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1 **Modelling competition, niche and coexistence between an invasive and a native species**
2 **in a two-species metapopulation**

3

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13

14 *Running Head: Coexistence of snail species*

15 4 figures, 2 tables, 2 online appendices

16

17 Abstract

18 Modelling the dynamics of competition and coexistence between species is crucial to predict
19 long-term impacts of invasive species on their native congeners. However, natural
20 environments are often fragmented and variable in time and space. In such contexts regional
21 coexistence depends on complex interactions between competition, niche differentiation and
22 stochastic colonization-extinction dynamics. Quantifying all these processes at landscape scale
23 has always been a challenge for ecologists. We propose a new statistical framework to evaluate
24 metapopulation parameters (colonization and extinction) in a two-species system and how they
25 respond to environmental variables and interspecific competition. It requires spatial surveys
26 repeated in time, but does not assume demographic equilibrium. We apply this model to a long-
27 term survey of two snails inhabiting a network of freshwater habitats in the West Indies. We
28 find evidence of reciprocal competition affecting colonization or extinction rates, modulated by
29 species-specific sensitivity to environmental variables. Simulations using model estimates
30 allow us to predict species dynamics and explore the role of various coexistence mechanisms
31 described by metacommunity theory in our system. The two species are predicted to stably
32 coexist, because niche partitioning, source-sink dynamics and interspecific differences in
33 extinction-colonization parameters all contribute to reduce the negative impacts of competition.
34 However, none of these mechanisms is individually essential. Regional coexistence is primarily
35 facilitated by transient co-occurrence of the two species within habitat patches, a possibility
36 generally not considered in theoretical metacommunity models. Our framework is general and
37 could be extended to guilds of several competing species.

38

39 *Key Words:* metacommunity, competition, environmental variability, extinction / colonization,

40 *Physa acuta, Aplexa marmorata, freshwater snails*

41

42 **INTRODUCTION**

43 Species coexistence is a long standing issue in community ecology (e.g., Gause 1934). A
44 critical question is why so many species coexist, particularly when they belong to the same
45 trophic level (Hutchinson 1959). Indeed, when two or more species live on the same resource,
46 competition can lead to the exclusion of the less competitive one (the competitive exclusion
47 principle; Darwin 1859, Gause 1934). In a constant and homogeneous environment, two main
48 mechanisms can counteract competitive exclusion. First, similar species (ecological
49 equivalence) may be subject to neutral dynamics (Bell 2001, Hubbell 2001). In that case,
50 coexistence is transient and species replacement follows a stochastic process, resulting in a slow
51 erosion of diversity that can be counteracted by migration and speciation (MacArthur and
52 Wilson 1963, Hubbell 2001). Second, dissimilar species may coexist through negative
53 frequency-dependent processes that favor species when they become rare, for example when
54 they use resources not or less efficiently exploited by other species (niche theory, Chase and
55 Leibold 2003). This negative frequency-dependence is a key component of the so-called
56 ‘modern coexistence theory’ (Chesson 2000, Barabás et al. 2018).

57 However, environments can be fragmented, unstable and variable in space (Amarasekare
58 2003, Gravel et al. 2011). In these situations, local equilibria are never permanent, and
59 colonization and extinctions affect local dynamics (Leibold et al. 2004). Coexistence is
60 therefore not only determined by local processes, but also by regional ones. The interplay
61 between local and regional processes has been encompassed under the metacommunity
62 framework in which source-sink and patch dynamics play an important role (Leibold et al. 2004,
63 Holyoak et al. 2005). Under source-sink dynamics, source populations with positive growth
64 rates maintain sink populations with negative growth rate through recurrent migrant flux
65 (Pulliam 1988). Under patch dynamics, species coexist by virtue of trade-offs among traits, for
66 example traits involved in competition *vs.* colonization (Tilman 1994, Calcagno et al. 2006) or

67 in dispersal *vs.* fecundity (Yu and Wilson 2001). Note that these metacommunity processes do
68 not exhaust all possibilities and are not mutually exclusive (Brown et al. 2017). For example,
69 their relative importance depends on environmental heterogeneity and species traits (Meynard
70 et al. 2013).

71 Disentangling the various processes that drive community assembly is a serious
72 challenge. Previous attempts have largely been based on the analysis of species occurrence or
73 co-occurrence, monitored at a (single) given time, often together with environmental
74 parameters, using statistical methods partitioning the impact of environment and/or space (e.g.,
75 Cottenie 2005, Pollock et al. 2014). We focus on more dynamical approaches that formally
76 account for environmental heterogeneity, local *vs.* regional dynamics and species interactions.
77 More specifically, we model competition and niche effects on colonization and extinction rates
78 at a metapopulation scale, based on temporal data of species occurrence. This general approach
79 has recently been implemented in several, closely related methods (e.g., Dorazio et al. 2010,
80 Miller et al. 2012, Yackulic et al. 2014, Davis et al. 2017). These studies take into account
81 imperfect species detection, a critical issue for any observational study, that, if neglected, can
82 lead to biased inferences (review in Guillera-Aroita 2017). They however present an important
83 drawback; colonization is not modelled as proportional to the fraction of already occupied sites
84 acting as propagule sources in a metapopulation. This proportionality should be considered
85 when this fraction varies in time, whether continuously (e.g., invasive species) or transiently
86 (Moilanen 2000). Effects of variation in occupancy can be modelled through auto-regressive
87 linear effects (e.g., Yackulic et al. 2014). However, this approach results in unwanted properties
88 for prediction, such as allowing colonization by regionally extinct species, or setting it to zero
89 below a certain occupancy. Moreover, some estimations assume that the system has reached a
90 quasi-stationary regime, or temporal variation is modelled through a “sampling year” factor

91 (Naujokaitis-Lewis and Fortin 2016), which precludes analysing and predicting non-stationary
92 dynamics, for example when invasive and native species are interacting.

93 We addressed these issues by developing a new model. Our approach extends the
94 spatially-implicit metapopulation model developed by Lamy et al. (2013a), which estimates
95 extinction and colonization rates as a function of environmental variables while considering
96 imperfect species detection. Our model includes, in addition, the impact of competitive
97 interactions on these parameters, and estimates colonization rates relative to occupancy as in
98 the original model of Levins (1969), therefore accounting for temporal changes in propagule
99 pressure. We focus on a two-species system for the sake of simplicity - the approach could
100 afford more species in principle. Importantly, we use the model outcomes to perform
101 simulations, in order to (i) predict the future dynamics of the interacting species, and (ii)
102 evaluate the impact of the various mechanisms mentioned above on species coexistence at
103 regional scale.

104 We used this approach to describe the joint dynamics of two species from the freshwater
105 snail metacommunity of Guadeloupe (Lesser Antilles) which has been monitored every year
106 since 2000 at 250 sites. These two species are closely related and ecologically similar. One is
107 native while the other was introduced at the end of the 20th century and started to spread in the
108 metacommunity at the beginning of the survey. We first evaluated whether competition actually
109 occurs, as previously suggested (Chapuis et al. 2017), and how each species may locally reduce
110 colonization (resource preemption) or increase extinction (competitive replacement) of the
111 other. We then assessed the impact of environmental heterogeneity, niche differentiation, and
112 source-sink dynamics (Pulliam 1988) on local and regional coexistence. Lastly, we explored
113 whether the negative impacts of competition could be compensated by differences in other
114 demographic traits, and whether such differences are promoting species coexistence, as in

115 patch-dynamics models of coexistence in metacommunities (Levins and Culver 1971, Tilman
116 1994, Calcagno et al. 2006).

117

118 **MATERIALS & METHODS**

119 *The freshwater snail metacommunity from Guadeloupe*

120 *Study area.* - The study area is the Grande-Terre island (570 km²) of Guadeloupe in the
121 Lesser Antilles, a limestone plateau harboring a large number of ponds (*ca.* 2000), a few small
122 intermittent rivers, and swamp grasslands connected to mangroves (hereafter back-mangrove).
123 The study system has been described in detail in previous studies (e.g., Lamy et al. 2012, 2013a,
124 Chapuis et al. 2017), and we report here the information relevant to the current work. Sites vary
125 in size (from a few m to a few hundreds of m), coverage by aquatic vegetation, connectivity,
126 and water permanence (some can be dry for up to several months). The latter two are markedly
127 influenced by the alternation between the dry season (December to June) and the rainy season
128 (hereafter RS) from July to December. A minor rainy episode often interrupts the dry season
129 from March to May (LRS for “little rainy season”) with a very variable intensity among years.
130 Strong precipitation often leads to flooding events, which can connect freshwater habitats and
131 create dispersal routes for their inhabitants. Snails are one of the dominant groups of
132 invertebrate communities in freshwater environments from Grande-Terre with 26 species in
133 total.

134 *Focal species.* – We focus on two pulmonate snails (*Aplexa marmorata* and *Physa acuta*)
135 belonging to the *Physidae* family. Both are currently abundant in Grande-Terre (Chapuis et al.
136 2017). *Aplexa marmorata* is native to Guadeloupe and is found on average in 59% of the sites
137 in our yearly surveys (see below). *Physa acuta* was introduced at the end of the 20th century,
138 probably through the trade of aquatic plants, but began spreading in Grande-Terre only around
139 2000 to now occupy *ca.* 50% of sites. These hermaphroditic species are phenotypically quite

140 similar, but differ in their mating systems. *Aplexa marmorata* reproduces mainly through
141 selfing (Escobar et al. 2011, Lamy et al. 2013b) while *P. acuta* is an outcrossing species (Henry
142 et al. 2005). Dispersal among sites, as in most freshwater snails, is mainly passive and can occur
143 through abiotic (e.g., floods) and biotic vectors (e.g., birds) and through human activities (Van
144 Leeuwen et al. 2013). Previous studies have highlighted competition between these species, as
145 the arrival of *P. acuta* results in both a decrease in densities and a rapid evolutionary shift in
146 life-history traits in *A. marmorata* (Chapuis et al. 2017).

147 *Field surveys and environmental variables.* – We surveyed around 250 sites yearly from
148 2001 to 2015, including mainly ponds, but also some intermittent rivers and back-mangroves.
149 A smaller number of sites (58) was surveyed in 2012 for technical reasons. Our protocol is
150 described in details in Lamy et al. (2013a, 2013b) and Chapuis et al. (2017). In each site we
151 noted the presence / absence of species (the primary data in the present study). Each year, a
152 randomly-chosen subset of sites (*ca.* 30) was visited twice in order to estimate species
153 detectability (see Mackenzie and Royle 2005, Lamy et al. 2013a). A set of environmental
154 characteristics was recorded in each site, including state (dry or wet), size (m), vegetation cover
155 (percent of total surface), water connectivity to neighboring freshwater habitats (four
156 categories), and water permanence (five levels, from fully permanent to frequently dry).

157

158 *Multistate occupancy model*

159 In order to estimate the demographic parameters of our two focal species in the
160 Guadeloupe metacommunity, we use the state-space modeling approach developed in Lamy et
161 al. (2013a), and derived from MacKenzie et al. (2003) and Royle and Kéry (2007). We extend
162 this approach to account for competition among species and dependency of colonization rates
163 on previous occupancy. The principle of the state-space approach is to distinguish between two
164 processes: a state process capturing transitions between states (occupied / not occupied) and an

165 observational process linking the data (observed or not) to the underlying state, accounting for
166 imperfect detection.

167 *The model.* – The model structure is reported in detail in Lamy et al. (2013a), and we
168 present here its general logic, as well as the extensions in the current version. The full details
169 are given in Appendix S2 and notations are summarized in Table 1. We model, simultaneously
170 for the two species, occupancy data in N sites (a metapopulation) over T occasions,
171 distinguishing between an observation status $y_{i,t}$ (=1 if the species is observed in site i at
172 occasion t , and 0 otherwise) and a true occupancy status $x_{i,t}$ (=1 if the species is present in site
173 i at t , and 0 otherwise). Two sampling occasions are separated by (successively) the dry season
174 during which extinction may occur and the rainy season during which colonization may occur.
175 The occupancy dynamics of a site (omitting the site index i for clarity) is modeled as a Bernoulli
176 draw with probability:

$$177 \quad P(x_{t+1} = 1) = x_t[\varphi + (1 - \varphi)(1 - e^{-c \bar{x}_t})] + (1 - x_t)(1 - e^{-c \bar{x}_t}) \quad (1)$$

178 with \bar{x}_t the overall metapopulation occupancy at the beginning of the cycle.

179 The temporal transitions between occupancy status within sites are governed by the
180 probabilities of local persistence φ (local extinction: $1 - \varphi$) and of colonization γ (probability
181 that an unoccupied site becomes occupied). Rather than estimating a constant colonization
182 probability as in Lamy et al. (2013a), we here modeled the metapopulation colonization rate c
183 (Levins 1969) which is connected to the colonization probability by $\gamma = 1 - e^{-c \bar{x}}$ where \bar{x} is
184 the proportion of occupied sites. The advantage of fitting c rather than γ is that γ automatically
185 follows year-to-year variation in \bar{x} as long as stationarity is not reached. For example, γ
186 increases during an invasion simply because more and more sites become occupied and produce
187 propagules. In contrast, c does not have this property, being the metapopulation analog of a per-
188 capita birth rate. This is a relevant property when considering invading species such as *P. acuta*
189 in Guadeloupe, or collapsing metapopulations. The negative exponential comes from the

190 assumption that colonization occurs as a continuous process in time and through propagules
 191 emitted by occupied sites at a constant rate, such that the probability that a site has not been
 192 colonized in one time unit (cycle) is $e^{-c\bar{x}}$ (*i.e.* the Poisson probability of no events in the time
 193 interval).

194 A peculiarity of our study system is that a given site can be either wet, or dry at different
 195 times. In what follows, wet and dry refer to site state observed at the time of sampling. Some
 196 snail species can persist buried in the ground in dry sites, where they cannot be detected
 197 (Pointier and Combes 1976, Lamy et al. 2013a). Species observation (y) in such sites is always
 198 0 as the site is in practice not sampled. Therefore, its estimated occupancy is a purely latent
 199 variable based upon occupancies during the previous and following wet periods. Following
 200 Lamy et al. (2013a), we estimated persistence probabilities separately for dry and wet sites (φ_D
 201 and φ_W respectively). We made a similar distinction for the colonization rate (c_D and c_W
 202 respectively), but preliminary tests showed that c_D was imprecisely estimated and its 95%
 203 credibility interval always included zero. Therefore we simply set c_D to zero, with no effect on
 204 the estimates of other parameters.

205 Imperfect species detection results in a possible mismatch between state and observation.
 206 Observation and state were linked by incorporating a detection probability (d) in both dry and
 207 wet sites (Appendix A). The detection probability was set to 0 in dry sites for both species, and
 208 estimated separately for each species in wet sites.

209 *Integrating environmental covariates and competition.* - Lamy et al. (2013a) modeled
 210 persistence and colonization in wet sites as functions of site and year-specific environmental
 211 covariates, and we extend their framework to account for competition. The final model reads
 212 for each species in site i between time t and $t+1$:

$$213 \quad \log(c_{W_{i,t}}) = \mu_{c_W} + \boldsymbol{\beta}_c \cdot \mathbf{X}_{c_{i,t}} + \alpha_c x'_{i,t} \quad (2a)$$

$$214 \quad \text{logit}(\varphi_{W_{i,t}}) = \mu_{\varphi_W} + \boldsymbol{\beta}_\varphi \cdot \mathbf{X}_{\varphi_{i,t}} + \alpha_\varphi x'_{i,t} \quad (2b)$$

215
$$c_D = 0 \quad (2c)$$

216
$$\text{logit}(\varphi_D) = \mu_{\varphi_D} \quad (2d)$$

217 where for each parameter μ is the intercept, $\boldsymbol{\beta}$ a row vector of regression coefficients, \mathbf{X} a vector
218 of environmental covariates (site and year specific), and α a regression coefficient modeling
219 the effect of the competitor species. x' represents the competitor occupancy in the focal site in
220 the previous year; it is a latent state predicted by the model, rather than an observation (as the
221 latter underestimates occupancy because of imperfect detection). Competition should result in
222 $\alpha < 0$ (the presence of the other species reduces colonization or persistence), while $\alpha > 0$ could
223 result from facilitation. Log and logit transformations, for c and φ respectively, rescale the
224 authorized intervals ($c \geq 0$ and $0 \leq \varphi \leq 1$) to $]-\infty; +\infty[$. We chose to model persistence in dry sites
225 (φ_D) as a constant: competition is unlikely to occur when sites are dry and snails are aestivating
226 (Eq. 2d). Moreover, the occurrence of dry sites is low in our dataset (5.8%), limiting the number
227 of parameters that can correctly be fitted.

228

229 *Application of the model to our study system*

230 *Species and environmental variables.* – We fit the dynamics and interactions of *P. acuta*
231 and *A. marmorata* in the Grande-Terre of Guadeloupe using a joint model that estimates the
232 intercepts μ and regression coefficients α and $\boldsymbol{\beta}$ for c_D and c_W , φ_D , the initial occupancy at
233 the beginning of the survey ψ , and the detection probability (in wet sites) d for each species.
234 The covariates included in our analysis were constructed from field and meteorological data,
235 and were site-specific, year-specific or site-and-year-specific (see Lamy et al. 2013a, 2013b).
236 The site-specific covariates are site type (pond vs. river and back-mangrove), site size,
237 vegetation cover and connectivity (Appendix S1: Tab. S1). We also considered stability, a
238 synthetic index negatively related to year-to-year fluctuations and perturbations within sites
239 (Lamy et al. 2013a, Appendix S1: Tab. S1). The two year-specific covariates were cumulative

240 rainfall over the little rainy season (LRS; when sites tend to shrink, reducing snail habitat) and
241 over the rainy season (RS; during which potential water connections are established among
242 sites) in the year preceding the survey. The last covariate (site- and year-specific) reflects the
243 local propagule pressure around the focal site ($D_{i,t}$ for site i at time t), an estimate of the number
244 of occupied sites surrounding the focal site in the preceding year (total number of water bodies
245 within a 4-km distance multiplied by the average x_{t-1} of the sites that were included in our
246 survey within this radius). This distance allows the inclusion of a large-enough number of sites
247 around each sampled site without encompassing a too large fraction of Grande-Terre (Lamy et
248 al. 2013a). Following Lamy et al. (2013a), the same set of covariates was used to model
249 colonization and persistence rates with a few exceptions: connectivity and local propagule
250 pressure were included only for colonization as they are related to the probability of receiving
251 propagules. Similarly, RS was included for colonization only, while LRS was included only for
252 persistence. Thus, the number of covariates was limited to those that are likely to have an effect,
253 in order to avoid overfitting.

254 In order to facilitate interpretation, the values of all environmental covariates were
255 standardized to zero mean and unit variance before analysis, such that model intercepts
256 represent colonization rate and persistence probability in an average site (*i.e.* in which all
257 environmental values are set to metapopulation means). We did not standardize x' (competitor
258 occupancy), meaning that the intercept μ estimates the colonization or persistence rate in an
259 average site when the competitor is absent ($x' = 0$) while $(\mu + \alpha)$ is the corresponding estimate
260 when it is present ($x' = 1$).

261

262 *Implementing the model.* – We fit the model to data using a Bayesian Markov Chain
263 Monte Carlo method. The analyses were conducted using JAGS (Just Another Gibbs Sampler,
264 Plummer 2003) implemented in the packages {rjags} and {coda} (Plummer et al. 2006) of R

265 (version 3.3.1, 2016). The model generates posterior probability distributions of all parameters
266 for both species. We used wide prior distributions for $\psi \sim U(0,1)$, $d \sim U(0,1)$, $\mu_c \sim \mathcal{N}(0,0.1)$,
267 $\mu_\varphi \sim \mathcal{N}(0,0.1)$, as well as for the $\beta \sim \mathcal{N}(0,0.1)$ and $\alpha \sim \mathcal{N}(0,0.1)$ coefficients (Normal
268 priors are expressed with a precision parameter). We ran three parallel Markov chains for 40000
269 iterations after a burn-in of 20000 iterations. Convergence was assessed by visual inspection
270 and using several diagnostics available in the {ggmcmc} (Fernández-i-Marín 2016). We report
271 potential scale reduction factor (\hat{R} , Brooks and Gelman 1998) in Appendix S1: Fig. S1,
272 posterior distributions of parameters in Appendix S1: Fig. S2 and pairwise correlations among
273 parameters in Appendix S1: Fig. S3. We report the medians and credibility intervals of posterior
274 distributions in Table 2.

275

276 *Projecting species dynamics to understand coexistence*

277 The results of the Bayesian approach were used to explore species dynamics, based on
278 simulations, with various aims. The first was to evaluate whether the model correctly
279 reproduced the observed dynamics of the two species at the time scale of our study. The second
280 aim was to make long-term projections (500 cycles) of occupancies and prospects of co-
281 existence of the two species in the Guadeloupe landscape. The third aim was to explore the
282 impact of various mechanisms (priority effects, environmental heterogeneity, and competition)
283 on the two-species dynamics by varying their intensity in the simulations.

284 For these purposes, we developed a stochastic simulation model of a two-species
285 metacommunity in a landscape of 250 sites mimicking the Guadeloupe system. The site-
286 specific covariates and geographical position of the simulated sites exactly matched those of
287 our dataset. At each cycle (corresponding to one year in the Guadeloupe system), we used LRS
288 and RS covariates, and a pattern of dry/wet sites, based on observed data; the first 15 years of
289 the simulations were as in the data, and the following years were drawn at random with

290 replacement from the first 15 years (*i.e.* assuming no temporal trend). The site and year-specific
291 covariate describing local propagule pressure ($D_{i,t}$) was computed for each site at each time
292 step, and standardized based on the mean and standard deviation from empirical data (the
293 appropriate scale to use the regression slope estimates produced by the Bayesian method).
294 Finally, occupancy was drawn at each time step from a Bernoulli distribution following Eqs. 1
295 and 2. We implemented the simulations in *Julia* (Bezanson et al. 2017, version 0.6.2), a fast
296 and user-friendly programming language, with 1000 replicates per parameter set (including 50
297 random initializations for RS, LRS and desiccation patterns, replicated twenty times each).
298 Simulations were run for 500 cycles (*i.e.* years). The values extracted from the simulations at
299 each cycle were the fraction of sites that were empty, occupied by a single species or occupied
300 by both species, as well as the transition frequencies among these states.

301 For aims 1 and 2 parameters were drawn for each replicate from the posterior joint
302 distribution obtained from the model. The first 15 years of simulations were used to compare
303 with empirical observations (aim 1) while the 500th year (after visually checking for stationarity,
304 see e.g., Appendix S1: Fig. S4) was used to predict the stationary state of the system (aim 2).

305 For aim 3, we changed some parameter values to investigate their impact. The other
306 parameters were again drawn from the joint posterior distribution generated from the statistical
307 model. We first evaluated possible priority effects by reversing the initial occupancies of the
308 two species (*ca.* 5% in the invasive *P. acuta* and *ca.* 50% in the native *A. marmorata*) in the
309 simulations of two-species metacommunity dynamics (see e.g., Hanski 1983). However, this
310 did not detectably influence the long-term behavior of the model (results not reported). Note
311 that 5% may already be high enough to overcome the initial stochasticity inherent to an invasion
312 process. Therefore, we also performed simulations initiated with a single occupied site (*i.e.*
313 0.4% of occupied sites) for one species, the other species being at its single-species stationary

314 occupancy. This was done for each species and used to estimate the probability of invasion
315 success.

316 Next, we studied the impact of environmental heterogeneity. To this end, we simulated
317 environmentally uniform landscapes, composed of 250 identical sites mimicking the conditions
318 of one of the 250 observed sites, for both species, including competition or setting it to zero.
319 This was done using each of the 250 sets of site-specific environmental covariates, and we
320 recorded for each set whether one or both species persisted on the long term. We could therefore
321 identify three categories of environments per species based on whether the metapopulation (i)
322 persisted in a landscape uniformly composed of this environment, even in competition with the
323 other species, (ii) persisted only in the absence of competition, or (iii) never persisted. By
324 analogy with classical concepts, we refer to category (i) as our metapopulation estimate of the
325 “realized niche” of the focal species, while the “fundamental niche” is represented by categories
326 (i) and (ii) together. By intersecting the realized and fundamental niches of the two species, we
327 ended up with six more precise categories of environments: (1) outside the two fundamental
328 niches (no species can persist), (2) within both realized niches (both species persist), (3) out of
329 the fundamental niche of *A. marmorata* but within that of *P. acuta* (only the latter persists), (4)
330 out of the realized niche of *A. marmorata* but within its fundamental niche (*A. marmorata*
331 persists only when *P. acuta* is absent). Categories (5) and (6) are as (3) and (4), swapping the
332 two species. We conducted a linear discriminant analysis (LDA) to determine which linear
333 combinations of the site-specific environmental variables (size, connectivity, vegetation cover,
334 stability, and site type) best differentiated among these six categories.

335 We explored the impact of competition asymmetry and difference in demographic
336 strategies on metapopulation persistence using two series of simulations. We first ran
337 simulations setting the competition coefficients (α) to zero for each species in turn (*i.e.* making
338 competition unidirectional rather than reciprocal). Second, we simulated a range of colonization

339 and extinction rates for each species, in presence and absence of competition, to determine how
340 the competitive effect exerted by the other species modifies the persistence thresholds. The two
341 series of simulations were performed both with and without environmental heterogeneity.

342

343 **RESULTS**

344 *Metacommunity parameters and the influence of environmental covariates and competition*

345 *Aplexa marmorata* (the native species) was found in 59% of the sites per year on average
346 (minimum 41%, maximum 77%), and was never observed in only 1.2% of the sites over the
347 whole period. Its detection probability was 0.84 (Table 2). The detection probability of *P. acuta*
348 (invasive) was slightly lower (0.75), and its dynamics differed, as it was detected in 1.4% of
349 the wet sites in 2000, steadily increased to 49% in 2015, and plateaued somewhat after 2011
350 (Fig. 1).

351 The intercepts for colonization and persistence (recall that intercepts represent
352 probabilities/rates in the absence of competition in a site with average environmental
353 characteristics) were very different between the two species (Table 2; posterior distributions are
354 reported in Appendix S1: Fig. S2). The colonization rate (c_w) of *A. marmorata* was almost
355 twice as high as that of *P. acuta* (1.24 vs. 0.70), while the persistence probability in wet sites
356 (φ_w) was much higher in *P. acuta* (0.99) than in *A. marmorata* (0.75). Interestingly, both
357 species persisted well in dry sites ($\varphi_D = 0.87$ and 0.81 in *A. marmorata* and *P. acuta*
358 respectively). Note that the φ_D 's were imprecisely estimated (see credibility intervals in Table
359 2) since they were calculated on a limited number of sites (5.8% of sites are dry on average per
360 year). However, the credibility intervals were well above zero, validating the inclusion of φ_D
361 in the model.

362 Habitat type, site size, vegetation cover and connectivity affected the two species in
363 different ways. In both species lower colonization rates were found in back-mangroves than in

364 other habitats (Table 2 and Appendix S1: Fig. S5). The reverse was true for persistence, with
365 higher values in back-mangroves, especially in *P. acuta* (Appendix S1: Fig. S5). However, a
366 lower persistence rate and a higher colonization rate were estimated in *A. marmorata* than in *P.*
367 *acuta* in all three habitat types. Note that the model predicted extremely low colonization and
368 extremely high persistence in *P. acuta* in back-mangroves (Appendix S1: Fig. S5). We
369 confirmed based on raw data that this reflects a real pattern. *P. acuta* is continuously present in
370 a few back-mangrove sites, and continuously absent in others, during the whole study period.
371 In the one hand, high vegetation cover had a markedly positive effect on the persistence of *A.*
372 *marmorata*, and a weaker, but still positive effect on its colonization. On the other hand,
373 vegetation cover decreased the colonization rate for *P. acuta* and its effect on persistence was
374 weak (credibility interval including zero). Site size and connectivity increased colonization in
375 *P. acuta*, but had no impact on *A. marmorata*. The rainfall variables (LRS and RS) had no
376 influence in *A. marmorata*, but in *P. acuta*, persistence was increased by LRS, while RS slightly
377 decreased the colonization rate (Table 2). The local propagule pressure covariate ($D_{i,t}$) had no
378 effect in either species.

379 Competition had a different effect on the two species (Table 2 and Fig. 2). The presence
380 of *P. acuta* strongly decreased the colonization rate of *A. marmorata* but had no effect on the
381 persistence of established populations. In contrast, the presence of *A. marmorata* strongly
382 decreased the persistence of *P. acuta*, and decreased its colonization to a lesser extent. These
383 effects are represented in Fig. 2. Competition drives both species closer to the extinction
384 threshold (when extinction overwhelms colonization), but each species would persist in a
385 hypothetical metapopulation completely occupied by its competitor.

386

387 *Simulated species dynamics: role of competition and environmental heterogeneity*

388 When all parameters were drawn from the posterior joint distribution, the simulated
389 dynamics matched the 15 years of data, both for each species separately and for the sites where
390 they co-occur (Fig. 1A). They also predicted that the two species could co-exist on the long
391 term and co-occur at equilibrium in a non-negligible fraction of the sites, despite the strong
392 reciprocal effects of competition detected above (Fig. 1A). In both species, however, the
393 predicted equilibrium occupancy was decreased by competition (60% instead of 85% in *A.*
394 *marmorata*, and 77% instead of 94% in *P. acuta*), and co-occurrence decreased from 80% to
395 42% (Fig. 1B). The influence of competition on the temporal turnover in site occupancy can be
396 represented in transition graphs extracted from simulations (Appendix S1: Fig. S6). In
397 simulations without competition, most sites (79.9%) were doubly occupied, a high fraction of
398 which stayed in this state between two successive years (88%). The largest predicted fluxes
399 were between doubly-occupied sites and sites with *P. acuta* only, reflecting frequent
400 extinction/colonization cycles in *A. marmorata*. With competition, the predicted fraction of
401 doubly-occupied sites strongly decreased; the probability to stay in this category the next year
402 was still high, but lower than without competition (70%). The turn-over rates were more
403 balanced, as the fluxes between singly- and doubly-occupied sites were comparable for the two
404 species (6.5 vs. 4.5%; Appendix S1: Fig. S6).

405 Possible priority effects were investigated by evaluating the invasion probability in
406 simulations initialized with a single randomly-chosen site occupied by one species, while
407 leaving the other species being at its equilibrium occupancy. The invasion probability decreased
408 from 0.97 to 0.78 in *P. acuta* (in the absence and presence of *A. marmorata* respectively), and
409 from 0.87 to 0.59 in *A. marmorata* (reciprocally).

410 We investigated the potential for coexistence of the two species in a (theoretical)
411 homogeneous landscape, by setting all sites to environmental conditions identical to those
412 observed in actual sites. These simulations showed that both species were able to maintain

413 viable metapopulations in most conditions in the absence of competitor (Fig. 3 and Fig. 4).
414 These conditions define the fundamental niche of the two species, which include 95% of the
415 sites for *A. marmorata* and 99% for *P. acuta*. A single site (0.4%) did not belong to either
416 fundamental niche. Competition decreased the number of favorable sites (realized niche, Fig.
417 3): 68% for *A. marmorata* and 93% for *P. acuta*. 64% of the site types would allow stable
418 coexistence of the two species in a homogeneous landscape, defining their shared realized
419 niche.

420 The first two axes of the LDA explained 72.3% and 24.4% of the total variance among
421 the six categories of sites based on realized and fundamental niches of the two species (Fig.
422 4A). Axis 1 was mainly related to vegetation cover, to which *A. marmorata* appeared to be very
423 sensitive. Very low values on this axis were outside its fundamental niche. Low to intermediate
424 values represent conditions under which *A. marmorata* could not maintain a viable
425 metapopulation in the presence of *P. acuta* (outside the realized niche; Fig. 4B). On the other
426 hand, only a few sites with low values on axis 2 were outside the fundamental niche of *P. acuta*
427 (Fig. 4C), and these were small, poorly connected and unstable sites. The conditions in which
428 *P. acuta* might be excluded by *A. marmorata* mostly combined relatively low values on axis 2
429 and high values on axis 1, *i.e.* sites that were relatively small, poorly connected, unstable and
430 vegetated (Fig. 4C). However, this exclusion domain was neither as large, nor as clearly
431 delimited as for *A. marmorata* (compare Fig. 4B and 4C).

432 Simulations of heterogeneous landscapes, in which all sites retained their actual
433 environmental characteristics, predicted positive occupancy probabilities in all sites, the lowest
434 values being 0.20 in *P. acuta*, 0.13 in *A. marmorata*, and 0.08 for local co-occurrence. Thus,
435 all sites, even the less favorable ones, were transiently occupied from time to time. Some sites
436 were predicted to be occupied more often, and others less often, in the real heterogeneous
437 landscape, than they would be in environmentally-homogeneous landscapes entirely composed

438 of sites similar to them. In both species, about 45% of sites belong to the first category
439 (Appendix S1: Fig. S7), which includes all sites outside the species' respective realized niches
440 (where the predicted occupancy is positive in a heterogeneous landscape, and zero in a
441 homogeneous one). Importantly, landscape heterogeneity overall resulted in more gain in
442 average occupancy in unfavorable sites than losses in favorable ones in both species (Appendix
443 S1: Fig. S7). This asymmetry is even more pronounced on the site-specific probability of co-
444 occurrence of both species (Appendix S1: Fig. S7).

445 We then ran simulations to evaluate the effects of competition on persistence. First, we
446 set the competitive effect of one species on the other to zero, leaving the reciprocal effect intact.
447 These simulations mimicked a situation of completely asymmetrical competition. When
448 removing the effect of *P. acuta* on *A. marmorata* colonization, the expected occupancy of *P.*
449 *acuta* decreased from 85% to 68% in the mean environment and from 77% to 74% in the
450 heterogeneous landscape, whereas *A. marmorata* occupancies increased by almost 30%, from
451 47% to 85% in the mean environment and from 60% to 87% in the heterogeneous landscape.
452 When removing the effect of *A. marmorata* on *P. acuta*, *A. marmorata* occupancies slightly
453 decreased both in the mean environment (47% to 41%) and in the heterogeneous landscape
454 (60% to 55%) whereas *P. acuta* occupancies increased by about 15%, from 85% to 97% in the
455 mean environment and from 77% to 94% in the heterogeneous landscape. The competitive
456 effect is therefore beneficial to the species exerting competition, but simulations suggest each
457 species would persist despite the competition exerted by the other, even without exerting any
458 reciprocal competitive effect.

459 Second, we investigated threshold values of species-specific demographic rates (ϕ and
460 c) allowing persistence at the metapopulation scale (Appendix S1: Fig. S8), focusing on the
461 component for which the species are performing better (*i.e.* colonization for *A. marmorata* and
462 persistence for *P. acuta*). The colonization rate of *A. marmorata* in the mean environment is

463 1.24, its lower limit for regional persistence being 0.29 without competition and 0.86 with
464 competition. The local persistence probability of *P. acuta* in the mean environment is 0.99, its
465 lower limit for regional persistence being 0.40 without competition and 0.91 when competition
466 occurs. The same values in the heterogeneous landscape are 0.06 and 0.19 (colonization) in *A.*
467 *marmorata* and 0.02 and 0.43 (persistence) in *P. acuta*.

468

469 DISCUSSION

470 *A methodology to predict the dynamics of competing species in a fragmented landscape*

471 Biological invasions create novel pairwise competitive interactions worldwide, with
472 uncertain outcomes (David et al. 2017). Invasive competitors often affect the demography of
473 native species at a local scale (Byers 1999, 2000). However, regional persistence in fragmented
474 landscapes depends on higher-scale impacts of competition on colonization and extinction rates
475 (Levins 1969, Leibold et al. 2004). Previous studies have used occupancy models to document
476 these impacts (e.g., Dugger et al. 2011, Yackulic et al. 2014) but did not provide useful
477 projections, as they did not account for natural feedbacks of occupancy on colonization in non-
478 equilibrium conditions inherent to ongoing invasions. In contrast, our model quantifies relative
479 colonization and extinction rates (as in Levins' model), and their sensitivity to competition. In
480 addition, our model accounts for imperfect species detection (MacKenzie et al. 2003, Guillera-
481 Arroita 2017). It accurately reproduces the trajectory of our system over the last 15 years,
482 suggesting that robust projections can be built without assuming equilibrium.

483

484 *Asymmetrical impacts of competition on colonization and extinction rates*

485 In the absence of competition the two snail species display striking differences in
486 demographic parameters: *A. marmorata* is a more fugitive species than *P. acuta*, with higher
487 colonization and lower persistence. Competition can affect both rates resulting in preemption

488 when an established competitor impedes colonization by other species, and/or replacement
489 when it drives it to local extinction (see e.g., Slatkin 1974, Hanski 1983, Calcagno et al. 2006,
490 Little and Altermatt 2018). Both forms markedly affect our two-species system, in an
491 asymmetric way: *P. acuta* reduces colonization in *A. marmorata* (preemption), while *A.*
492 *marmorata* mostly reduces persistence in *P. acuta* (replacement). Although it has been
493 theorized for a long time that competition might act on both colonization and persistence in
494 metacommunities (e.g., Levins and Culver 1971, Slatkin 1974, Hanski and Ranta 1983), this
495 has been quantified in surprisingly few studies – possibly because long-term data are required
496 (see Hastings 1987). For example, Bengtsson (1989) identified effects on extinction, though
497 not on colonization, in *Daphnia* species. Dugger et al. (2011) demonstrated the invasive barred
498 owl decreased both colonization and persistence of the Spotted Owl in North America, but the
499 barred owl dynamics was not quantified. Naujokaitis-Lewis and Fortin (2016) highlighted
500 reciprocal competition on the two components between two warbler species. However, they
501 estimated environmental effects and competition sequentially rather than simultaneously,
502 potentially biasing competition estimates. Our study therefore adds to these few examples, and
503 goes a step forward by simultaneously fitting two-species dynamics dependent on environment
504 and species interactions, and by considering per-capita colonization rates instead of absolute
505 ones (Moilanen 2000).

506 We observed differences in colonization, extinction, and competition that may be related
507 to species traits. Colonization has classically been related to “fast” life-history and self-
508 fertilization ability, often found in early-succession stages (Baker 1955, Baker 1974, Grime
509 1977). In the laboratory, Guadeloupe populations of *A. marmorata* reproduce earlier, have a
510 lower fecundity and adult body volume, and a higher juvenile survival, but a shorter adult
511 lifespan than populations of *P. acuta* (Chapuis et al. 2017). The latter is also a preferential
512 outcrosser that can self-fertilize only after a long waiting time (Tsitrone et al. 2003), and at the

513 cost of strong inbreeding depression (Jarne et al. 2000, Escobar et al. 2011). In contrast, *A.*
514 *marmorata* is a preferential selfer subject to none of these two constraints (Escobar et al. 2011).
515 Thus, both life-history traits and mating system may favor the ability of *A. marmorata* to rapidly
516 grow in numbers from an initial low-density population in a context of abundant resources (high
517 colonization rate), while *P. acuta* might be more efficient at maintaining an established
518 population dominated by long-lived adults tolerating low resource levels (high persistence rate).
519 In consistency with this hypothesis, *A. marmorata* depends on the abundant food and shelter
520 provided by aquatic vegetation for persistence. Positive effects of site size and water
521 connectivity on colonization in *P. acuta* suggest a limitation by propagule pressure: founding a
522 new population may require more attempts than in *A. marmorata*. Competitive preemption by
523 *P. acuta* may occur because established populations keep resources at a low level, especially
524 when vegetation is rare, reducing the colonization probability of *A. marmorata*. The
525 competitive replacement ability of *A. marmorata* is more difficult to explain, perhaps resulting
526 from a faster exploitation of ephemeral resources (e.g., vegetation patches) during contraction-
527 expansion cycles of waterbodies in the dry season, reducing the population growth rate of *P.*
528 *acuta*.

529

530 *Coexistence, competition and species sorting at the landscape scale*

531 Our simulations do not predict competitive exclusion. However, (i) the invasion of each
532 species is predicted to be slightly slower and more uncertain when the other species is
533 established; (ii) the model predicts competition should reduce the equilibrium occupancy of
534 each species by 15 to 20%, and the number of co-occupied sites by nearly 50%. We used
535 additional simulations to disentangle the contribution of various processes modulating these
536 effects, thus favoring or disfavoring local and regional coexistence of the two species.

537 The first process indicated by our simulations is a species-specific response to
538 environmental heterogeneity. Specialization in different patch types may facilitate coexistence
539 through “species sorting”, *i.e.* niche partitioning at the landscape scale (Amarasekare et al.
540 2004, Leibold et al. 2004). However, mapping favorable sites for each species is not a simple
541 task in a metapopulation. Classical niche models such as species distribution models, based on
542 the presence of a species in a given environment (e.g., see Guisan and Thuiller 2005 for review),
543 cannot be applied at this scale because migration from favorable habitats maintains species in
544 patch types that would not, in the absence of other types, sustain a stable metapopulation
545 (source-sink dynamics; Pulliam 1988, Loreau and Mouquet 1999). This led us to propose an
546 operational definition of the niche in a metapopulation context: the region in the environmental
547 space where a species could potentially maintain a viable metapopulation in the absence of
548 heterogeneity among patches. Although homogeneous landscapes do not exist, simulating them
549 allows one to identify species-specific sink and source habitats, to express competition effects
550 in the form of realized *vs.* fundamental niches, and to evaluate the reduction in local co-
551 occurrence due to species sorting. We observed, for example, contrasted responses to vegetation
552 cover in the two species. Nevertheless, the two fundamental niches still largely overlapped.
553 Adding inter-specific competition to the model reduced this overlap, but not to a dramatic
554 extent. At least half of the sites harbor environments that, if generalized to the whole landscape,
555 would result in stable coexistence of the two species (shared realized niche).

556

557 *Competition and coexistence theory*

558 As our results suggest that environmental species-sorting is not necessary for coexistence,
559 are there environment-independent mechanisms at play? Metacommunity theory has
560 highlighted two such mechanisms (Leibold et al. 2004): (i) ecological neutrality (Bell 2001,
561 Hubbell 2001), under which competition is approximately symmetrical. However, neutrality is

562 here contradicted by the very different estimates of metapopulation vital rates and asymmetrical
563 impacts of competition between the two species; (ii) trade-offs among species traits, whereby
564 competitive inferiority of one species is compensated by an advantage in some other trait,
565 usually colonization (Kneitel and Chase 2004). Classical models of the colonization-
566 competition tradeoff (Levins and Culver 1971, Tilman 1994) assume hierarchical competitive
567 effects resulting in instantaneous eviction of the inferior species, and precluding local co-
568 occurrence. Our system differs from this idealized situation in two ways: competition is not
569 efficient enough to preclude co-occurrence within patches (70% of doubly-occupied patches
570 remain in this state from one year to the next), and species may compensate for differences in
571 competitive replacement ability not only by colonization, but also by persistence and
572 competitive preemption (here, *A. marmorata* has stronger replacement effects, and *P. acuta*
573 stronger preemption effects). The available models that best capture these characteristics are
574 metapopulation models of two competing species (Slatkin 1974, Taneyhill 2000) in which
575 conditions for coexistence at the landscape scale are not as stringent as in classical competition-
576 colonization metacommunity models. For example, competition may elevate the threshold
577 colonization rate below which a species cannot persist, but this threshold does not have to
578 exceed the colonization rate of the competitor (e.g., Taneyhill 2000). Accordingly, our
579 simulations suggest that although *A. marmorata* has a greater basal colonization rate than *P.*
580 *acuta*, and *P. acuta* a higher basal local persistence rate than *A. marmorata*, these conditions
581 were not required for them to co-exist. Similarly, compensation between two components of
582 competition occurs (*A. marmorata* has stronger replacement effects, and *P. acuta* stronger
583 preemption effects) and affects equilibrium occurrences, but does not seem necessary for
584 coexistence.

585 Overall, a diversity of mechanisms (species sorting, differences in colonization and
586 persistence rates, reciprocal competitive effects) contribute to increase the levels of occurrence

587 and co-occurrence of the two species in our system, none of which appears individually
588 essential in our simulations. As mentioned above, one reason might be that competition itself
589 is not strong enough to preclude transient local coexistence. Local co-occurrence between
590 competitors is common in many empirical studies, for example in small mammals (Guélat et
591 al. 2008), birds (Dugger et al. 2011) or frogs (Lehtinen and Carfagno 2011). In this respect,
592 classical competition-colonization trade-offs models, although useful to conceptualize
593 coexistence, are caricatural representations of true metacommunities as they implicitly assume
594 extremely high and asymmetrical impacts of competition, and conceal the stochastic and
595 multifarious nature of the processes and trade-offs at play. These models may be more
596 applicable to sets of individual sites (*i.e.* can be occupied by at most one individual of one
597 species) than to true metacommunities, where patches are occupied by entire populations,
598 possibly of two or more species.

599

600 *Limitations and future directions*

601 There are some limitations in our study. (i) As for any study incorporating niche
602 differentiation, unmeasured variables might affect colonization and extinction, potentially
603 biasing estimates of competition (see e.g. Chase and Leibold 2003). Unfortunately, including
604 too many covariates may result in overfitting instead of model improvement; therefore, we tried
605 to rely on a limited set of variables that appeared most relevant for the species considered (Lamy
606 et al. 2013a). (ii) We only modelled coexistence at the landscape scale. The conclusion that
607 transient co-occurrence is possible in many site types and facilitates coexistence at landscape
608 scale does not specify the underlying local mechanisms. Microhabitat differentiation within
609 sites could exist in our system, and may facilitate local coexistence. (iii) Our model is spatially
610 implicit. A spatially-explicit model may be required in systems with strong dispersal limitation.

611 Our method could be generalized to accommodate more species and/or environment-
612 dependent competition. However this would rapidly increase the number of parameters,
613 especially competition parameters if all pairwise coefficients are estimated. A solution might
614 be to consider independently small groups of species for which we have *a priori* expectations
615 of stronger interactions, or decomposing the interaction matrix in order to reduce its
616 dimensionality (see e.g., Warton et al. 2015, Godoy et al. 2017). One could also make use of
617 regularization methods (e.g., using “spike and slab” priors or L1 regularization – Laplacian
618 prior) in order to produce more sparse coefficient matrices. None of these solutions may be
619 perfect, but exploring them is a worthy objective for future research in order to deepen our
620 understanding of metacommunity dynamics.

621

622 *Conclusion*

623 Our study is the first attempt to estimate metapopulation vital rates of two related species
624 in a fragmented landscape, including reciprocal competitive effects on both colonization and
625 persistence, as a first step towards understanding more complex metacommunities. Simulations
626 based on our estimates accurately reproduce the observed trajectory of the two species during
627 15 successive years, and provide the opportunity to project the long-term trajectory of the
628 system. We also explore hypothetical trajectories that serve as thought experiments to
629 understand coexistence conditions. The metacommunity framework organizes coexistence
630 mechanisms in fragmented landscapes along four idealized paradigms: neutral dynamics,
631 species-sorting, mass-effects, and patch-dynamics (Leibold et al. 2004, Holyoak et al. 2005).
632 Empirical studies have mainly tried to classify observed communities along these axes
633 (reviewed by Logue et al. 2011), essentially using pattern-based methods (e.g., variation
634 partitioning, Cottenie 2005). However, these processes are not exclusive (e.g., Winegardner et
635 al. 2012, Brown et al. 2017). Our case study illustrates how they can interact. We observe

636 species-sorting, although recurrent migration among sites allows species to occur or co-occur
637 in unfavorable habitats (*i.e.* mass-effects). However, the coexistence of snail species would be
638 possible even without environmental heterogeneity. Thus, providing evidence for niche
639 partitioning is not sufficient to argue that it plays a large role in coexistence. We also show that
640 theoretical models that inspire the patch-dynamic perspective often rely on assumptions
641 unlikely to be met in metacommunities, and that models integrating doubly-occupied sites and
642 transient co-occurrence (Slatkin 1974, Taneyhill 2000) may provide parsimonious explanations
643 to regional coexistence, even in the case of similar species.

644

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837

838 TABLE 1. Description of model parameters. All parameters are species-specific (species index
839 was omitted for clarity). Subscript i and t refer respectively to site and year. Parameters without
840 subscripts are identical among sites and years.

841

Parameters	Values	Description
$x_{i,t}$	$\{0,1\}$	Presence of focal species (latent variable)
$y_{i,t}$	$\{0,1\}$	Observation of focal species (observed variable)
$x'_{i,t}$	$\{0,1\}$	Presence of competitor (latent variable)
$\gamma_{i,t}$	$[0;1]$	Colonization probability of wet sites
$c_{W_{i,t}}$	$[0; +\infty[$	Per capita colonization rate of wet sites
c_D	0	Per capita colonization rate of dry sites
$\varphi_{W_{i,t}}$	$[0;1]$	Persistence probability in wet sites
$\varphi_{D_{i,t}}$	$[0;1]$	Persistence probability in dry sites
μ_{c_W}	$] -\infty; +\infty [$	Model intercept for colonization of wet sites
μ_{φ_W}	$] -\infty; +\infty [$	Model intercept for persistence in wet sites
μ_{φ_D}	$] -\infty; +\infty [$	Model intercept for persistence in dry sites
β_c	$] -\infty; +\infty [$	Vector of regression coefficients for colonization
β_φ	$] -\infty; +\infty [$	Vector of regression coefficients for persistence
α_c	$] -\infty; +\infty [$	Competitor effect on focal species colonization
α_φ	$] -\infty; +\infty [$	Competitor effect on focal species persistence
d	$[0;1]$	Detection probability ($P(y = 1 x = 1) = d$)
ψ	$[0;1]$	Initial occupancy (at $t = 0$)

842

843 TABLE 2. Parameter estimates from the Bayesian model (median and 95% credibility intervals)
844 in the two species studied. The estimated values of φ (persistence) and c (colonization) in wet
845 (W) and dry (D) sites are the intercept from Eqs. 2, and have been estimated on logit and log
846 scale respectively. d is the detection probability in wet sites. β_φ and β_c are the regression
847 coefficient for the effect of environmental parameters, and α_c and α_φ those of competitive
848 effects of the other species on colonization and persistence respectively. Bold characters (for
849 ‘effects’ and ‘competition coefficients’) highlight cases in which the credibility interval does
850 not include 0.
851

Parameters	<i>Aplexa marmorata</i>	<i>Physa acuta</i>
logit(φ_W)	1.10 (0.06, 1.93)	4.43 (2.84, 7.06)
φ_W	0.75 (0.52, 0.87)	0.99 (0.94, 1)
logit(φ_D)	1.95 (0.12, 6.51)	1.45 (-0.91, 6.30)
φ_D	0.87 (0.53, 1)	0.81 (0.28, 1)
log(c_W)	0.22 (-0.06, 0.53)	-0.35 (-0.90, 0.12)
c_W	1.24 (0.94, 1.70)	0.70 (0.41, 1.13)
d	0.84 (0.82, 0.86)	0.75 (0.72, 0.78)
Effect on persistence (β_φ)		
Size	0.12 (-0.31, 0.54)	0.24 (-0.31, 0.80)
Vegetation	1.99 (1.34, 2.69)	0.45 (-0.03, 0.94)
Stability	-0.25 (-0.66, 0.12)	0.39 (-0.15, 0.95)
Back-mangrove	0.14 (-0.21, 0.56)	2.48 (0.86, 6.53)
River	-0.04 (-0.43, 0.36)	0.33 (-0.13, 0.84)
LRS	-0.02 (-0.34, 0.30)	0.56 (0.15, 1.03)

Effect on colonization (β_c)

Size	-0.02 (-0.20, 0.16)	0.37 (0.17, 0.57)
Vegetation	0.08 (-0.07, 0.25)	-0.49 (-0.66, -0.34)
Stability	0.10 (-0.06, 0.27)	-0.03 (-0.19, 0.14)
Connectivity	0.05 (-0.14, 0.23)	0.52 (0.31, 0.72)
Back-mangrove	-0.34 (-0.57, -0.14)	-1.13 (-1.83, -0.76)
River	-0.04 (-0.22, 0.15)	-0.19 (-0.39, 0.02)
RS	0 (-0.13, 0.13)	-0.31 (-0.52, -0.12)
D	-0.02 (-0.14, 0.08)	0.02 (-0.12, 0.15)
α_φ	-0.03 (-0.98, 1.13)	-2.60 (-5.19, -1.14)
α_c	-1.15 (-1.56, -0.78)	-0.41 (-0.96, 0.16)

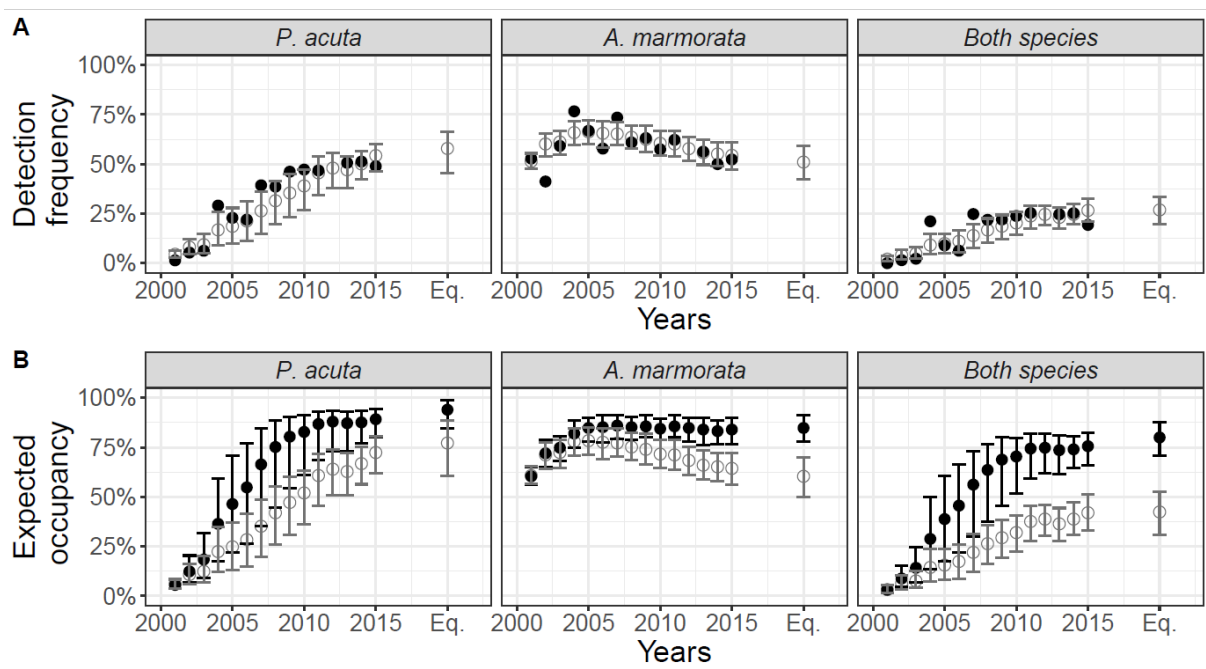
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854 FIGURE LEGENDS

855

856 FIGURE 1. Occupancy in a two-species metacommunity dynamics over time. (A) Empirical
 857 (black dots) and simulated (grey empty dots; predicted occupancy multiplied by detection
 858 probability) detection frequency (proportion of sites in which the species is detected). (B)
 859 Simulated occupancies (without correction for detectability) when competition is (grey empty
 860 dots) or is not (black dots) taken into account. The grey dots in A and B represent the same
 861 dynamics, and differ because of correction (A) or no correction (B) for detectability. The left
 862 and central panels represent the dynamics of *P. acuta* and *A. marmorata*, and the right panel,
 863 sites in which the two species co-occur. Dots on the extreme right of each panel are equilibrium
 864 values (500th generation). Estimates are reported with 95% confidence intervals.



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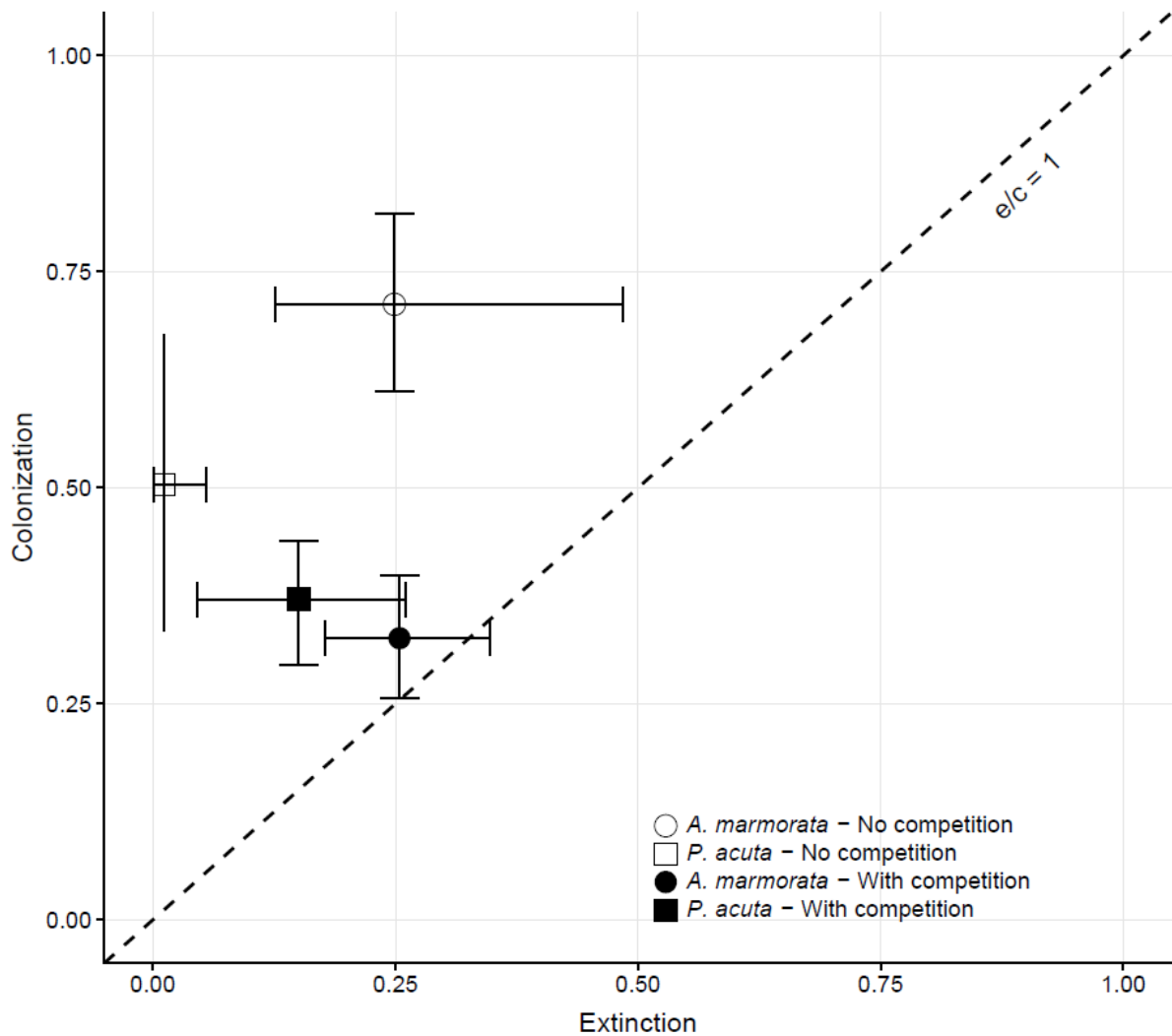
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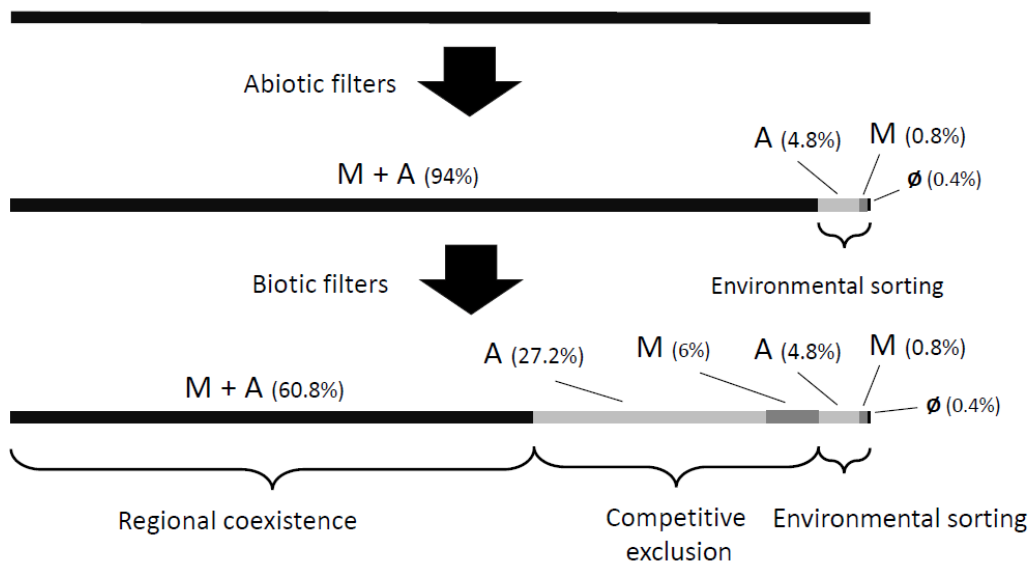
870 FIGURE 2. Colonization and extinction probabilities (per year) without / with competition, in a
 871 site with average environmental characteristics. The median estimates without competition are
 872 derived from the intercept of the regression model (Eq. 2), while those with competition are
 873 derived from intercepts plus competition effect ($\mu+\alpha$ in Eq. 2, *i.e.* assuming that the competitor
 874 occupies all the metapopulation). To express extinction and colonization on the same
 875 probability scale, the estimates of colonization rate c from the models were converted into
 876 colonization probabilities (per year), computed as $1 - e^{-c}$. Extinction is simply defined as
 877 $(1 - \varphi)$. Error bars represent the 95% values from posterior distributions of parameters. The
 878 dotted line represents the extinction border under which the metapopulation is no longer viable.



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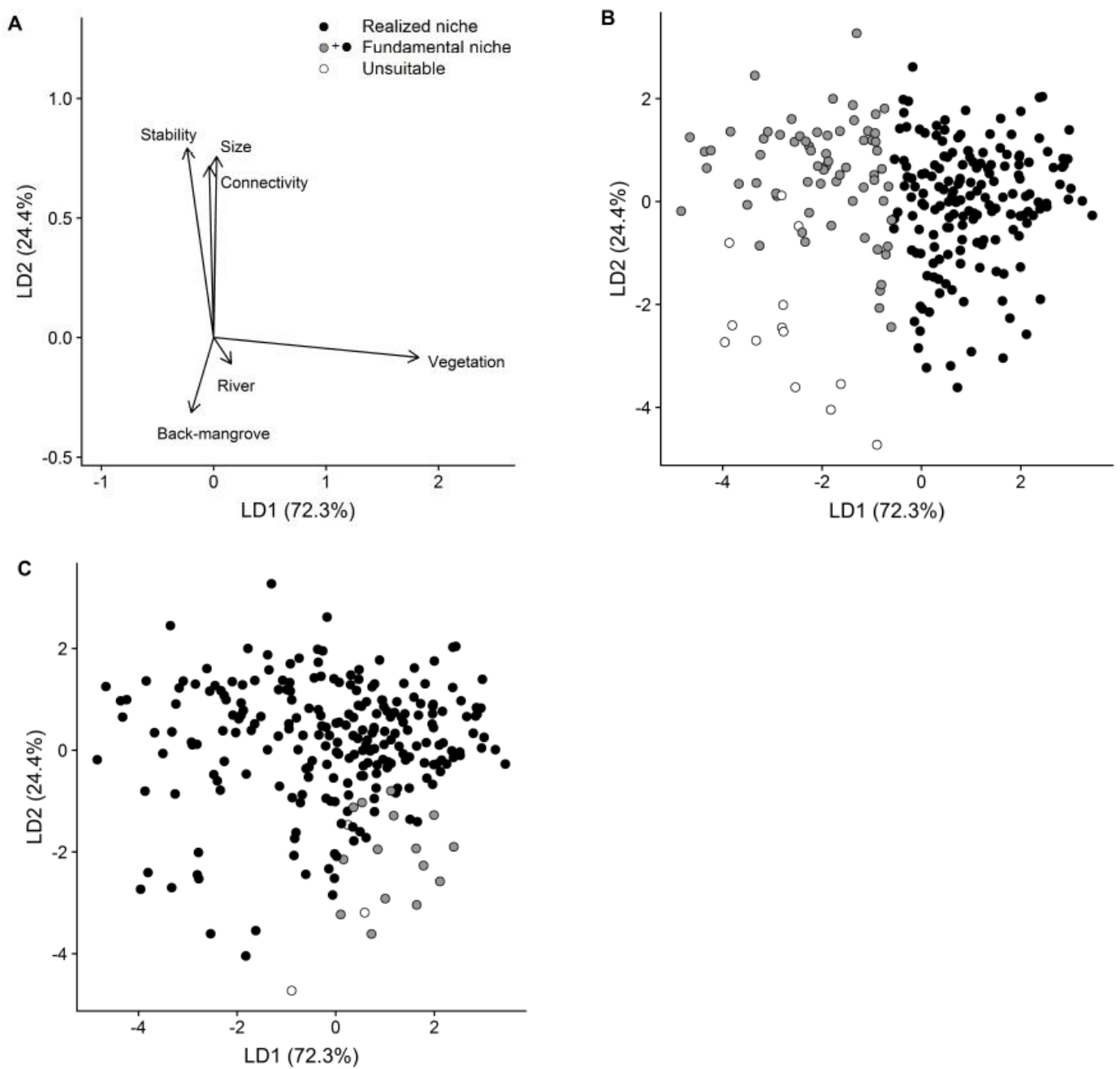
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881 FIGURE 3. Proportions of sites belonging to the fundamental and realized niches based on
 882 simulated metacommunities under homogeneous environmental conditions. The first line
 883 represents all environmental conditions typical of each of the (250) sites. The second one shows
 884 the fraction of conditions that can harbor viable metapopulations for no, one, or both species in
 885 the absence of competition (fundamental niches). The third line subdivides the last category,
 886 based on the persistence of one or both species in the presence of competition (realized niche).
 887 The domains in which species cannot coexist because of environmental sorting (one species
 888 does not tolerate the abiotic conditions while the other can; 2nd line) or competitive exclusion
 889 (both tolerate the abiotic conditions, but one excludes the other; 3rd line) are indicated. Dark
 890 grey: *A. marmorata* only (M); light grey: *P. acuta* only (A); black: both species (M+A); black
 891 portion on the right (\emptyset): no species.



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897 FIGURE 4. Axes 1 and 2 of a linear discriminant analysis (explaining 96.7% of the among-group
 898 variance) on environmental variables. Distribution of the site categories is represented in the
 899 environmental space. The contributions of variables to axis are reported in (A). The conditions
 900 where each species cannot persist at all (empty dots, unsuitable sites), persists only without
 901 competitor (grey symbols; belonging to the fundamental but not to the realized niche) and
 902 persists both with and without competitor (black symbols; realized niche) are reported for A.
 903 *marmorata* in (B) and *P. acuta* in (C).



904 Dubart et al. Modelling competition, niche and coexistence between an invasive and a native
905 species in a two-species metapopulation

906 **Appendix S1:** Supplementary figures and tables.

907

908 **Table. S1.** Environmental variables used to describe each site.

909 **Figure. S1.** Potential scale reduction factor (\hat{R}) for model convergence.

910 **Figure. S2.** Posterior distributions.

911 **Figure. S3.** Pairwise correlations amongst parameters

912 **Figure. S4.** Full long-term metapopulations dynamic.

913 **Figure. S5.** Effects of covariates on the colonization rate and persistence probability of the two
914 species studied.

915 **Figure. S6.** Transition graphs among patch states in the simulated metacommunities.

916 **Figure. S7.** Comparison of site-specific probability of occurrence in an environmentally
917 homogeneous landscape *versus* in the real heterogeneous landscape.

918 **Figure. S8.** Comparison of persistence thresholds in the mean environment (homogeneous
919 landscape) *vs.* in the whole environment (heterogeneous landscape), depending on
920 competition

921

922 TABLE S1. Environmental variables used to describe each site. Connectivity, size, and
 923 vegetation cover are site-specific variables (obtained by averaging an environmental variable
 924 over years); propagule pressure varies among sites and years. Stability is a site-specific variable,
 925 obtained as the value on the first axis of a principal component analysis including the
 926 hydrological regime (five levels from very regularly dry to fully permanent, averaged over
 927 years), the average frequency of dry state over years, and the variance of both site size and
 928 vegetation cover over years (more details in Lamy et al. 2012). The transformation used for
 929 statistical analyses is given in the last column. All variables are quantitative except when
 930 “factor” is indicated.

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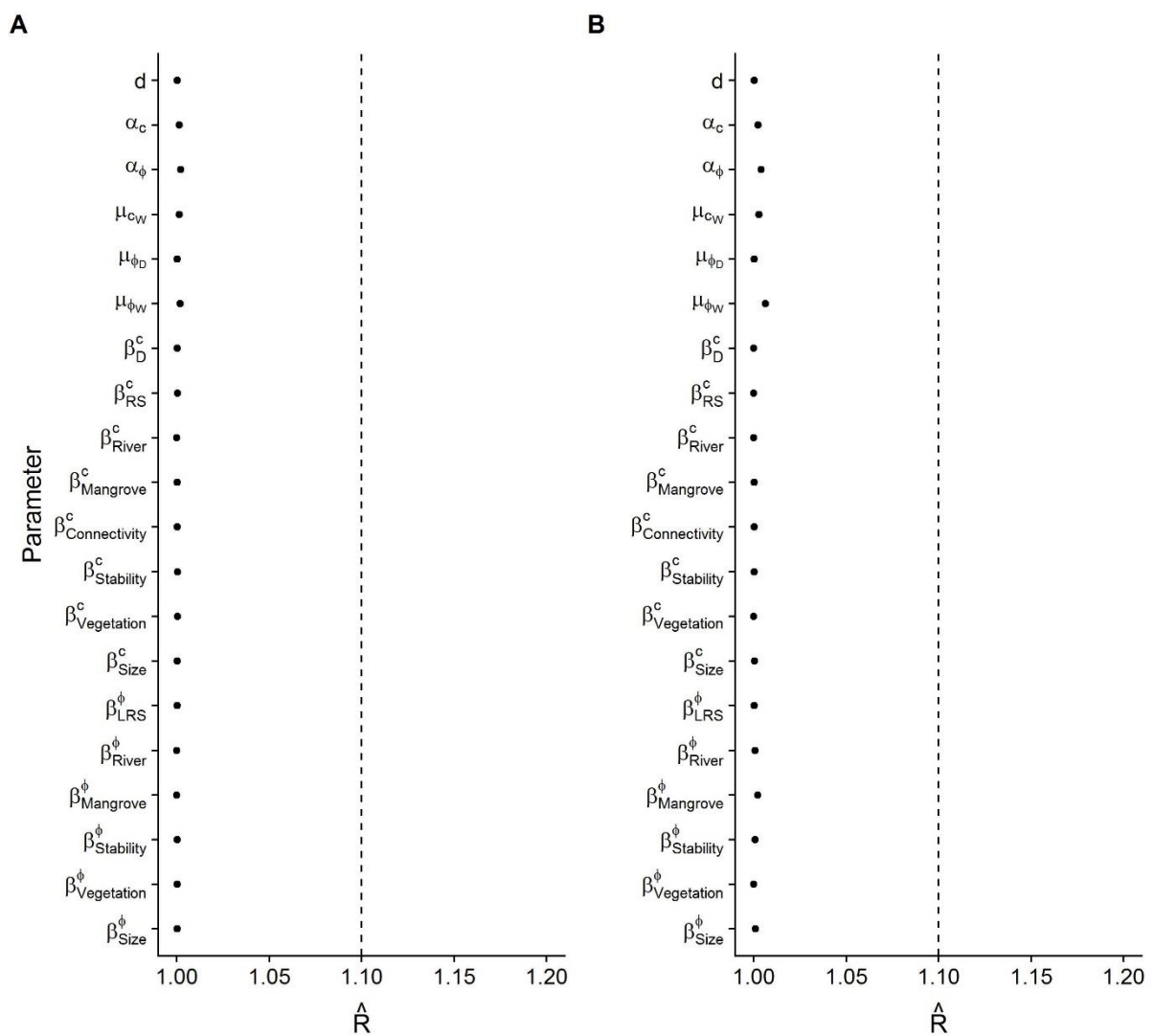
Variable	Description	Transformation
Type (factor)	Pond, back-mangrove, river	-
State (factor)	Dry vs. wet	-
Size	Pond diameter / river width / back-mangrove extent in meters	$\log_{10}(1+X)$, then averaged over years
Vegetation cover	Fraction of site covered by aquatic vegetation (in %)	$\log_{10}(1+X)$, then averaged over years
Connectivity	Connectivity to neighboring sites (four levels 1 to 4, from never to always)	averaged over years
Stability	Composite index (see legend)	-
Propagule pressure	N occupied sites within four km	-

932

933

934 FIGURE S1. Potential scale reduction factor (\hat{R}) for model convergence (Gelman & Rubin,
 935 1992). This statistic allows to assess model convergence by comparing the estimated among-
 936 chains and within-chain variances for each parameter and tends toward one when the model has
 937 converged. If \hat{R} is inferior to 1.2 for all parameters, one can consider that convergence has been
 938 reached (Brooks & Gelman, 1998). We chose a threshold of 1.1 (indicated by dashed lines). For
 939 *A. marmorata* in panel A and *P. acuta* in B.

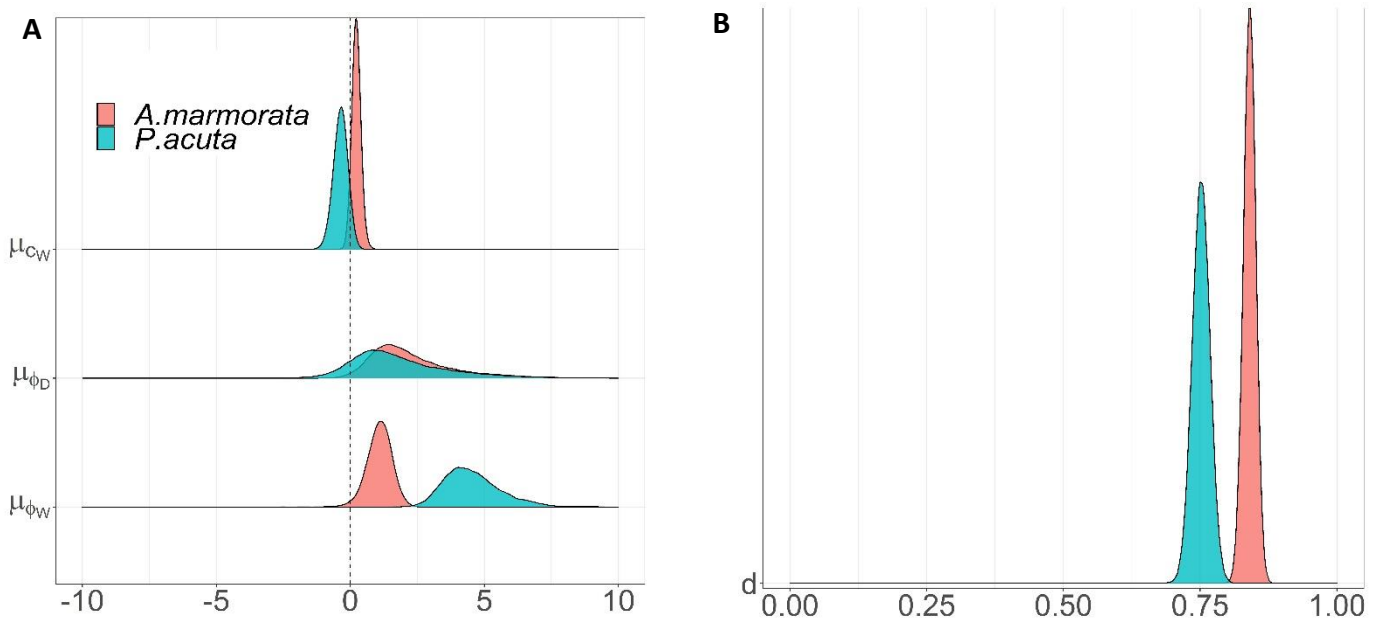
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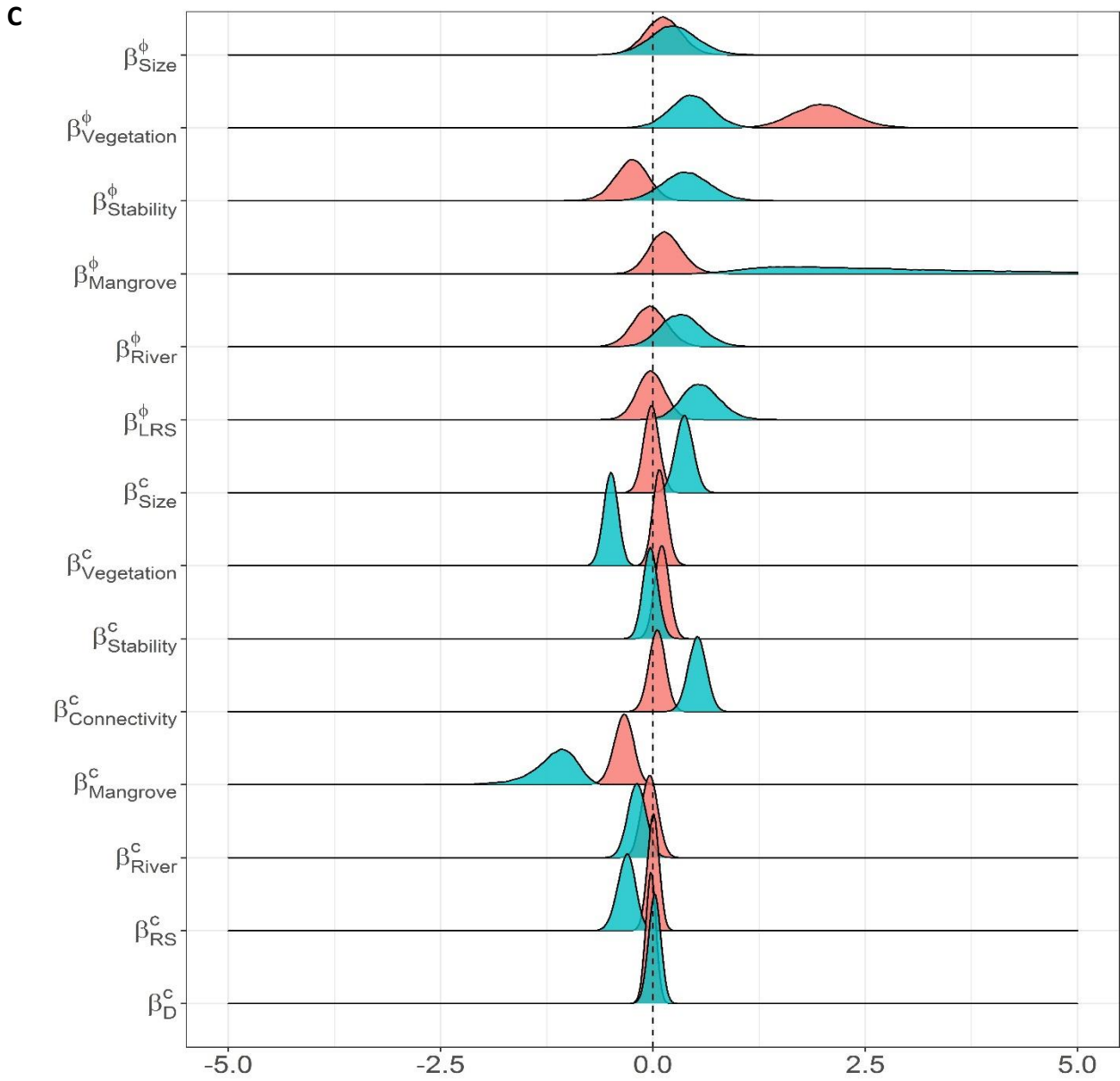
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943 FIGURE S2. Posterior distributions of the parameters estimated from the statistical (Bayesian)
 944 model in the native (*Aplexa marmorata*) and invasive (*Physa acuta*) species (see Table 2 for
 945 parameter estimates and their credibility intervals). We do not represent prior distributions as
 946 they appear as horizontal lines almost superimposed on the x-axis. The demographic rates
 947 (persistence φ and colonization c) are reported in panel A for wet (W) and dry (D) sites. The
 948 detection probability in wet sites (d) is reported in panel B. The regression coefficient for the
 949 effect of environmental parameters on colonization (β_c) and persistence (β_φ) are given in panel
 950 C. Panel D reports the distribution of competition coefficients (α). Interactions are represented
 951 with the α Greek letter, where the superscript designates the concerned parameter (colonization
 952 or extinction) and the subscript the interaction direction (e.g. α^φ_{12} : effect of species n°2 –
 953 *P.acuta*, on species n°1 – *A.marmorata* for the persistence).



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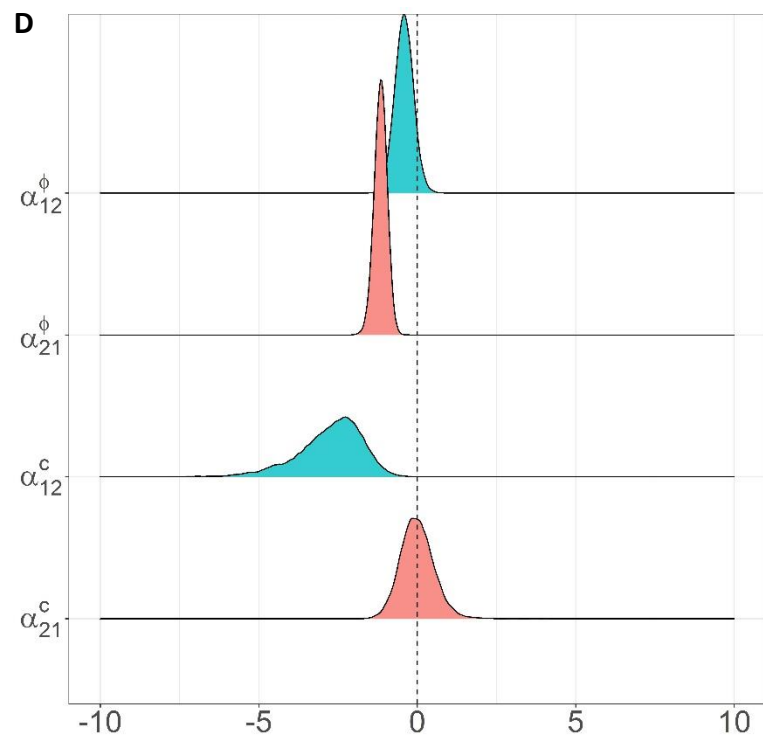
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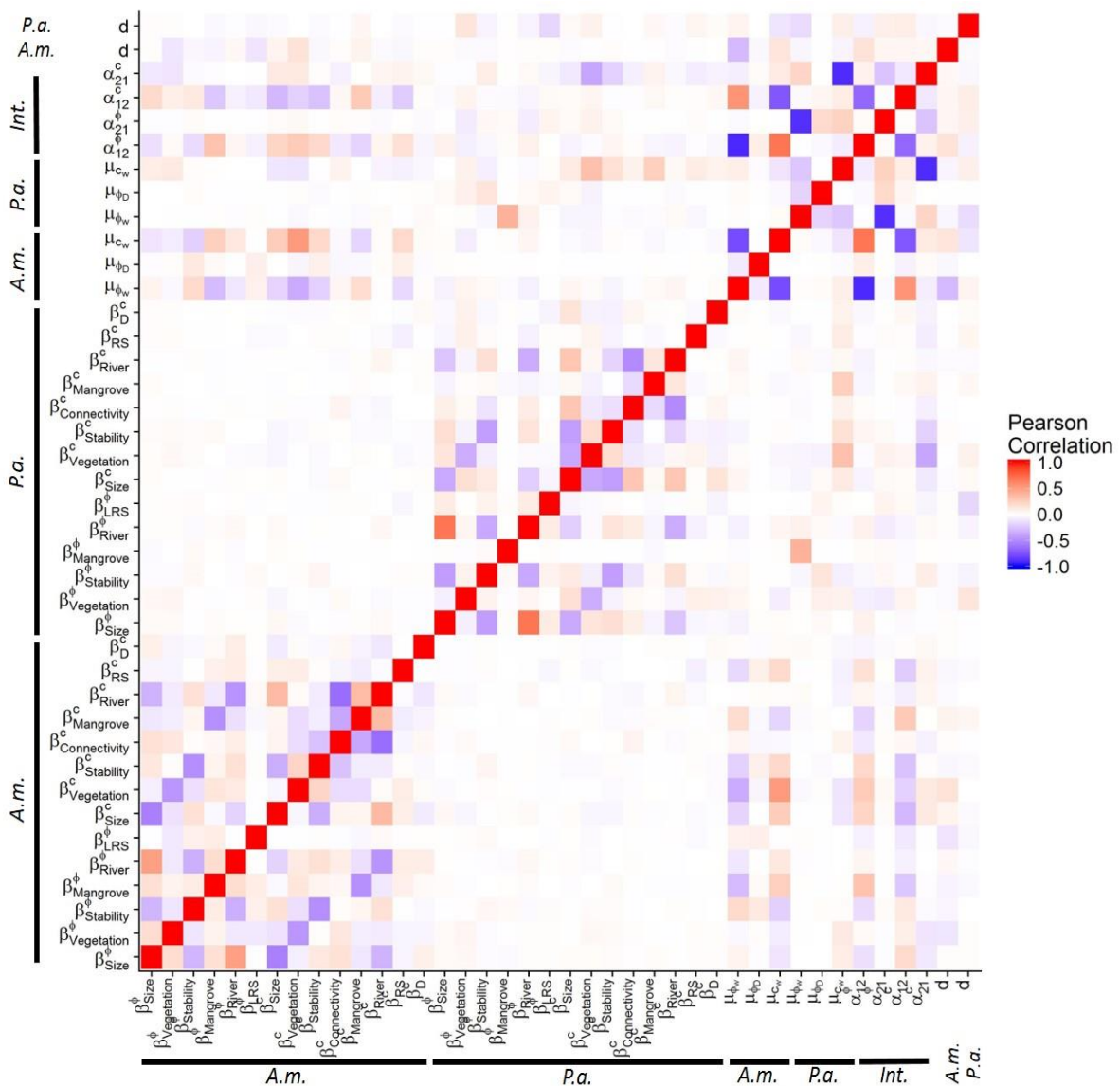
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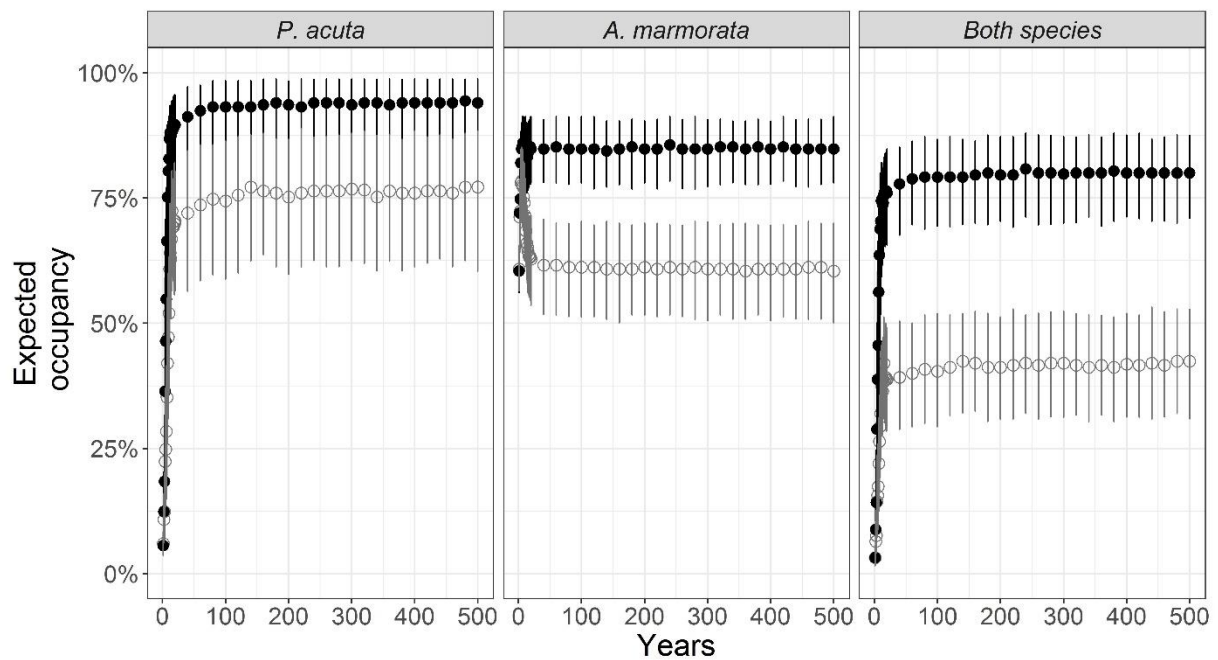
963 FIGURE S3. Pairwise (Pearson) correlation coefficients among parameters in the analysis of
 964 Guadeloupe data based on the Bayesian model in the native (*A.m.* holding for *Aplexa*
 965 *marmorata*) and invasive (*P.a.* holding for *Physa acuta*) species.

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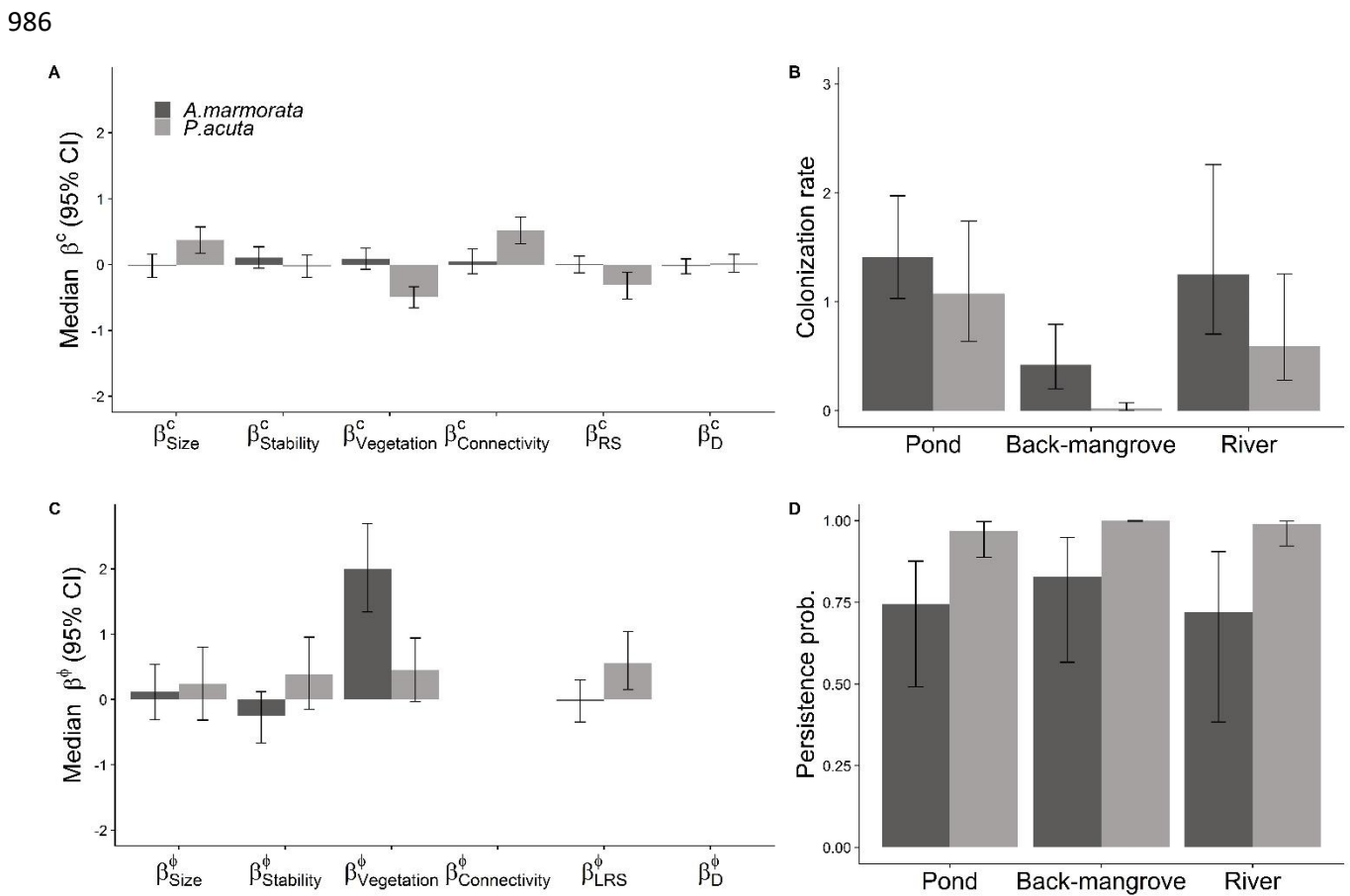
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968 FIGURE S4. Long-term (500 years) occupancy in a two-species metacommunity (see also Fig.
969 1). Full / empty circles represent the dynamics without / with species interactions. The left and
970 central panels represent the dynamics of *P. acuta* and *A. marmorata*, and the right panel, sites
971 in which the two species co-occur (uncorrected for detectability in the three cases). Estimates
972 are reported with 95% confidence intervals (over 1000 replicates). Note that this variance
973 includes both uncertainty on parameter estimates and the stochasticity inherent to any
974 metapopulation model with a finite number of patches.
975



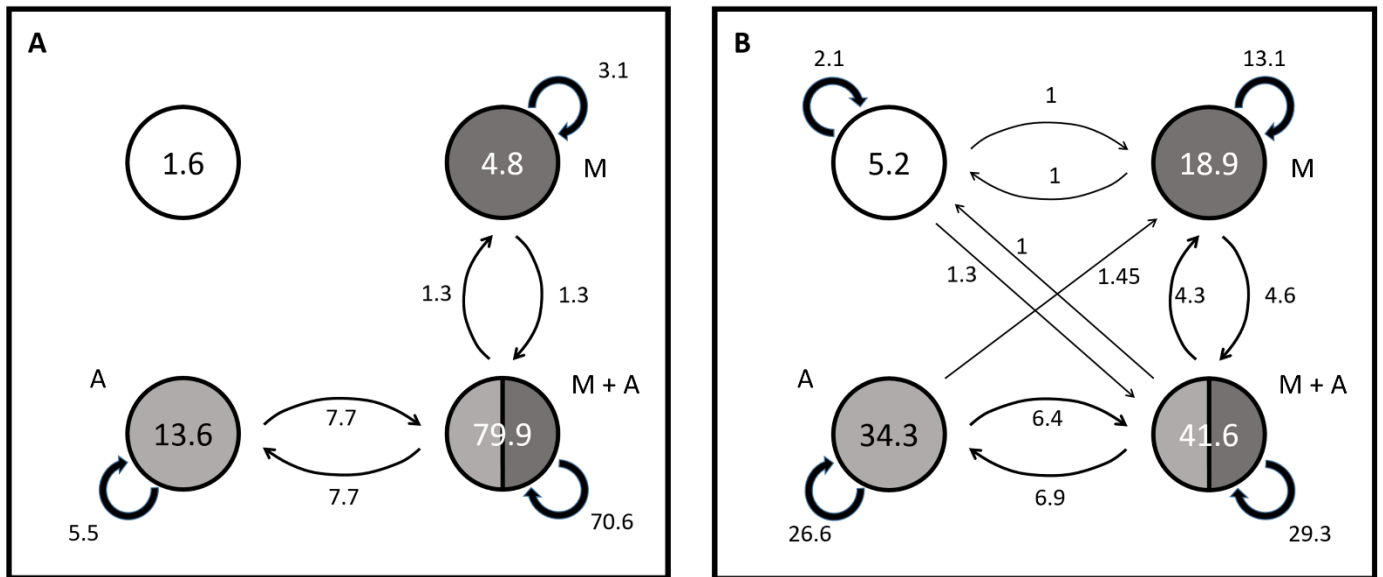
976 FIGURE S5. Effects of covariates (median and 95% credibility interval) on the colonization rate
 977 and persistence probability of the two species studied. In panels A and C, we present estimates
 978 of regression coefficients (model outputs), *i.e.* the change in log(colonization rate) or
 979 logit(persistence) when the covariate increases by one standard deviation. In order to facilitate
 980 interpretation, the effect of covariates related to habitat type (panels B and D) is presented as
 981 colonization and persistence rates in their natural scales for each of the three habitats, all other
 982 environmental covariates being set to their population average, and the competitor occurrence
 983 set to zero. Note that the effect of connectivity, propagule pressure (*D*) and RS were not
 984 estimated for persistence and that of LRS was not estimated for colonization (see Materials &
 985 Methods). Dark grey: *A. marmorata*; light grey: *P. acuta*.



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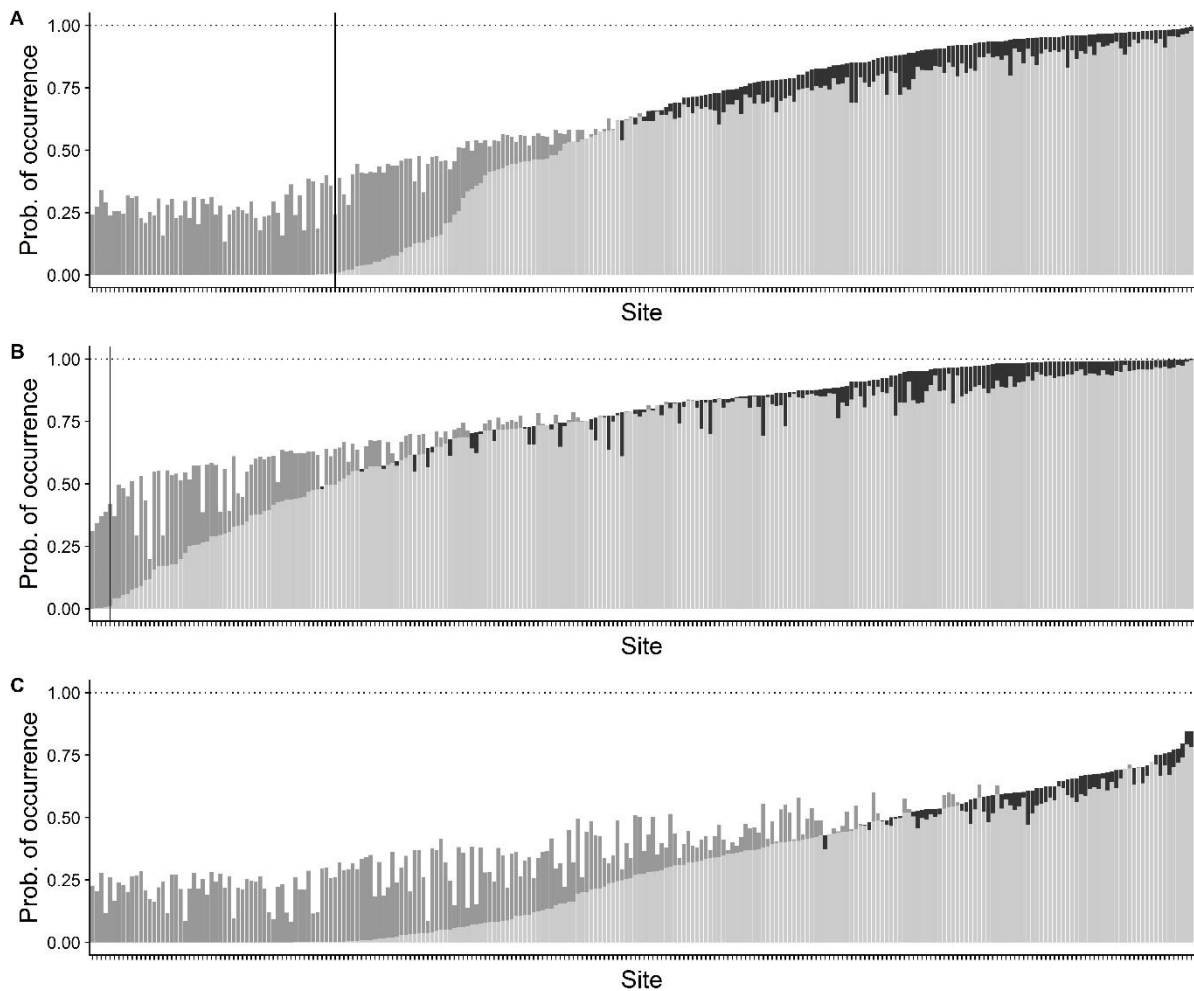
989 FIGURE S6. Transition graphs among patch states in the simulated metacommunities. The
 990 circles represent the fraction (in %) of unoccupied and occupied sites and arrows the transitions
 991 between states across successive generations at equilibrium when all covariates are taken into
 992 account. (A) No competition. (B) With competition. White circles: no species; light grey
 993 circles: *P. acuta* only (A); dark grey circles: *A. marmorata* only (M); mixed grey circles: both
 994 species (M+A). Arrows were omitted for transition probabilities < 1%. Note that these values
 995 include the possibility of extinction followed by recolonization within a cycle.
 996



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999 FIGURE S7. Comparison of site-specific probability of occurrence in an environmentally
1000 homogeneous landscape *versus* in the real heterogeneous landscape. Panel A: *A. marmorata*;
1001 B: *P. acuta* and C: co-occurrence. Light grey bars represent site-specific probabilities when
1002 considering a homogeneous landscape (250 sites, ranked by increasing probabilities). Dark grey
1003 (resp. black) bars represent how this site-specific probability increases (resp. decreases) when
1004 the considered site is included in the real heterogeneous landscape. Vertical lines in panel A
1005 and B give the realized niche limit.
1006



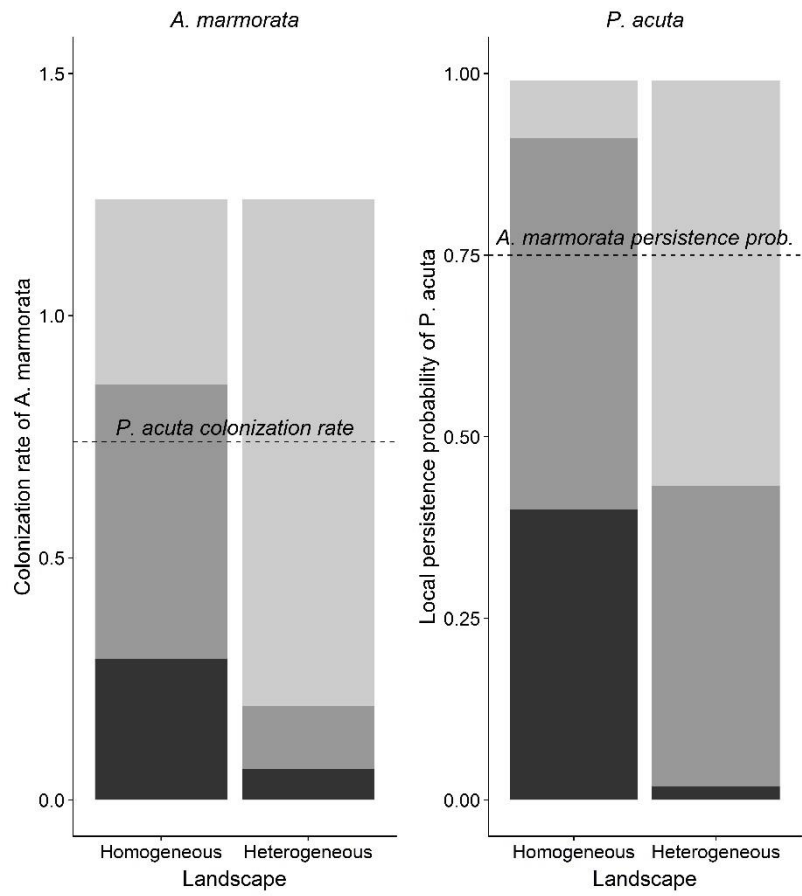
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1009 FIGURE S8. Comparison of persistence thresholds in the mean environment (homogeneous
1010 landscape) vs. in the whole environment (heterogeneous landscape), with or without
1011 competitive effects, based on simulations of a range of colonization rates (*A. marmorata*) and
1012 local persistence rate (*P. acuta*). In the case of heterogeneous landscape, we modified only the
1013 intercepts in the model with all environmental covariates. For comparison, these intercepts were
1014 converted back from log- or logit-scale to natural scale. Light grey zone: range of values in
1015 which the metapopulation persists in the presence of the competitor species (maximum value
1016 set at the actual parameter of the focal species); dark grey zone: range in which the
1017 metapopulation persists only without competitor; black zone: range in which the
1018 metapopulation gets extinct with or without competitor. The corresponding rates in the
1019 competitor species are indicated for comparison.

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1024 LITERATURE CITED

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1026 genetic, demographic and ecological data. *Molecular Ecology* 21:1394–1410.

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1051 Dubart et al. Modelling competition, niche and coexistence between an invasive and a native
 1052 species in a two-species metapopulation

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1054 **Appendix S2** – Mathematical formulation of the model.

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1056 The occupancy probability at $t+1$ is described as a function of the occupancy at t (Eq. 1 in main
 1057 text; subscripts not included for clarity):

$$1058 \quad P(x_{t+1} = 1) = x_t[\varphi + (1 - \varphi)(1 - e^{-c \bar{x}_t})] + (1 - x_t)(1 - e^{-c \bar{x}_t}) \quad [\text{Eq. S1}]$$

1059 The occupancy probability of species s in site i at time $t+1$ reads:

$$1060 \quad P(x_{s,i,t+1} = 1) = x_{s,i,t} \cdot T_{1 \rightarrow 1}^{s,i,t} + (1 - x_{s,i,t}) \cdot T_{0 \rightarrow 1}^{s,i,t} \quad [\text{Eq. S2}]$$

1061 where $T_{1 \rightarrow 1}^{s,i,t}$ gives the transition probability from an occupied to an occupied site (i) for species
 1062 s between time t and $t+1$, and $T_{0 \rightarrow 1}^{s,i,t}$ gives the transition probability from empty to occupied
 1063 sites. The transition from empty to occupied ($T_{0 \rightarrow 1}$) occurs through colonization, whereas the
 1064 transition from occupied to occupied ($T_{1 \rightarrow 1}$) can be achieved by persisting or by becoming
 1065 extinct and recolonized during the same time-step. The transition probabilities are given by:

$$1066 \quad T_{0 \rightarrow 1}^{s,i,t} = 1 - e^{-\Delta_c^{s,i,t}} \quad [\text{Eq. S3a}]$$

$$1067 \quad T_{1 \rightarrow 1}^{s,i,t} = \Delta_\varphi^{s,i,t} + (1 - \Delta_\varphi^{s,i,t})(1 - e^{-\Delta_c^{s,i,t}}) \quad [\text{Eq. S3b}]$$

1068 Species, site- and year-specific colonization rates ($\Delta_c^{s,i,t}$) and persistence probabilities ($\Delta_\varphi^{s,i,t}$)
 1069 are given by:

$$1070 \quad \Delta_c^{s,i,t} = [X_{i,t+1} \cdot c_D + (1 - X_{i,t+1}) \cdot c_W^{s,i,j}] \cdot \bar{x}_t \quad [\text{Eq. S4a}]$$

$$1071 \quad \Delta_\varphi^{s,i,t} = X_{i,t} \cdot \varphi_D + (1 - X_{i,t}) \cdot \varphi_W^{s,i,j} \quad [\text{Eq. S4b}]$$

1072

1073 Where subscript W and D stand for rate/probability in wet and dry sites respectively. $X_{i,t}$ is an
 1074 indicator variable taking value 1/0 if site i at time t was dry/wet, allowing to condition rates on

1075 site status (dry/wet). Following Lamy et al. (2013a) colonization between t and $t+1$ depends on
1076 site status at time $t+1$ whereas persistence depends on site status at time t . Remember that we
1077 set $c_D = 0$.

1078
$$\bar{x}_t = \frac{1}{N} \sum_{i=1}^N x_{i,t} \quad [\text{Eq. S5}]$$

1079 is the metapopulation occupancy at time t ($x_{i,t}$ is an indicator variable taking value 1 when sites
1080 are occupied, and 0 otherwise).

1081

1082 Linking states ($x_{i,t}$) and observations ($y_{i,t}$)

1083 We linked occupancy probabilities ($x_{i,t}$) to probabilities of observation ($y_{i,t}$) as follows :

1084
$$P(y_{i,t} = 1) = d \cdot (1 - X_{i,t}) \cdot x_{i,t} \quad [\text{Eq. S6}]$$

1085 where d is the detection probability (probability of species being observed given that it is
1086 present, in a wet site).

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