varies along
392 with competitiveness and reproductive investment. However, interestingly, an association
393 between these traits emerges when species are grouped by specialisation levels.

394 When no disturbance occurs and there is no generation overlap, recruitment is high and
395 homogeneous, favouring species with both reduced dispersal and increased reproductive
396 investment (Ronce and Olivieri 1997). In contrast, when disturbance rate and generation
397 overlap both occur, generalist species disperse effectively and invest greatly in reproduction.

398 This situation is similar to gap creation in rain forests or coral reefs, leading to a "fugitive
399 species syndrome" (Connell 1978, Tilman 1994).

400 Our results demonstrate that there is not a unique association between specialisation, dispersal
401 ability and reproductive investment. These associations are instead driven by recruitment
402 opportunities that are determined by disturbance rate and generation overlap. Similar results

403 were obtained by Venable and Brown (1988), who show that the relative importance of seed
404 traits (e.g. size, dispersal, dormancy) depends on dispersal limitation, spatial and temporal
405 autocorrelation and disturbance.

406

407 *Model discussion and perspectives*

408 The approach adopted in our model consisted of generating species rich metacommunities in
409 which each species has random trait values. We subsequently observed the selection of
410 strategies that allowed species survival. This corresponds to community assembly processes,
411 which are adopted less often than genetic approaches (but see for example Kallimanis et al.
412 2006, Devictor and Robert 2009). During simulations, traits did not evolve and the invasion
413 of new or formerly extinct species was not allowed. We assumed that the time scale of the
414 processes studied did not allow for trait evolution, as, our system is meant to mimic, for
415 example, the colonisation of a novel habitat by competing species or a community
416 experiencing a rapid change of its environment, as expected with anthropogenic changes. The
417 use of a simulation model was necessary given the multiplicity of the traits considered and
418 number of processes involved, as such a system would not be analytically tractable.
419 Simulations also allow a thorough characterization of the successful strategies under different
420 conditions. Finally, our simulation framework complements common models used to test
421 theoretical metacommunity paradigms (see review in Logue et al. 2011).
422 Here, we considered 50 replicates of simulations, each starting with 100 species. This
423 translated into a random sample of 100 x 50 combinations of trait values. This procedure
424 allowed for the exploration of a large range of trait values. The number of species considered
425 in our simulation set up is representative of what is generally observed in natural
426 communities. Indeed, species richness is generally around 20-40 species and rarely goes
427 beyond 100 species in temperate grasslands and forests (e.g. Proulx and Mazumder 1998,

428 Klimek et al. 2007, Morin et al. 2011, Axmanova et al. 2012). Accounting for a larger number
429 of initial species does not qualitatively change the results (see results for 1000 species in the
430 Supplementary Material Appendix 2). However, it has the consequence of generating many
431 highly specialised species that occupy the whole range of environmental space. This process
432 drives generalist species to extinction; we therefore cannot effectively describe strategies for
433 generalist species under this condition. When a reduced number of species is considered (see
434 results for 10 species in the Supplementary Material Appendix 2), the resulting
435 metacommunity poorly represents the potential diversity of strategies and combine few traits
436 values. In this case, competition is very low and almost all species are maintained in the
437 metacommunity, and strategies are thus not easy to identify.

438 In our simulations, the associations found between niche breadth and other traits are generally
439 quantitatively but not qualitatively impacted by spatial autocorrelation (see Supplementary
440 Material Appendix 3). The main differences are observed in the presence of disturbance. We
441 expect a more drastic effect if this environmental autocorrelation is associated with
442 autocorrelation in disturbance (as predicted for fire, hurricane, or drought). Indeed it has been
443 shown, in a metapopulation context, that the effect of autocorrelated disturbance can interact
444 with habitat configuration (Vuilleumier et al. 2007). In this situation, specialist species might
445 be driven to extinction by aggregated disturbance in their clustered habitats while generalist
446 species might find refuge in more type of habitats, allowing re-colonisation following
447 disturbance events.

448 The exact form of a trade-off can influence the species coexistence outcome (Levins 1968, Yu
449 and Wilson 2001, Levine and Rees 2002, Nurmi and Parvinen 2008). Our simulations
450 considered two trade-offs: one with habitat specialisation, and the other with investment in
451 competition and reproduction. The specialisation trade-off considered here is based on the
452 species growth rate, which might be more detrimental to generalist species than specialist

453 ones (Nurmi and Parvinen 2008). The trade-off between competition and reproduction
454 modelled here was inspired by the well-documented trade-off between number and size of
455 flowering plants' seed (Leishman 2001). While this trade-off has been shown to promote
456 coexistence (Tilman 1994, Yu and Wilson 2001), its role in shaping natural communities'
457 composition, and its consequences in terms of species performance, have often been
458 questioned (Leishman 2001, Moles and Westoby 2006, Agrawal et al. 2010). Moreover,
459 trade-offs are expected to vary among species and depend on the environments experienced
460 by the species (Agrawal et al. 2010). How such variability impacts species' coexistence in a
461 community remain to be investigated.

462 Our results show that dispersal is a critical factor in shaping trait associations in
463 metacommunities. To gain further insights on its impact on community composition, we
464 suggest that dispersal rate and dispersal distance should be considered as two independent
465 factors. We expect that specialist species would benefit from rare, long distance dispersal
466 events but do not require a high dispersal rate.
467 Specialist species are currently declining worldwide (Warren et al. 2001, Munday 2004,
468 Clavel et al. 2010). However, our results demonstrate that specialists could be successful even
469 in the presence of disturbance. This counterintuitive result could be explained by the large
470 availability of habitats for specialist species in our study, while in natural ecosystems,
471 specialist species suffer from important habitat loss. The impact of habitat loss on the
472 coexistence of specialist and generalist species, and on the association of specialisation with
473 the other traits, especially dispersal ability, would thus deserve further investigation.

474 Very few experimental investigations on the association of specialisation and other life
475 history traits exist. However, recently, two experimental studies on trait co-variation with
476 specialisation reported interesting and unexpected results. First, Khokhlova et al. (2014)
477 demonstrated, using fleas, that stronger trade-offs between quantity and quality of offspring

478 are found for generalist species compared to specialist ones. Second, Condon et al. (2014)
479 showed, using *Drosophila melanogaster*, that specialist and generalists genotypes do not
480 necessary evolve in spatially constant and variable environments, respectively. We hope that
481 our results will stimulate further experimental tests.

482

483 *Conclusions*

484 Our results show that distinct ecological strategies emerge principally for generalist species,
485 whereas specialist species have much larger ranges of trait values and associations. The
486 drivers of strategies are disturbance, in interaction with species dispersal ability and local
487 recruitment opportunities. In natural habitats, these processes are strongly impacted by
488 anthropogenic changes, such as increased disturbance, habitat fragmentation and habitat loss.
489 This could explain the important changes in the degree of specialisation seen in natural
490 communities (Warren et al. 2001, Munday 2004, Clavel et al. 2010). A better understanding
491 of the characteristics linked to specialisation is therefore essential, as specialists are currently
492 declining worldwide. In particular, the association of specialisation with other life-history
493 traits would benefit from further empirical evidence.

494

495

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649 **Supplementary material**

650 Supplementary material (Appendix oik.XXXXX at
651 <www.oikosjournal.org/readers/appendix>). Appendix 1-4.
652

For Review Only

653 **Table 1:** Values of the parameters used in the simulations. In bold the parameters varying
 654 between simulations.

Parameters	Symbols	Values
Niche optimum	μ_s	random [-2.5 - 2.5]
Niche breadth	σ_s	random [0.01 - 1]
Competitiveness	k_s	1 ; random* [0.1 - 10]
Reproductive investment	ω_s	1 ; random* [0.1 - 10]
Dispersal ability	δ_s	0.1 ; random [0 - 1]
Survival rate	ψ_s	0.95 ; 0
Disturbance rate	T	0 ; 0.01 ; 0.25

*trade-off: $k_s \times \omega_s = 1$

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667 **Figure legends**

668 **Figure 1:** Expectations for trait strategies from different empirical and theoretical studies. A,
669 B and C: relationship between dispersal and niche breadth, D. relationship between
670 competitiveness (in trade-off with reproductive investment) and niche breadth, E: relationship
671 between competitiveness and dispersal, in stable and disturbed habitats.

672

673 **Figure 2:** Association between dispersal and niche breadth values in communities
674 experiencing different strength of disturbance: $T = 0$: upper row, $T = 0.01$: middle row, $T =$
675 0.25 : lower row. Results are presented for species with competitiveness and reproductive
676 investment equal to 1, without and with generation overlap (survival rate at each generation is
677 either 0 or 0.95). The grey dots represent the strategies of the surviving species, the black line
678 is the mean dispersal, weighted by species abundances, computed for five categories of niche
679 breadth (0.0-0.1; 0.1-0.2; 0.2-0.4; 0.4-0.6; 0.6-1.0). Each graph represents the pooled results
680 over the 50 replicates.

681

682 **Figure 3:** Association between competitiveness (on a logarithmic scale) and niche breadth in
683 communities experiencing different strength of disturbance, $T = 0$: upper row, $T = 0.01$:
684 middle row, and $T = 0.25$: lower row. Results are presented for species with limited dispersal,
685 without and with generation overlap (survival rate at each generation is either 0 or 0.95). The
686 grey dots represent the strategies of the surviving species, the black line is the mean
687 competitiveness, weighted by species abundances, computed for five categories of niche
688 breadth (0.0-0.1; 0.1-0.2; 0.2-0.4; 0.4-0.6; 0.6-1.0). Each graph represents the pooled results
689 over the 50 replicates.

690

691 **Figure 4:** Association between dispersal and niche breadth values in communities
692 experiencing different strength of disturbance: $T = 0$: upper row, $T = 0.01$: middle row, $T =$
693 0.25 : lower row. Results are presented for species with variable values of competitiveness and
694 reproductive investment, without and with generation overlap (survival rate at each generation
695 is either 0 or 0.95). The grey dots represent the strategies of the surviving species, the black
696 line is the mean dispersal, weighted by species abundances, computed for five categories of
697 niche breadth (0.0-0.1; 0.1-0.2; 0.2-0.4; 0.4-0.6; 0.6-1.0). Each graph represents the pooled
698 results over the 50 replicates.

699

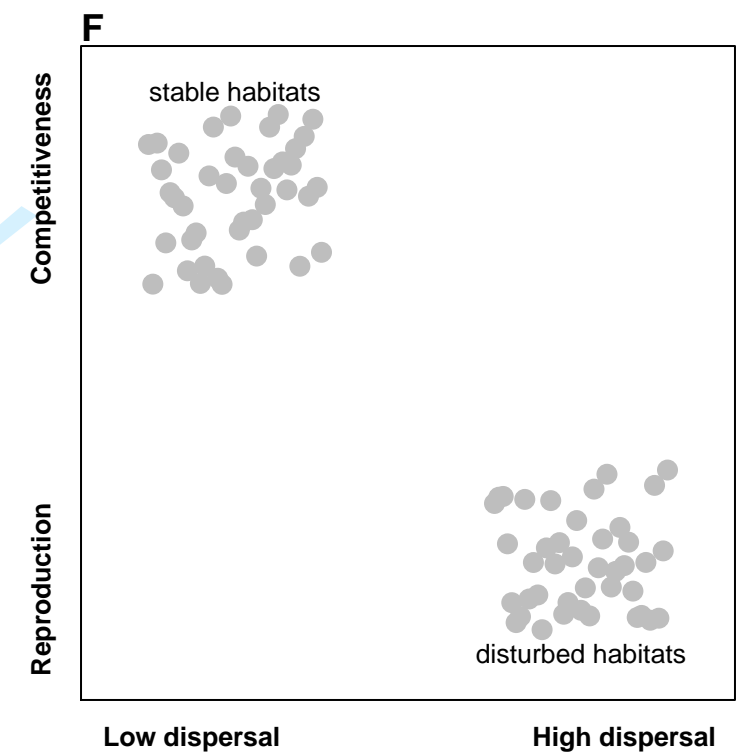
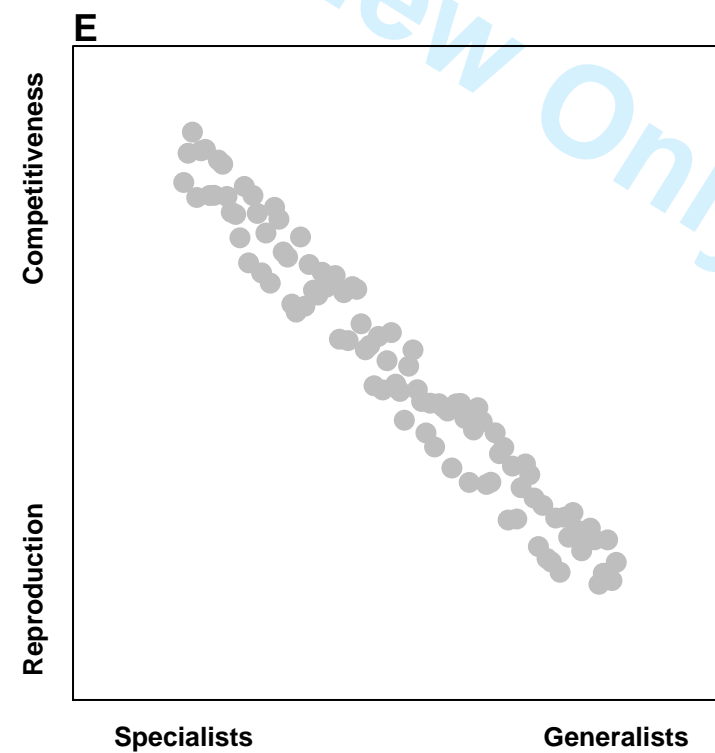
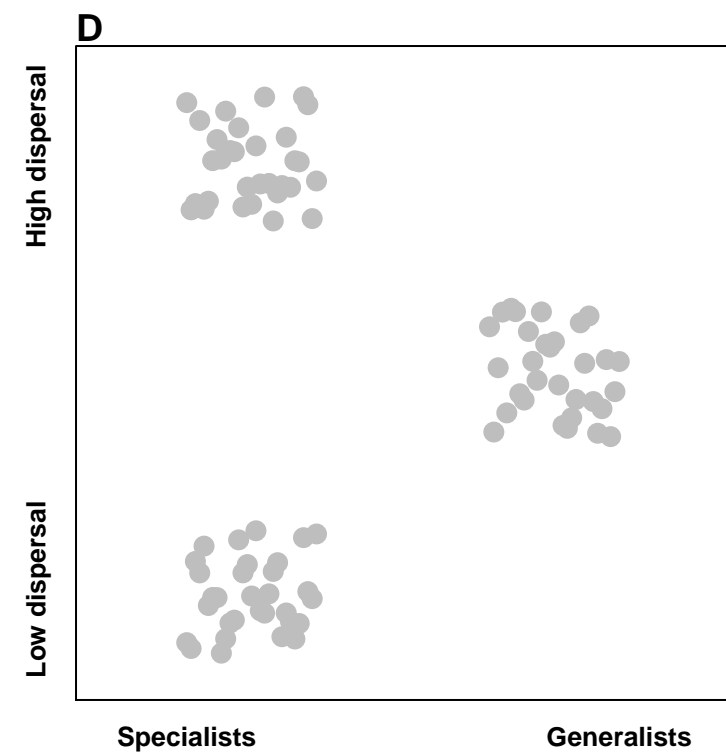
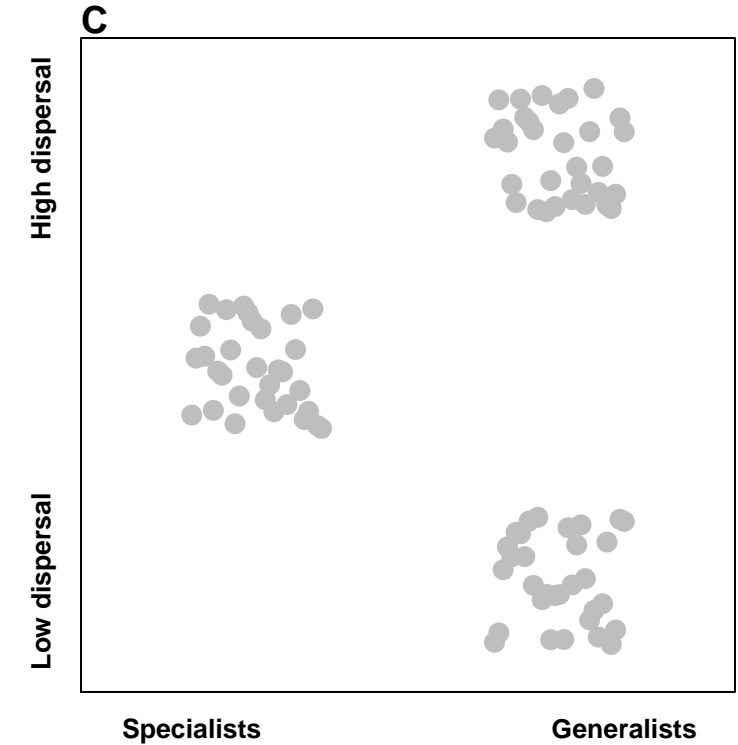
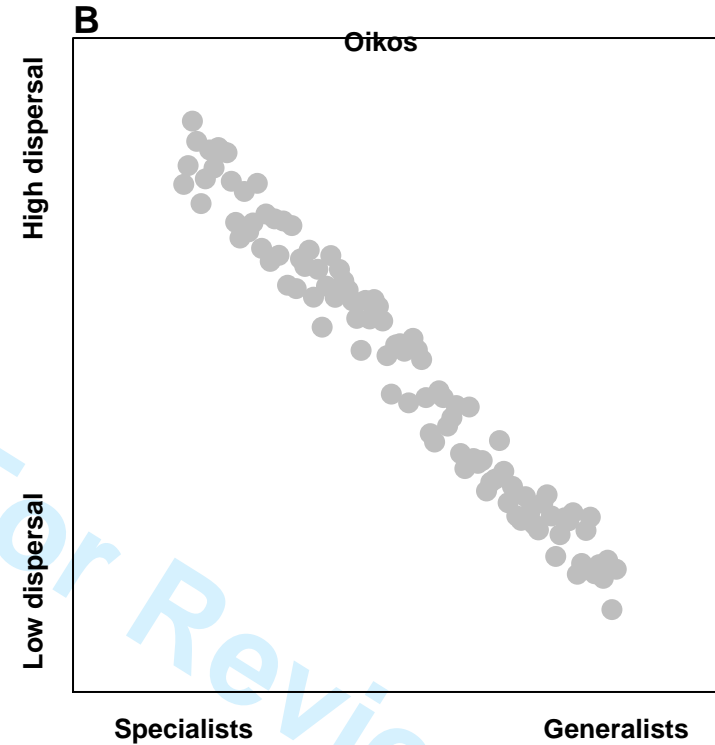
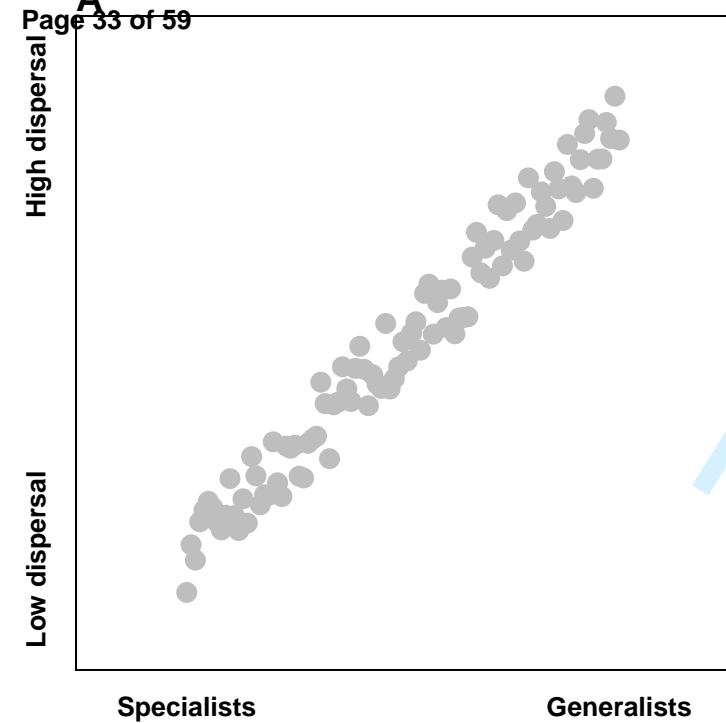
700 **Figure 5:** Association between competitiveness (on a logarithmic scale) and niche breadth
701 values in communities experiencing different strength of disturbance: $T = 0$: upper row, in
702 the $T = 0.01$: middle row, $T = 0.25$: lower row. Results are presented for species with
703 randomly assigned dispersal values, with and without generation overlap (survival rate at each
704 generation is either 0 or 0.95). The grey dots represent the strategies of the surviving species,
705 the black line is the mean competitiveness, weighted by species abundances, computed for
706 five categories of niche breadth (0.0-0.1; 0.1-0.2; 0.2-0.4; 0.4-0.6; 0.6-1.0). Each graph
707 represents the pooled results over the 50 replicates.

708

709 **Figure 6:** Association between dispersal ability and competitiveness (log values) for five
710 categories of niche breadth. The mean values are the average over the 50 replicates of the
711 values observed in all surviving individuals. The numbers correspond to the five niche
712 breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1;
713 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean values of the
714 metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$),
715 dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T =$

716 0.25). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping
717 generations (survival rate $\psi_s = 0.95$).
718

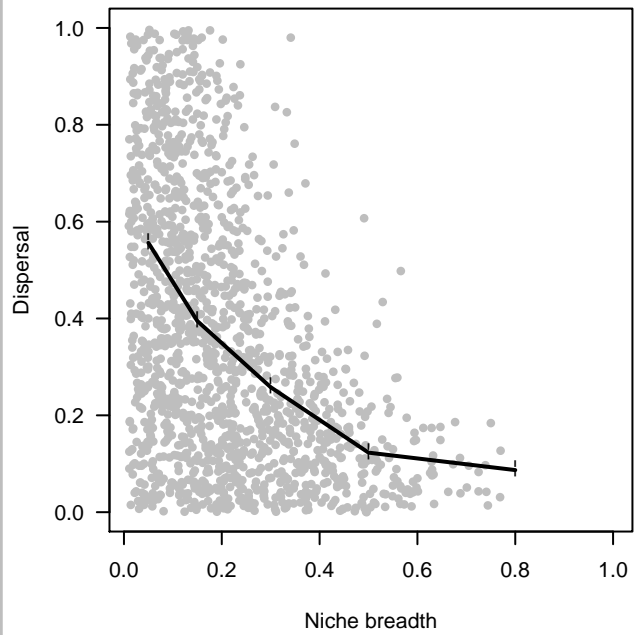
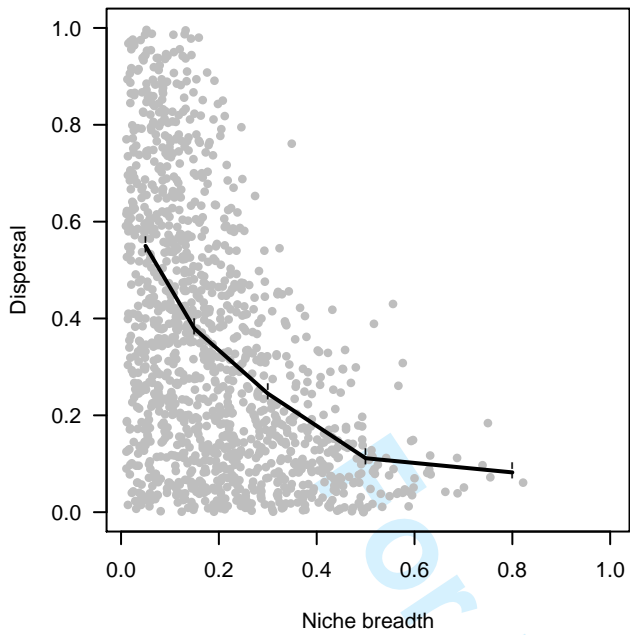
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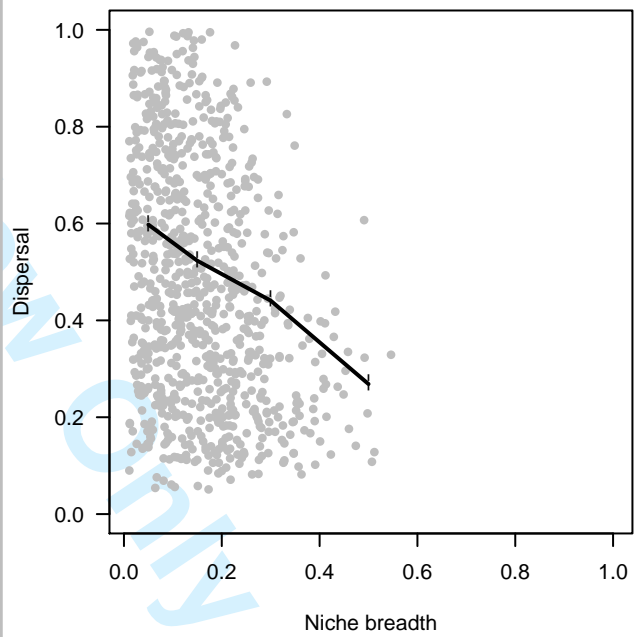
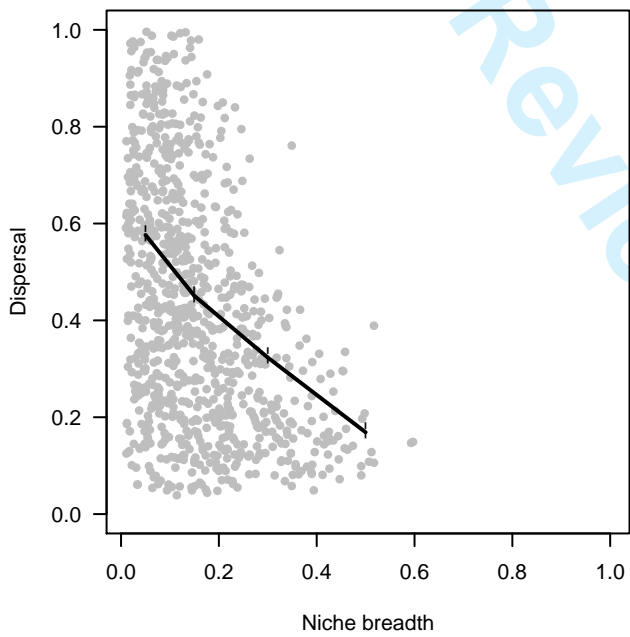
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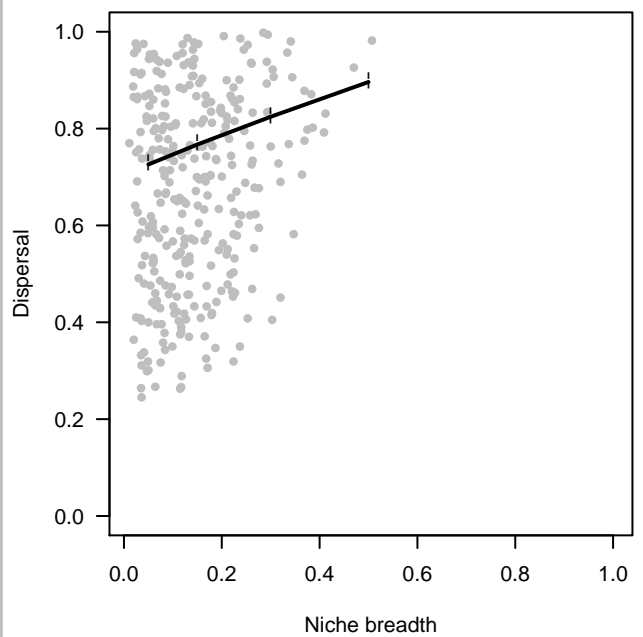
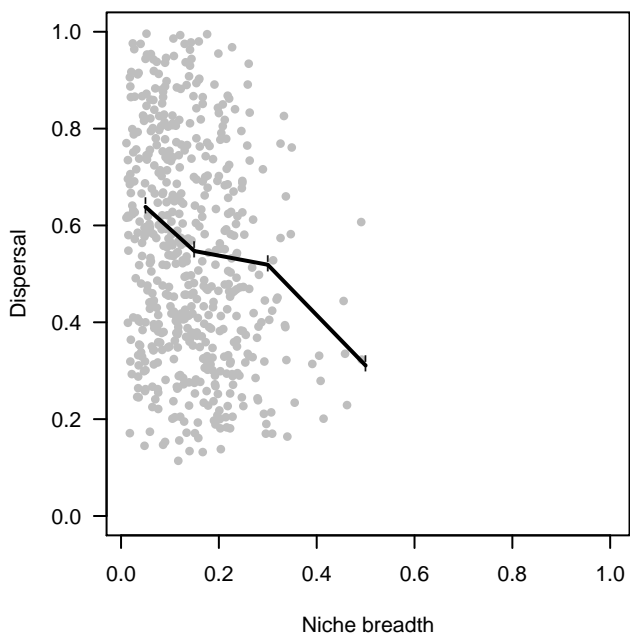
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T = 0.01



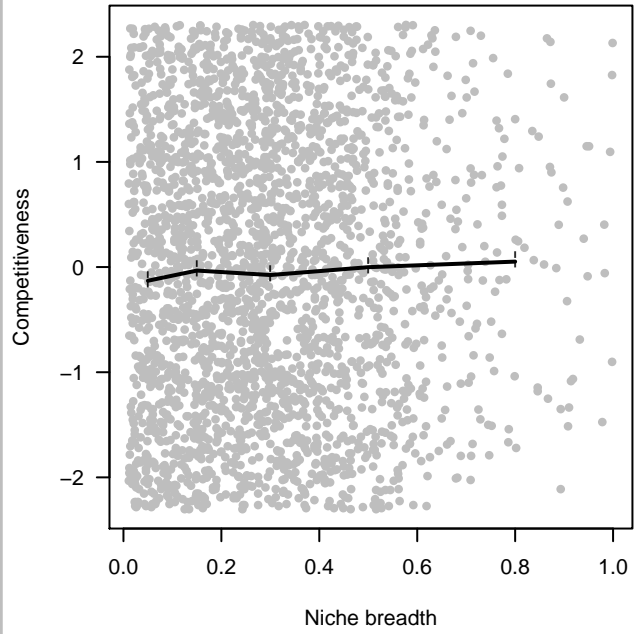
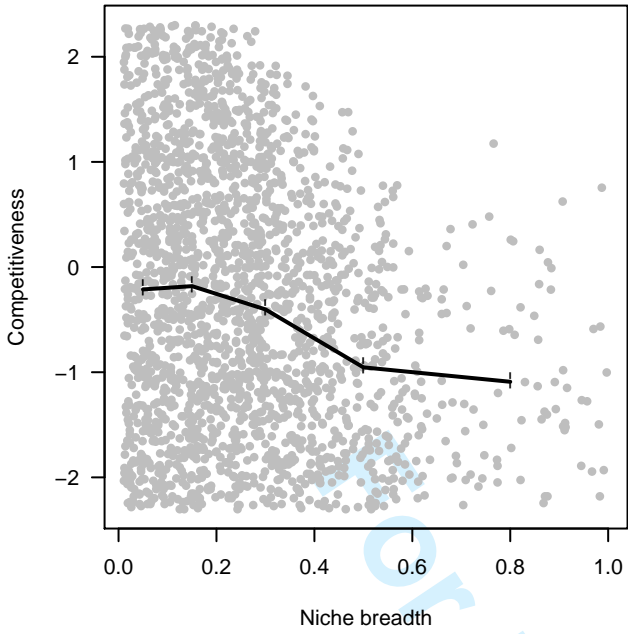
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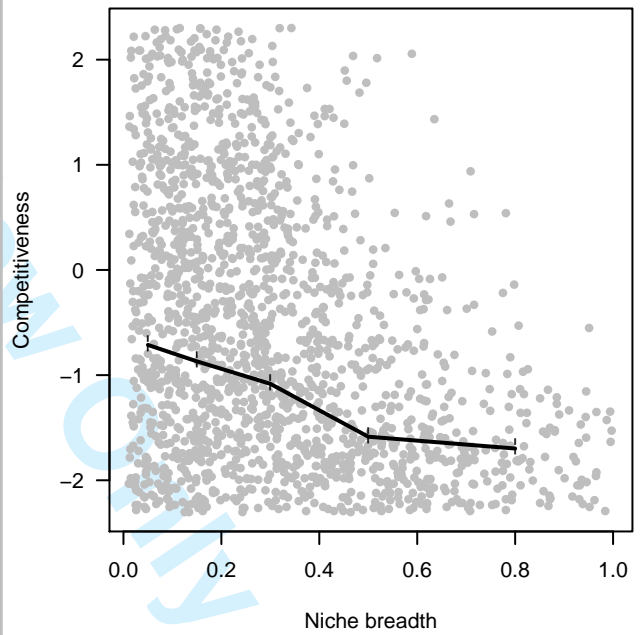
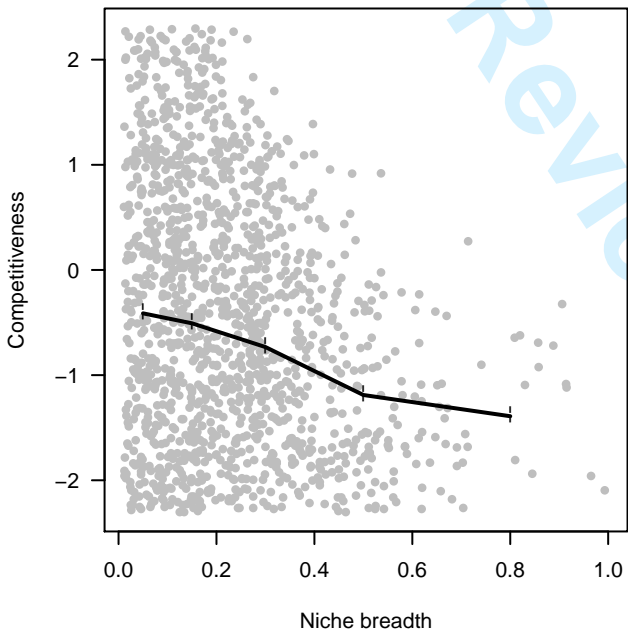
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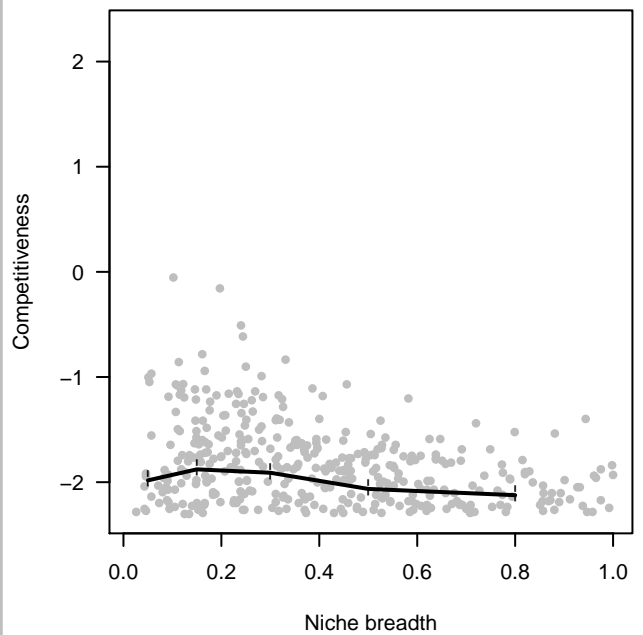
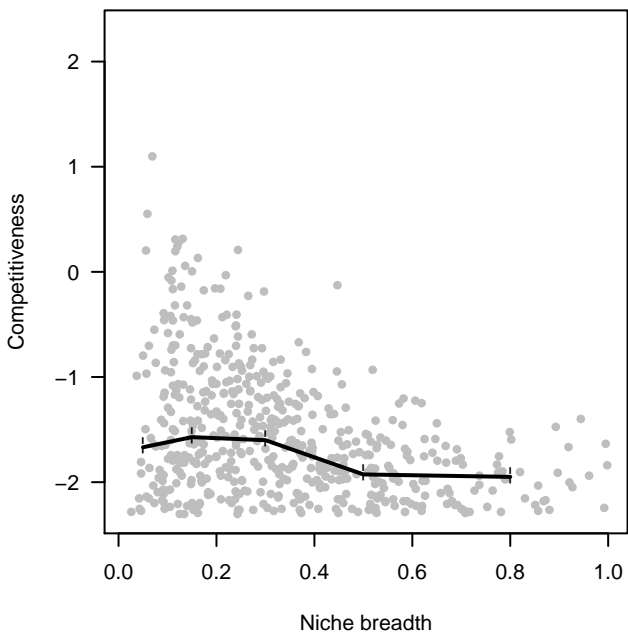
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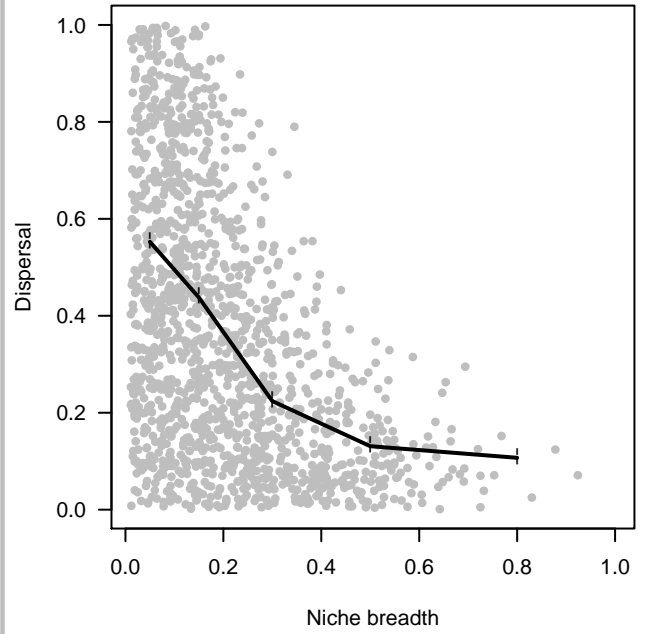
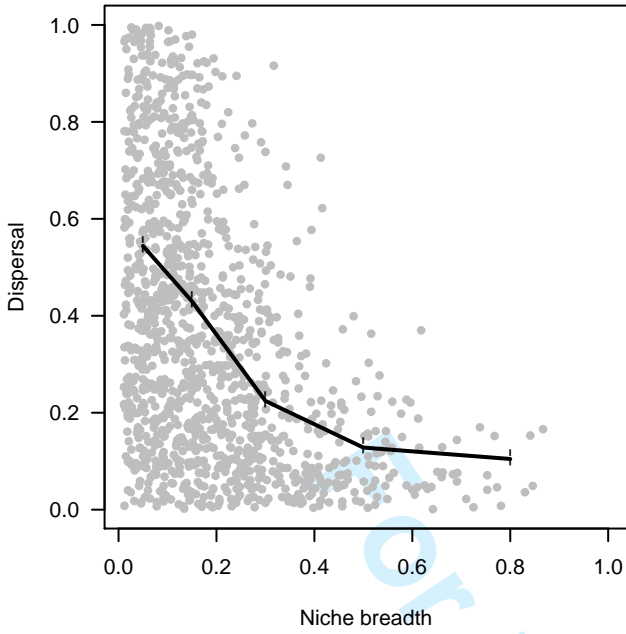
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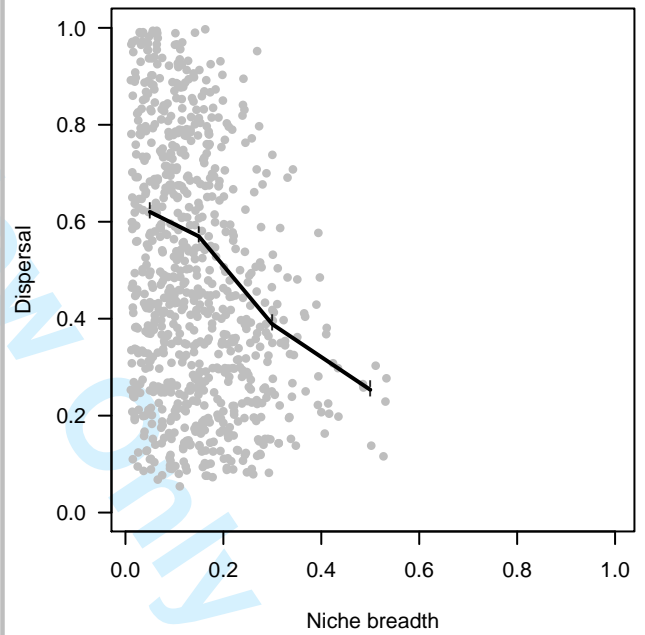
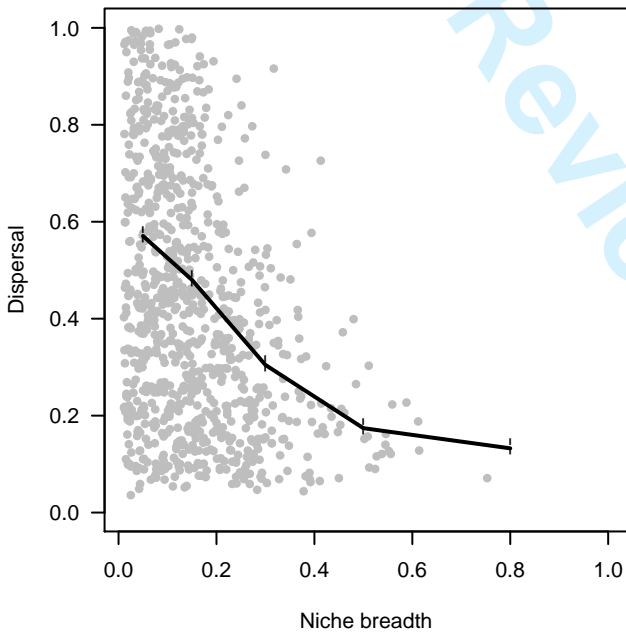
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survival = 0.95

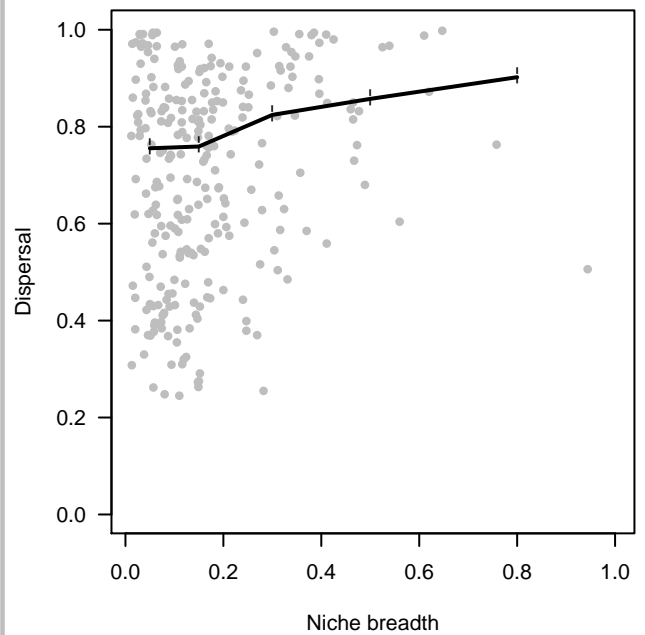
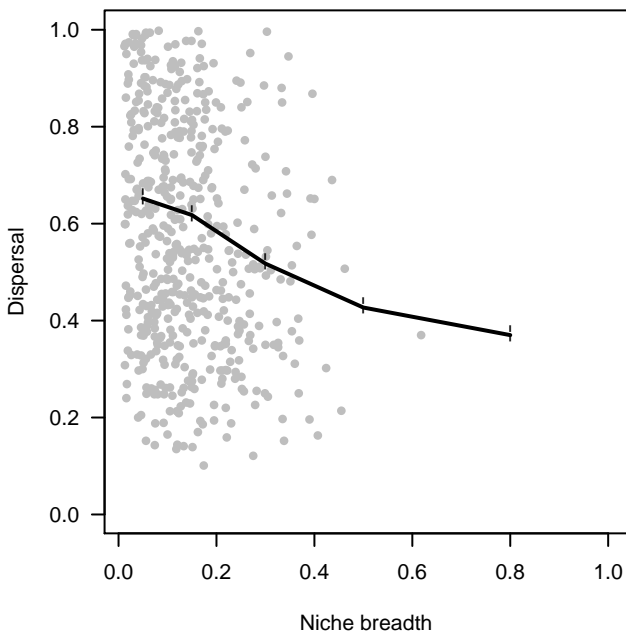
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T = 0.01



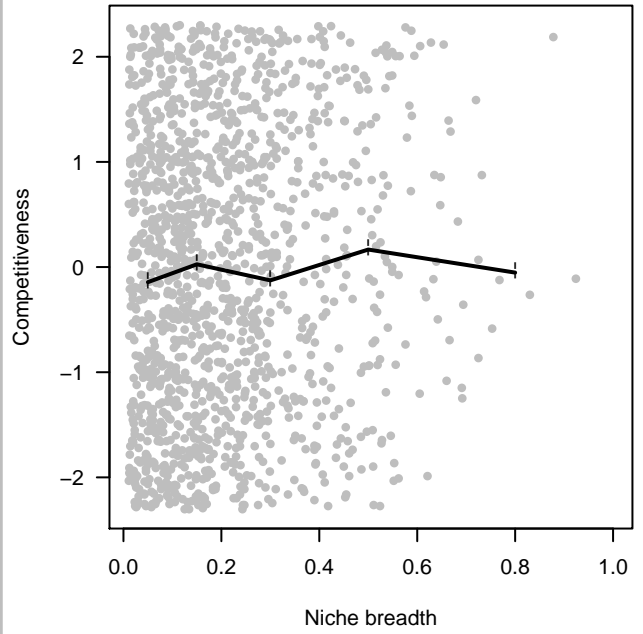
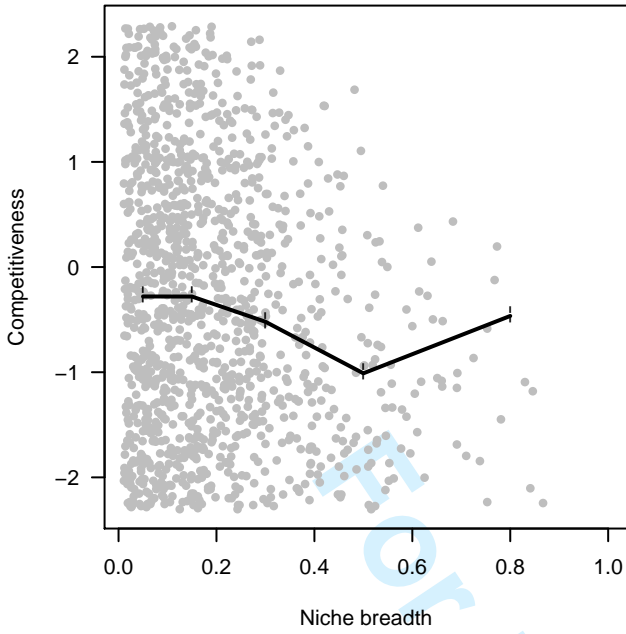
T = 0.25



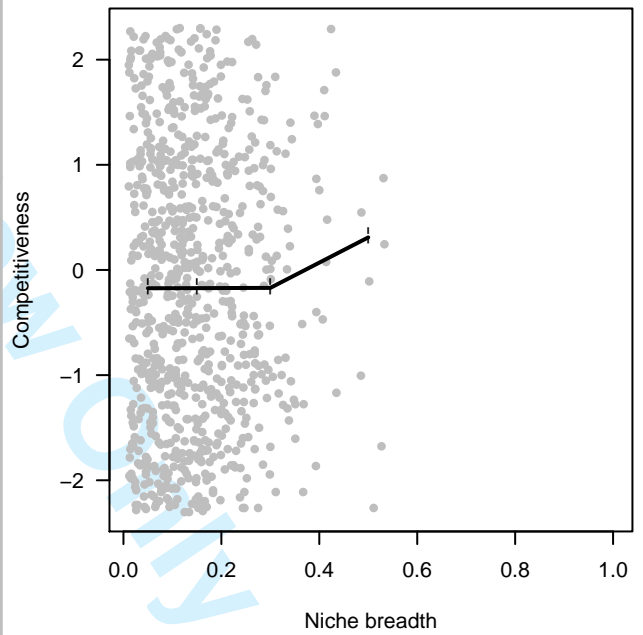
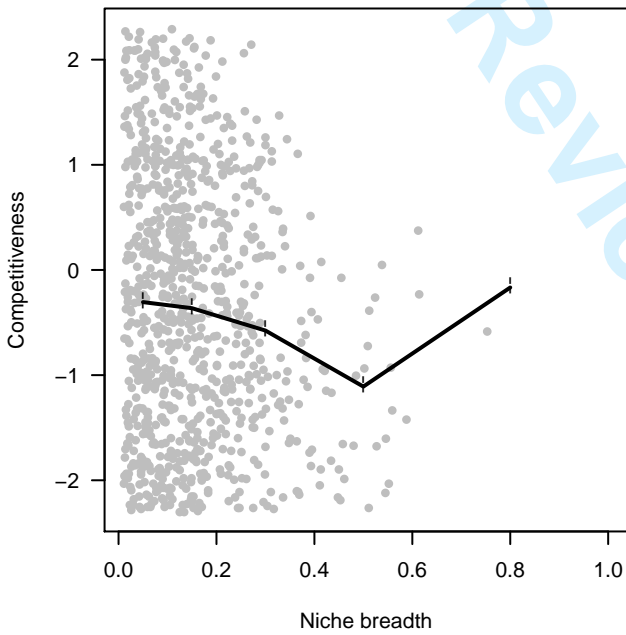
survival = 0

survival = 0.95

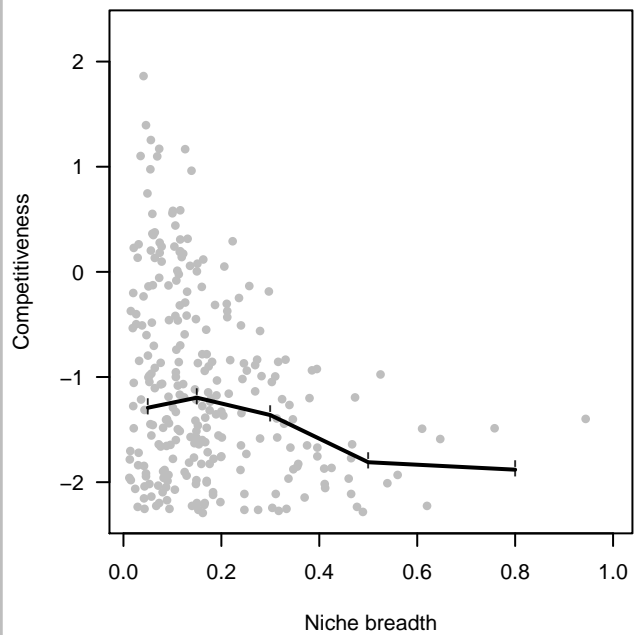
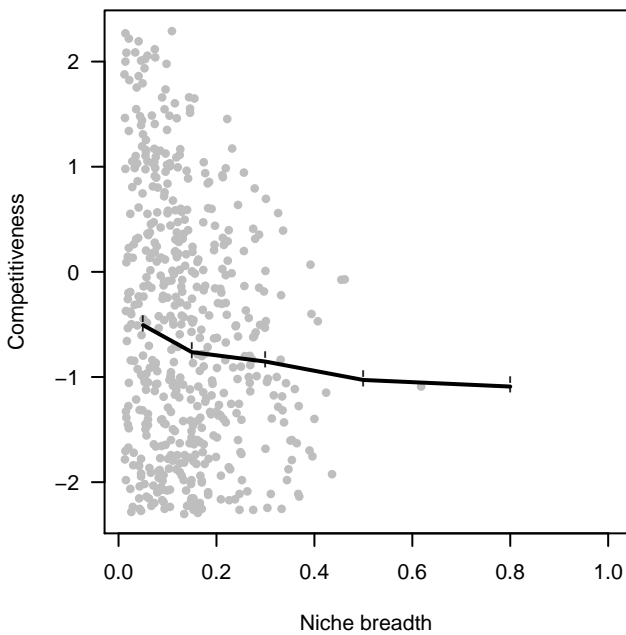
T = 0

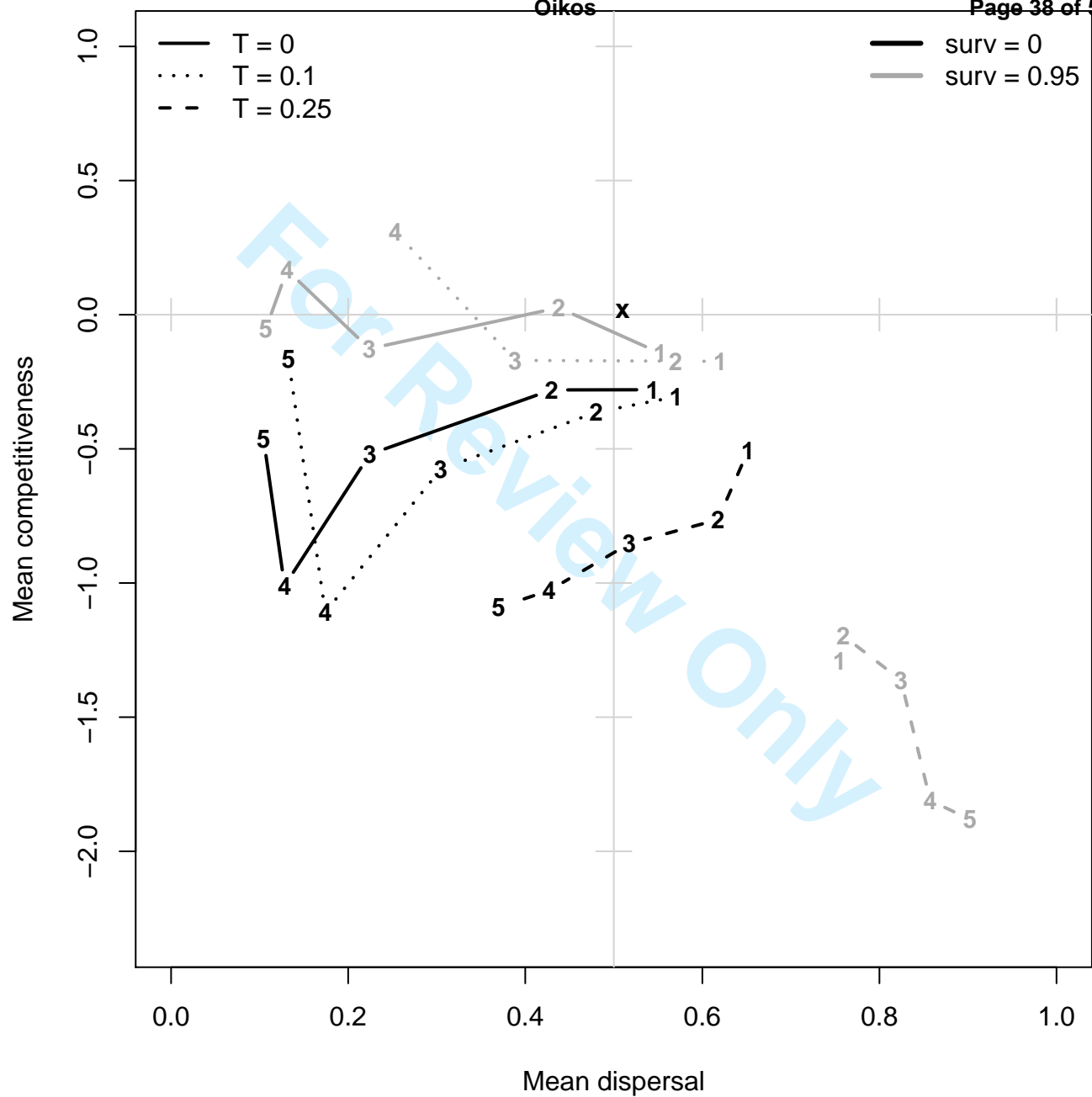


T = 0.01



T = 0.25





Büchi, L. and Vuilleumier, S. 2015 Ecological strategies in stable and disturbed environments depend on species specialisation – *Oikos* 000:000–000.

Appendix 1: Dynamics of species richness and mean weighted traits

In this Appendix, the trajectories through time of the values of species richness (Figure A1), mean weighted niche breadth (Figure A2), mean weighted competitiveness (Figure A3) and mean weighted dispersal (Figure A4) are represented.

In each figure, four panels are displayed. They correspond to the four cases with different values of dispersal ability and generation overlap. A. random dispersal ability δ_s and annual survival rate $\psi_s = 0$, B. random dispersal ability δ_s and annual survival rate $\psi_s = 0.95$, C. dispersal ability $\delta_s = 0.1$ and annual survival rate $\psi_s = 0$, D. dispersal ability $\delta_s = 0.1$ and annual survival rate $\psi_s = 0.95$.

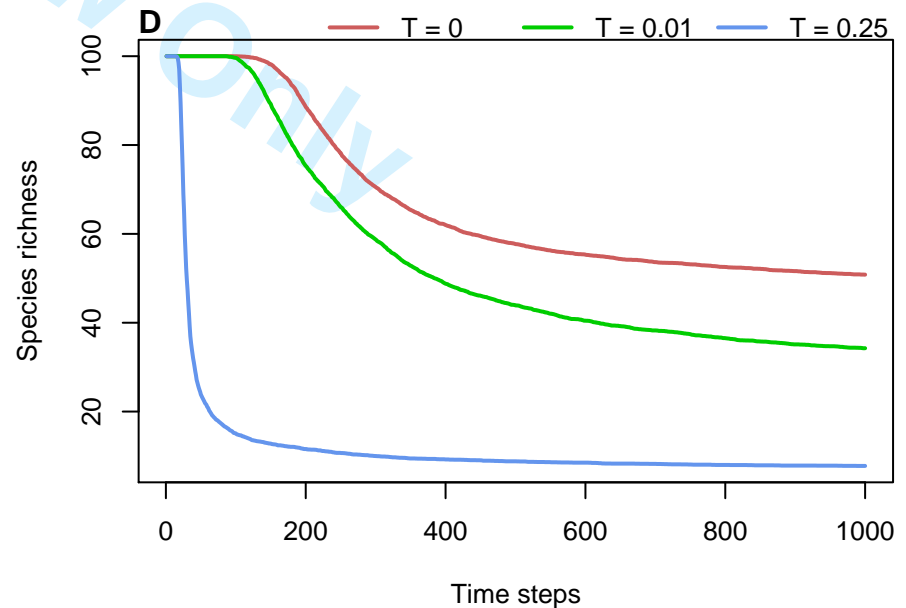
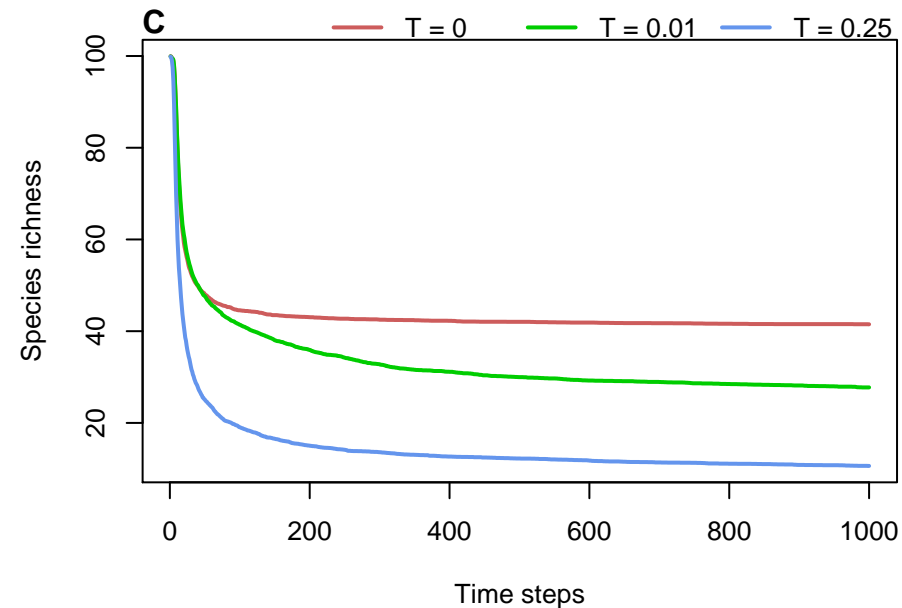
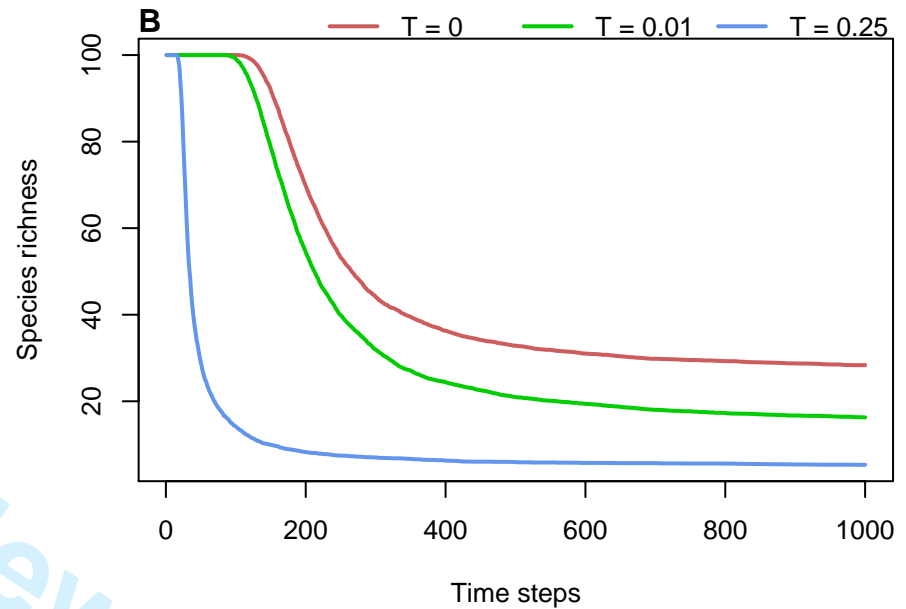
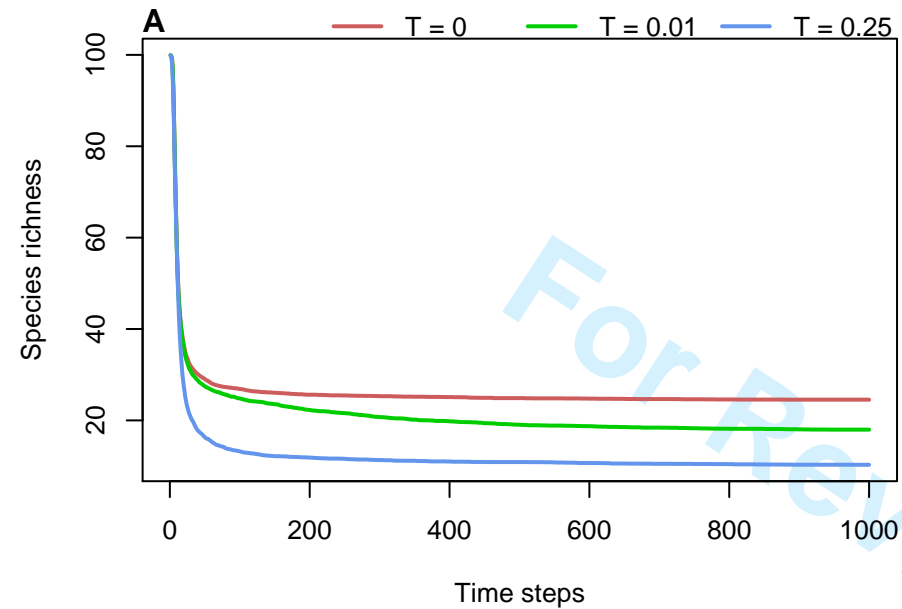
For all panels, the x axis represents the number of time steps (each time step is a full life cycle) and the y axis represents the value of either species richness (Figure A1), mean weighted niche breadth (Figure A2), mean weighted competitiveness (Figure A3) and mean weighted dispersal (Figure A4). In each panel, three lines are represented, the colours of the lines describing different disturbance rate T ; red: $T = 0$, green: $T = 0.01$, blue: $T = 0.25$. Each line represents the mean value over 50 replicates.

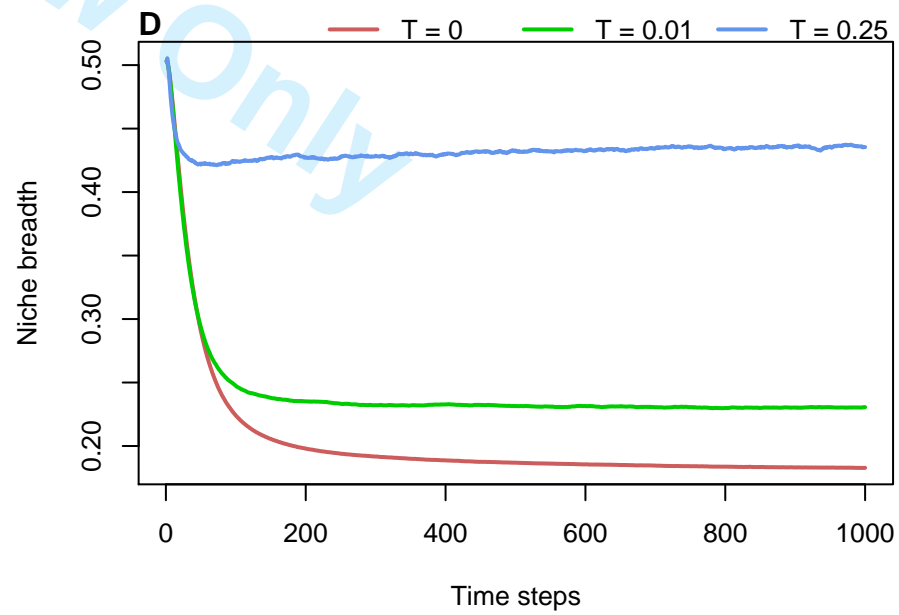
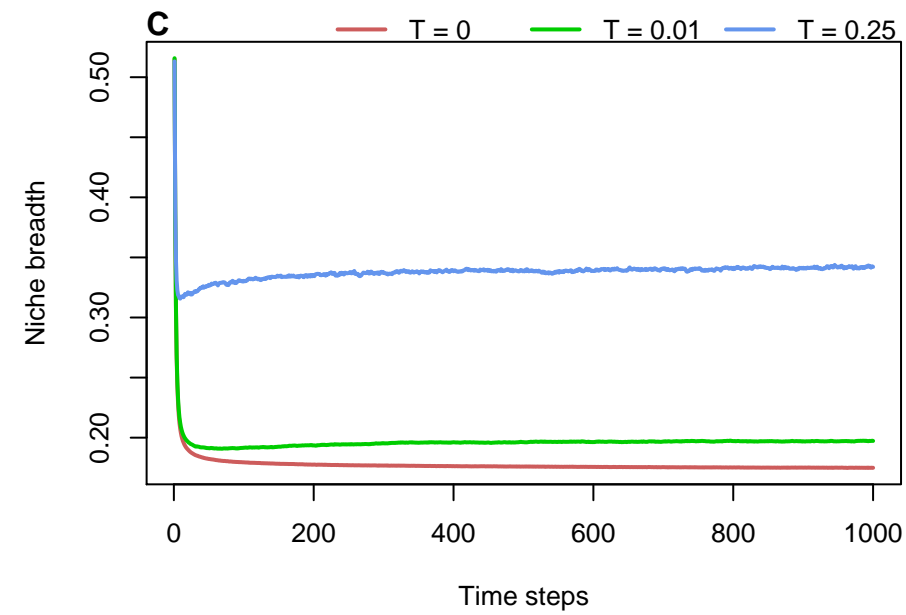
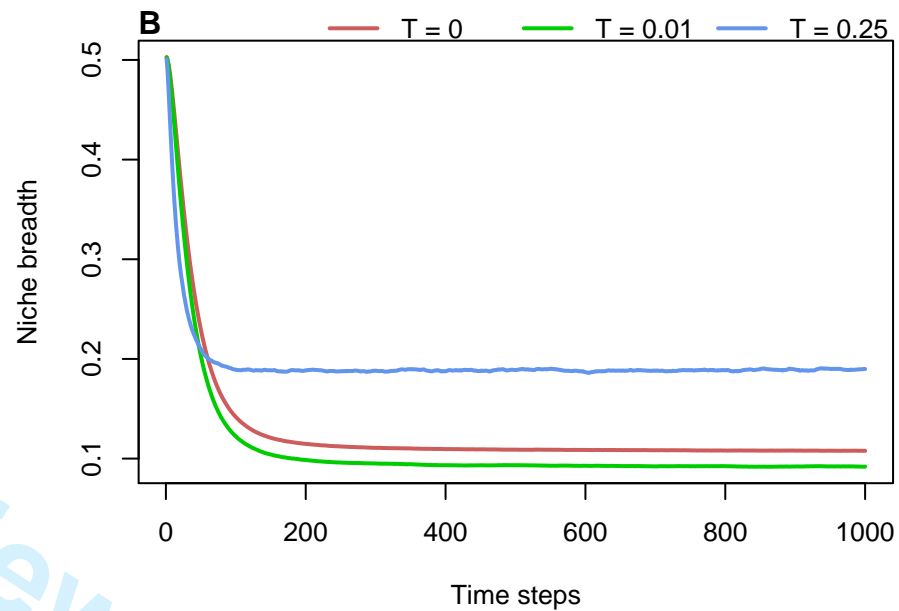
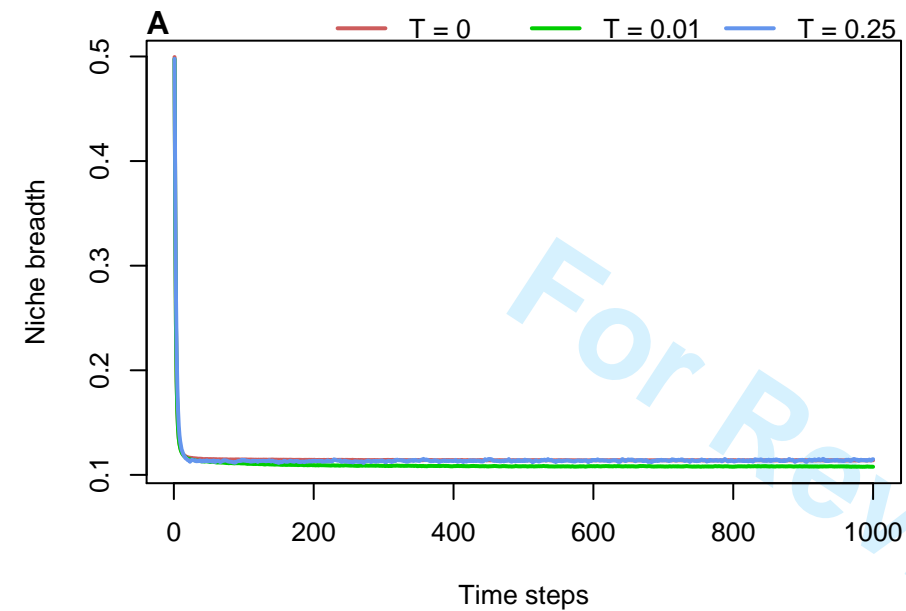
Figure A1: Values of species richness through time.

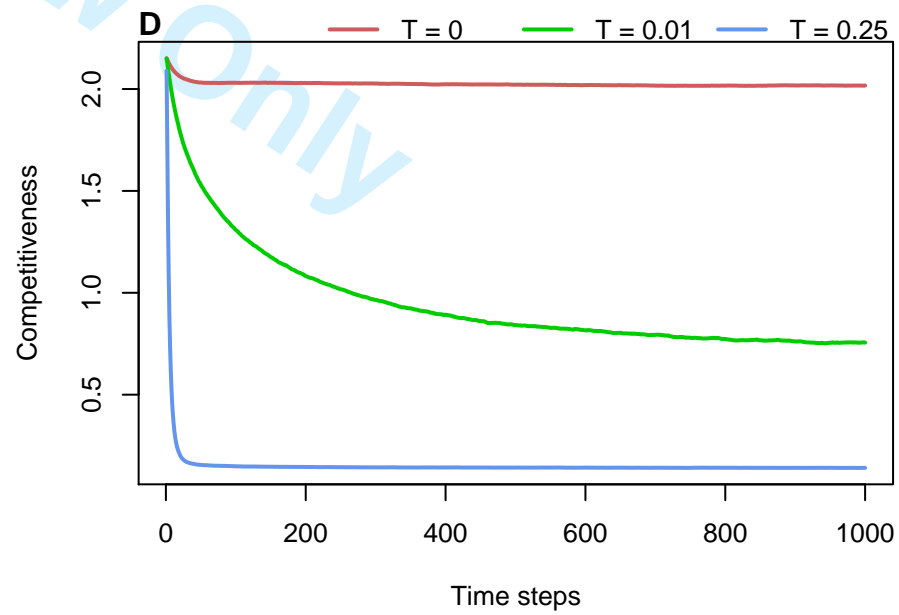
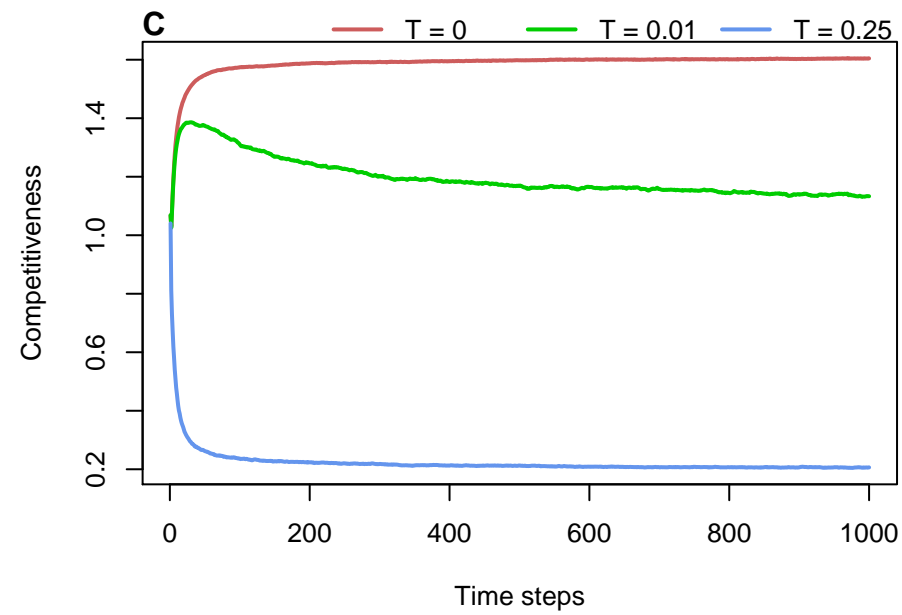
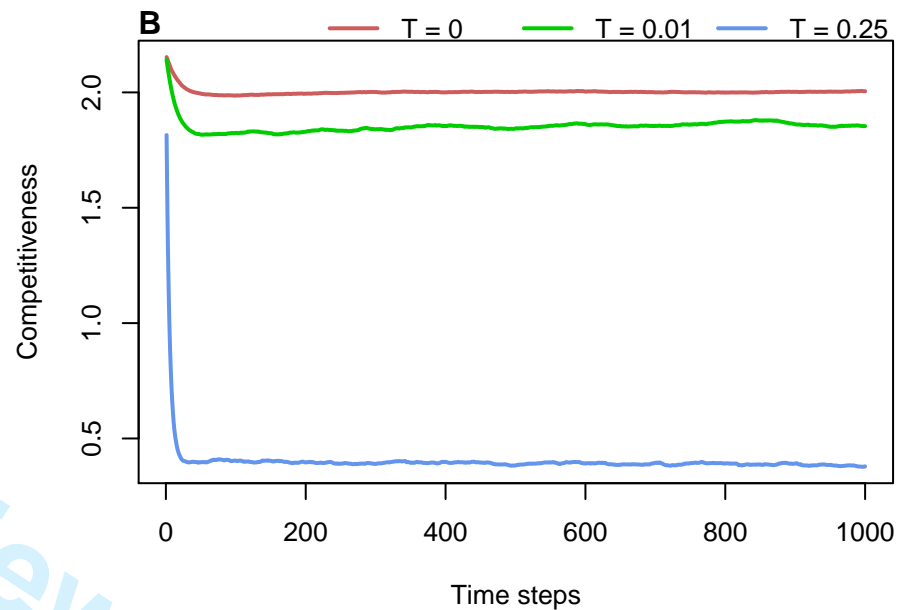
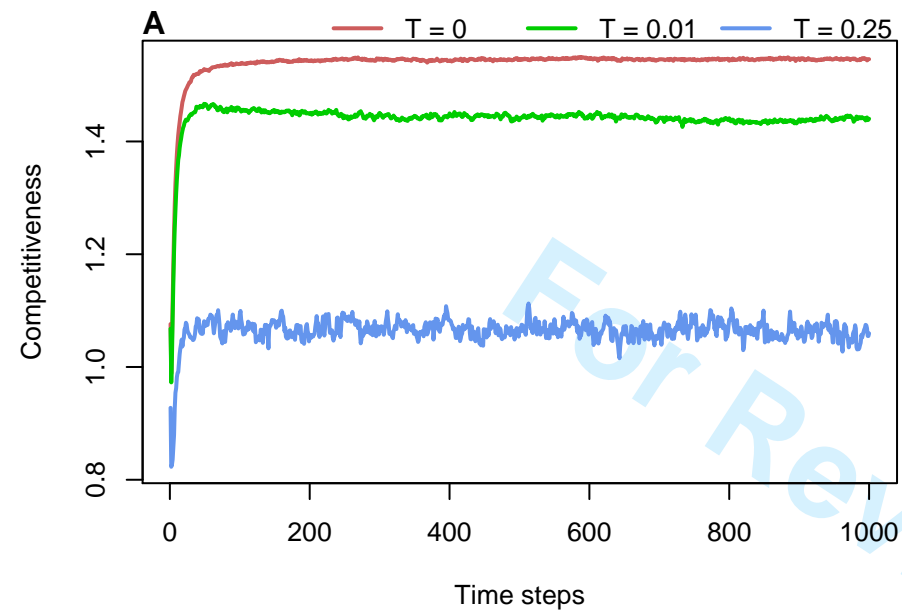
Figure A2: Values of the mean weighted niche breadth through time.

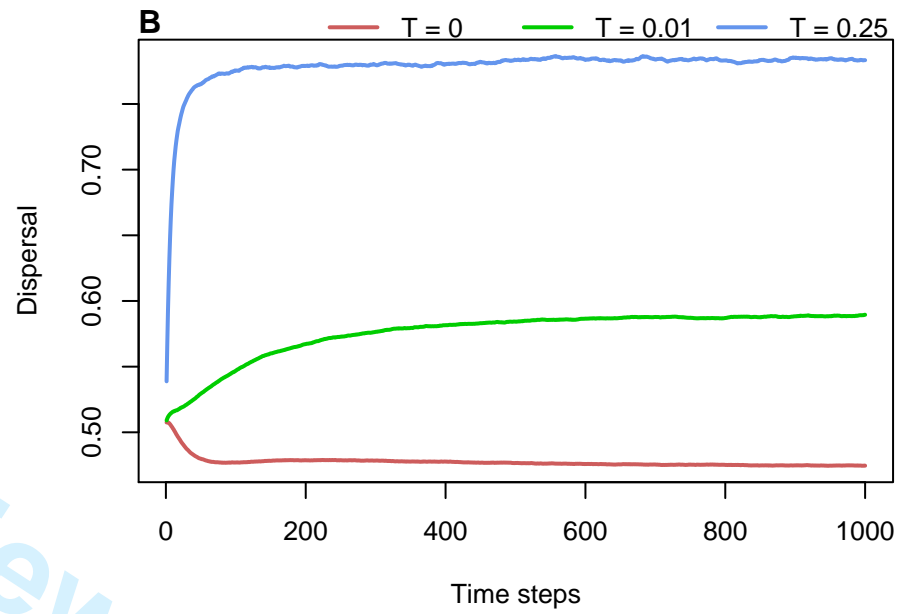
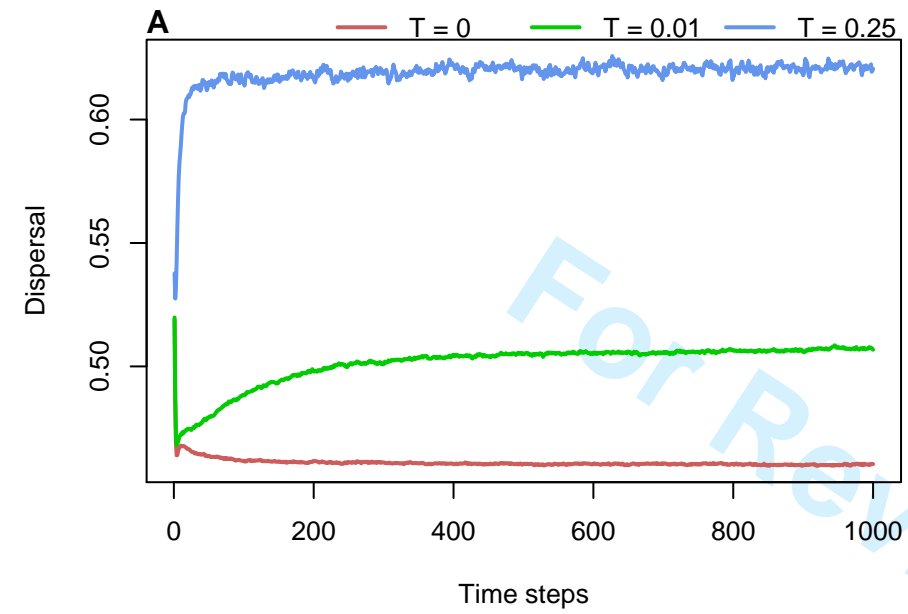
Figure A3: Values of the mean weighted competitiveness through time.

Figure A4: Values of the mean weighted dispersal through time.









Appendix 2: Effect of the number of initial species on the emerging trait strategies

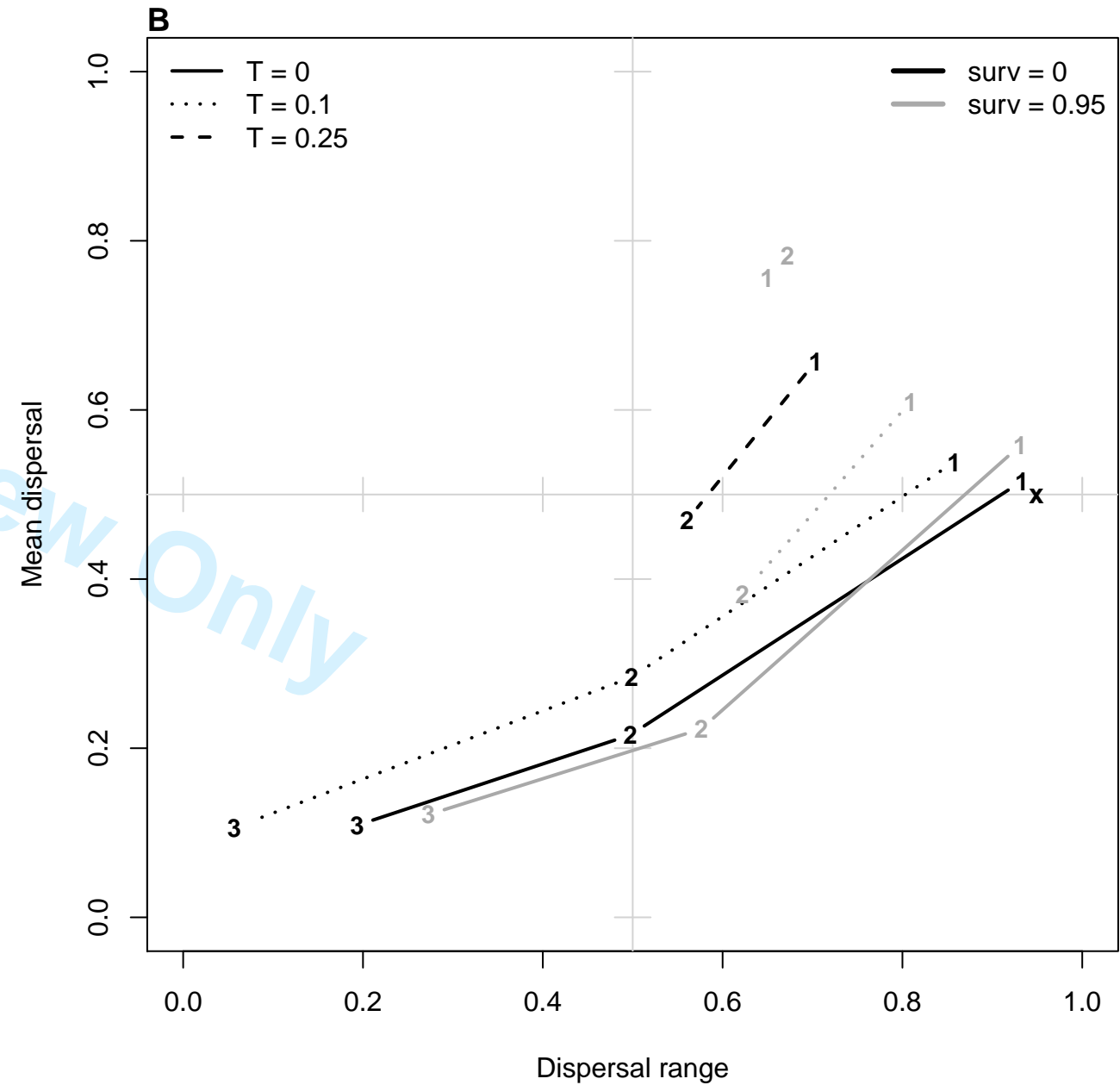
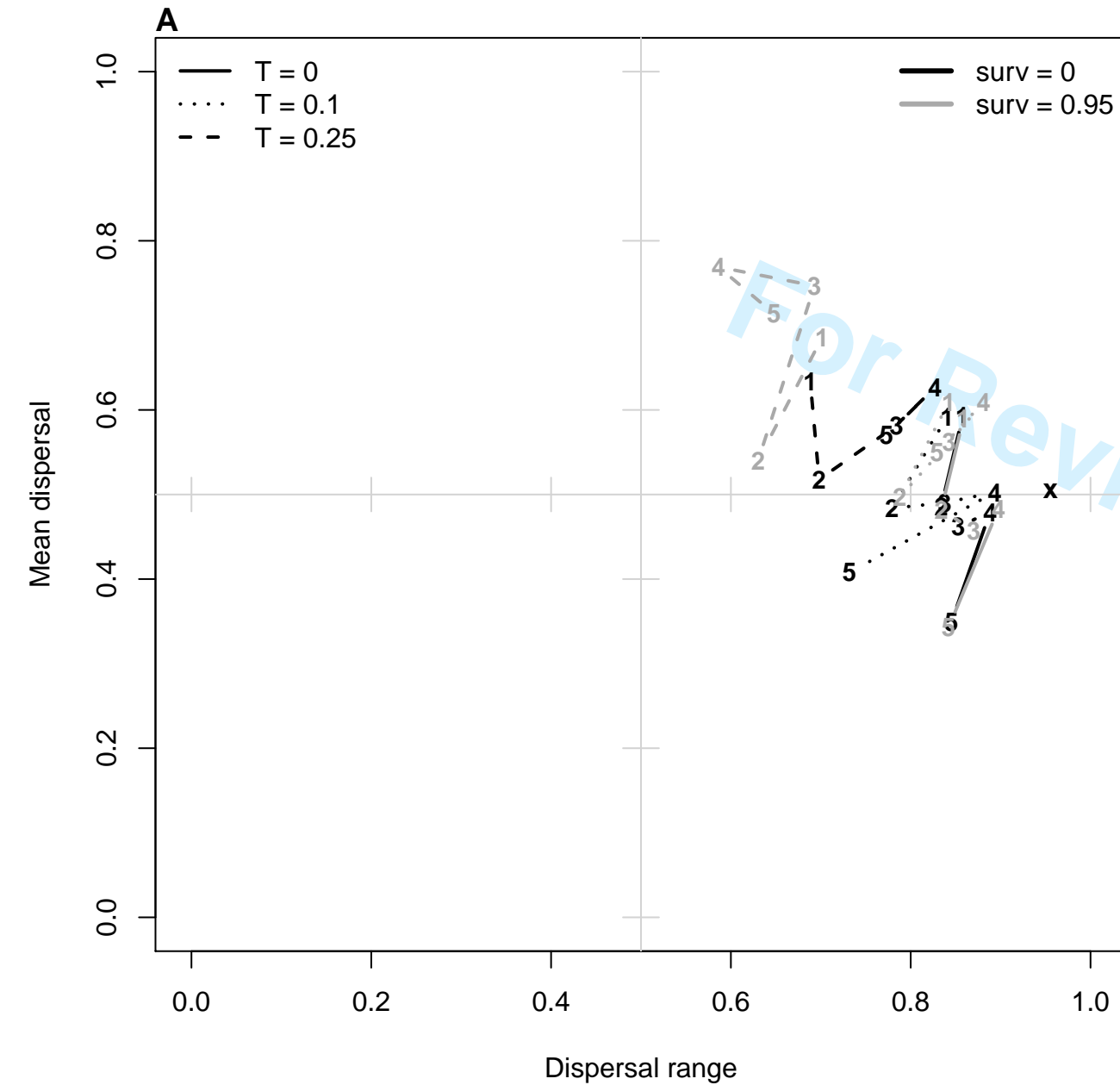
Figure A1: Association of dispersal ability with niche breadth, considering values of species competitiveness and reproductive investment each equals to 1 with (A) 10 species at the beginning of the simulations and (B) 1000 species at the beginning of the simulations. The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The dispersal range is the difference between the 97.5% and 2.5% quantiles of the distribution of dispersal values among the surviving species. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean and range value of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).

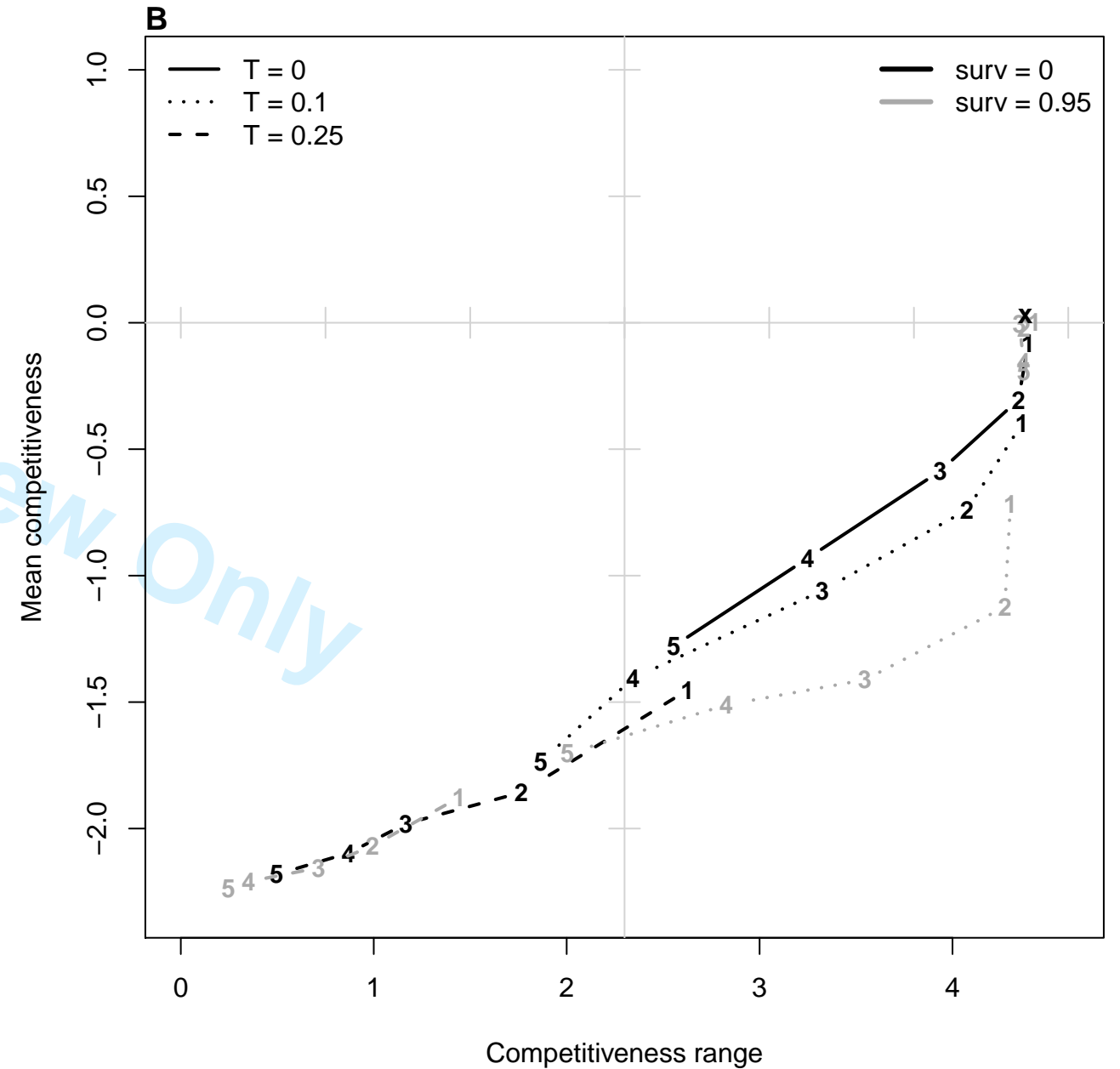
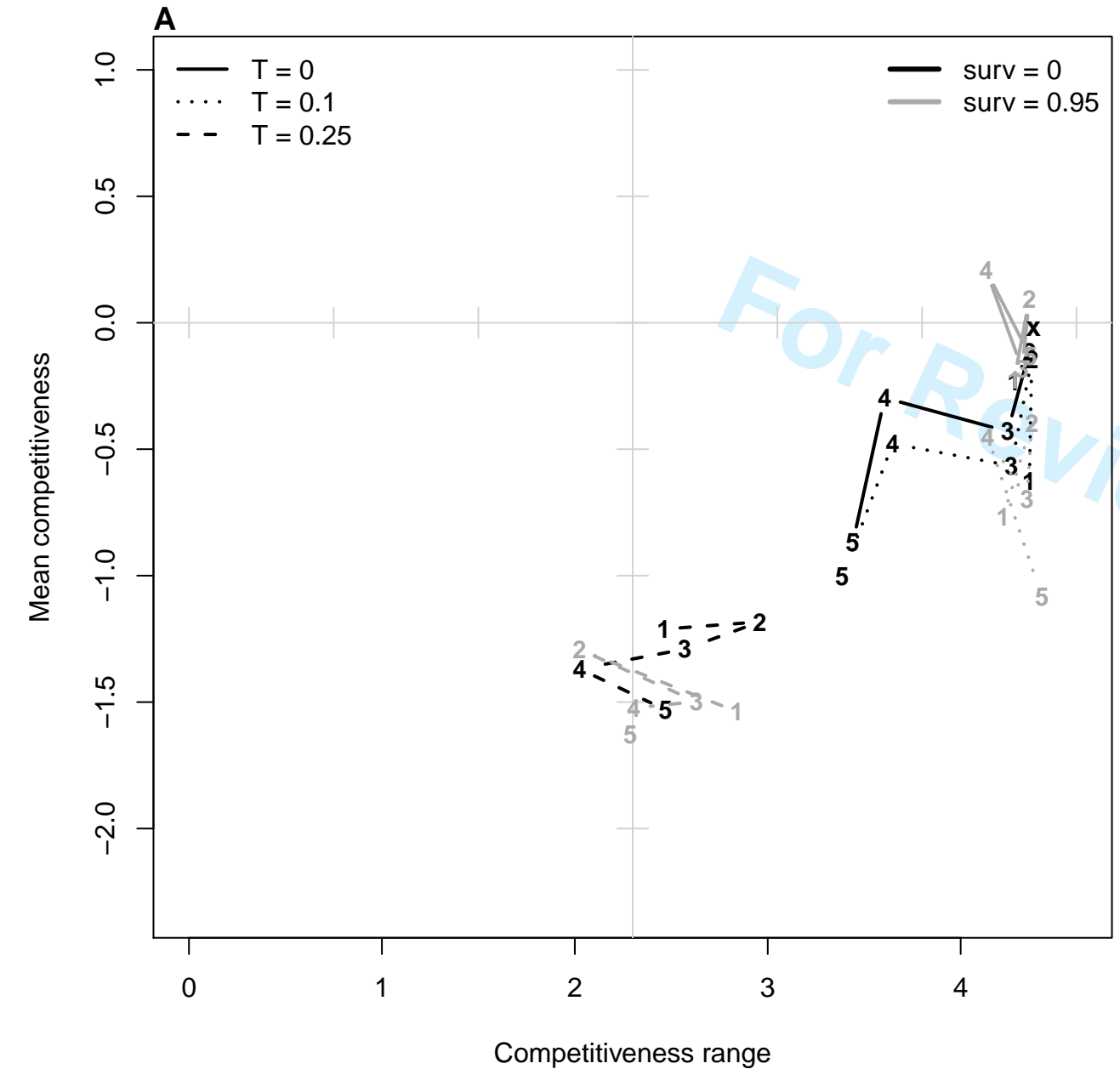
Figure A2: Association between competitiveness (log values) and niche breadth, considering values of dispersal ability equals to 0.1 with (A) 10 species at the beginning of the simulations and (B) 1000 species at the beginning of the simulations. The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The competitiveness range is the difference between the 97.5% and 2.5% quantiles of the distribution of competitiveness values among the surviving species. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean and range value of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).

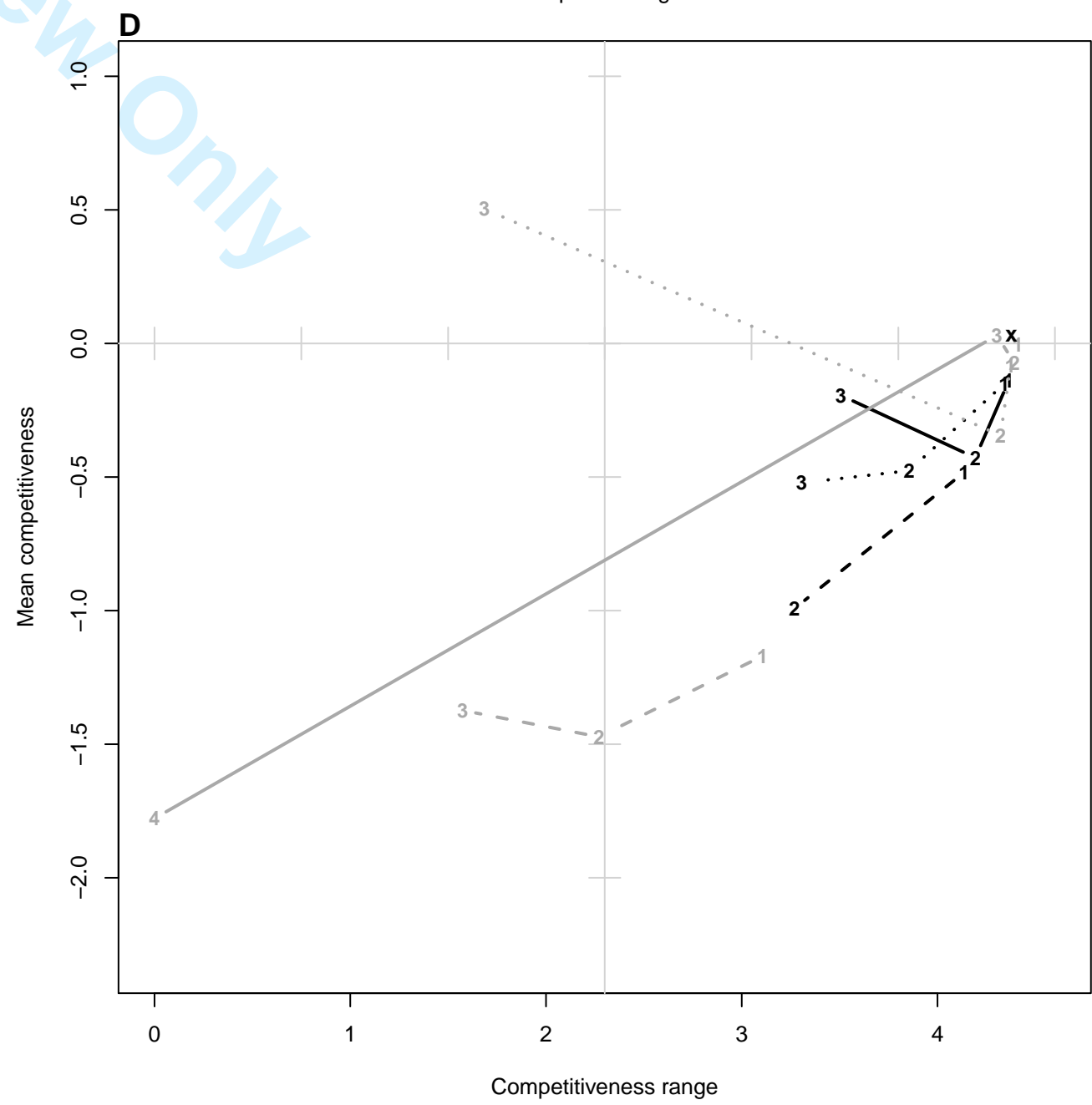
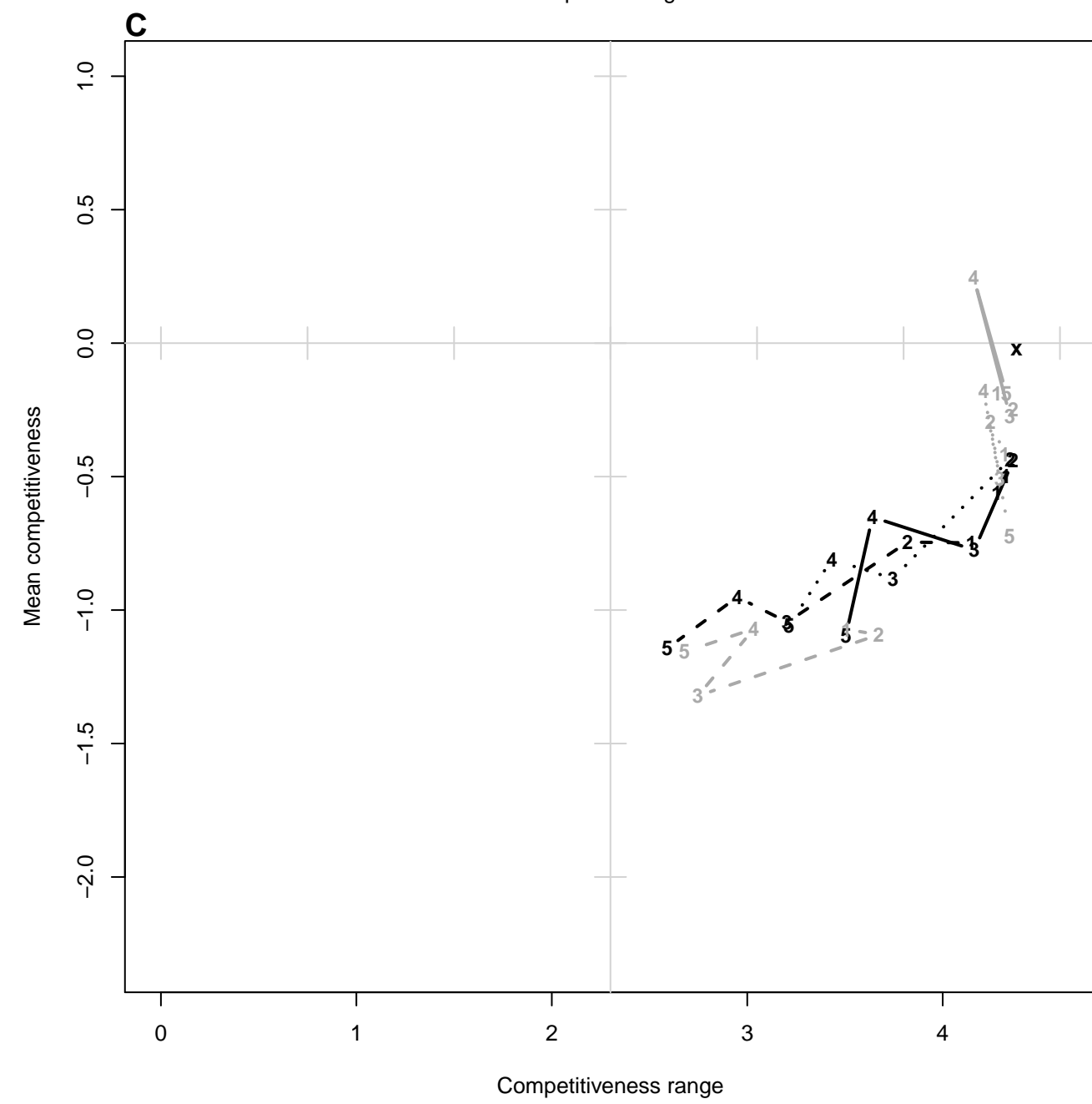
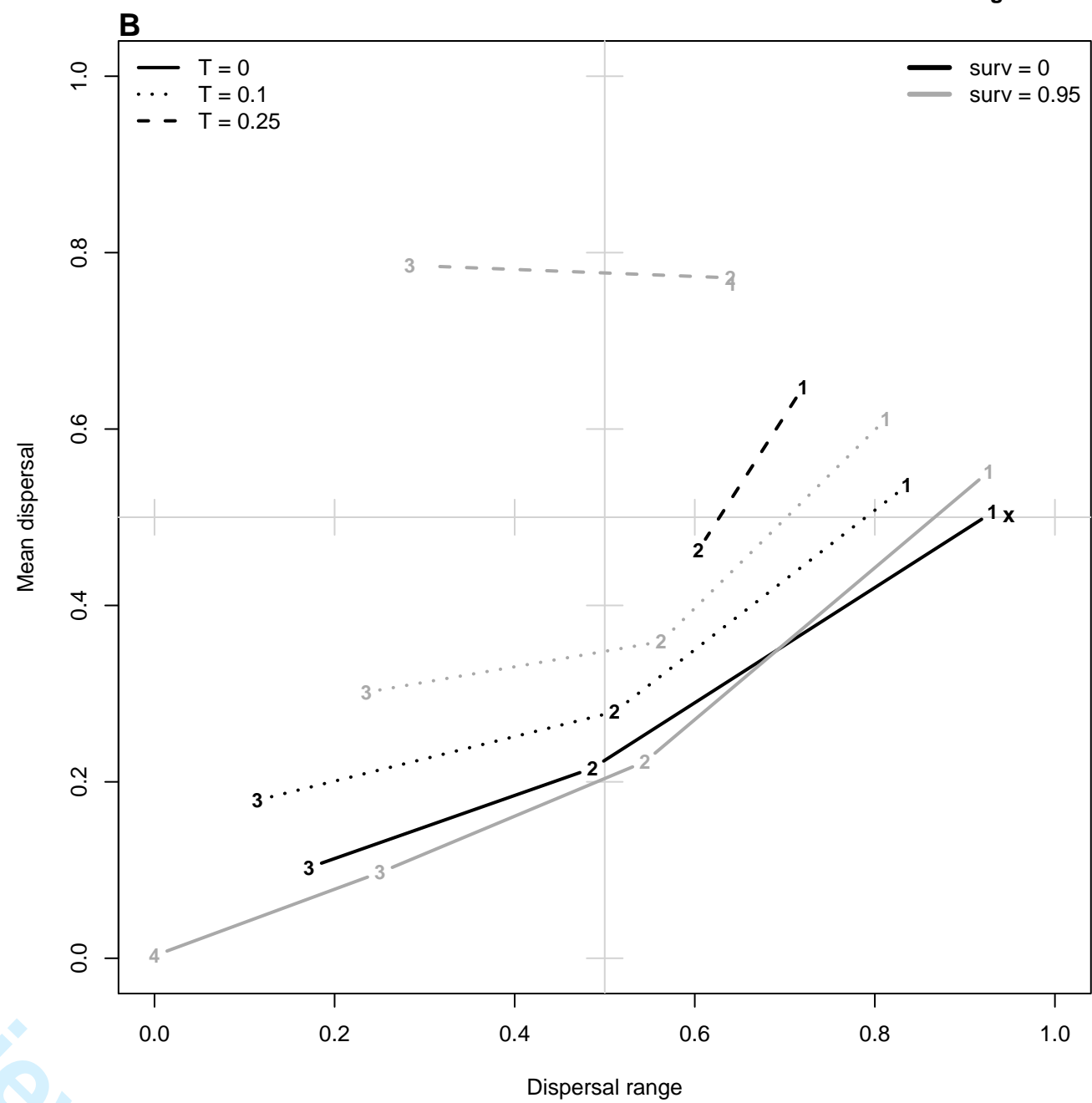
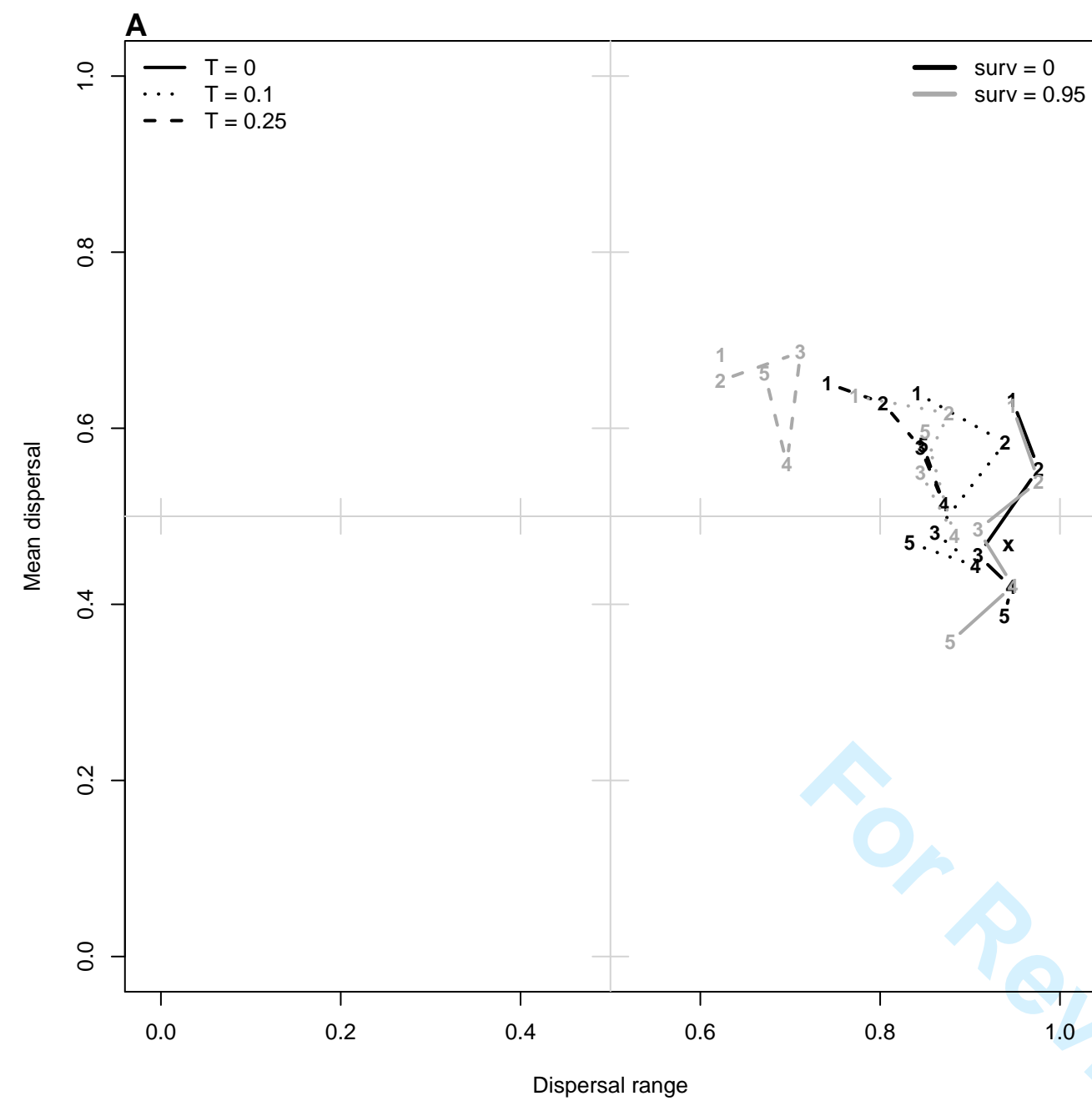
Figure A3: Association between niche breadth and (A, B) dispersal ability (C, D), competitiveness (log values), considering either (A, C) 10 species at the beginning of the simulations or (B, D) 1000 species at the beginning of the simulations. The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The

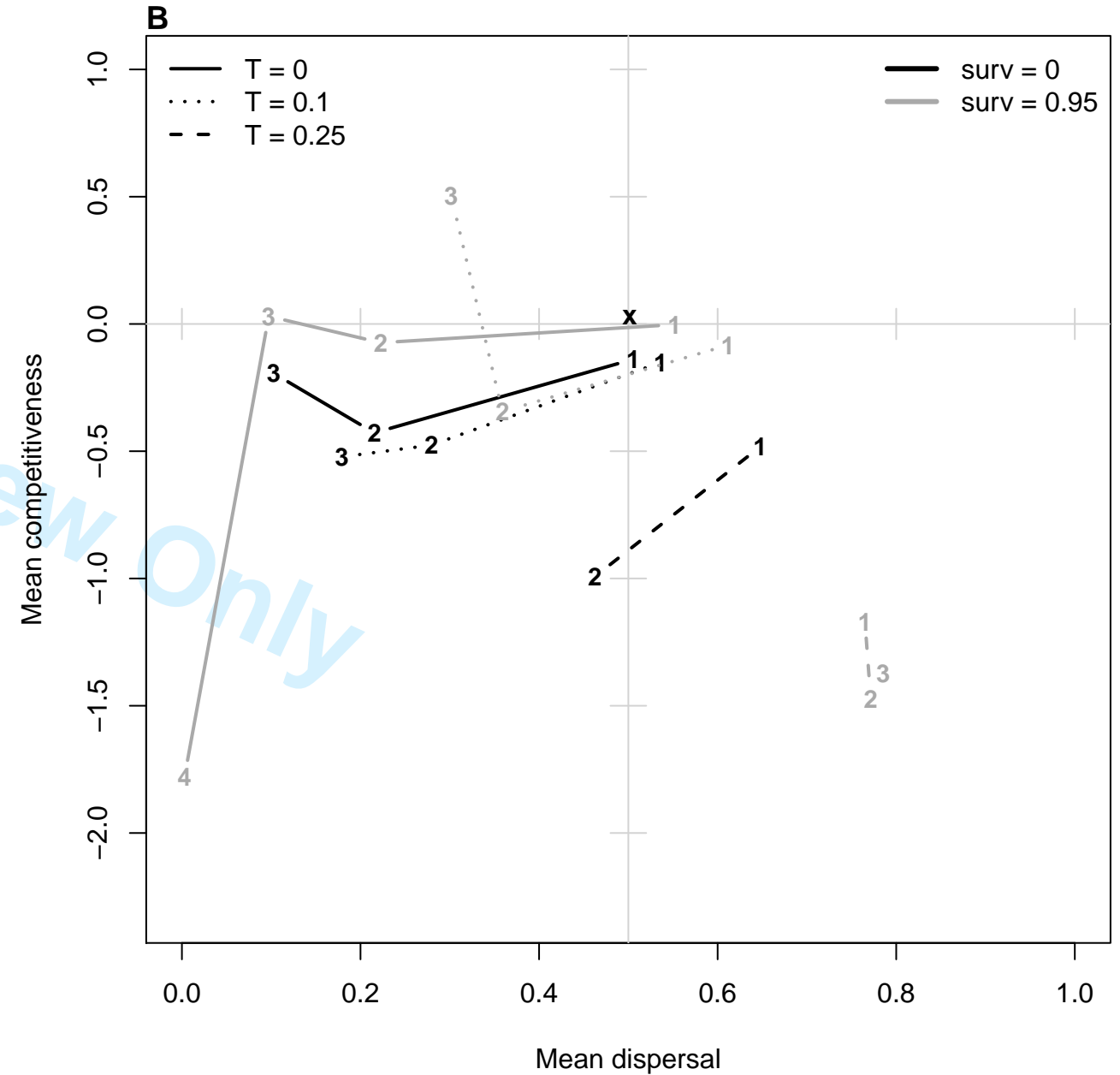
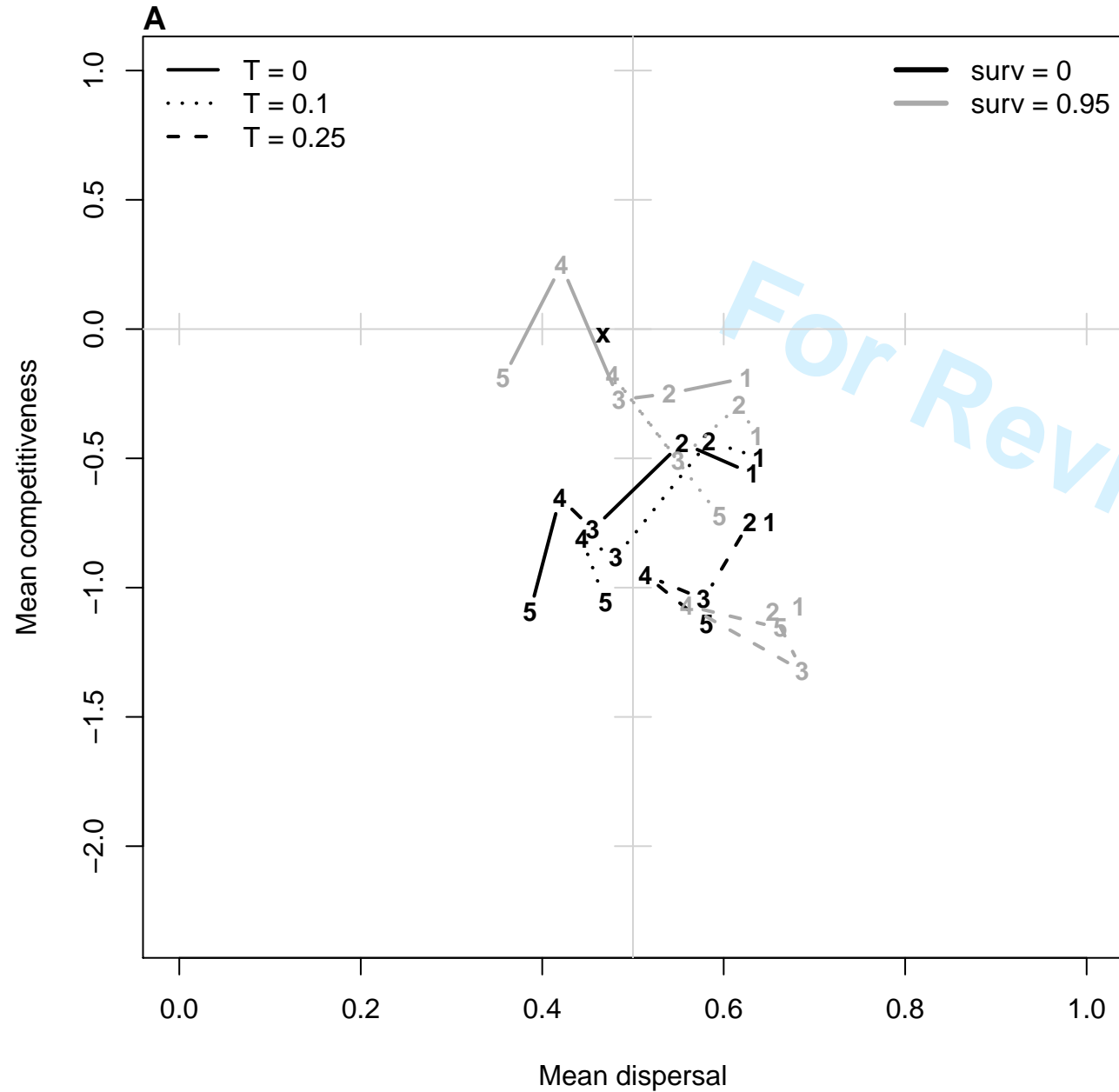
range is the difference between the 97.5% and 2.5% quantiles of distribution of trait values among the surviving species. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean and range value of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).

Figure A4: Association between dispersal ability and competitiveness (log values) for five categories of niche breadth considering either (A) 10 species at the beginning of the simulations or (B) 1000 species at the beginning of the simulations. The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean values of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).









Appendix 3: Effect of spatial autocorrelation on emerging trait strategies

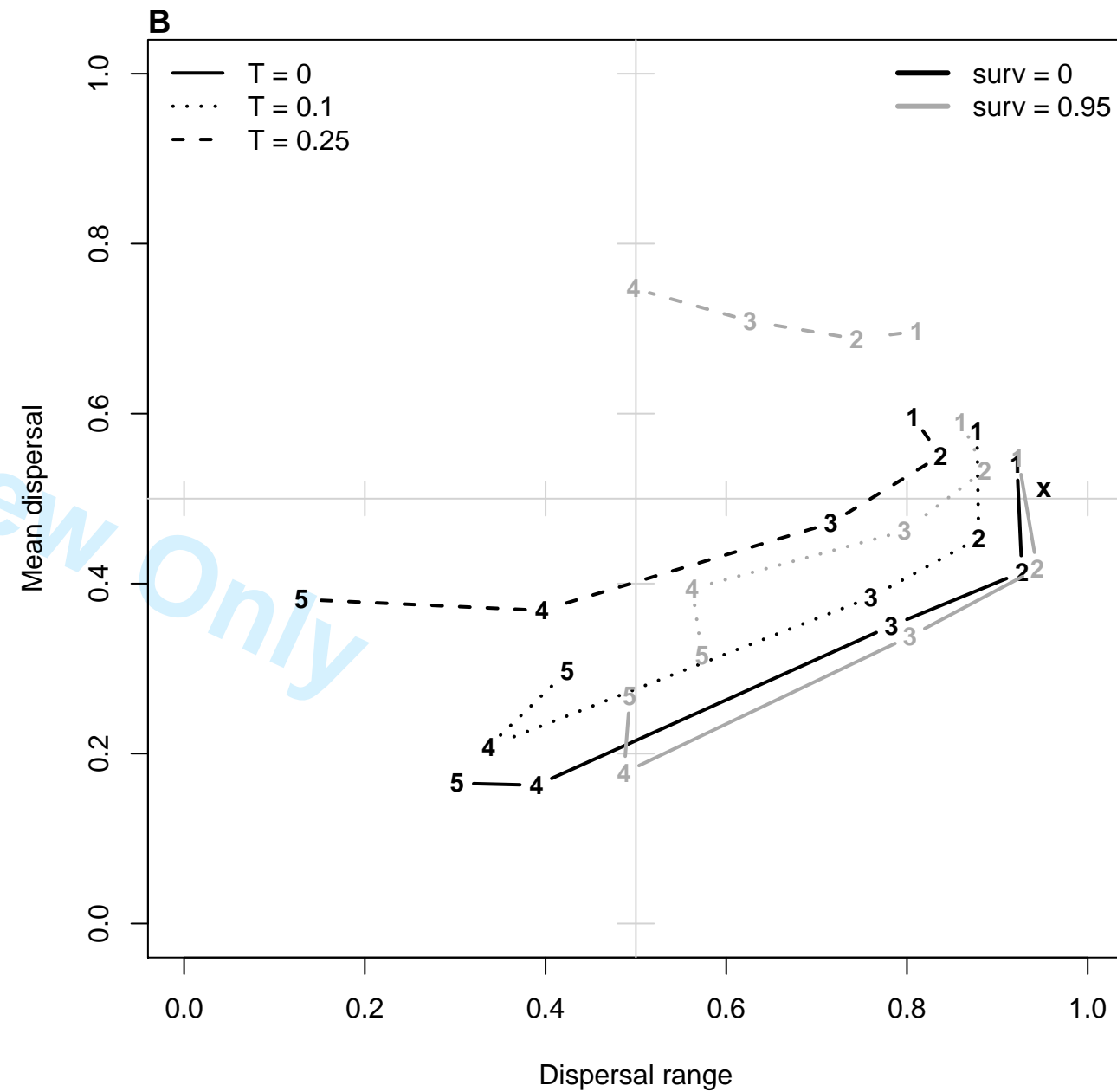
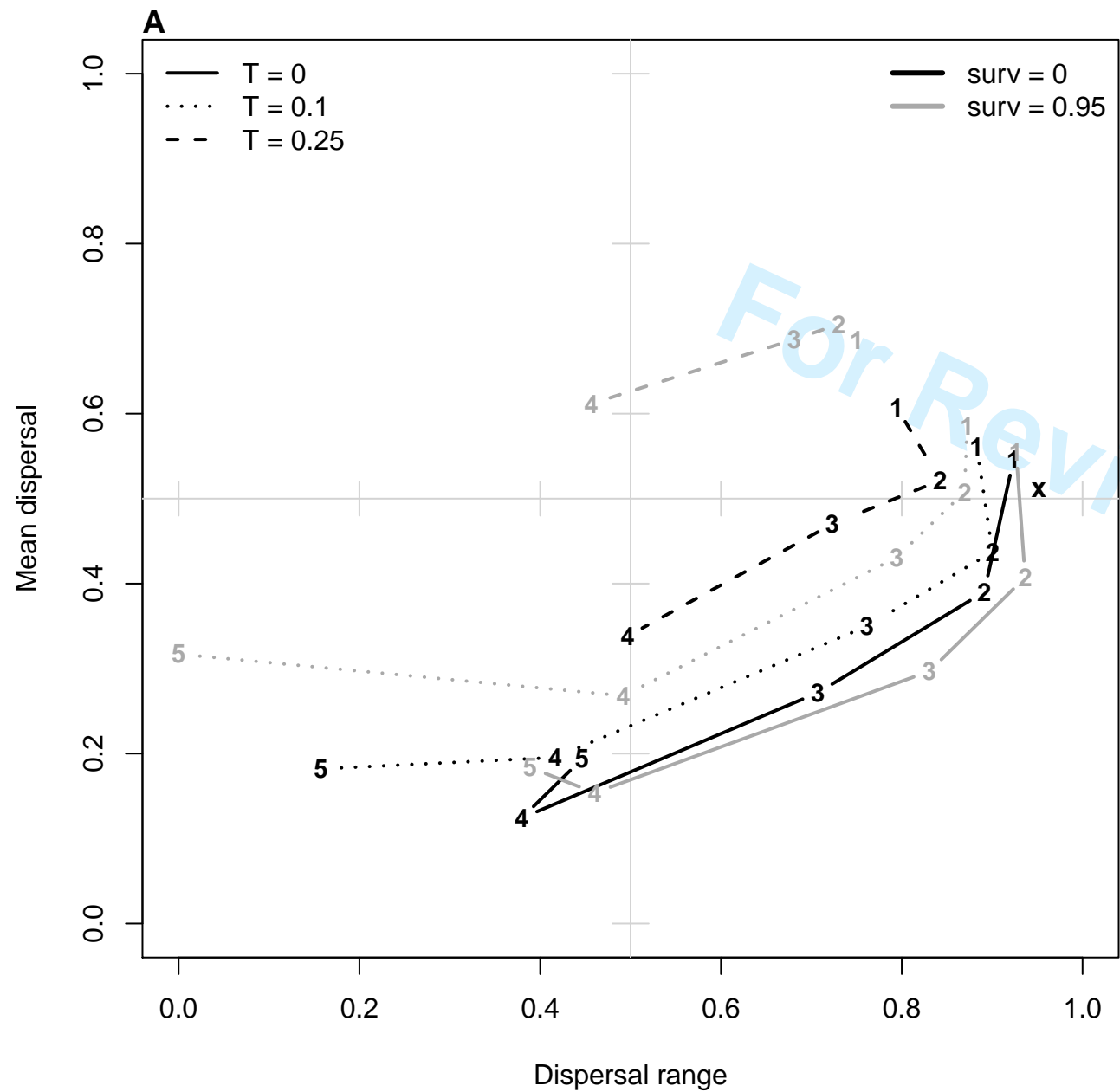
Figure A1: Association between dispersal ability and niche breadth, considering species competitiveness and reproductive investment each equals to 1. (A) with moderate spatial autocorrelation ($\alpha = 5$) and (B) with strong spatial autocorrelation ($\alpha = 10$). The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The dispersal range is the difference between the 97.5% and 2.5% quantiles of the distribution of dispersal values among the surviving species. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean and range value of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).

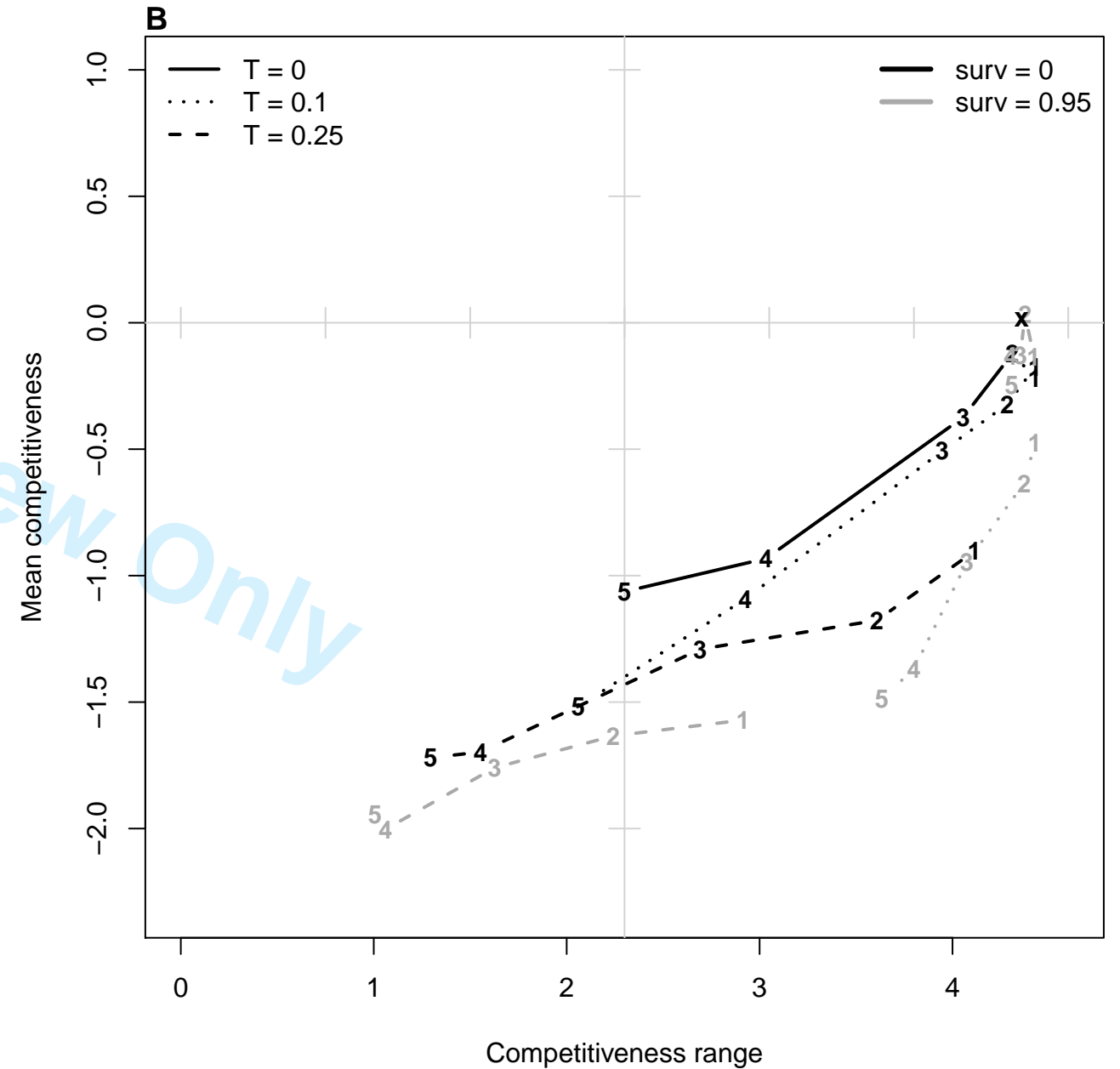
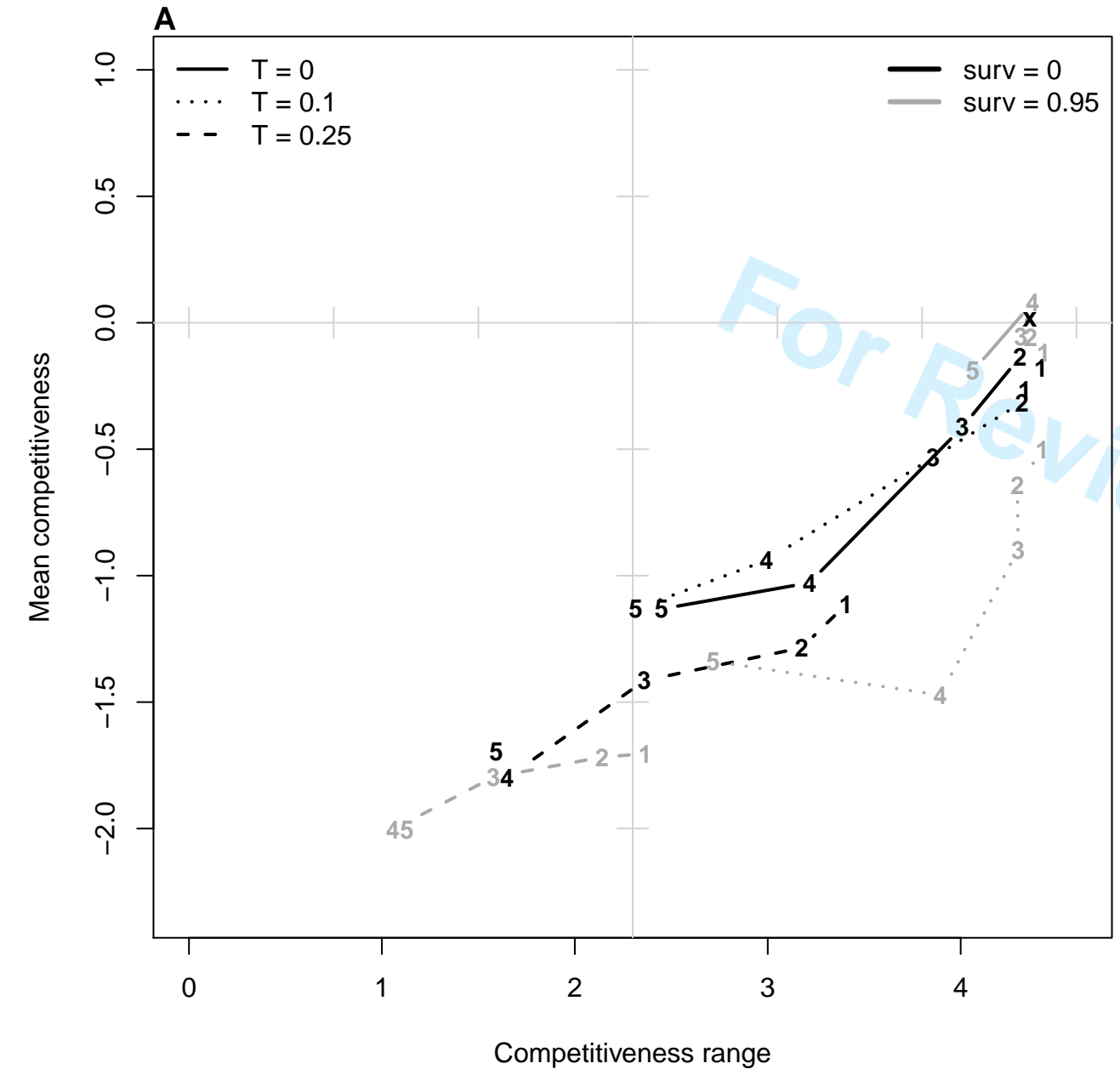
Figure A2: Association between competitiveness (log values) and niche breadth, considering values of dispersal ability equals to 0.1 (A) with moderate spatial autocorrelation ($\alpha = 5$) and (B) with strong spatial autocorrelation ($\alpha = 10$). The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The competitiveness range is the difference between the 97.5% and 2.5% quantiles of the distribution of competitiveness values among the surviving species. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean and range value of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).

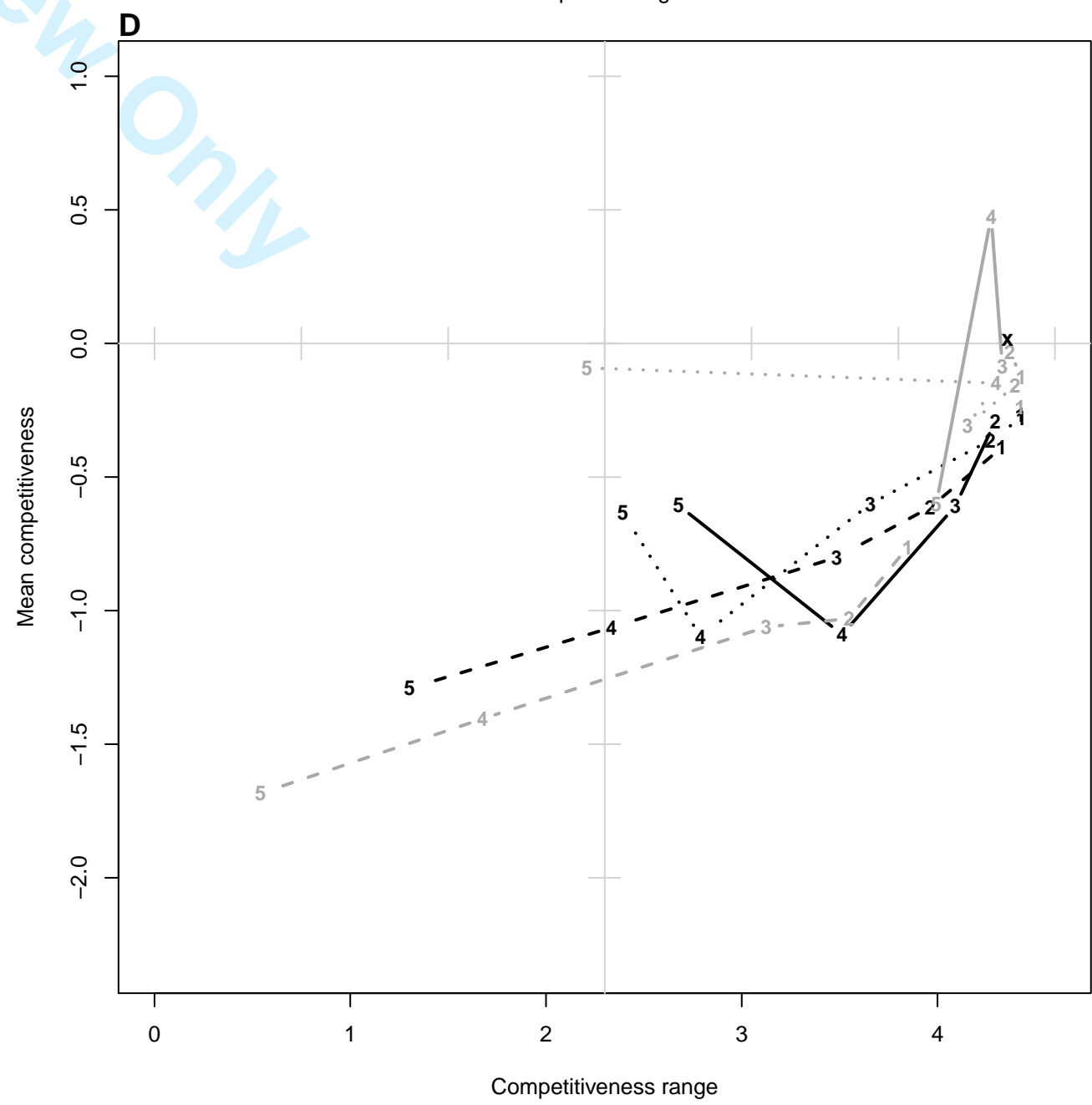
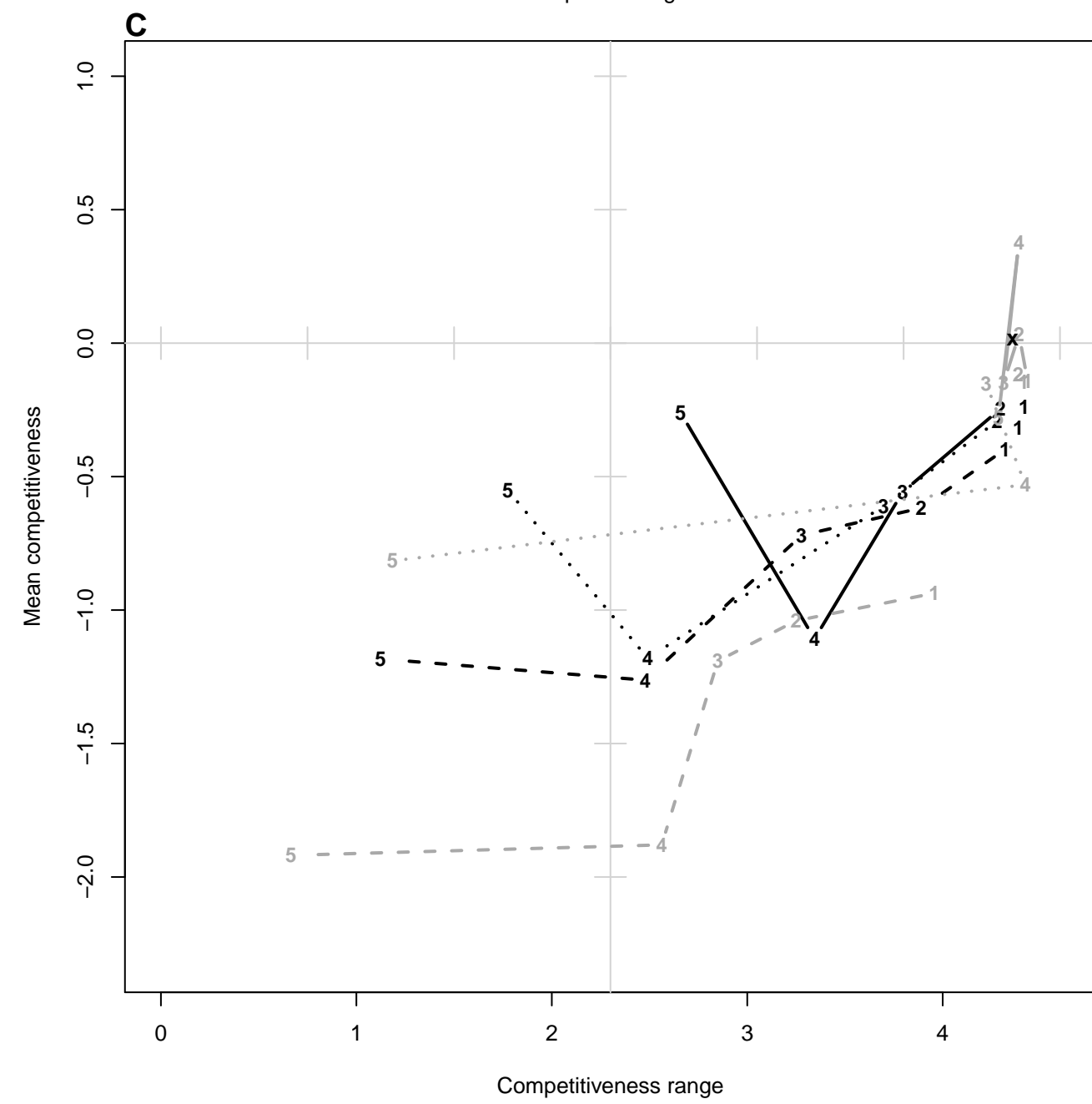
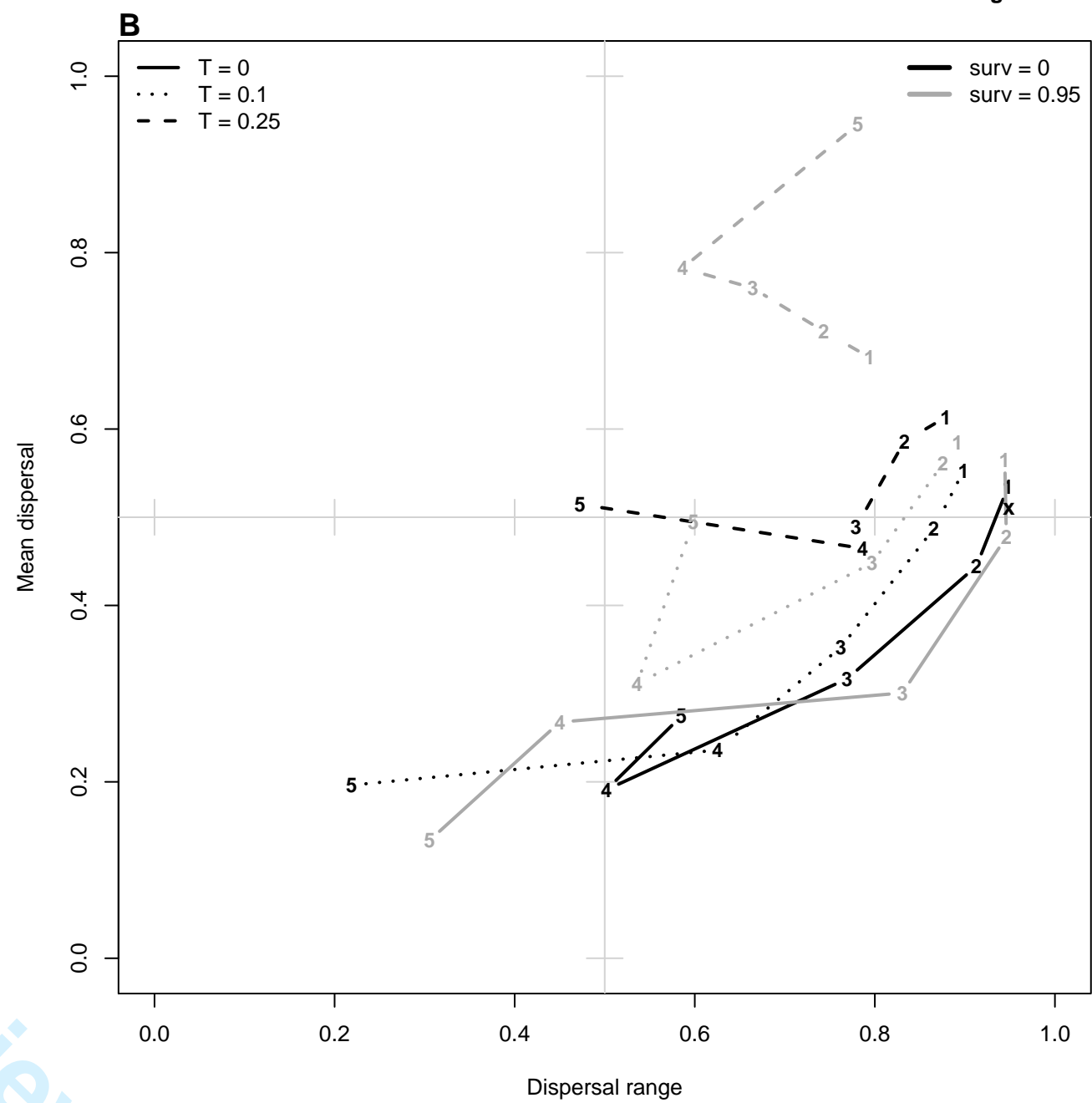
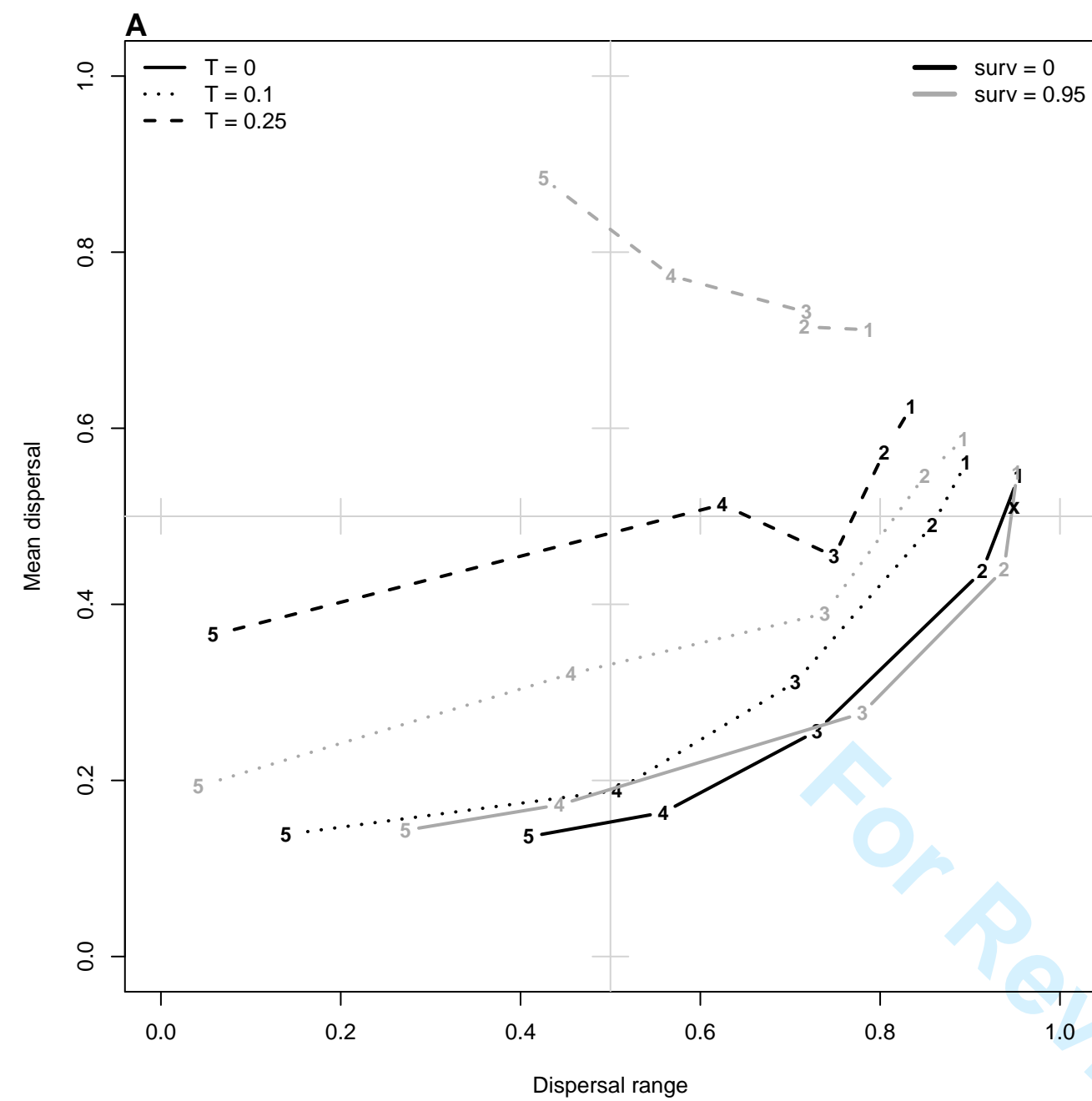
Figure A3: Association between niche breadth and (A, B) dispersal ability, (C, D) competitiveness (log values), considering either (A, C) moderate spatial autocorrelation ($\alpha = 5$) or (B, D) strong spatial autocorrelation ($\alpha = 10$). The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The range is the difference between the 97.5% and 2.5% quantiles of distribution of trait values among the surviving

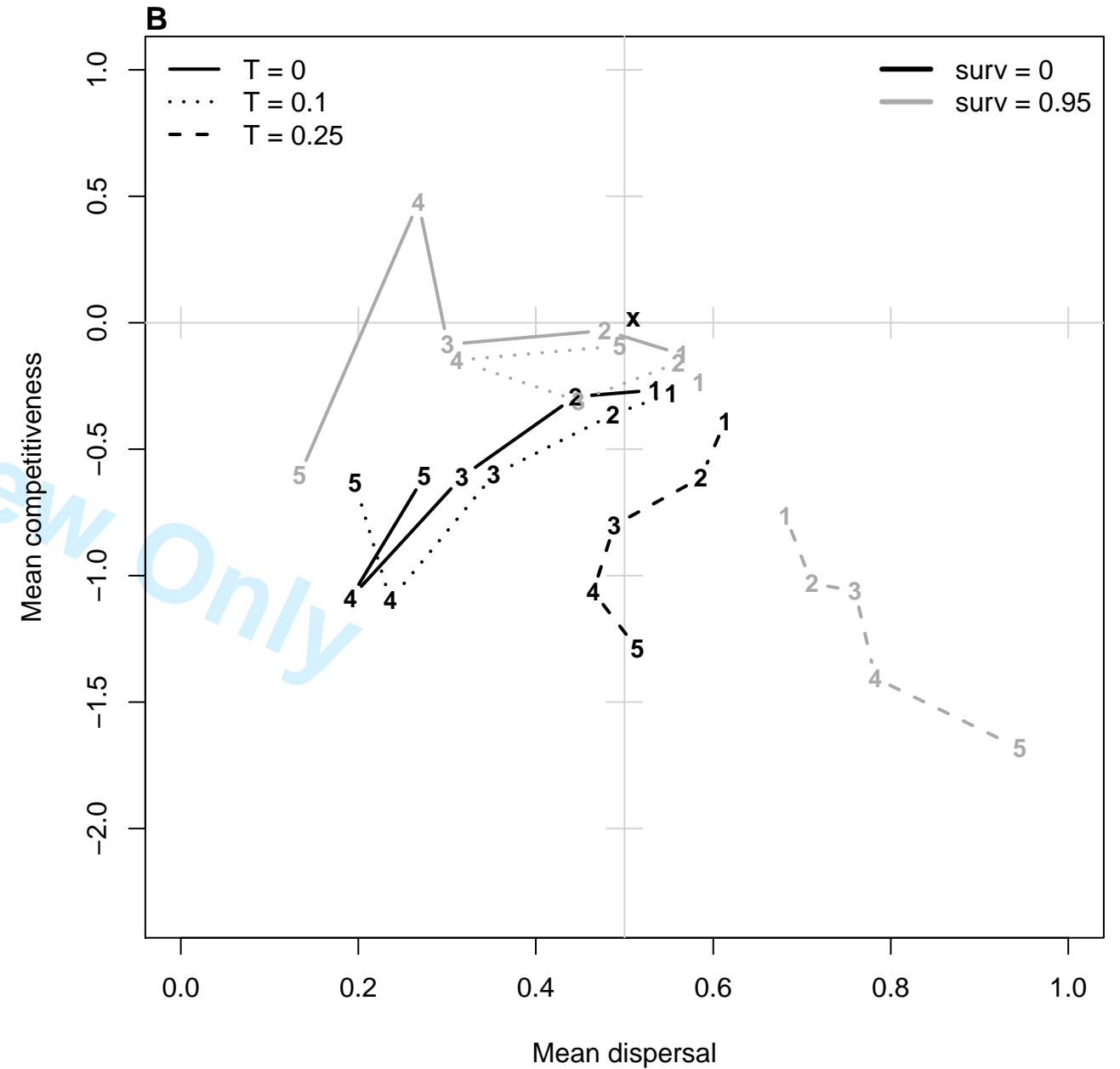
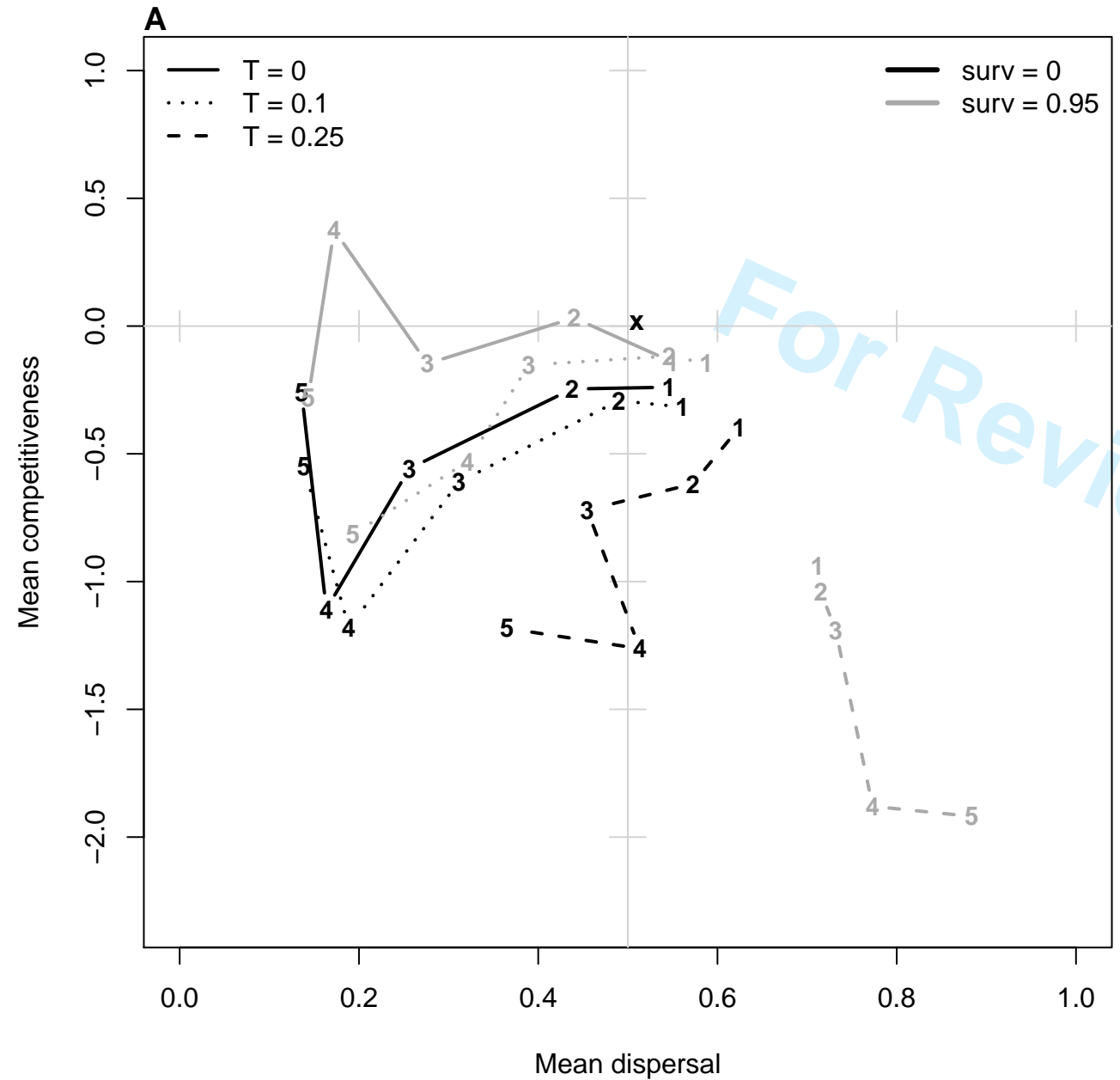
species. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean and range value of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).

Figure A4: Association between dispersal ability and competitiveness (log values) for five categories of niche breadth considering either (A) moderate spatial autocorrelation ($\alpha = 5$) or (B) strong spatial autocorrelation ($\alpha = 10$). The mean values are the average over the 50 replicates of the values observed in all surviving individuals. The numbers correspond to the five niche breadth categories from the most specialist species to the most generalist species: 1: 0.0-0.1; 2: 0.1-0.2; 3: 0.2-0.4; 4: 0.4-0.6; 5: 0.6-1.0. The cross shows the mean values of the metacommunity at the initial stage of the simulations. Plain lines: no disturbance ($T = 0$), dotted lines: intermediate disturbance rate ($T = 0.01$), dashed lines: high disturbance rate ($T = 0.25$). In black, non-overlapping generations (survival rate $\psi_s = 0$) and in grey overlapping generations (survival rate $\psi_s = 0.95$).









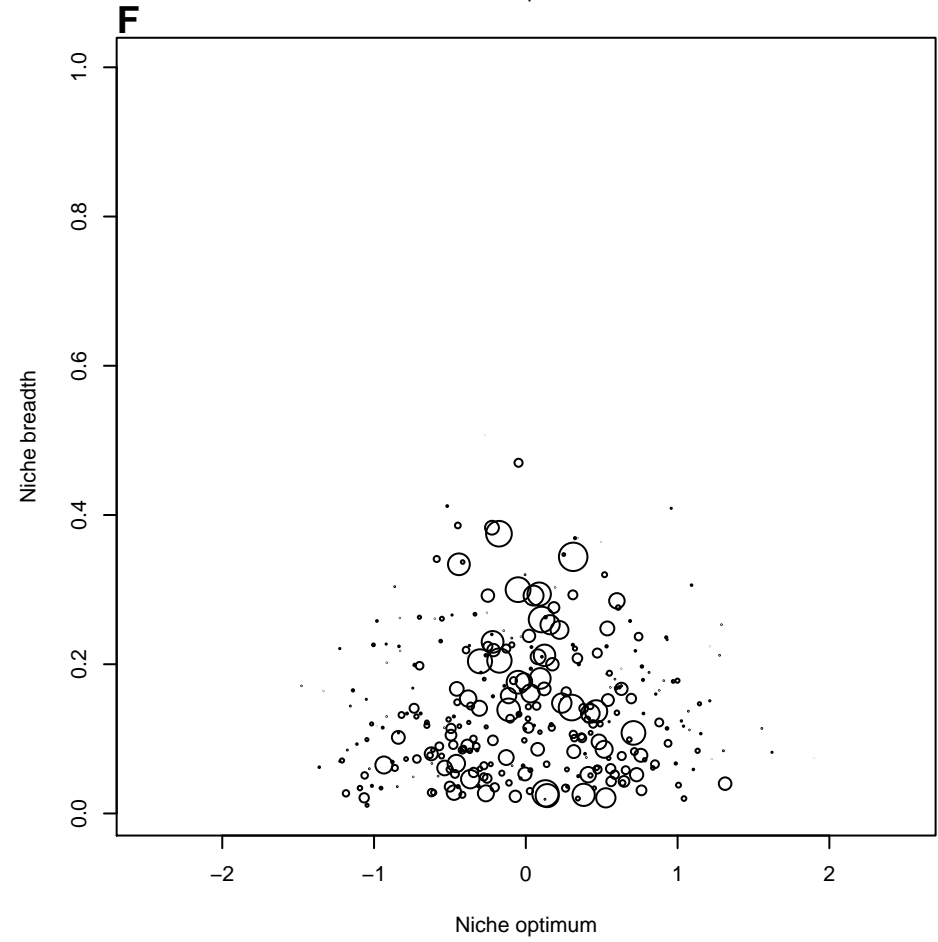
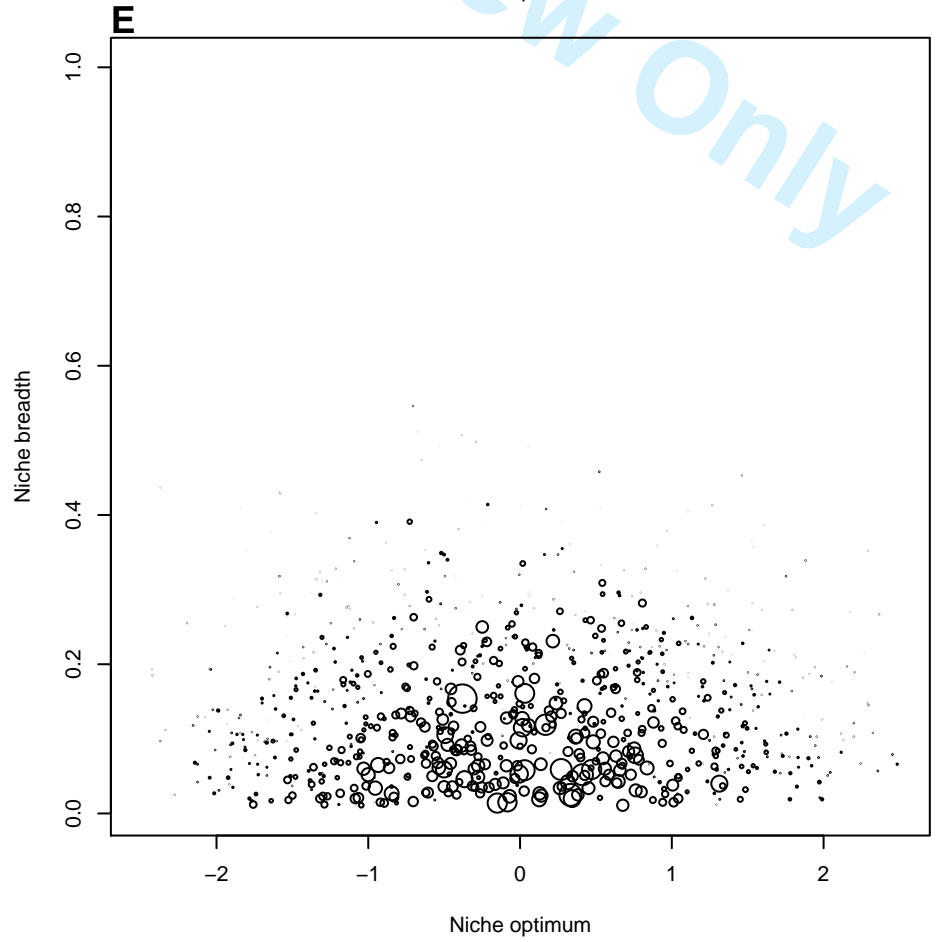
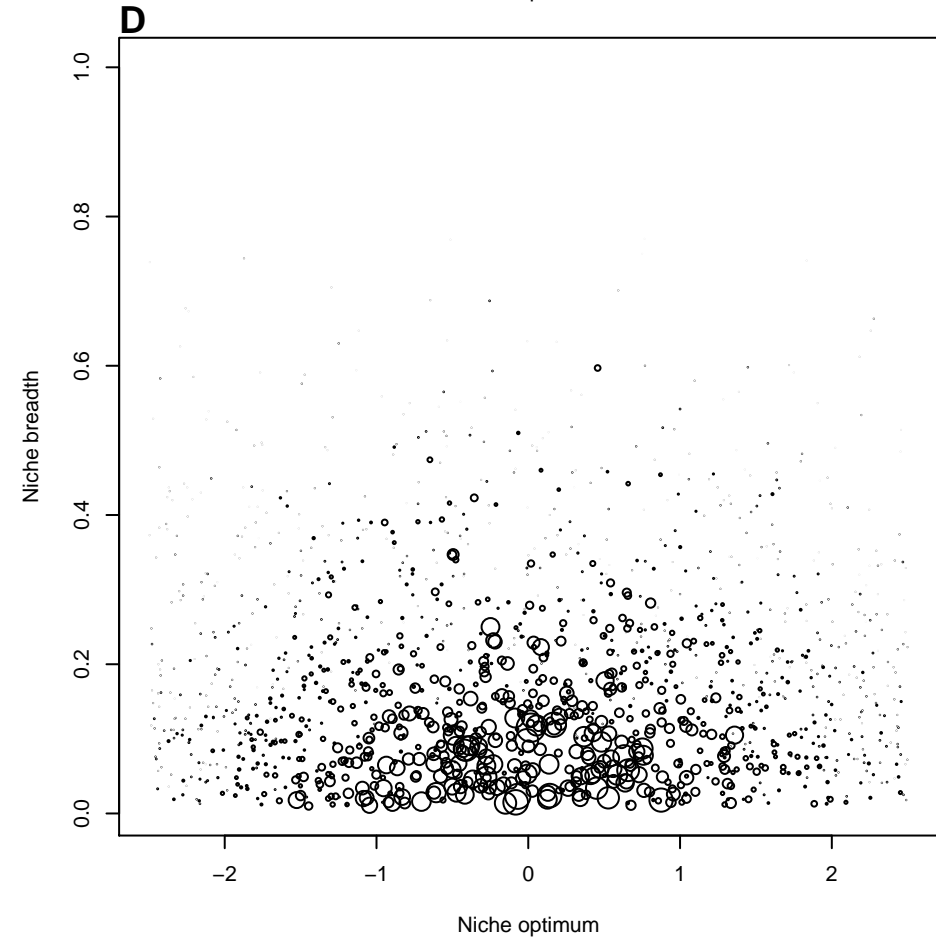
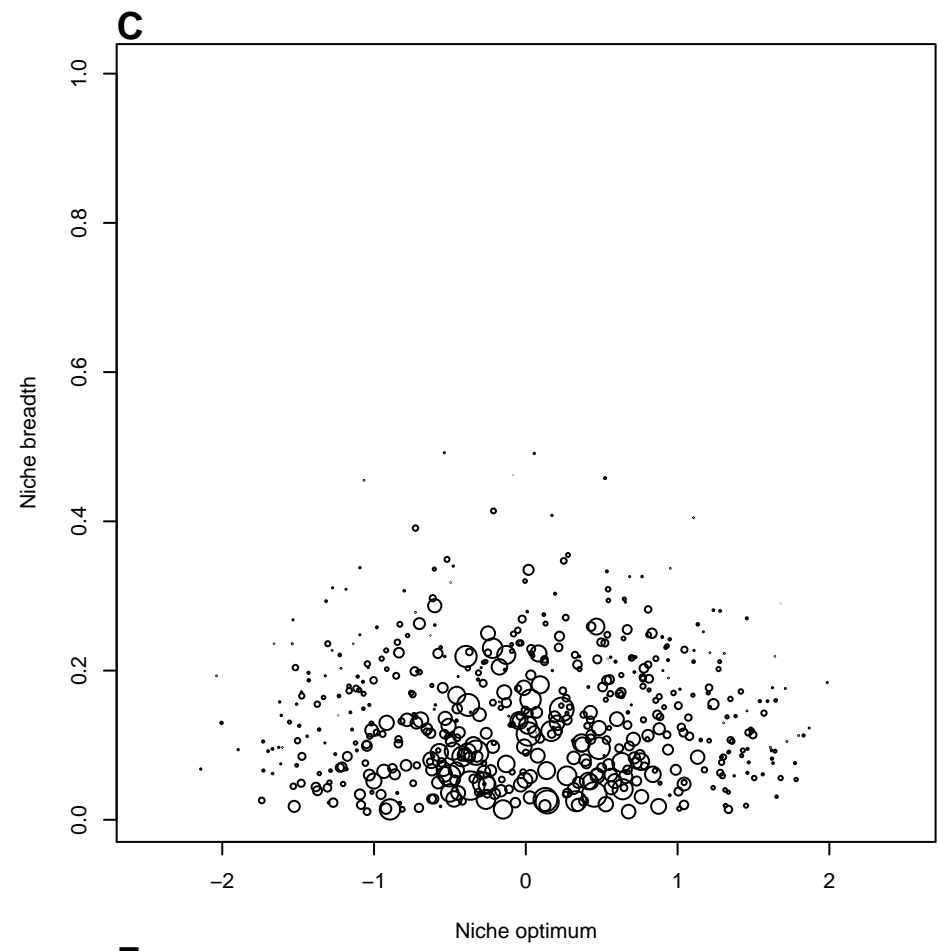
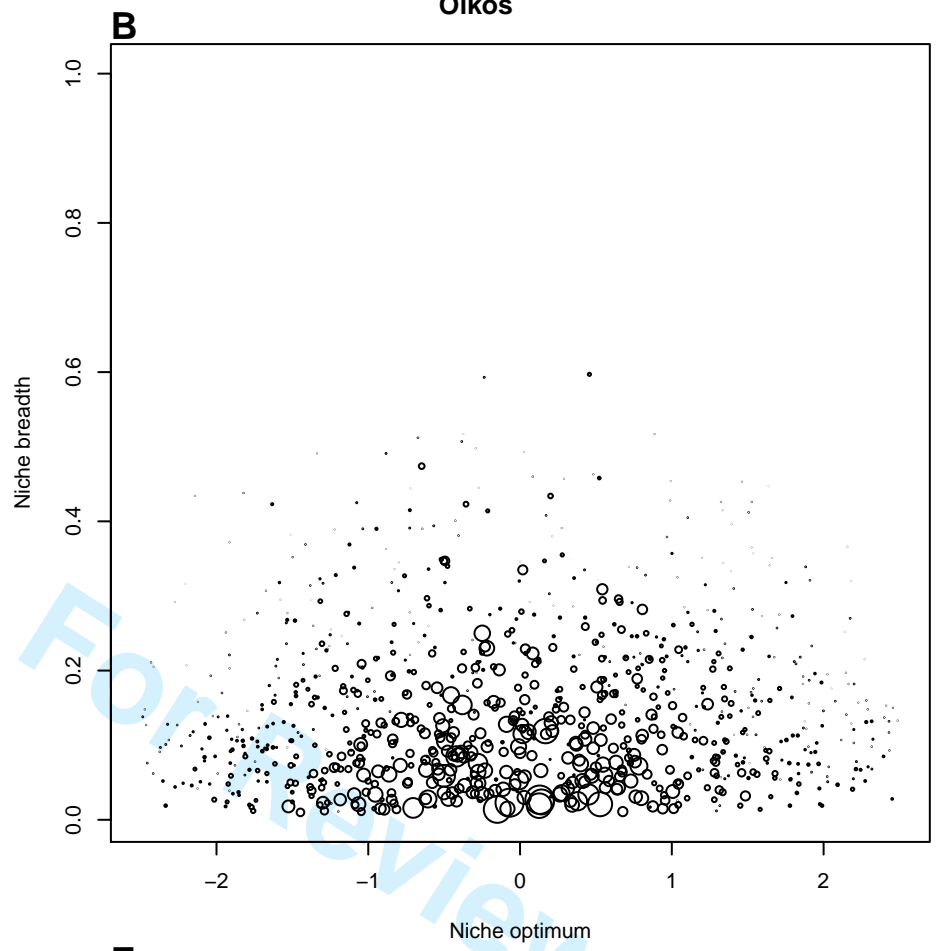
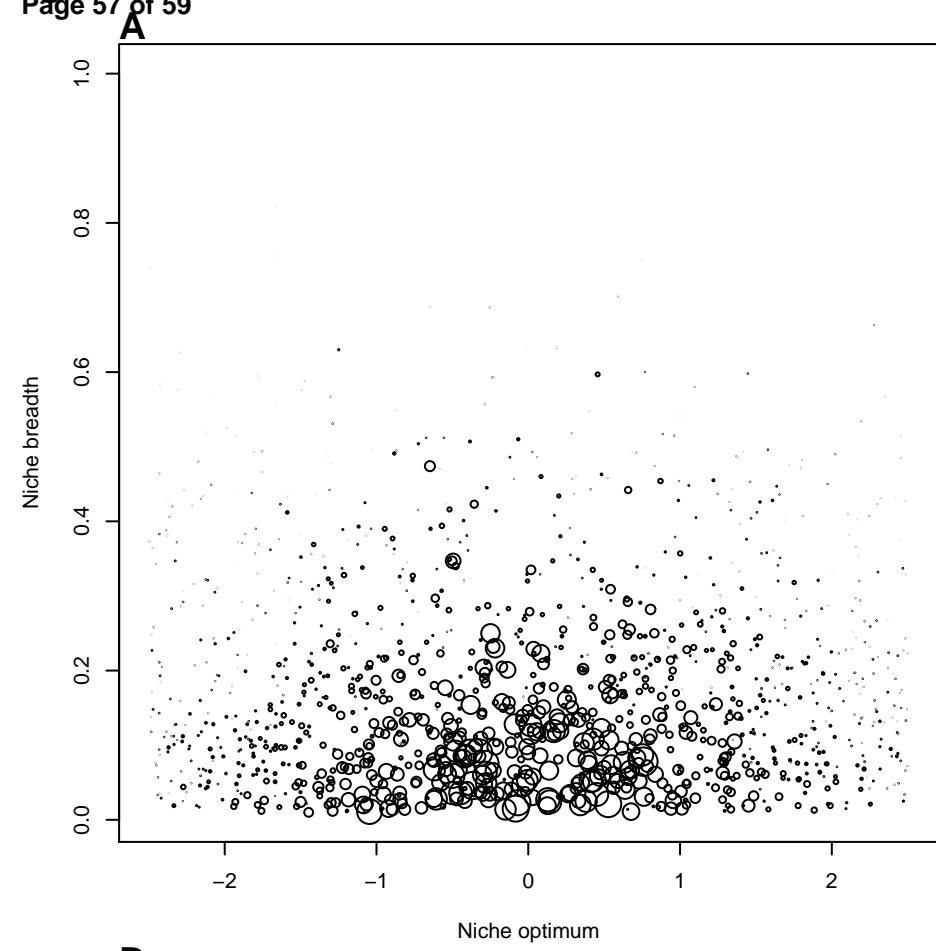
Appendix 4: Relationship between niche breadth and niche optimum

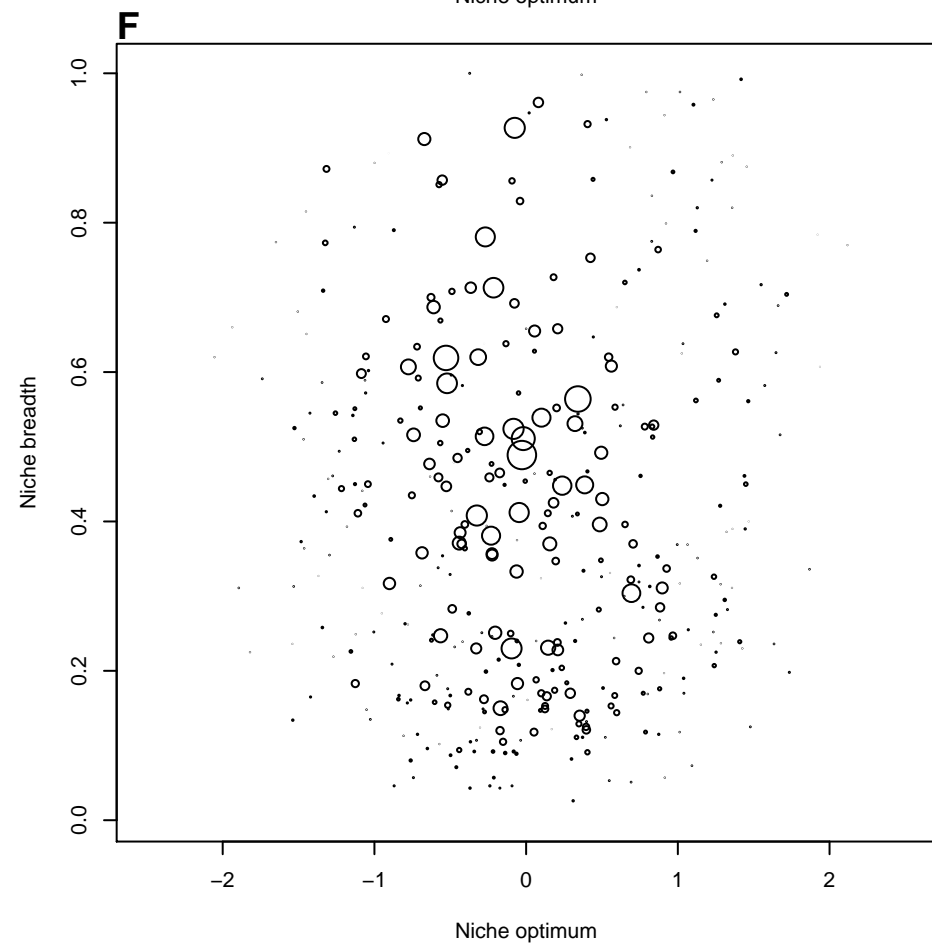
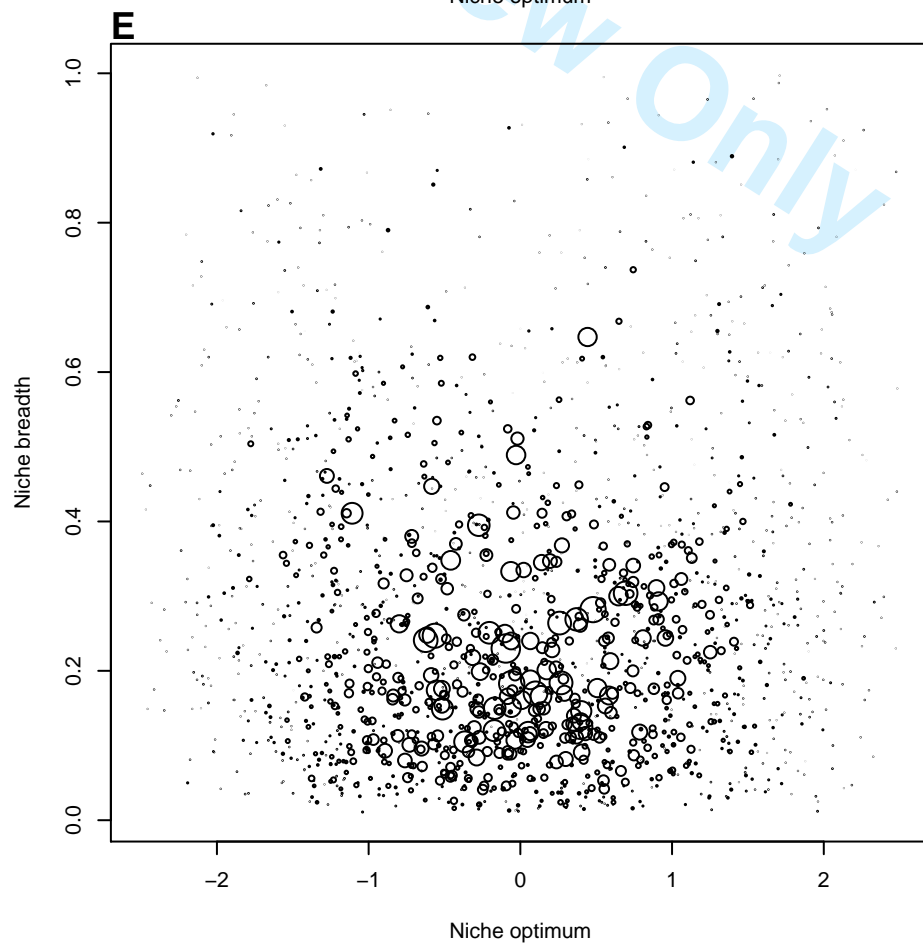
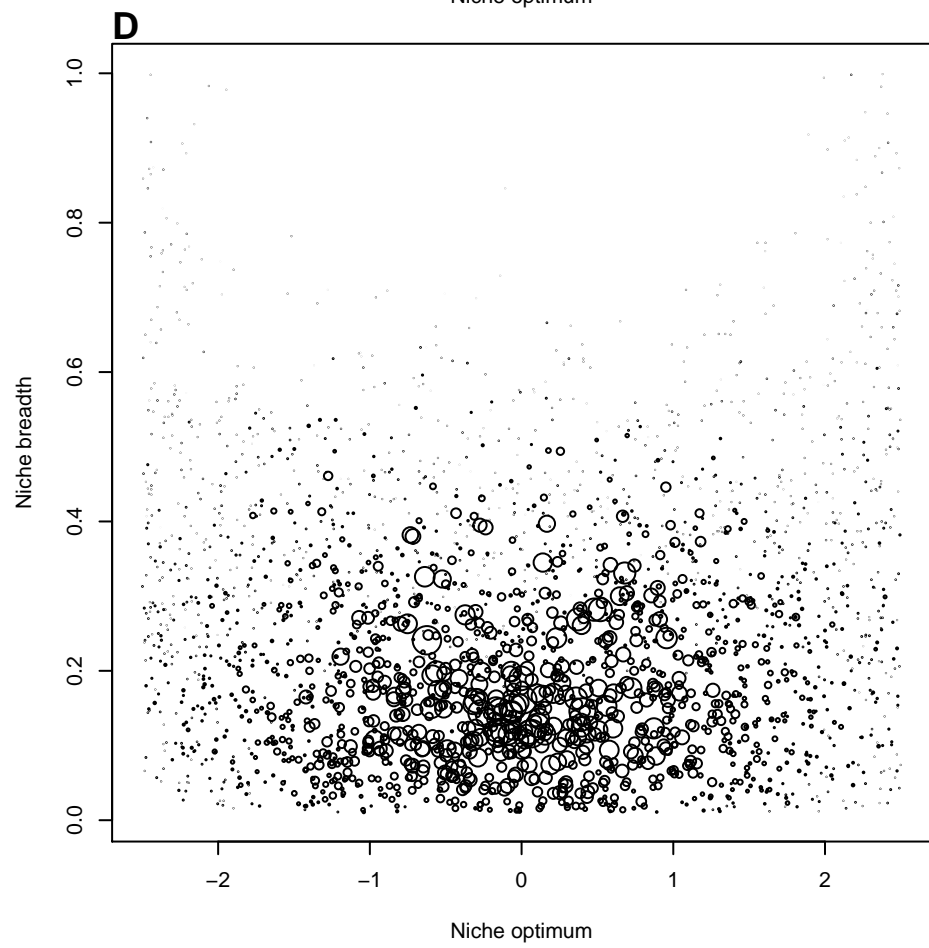
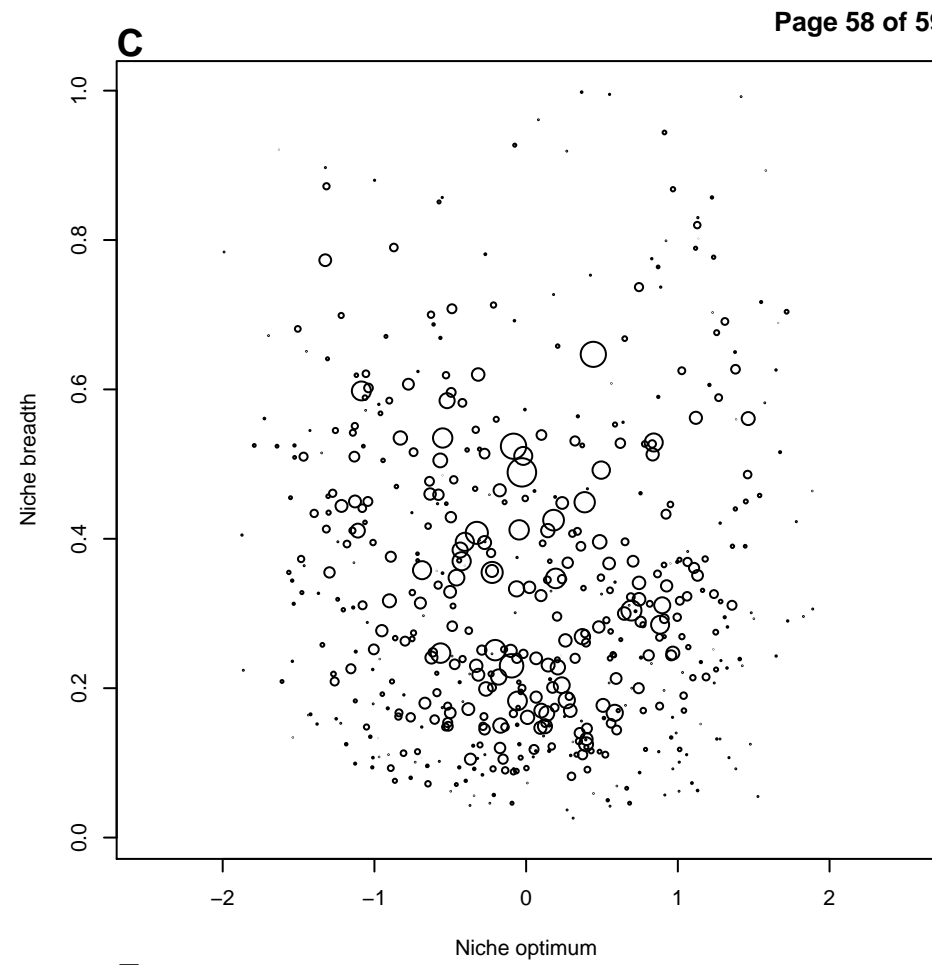
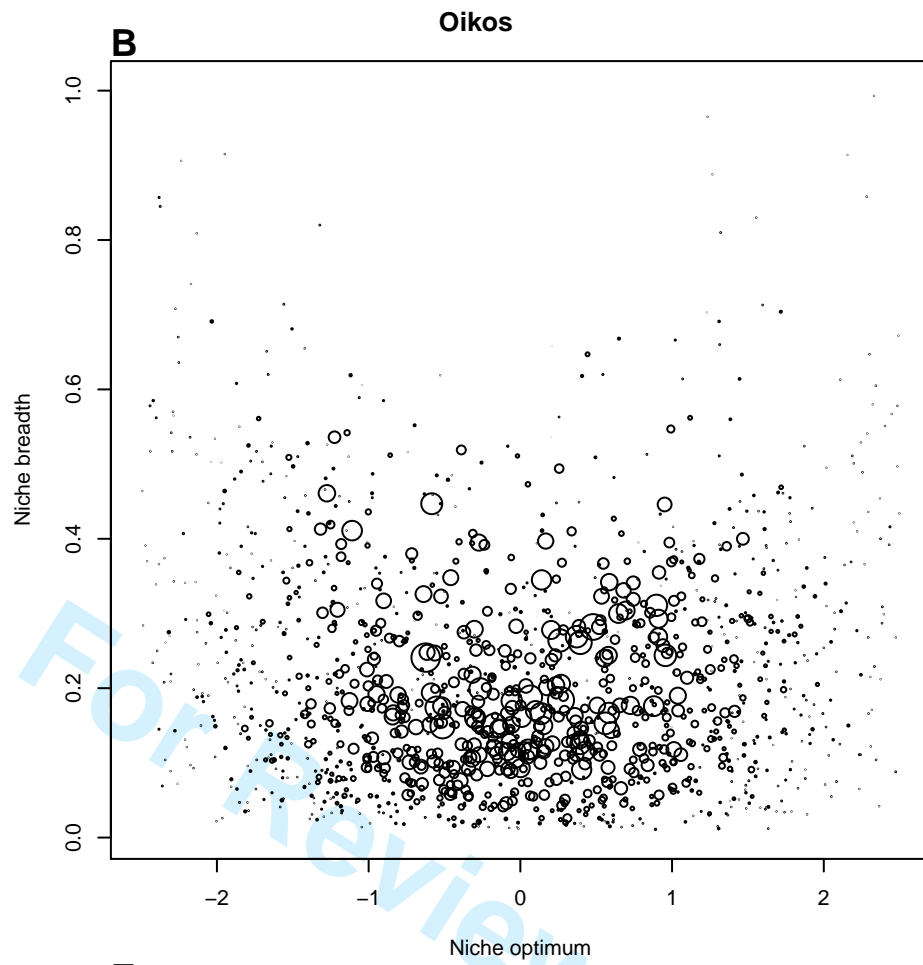
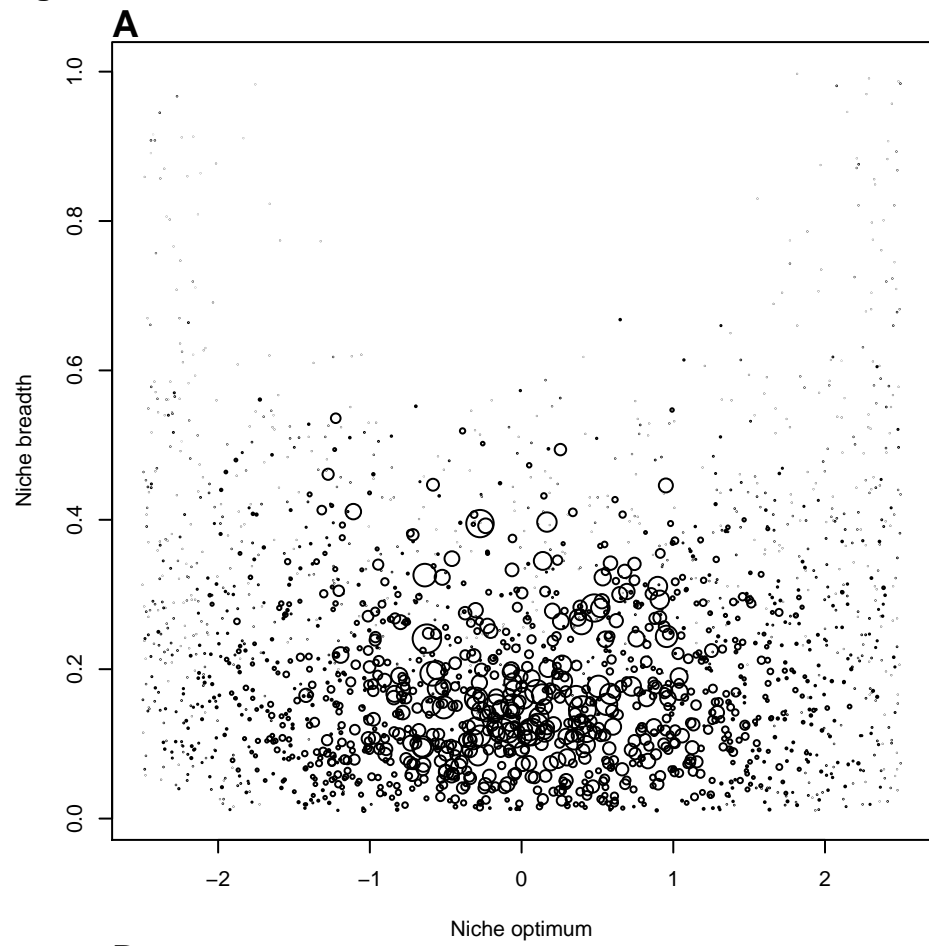
Figure A1: Relationship between niche breadth and niche optimum, with variable dispersal ability, and competitiveness and reproductive investment each equals to 1. (A) without disturbance ($T = 0$) and non-overlapping generations (survival rate $\psi_s = 0$), (B) with low disturbance rate ($T = 0.01$) and non-overlapping generations (survival rate $\psi_s = 0$), (C) with high disturbance rate ($T = 0.25$) and non-overlapping generations (survival rate $\psi_s = 0$), (D) without disturbance ($T = 0$) and overlapping generations (survival rate $\psi_s = 0.95$), (E) with low disturbance rate ($T = 0.01$) and overlapping generations (survival rate $\psi_s = 0.95$), (F) with high disturbance rate ($T = 0.25$) and overlapping generations (survival rate $\psi_s = 0.95$). The size of each point is proportional to the relative abundance of the species.

Figure A2: Relationship between niche breadth and niche optimum, with dispersal ability equals to 0.1, and variable competitiveness and reproductive investment. (A) without disturbance ($T = 0$) and non-overlapping generations (survival rate $\psi_s = 0$), (B) with low disturbance rate ($T = 0.01$) and non-overlapping generations (survival rate $\psi_s = 0$), (C) with high disturbance rate ($T = 0.25$) and non-overlapping generations (survival rate $\psi_s = 0$), (D) without disturbance ($T = 0$) and overlapping generations (survival rate $\psi_s = 0.95$), (E) with low disturbance rate ($T = 0.01$) and overlapping generations (survival rate $\psi_s = 0.95$), (F) with high disturbance rate ($T = 0.25$) and overlapping generations (survival rate $\psi_s = 0.95$). The size of each point is proportional to the relative abundance of the species.

Figure A3: Relationship between niche breadth and niche optimum, with variable dispersal ability and species competitiveness and reproductive investment. (A) without disturbance ($T = 0$) and non-overlapping generations (survival rate $\psi_s = 0$), (B) with low disturbance rate ($T = 0.01$) and non-overlapping generations (survival rate $\psi_s = 0$), (C) with high disturbance rate ($T = 0.25$) and non-overlapping generations (survival rate $\psi_s = 0$), (D) without disturbance ($T = 0$) and overlapping generations (survival rate $\psi_s = 0.95$), (E) with low disturbance rate ($T = 0.01$) and overlapping generations (survival rate $\psi_s = 0.95$), (F) with high disturbance rate ($T = 0.25$) and overlapping generations (survival rate $\psi_s = 0.95$). The size of each point is proportional to the relative abundance of the species.

Oikos





Oikos

