



Modeling competition, niche, and coexistence between an invasive and a native species in a two-species metapopulation

Maxime Dubart, Jelena Pantel, Jean-pierre Pointier, Philippe Jarne, Patrice David

► To cite this version:

Maxime Dubart, Jelena Pantel, Jean-pierre Pointier, Philippe Jarne, Patrice David. Modeling competition, niche, and coexistence between an invasive and a native species in a two-species metapopulation. *Ecology*, 2019, 100 (6), 10.1002/ecy.2700 . hal-02148415

HAL Id: hal-02148415

<https://univ-perp.hal.science/hal-02148415>

Submitted on 30 Nov 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

MAXIME DUBART^{1,4}, JELENA H. PANTEL^{1,2}, JEAN-PIERRE POINTIER³, PHILIPPE JARNE¹ AND
PATRICE DAVID¹

¹ *CEFE UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier –
IRD - EPHE, 1919 route de Mende, 34293 Montpellier cedex 5, France*

² *Department of Biology, The College of William and Mary, P.O. Box 8795, Williamsburg,
Virginia, United States of America*

³ *CRILOBE, USR 3278 CNRS–EPHE, Université de Perpignan, 66880 Perpignan cedex, France*

⁴ Corresponding author: maxime.dubart@cefe.cnrs.fr

Running Head: Coexistence of snail species

4 figures, 2 tables, 2 online appendices

Abstract

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

Key Words: metacommunity, competition, environmental variability, extinction / colonization, *Physa acuta*, *Aplexa marmorata*, freshwater snails

INTRODUCTION

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

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

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

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

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

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

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

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

MATERIALS & METHODS

The freshwater snail metacommunity from Guadeloupe

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

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

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

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

Multistate occupancy model

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

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

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

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

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

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

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

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

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

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

$$\log(c_{W,i,t}) = \mu_{c_W} + \beta_c \cdot \mathbf{X}_{c,i,t} + \alpha_c x'_{i,t} \quad (2a)$$

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

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

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

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

Application of the model to our study system

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

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

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

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

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

Projecting species dynamics to understand coexistence

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

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

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

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

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

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

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

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

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

RESULTS

Metacommunity parameters and the influence of environmental covariates and competition

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

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

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

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

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

Simulated species dynamics: role of competition and environmental heterogeneity

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

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

We investigated the potential for coexistence of the two species in a (theoretical) homogeneous landscape, by setting all sites to environmental conditions identical to those 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

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

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

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

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

DISCUSSION

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

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

Asymmetrical impacts of competition on colonization and extinction rates

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

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

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

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

Coexistence, competition and species sorting at the landscape scale

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

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

Competition and coexistence theory

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

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

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

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

Limitations and future directions

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

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

Conclusion

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

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

ACKNOWLEDGEMENTS

We thank two reviewers for insightful comments and the numerous people who participated to metacommunity sampling in Guadeloupe over the last two decades: N. Bonel, V. Calcagno, E. Chapuis, M.-P. Dubois, G. Epinat, J.S. Escobar, N. Juillet, T. Lamy, F. Laroche, F. Massol, and A. Ségard. MD is supported by a PhD fellowship from the University of Montpellier. The research conducted here was supported by grants from the Agence National de la Recherche (AFFAIRS, ANR-12SV005, and NGB, ANR-17CE32-0011-05) to PD and by the CNRS. Analyses benefited from facilities from the Montpellier Bioinformatics Biodiversity platform (CeMEB LabEx).

654 LITERATURE CITED

- 655 Amarasekare, P. 2000. The geometry of coexistence. *Biological Journal of the Linnean*
656 *Society* 71:1–31.
- 657 Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: A
658 synthesis. *Ecology Letters* 6:1109–1122.
- 659 Amarasekare, P., M. F. Hoopes, N. Mouquet, and M. Holyoak. 2004. Mechanisms of
660 coexistence in competitive metacommunities. *The American naturalist* 164:310–326.
- 661 Baker, H. G. 1955. Self-compatibility and establishment after “long-distance” dispersal.
662 *Evolution* 9:347–349.
- 663 Baker, H. G. 1974. The evolution of weeds. *Annu. Rev. Ecol. Syst* 5:1–24.
- 664 Barabás, G., R. D’Andrea, and S. M. Stump. 2018. Chesson’s coexistence theory. *Ecological*
665 *Monographs*.
- 666 Bell, G. 2001. Ecology - neutral macroecology. *Science* 293:2413–2418.
- 667 Bengtsson, J. 1989. Interspecific competition increases local extinction rate in a
668 metapopulation system. *Nature* 340.
- 669 Bezanson, J., A. Edelman, S. Karpinski, and V. B. Shah. 2017. Julia: A fresh approach to
670 numerical computing. *SIAM review* 59:65–98.
- 671 Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative
672 simulations. *Journal of Computational and Graphical statistics* 7:434–455.
- 673 Brown, B. L., E. R. Sokol, J. Skelton, and B. Tornwall. 2017. Making sense of
674 metacommunities : dispelling the mythology of a metacommunity typology. *Oecologia*
675 183:643–652.
- 676 Byers, J. E. 1999. The distribution of an introduced mollusc and its role in the long-term
677 demise of a native confamilial species. *Biological Invasions* 1:339–352.
- 678 Byers, J. E. 2000. Competition between two estuarine snails: implications for invasions of

679 exotic species. *Ecology* 81:1225–1239.

680 Calcagno, V., N. Mouquet, P. Jarne, and P. David. 2006. Coexistence in a metacommunity:
681 The competition-colonization trade-off is not dead. *Ecology Letters* 9:897–907.

682 Chapuis, E., T. Lamy, J.-P. Pointier, N. Juillet, A. Ségard, P. Jarne, and P. David. 2017.
683 Bioinvasion triggers rapid evolution of life histories in freshwater snails. *American*
684 *Naturalist* 190.

685 Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary
686 approaches. University of Chicago Press.

687 Chesson, P. 2000. General theory of competitive coexistence in spatially-varying
688 environments. *Theoretical population biology* 58:211–37.

689 Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community
690 dynamics. *Ecology Letters* 8:1175–1182.

691 Darwin, C. 1859. On the origins of species by means of natural selection. London: Murray
692 247.

693 David, P., E. Thébault, O. Anneville, P. F. Duyck, E. Chapuis, and N. Loeuille. 2017. Impacts
694 of invasive species on food webs: A review of empirical data. *Advances in Ecological*
695 *Research* 56:1–60.

696 Davis, C. L., D. A. W. Miller, S. C. Walls, W. J. Barichivich, J. W. Riley, and M. E. Brown.
697 2017. Species interactions and the effects of climate variability on a wetland amphibian
698 metacommunity. *Ecological Applications* 27:285–296.

699 Dorazio, R. M., M. Kéry, J. A. Royle, and M. Plattner. 2010. Models for inference in dynamic
700 metacommunity systems. *Ecology* 91:2466–2475.

701 Dubois, M. P., A. Nicot, P. Jarne, and P. David. 2008. Characterization of 15 polymorphic
702 microsatellite markers in the freshwater snail *Aplexa marmorata* (Mollusca, Gastropoda).
703 *Molecular Ecology Resources* 8:1062–1064.

704 Dugger, K., R. Anthony, and L. Andrews. 2011. Transient dynamics of invasive competition:
 705 Barred Owls, Spotted Owls, habitat, and the demons of competition present. *Ecological*
 706 *Applications* 21:2459–2468.

707 Escobar, J. S., J. R. Auld, A. C. Correa, J. M. Alonso, Y. K. Bony, M. A. Coutellec, J. M.
 708 Koene, J. P. Pointier, P. Jarne, and P. David. 2011. Patterns of mating-system evolution
 709 in hermaphroditic animals: Correlations among selfing rate, inbreeding depression, and
 710 the timing of reproduction. *Evolution* 65:1233–1253.

711 Fernández-i-Marín, X. 2016. **ggmcmc** : Analysis of MCMC Samples and Bayesian Inference.
 712 *Journal of Statistical Software* 70.

713 Gause, G. F. 1934. *The struggle for existence*. Baltimore. Wilkins Williams.

714 Godoy, O., D. B. Stouffer, N. J. B. Kraft, and J. M. Levine. 2017. Intransitivity is infrequent
 715 and fails to promote annual plant coexistence without pairwise niche differences.
 716 *Ecology* 98.

717 Gravel, D., F. Guichard, and M. E. Hochberg. 2011. Species coexistence in a variable world.
 718 *Ecology Letters* 14:828–839.

719 Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its
 720 relevance to ecological and evolutionary theory.

721 Guélat, J., J. Jaquière, L. Berset-Brändli, E. Pellegrini, R. Moresi, T. Broquet, A. H. Hirzel,
 722 and N. Perrin. 2008. Mass effects mediate coexistence in competing shrews. *Ecology*
 723 89:2033–2042.

724 Guillera-Aroita, G. 2017. Modelling of species distributions, range dynamics and
 725 communities under imperfect detection: advances, challenges and opportunities.
 726 *Ecography*.

727 Guisan, A., and W. Thuiller. 2005. Predicting species distribution: Offering more than simple
 728 habitat models. *Ecology Letters* 8:993–1009.

729 Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* 64:493–500.

730 Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment: Three species of
731 *Daphnia* in rock pools. *Journal of Animal Ecology* 52:263–279.

732 Hastings, A. 1987. Can Competition Be Detected Using Species Co-Occurrence Data ?
733 *Ecology* 68:117–123.

734 Henry, P. Y., L. Bousset, P. Sourrouille, and P. Jarne. 2005. Partial selfing, ecological
735 disturbance and reproductive assurance in an invasive freshwater snail. *Heredity* 95:428–
736 436.

737 Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: spatial dynamics and
738 ecological communities. University of Chicago Press.

739 Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton
740 University Press.

741 Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of
742 animals ? *The American naturalist* 93.

743 Jarne, P., M. A. Perdieu, A. F. Pernot, B. Delay, and P. David. 2000. The influence of self-
744 fertilization and grouping on fitness attributes in the freshwater snail *Physa acuta*:
745 Population and individual inbreeding depression. *Journal of Evolutionary Biology*
746 13:645–655.

747 Kappes, H., and P. Haase. 2012. Slow, but steady: Dispersal of freshwater molluscs. *Aquatic*
748 *Sciences* 74:1–14.

749 Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: Linking spatial
750 scales and species coexistence. *Ecology Letters* 7:69–80.

751 Lamy, T., O. Gimenez, J.-P. Pointier, P. Jarne, and P. David. 2013a. Metapopulation
752 dynamics of species with cryptic life stages. *The American Naturalist* 181:479–491.

753 Lamy, T., P. Jarne, F. Laroche, J. P. Pointier, G. Huth, A. Segard, and P. David. 2013b.

754 Variation in habitat connectivity generates positive correlations between species and
755 genetic diversity in a metacommunity. *Molecular Ecology* 22:4445–4456.

756 Lamy, T., J. P. Pointier, P. Jarne, and P. David. 2012. Testing metapopulation dynamics using
757 genetic, demographic and ecological data. *Molecular Ecology* 21:1394–1410.

758 Van Leeuwen, C. H. A., N. Huig, G. Van Der Velde, T. A. Van Alen, C. A. M. Wagemaker,
759 C. D. H. Sherman, M. Klaassen, and J. Figuerola. 2013. How did this snail get here?
760 Several dispersal vectors inferred for an aquatic invasive species. *Freshwater Biology*
761 58:88–99.

762 Lehtinen, R. M., and G. L. F. Carfagno. 2011. Habitat Selection , the Included Niche , and
763 Coexistence in Plant-Specialist Frogs from Madagascar. *Biotropica* 43:58–67.

764 Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D.
765 Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The
766 metacommunity concept: A framework for multi-scale community ecology. *Ecology*
767 Letters 7:601–613.

768 Leibold, M. A., and G. M. Mikkelsen. 2002. Coherence, species turnover, and boundary
769 clumping: elements of meta-community structure. *Oikos* 97:237–250.

770 Levins, R. 1969. Some demographic and genetic consequences of environmental
771 heterogeneity for biological control. *Bulletin of the Entomological Society of America*
772 15:237–240.

773 Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between
774 rare species. *Proceedings of the National Academy of Sciences* 68:1246–1248.

775 Little, C. J., and F. Altermatt. 2018. Do priority effects outweigh environmental filtering in a
776 guild of dominant freshwater macroinvertebrates? *Proceedings of the Royal Society B:*
777 *Biological Sciences* 285.

778 Logue, J. B., N. Mouquet, H. Peter, and H. Hillebrand. 2011. Empirical approaches to

779 metacommunities: A review and comparison with theory. *Trends in Ecology and*
780 *Evolution* 26:482–491.

781 Loreau, M., and N. Mouquet. 1999. Immigration and the Maintenance of Local Species
782 Diversity. *The American Naturalist* 154:427–440.

783 MacArthur, R., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography.
784 *Evolution* 17:373–387.

785 MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003.
786 Estimating site occupancy, colonization, and local extinction when a species is detected
787 imperfectly. *Ecology* 84:2200–2207.

788 Mackenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: General advice and
789 allocating survey effort. *Journal of Applied Ecology* 42:1105–1114.

790 Meynard, C. N., S. Lavergne, I. Boulangeat, and L. Garraud. 2013. Disentangling the drivers
791 of metacommunity structure across spatial scales. *Journal of Biogeography* 40:1560–
792 1571.

793 Miller, D. A. W., C. S. Brehme, J. E. Hines, J. D. Nichols, and R. N. Fisher. 2012. Joint
794 estimation of habitat dynamics and species interactions: Disturbance reduces co-
795 occurrence of non-native predators with an endangered toad. *Journal of Animal Ecology*
796 81:1288–1297.

797 Moilanen, A. 2000. The equilibrium assumption in estimating the parameters of
798 metapopulation models. *Journal of Animal Ecology* 69:143–153.

799 Naujokaitis-Lewis, I., and M. J. Fortin. 2016. Spatio-temporal variation of biotic factors
800 underpins contemporary range dynamics of congeners. *Global Change Biology* 22:1201–
801 1213.

802 Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs
803 sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical*

804 Computing (DSC 2003):20–22.

805 Plummer, M., N. Best, and K. Cowles. 2006. CODA: convergence diagnosis and output
806 analysis for MCMC. R News 6.

807 Pointier, J. P., and C. Combes. 1976. La saison sèche en Guadeloupe et ses conséquences sur
808 la démographie des mollusques dans les biotopes à *Biomphalaria glabrata* (Say, 1818),
809 vecteur de la bilharziose intestinale.

810 Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O. Hara, K. M. Parris, P. A. Vesk,
811 and M. A. Mccarthy. 2014. Understanding co-occurrence by modelling species
812 simultaneously with a Joint Species Distribution Model (JSDM):397–406.

813 Pulliam, H. R. 1988. Sources, sinks and population regulation. The American Naturalist
814 132:652–661.

815 Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy
816 models. Ecology 88:1813–1823.

817 Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. Vegetatio
818 58:29–55.

819 Slatkin, M. 1974. Competition and regional coexistence. Ecology 55:128–134.

820 Taneyhill, D. E. 2000. Metapopulation dynamics of multiple species : the geometry of
821 competition in a fragmented habitat. Ecological Monographs 70:495–516.

822 Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–
823 16.

824 Tsitrone, A., P. Jarne, and P. David. 2003. Delayed selfing and resource reallocations in
825 relation to mate availability in the freshwater snail *Physa acuta*. The American Naturalist
826 162:474–488.

827 Warton, D. I., F. G. Blanchet, R. B. O’Hara, O. Ovaskainen, S. Taskinen, S. C. Walker, and F.
828 K. C. Hui. 2015. So many variables: Joint modeling in community ecology. Trends in

829 Ecology and Evolution 30:766–779.

830 Winegardner, A. K., B. K. Jones, I. S. Y. Ng, T. Siqueira, and K. Cottenie. 2012. The

831 terminology of metacommunity ecology. Trends in Ecology and Evolution 27:253–254.

832 Yackulic, C. B., J. Reid, J. D. Nichols, J. E. Hines, R. Davis, and E. Forsman. 2014. The roles

833 of competition and habitat in the dynamics of populations and species distributions.

834 Ecology 95:265–279.

835 Yu, D. W., and H. B. Wilson. 2001. The competition-colonization trade-off is dead; Long live

836 the competition-colonization trade-off. The American Naturalist 158:49–63.

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

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

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)

852

853

FIGURE LEGENDS

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

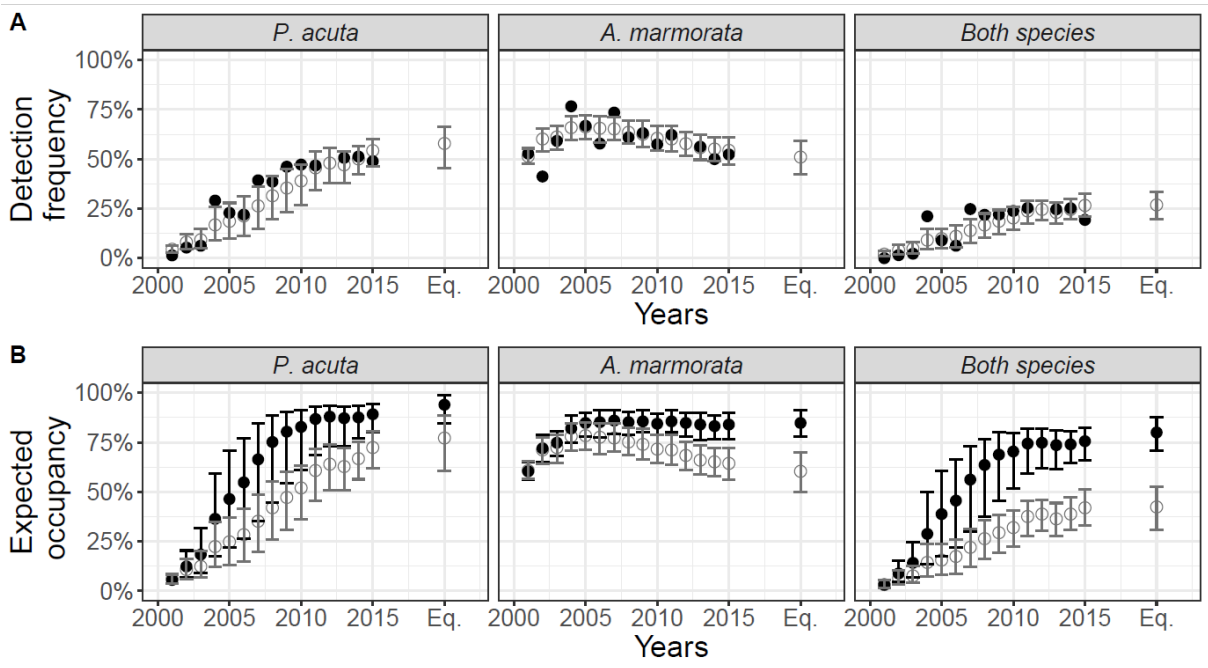


FIGURE 2. Colonization and extinction probabilities (per year) without / with competition, in a site with average environmental characteristics. The median estimates without competition are derived from the intercept of the regression model (Eq. 2), while those with competition are derived from intercepts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

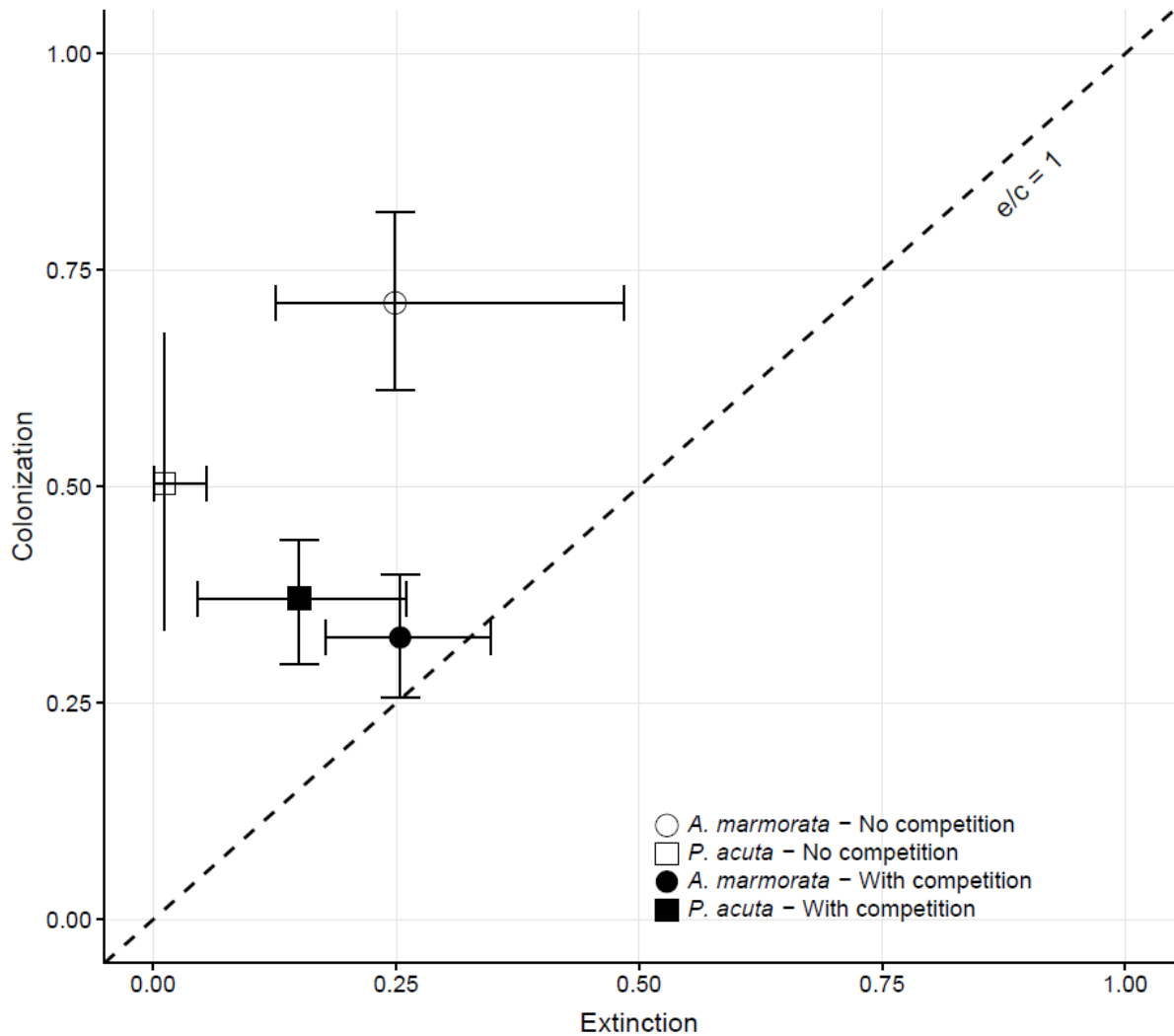


FIGURE 3. Proportions of sites belonging to the fundamental and realized niches based on simulated metacommunities under homogeneous environmental conditions. The first line represents all environmental conditions typical of each of the (250) sites. The second one shows the fraction of conditions that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

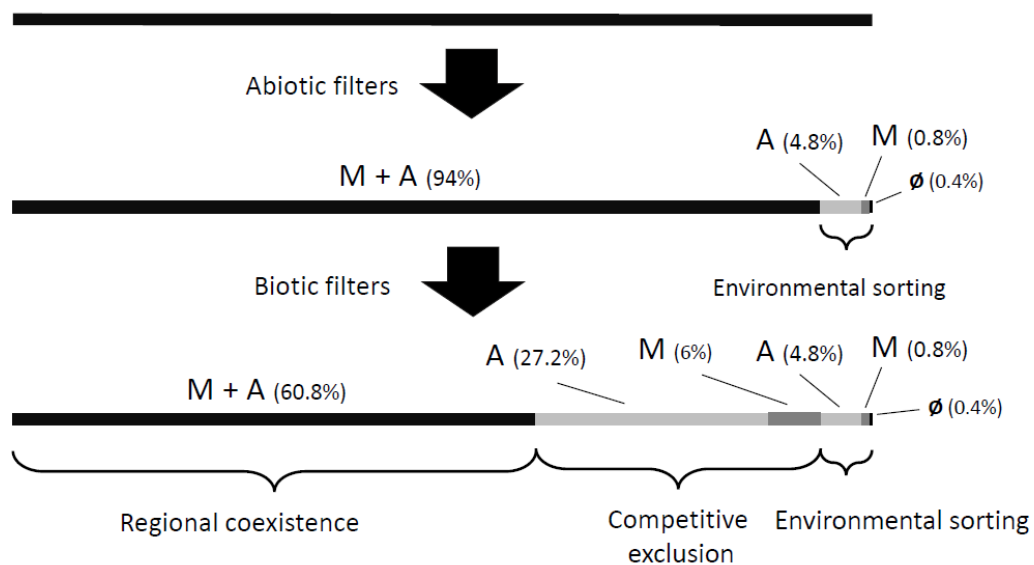
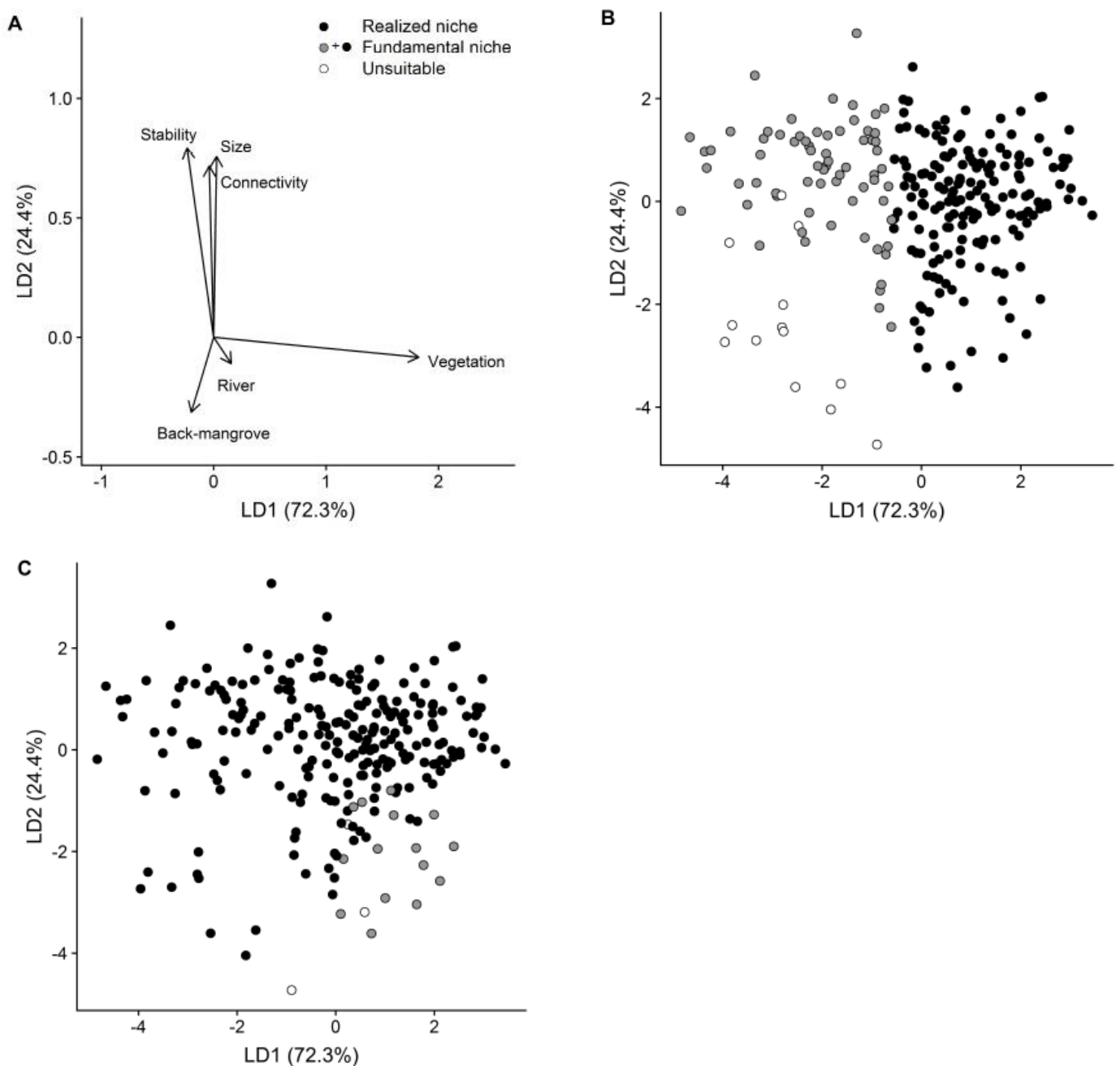


FIGURE 4. Axes 1 and 2 of a linear discriminant analysis (explaining 96.7% of the among-group variance) on environmental variables. Distribution of the site categories is represented in the environmental space. The contributions of variables to axis are reported in (A). The conditions where each species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



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

Appendix S1: Supplementary figures and tables.

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

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

Figure. S2. Posterior distributions.

Figure. S3. Pairwise correlations amongst parameters

Figure. S4. Full long-term metapopulations dynamic.

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

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

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

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

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

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	-

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

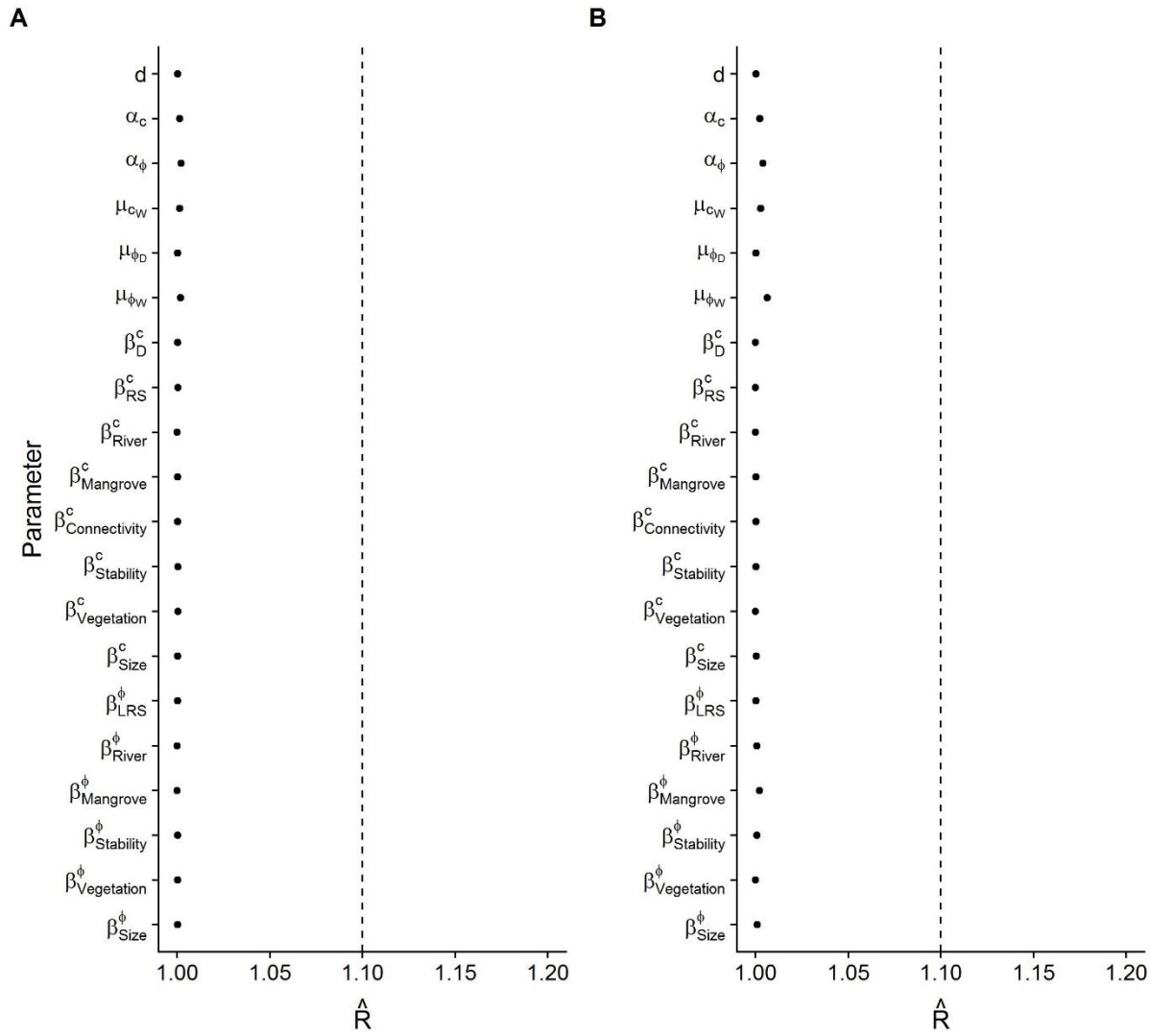
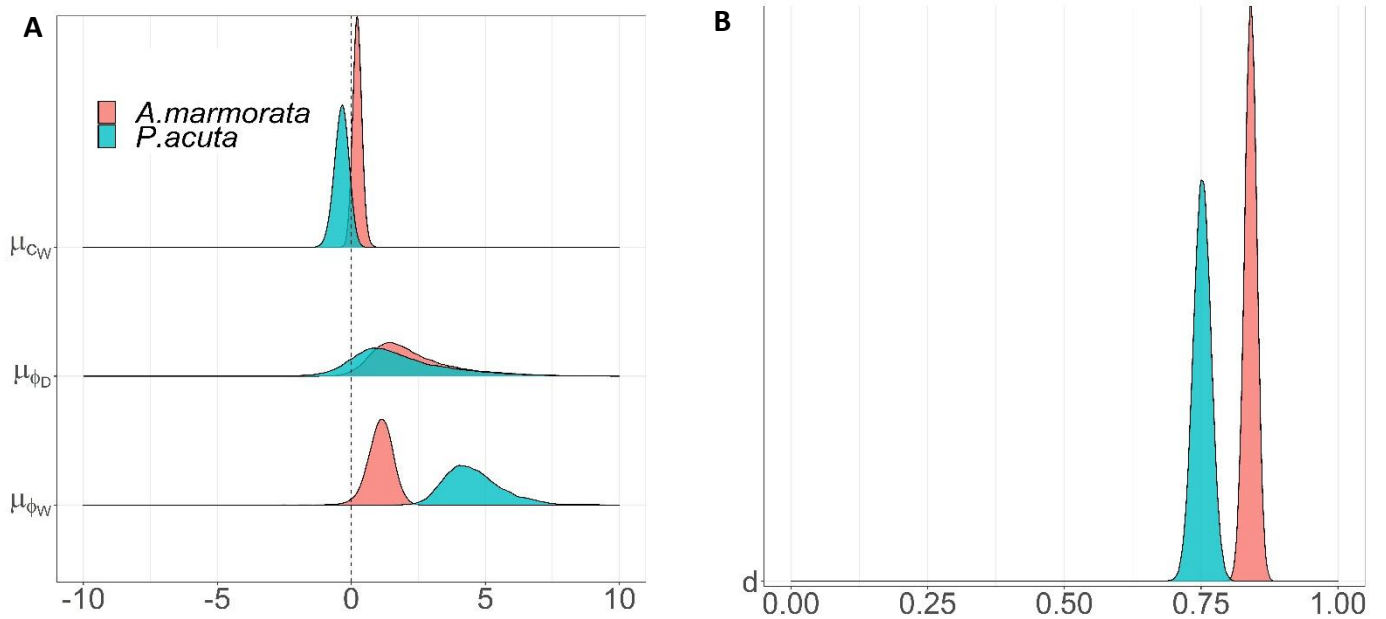
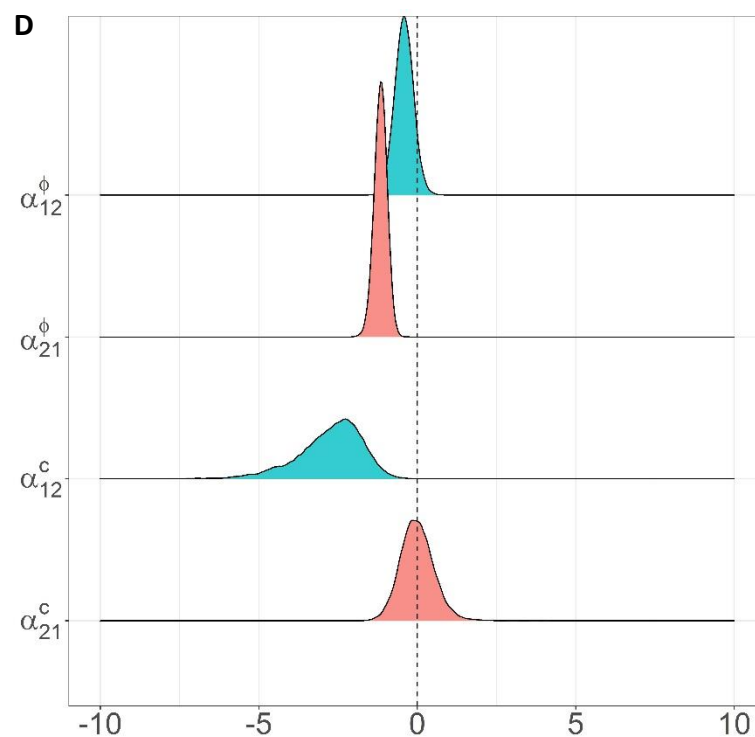
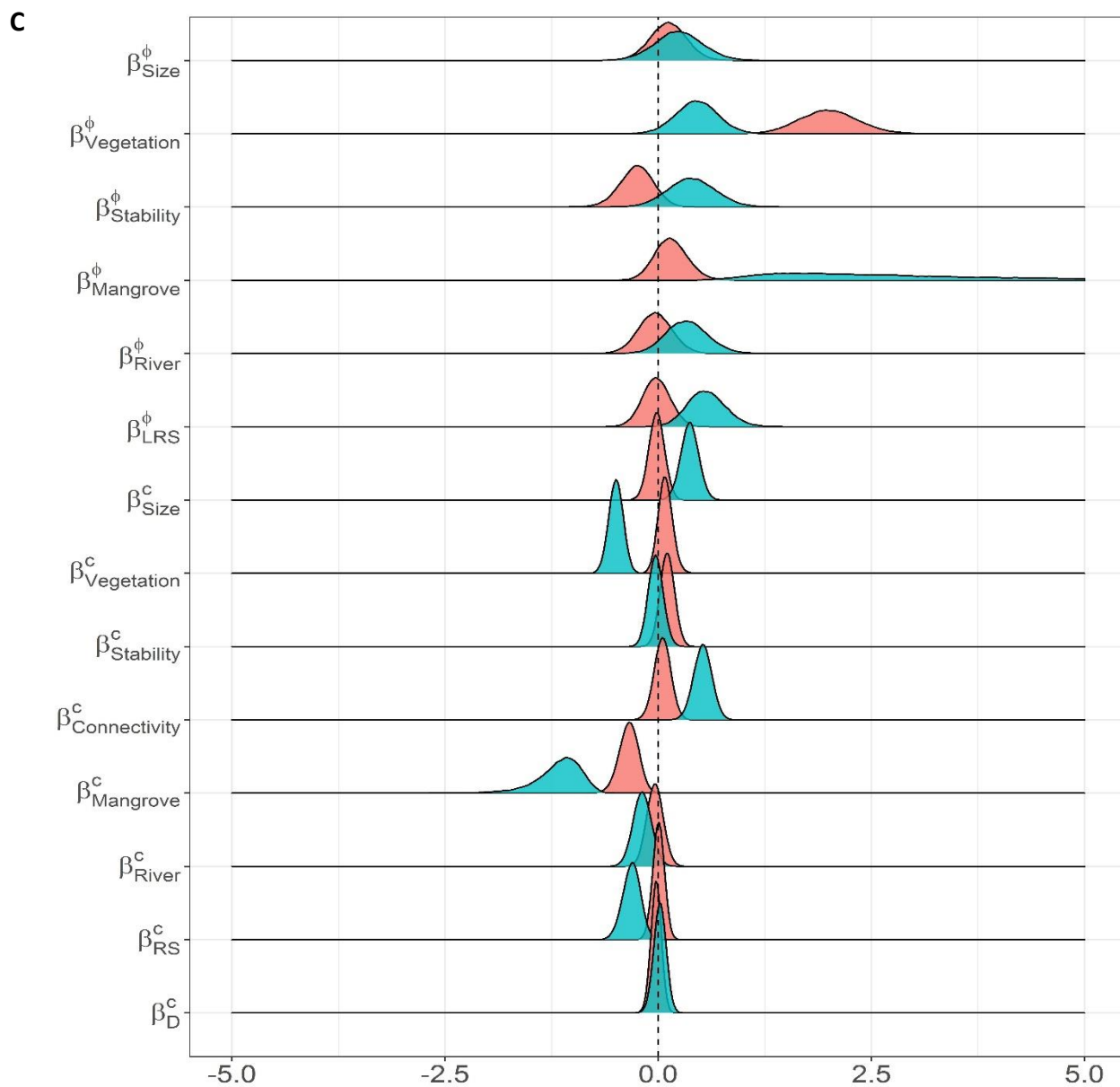
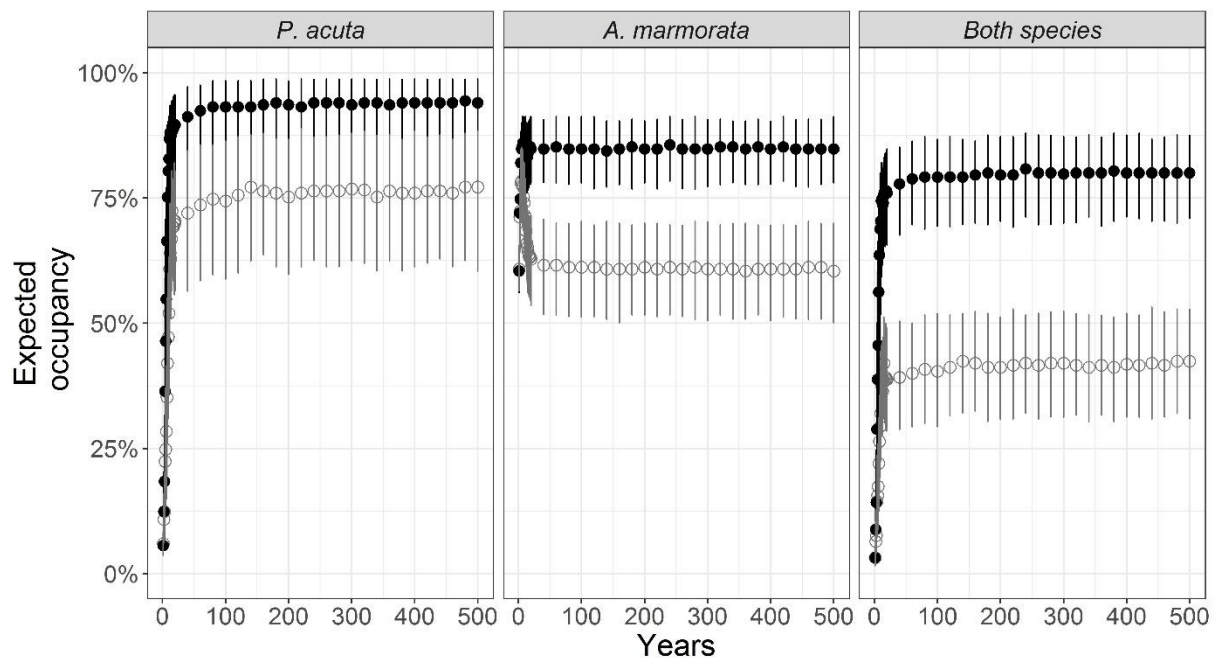


FIGURE S2. Posterior distributions of the parameters estimated from the statistical (Bayesian) model in the native (*Aplexa marmorata*) and invasive (*Physa acuta*) species (see Table 2 for parameter estimates and their credibility intervals). We do not represent prior distributions as they appear as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





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*.

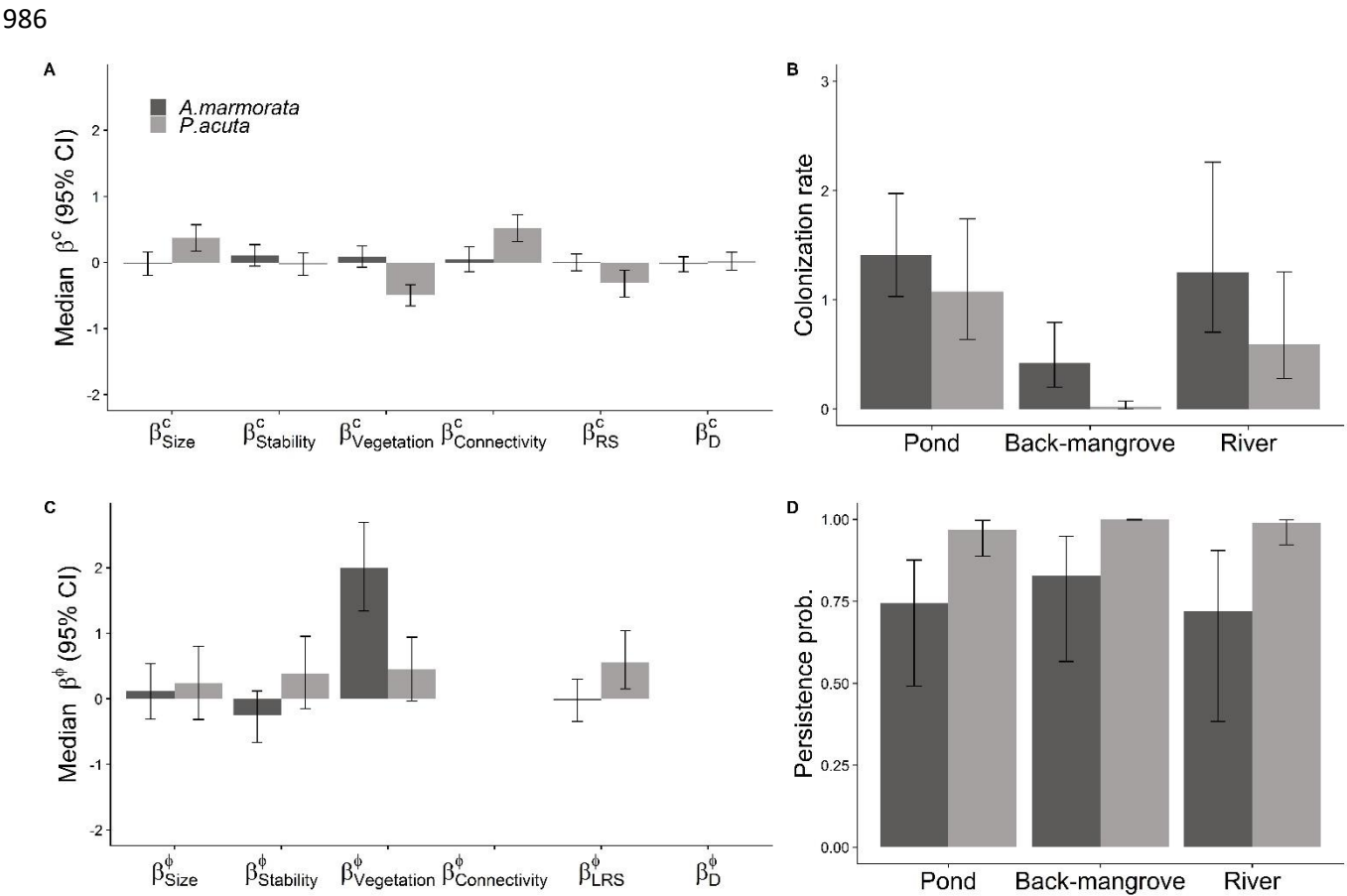


FIGURE S6. Transition graphs among patch states in the simulated metacommunities. The circles represent the fraction (in %) of unoccupied and occupied sites and arrows the transitions between states across successive generations at equilibrium when all covariates are taken into account. (A) No competition.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

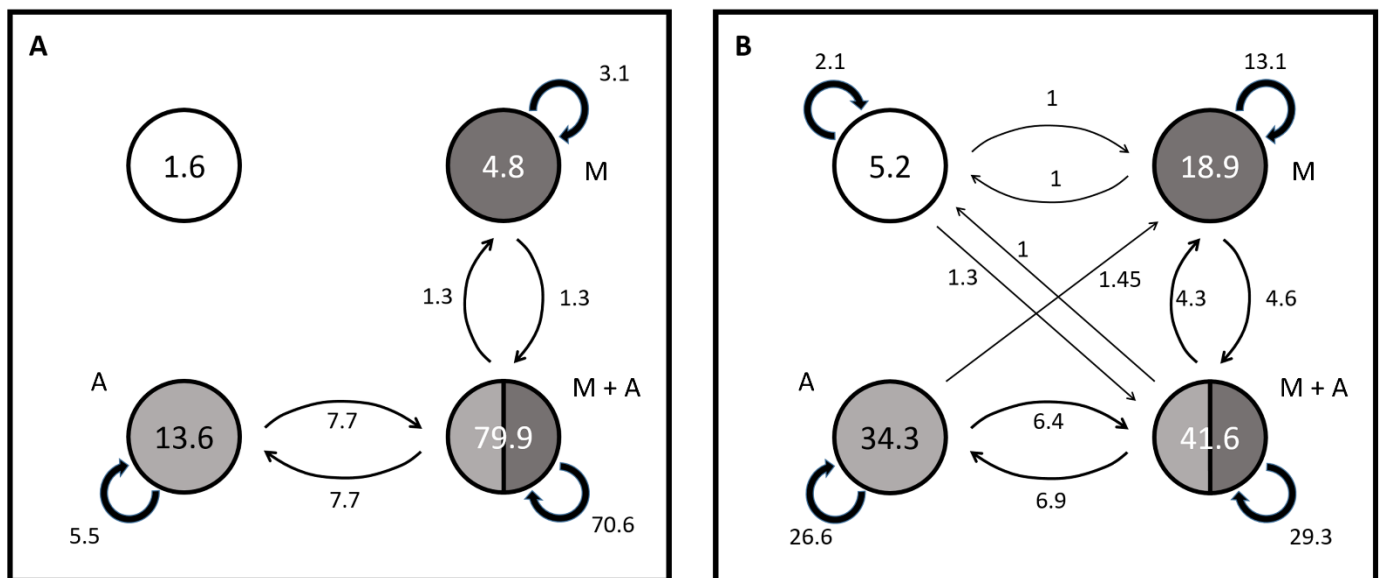


FIGURE S7. Comparison of site-specific probability of occurrence in an environmentally homogeneous landscape *versus* in the real heterogeneous landscape. Panel A: *A. marmorata*; Panel B: *P. acuta* and Panel C: co-occurrence. Light grey bars represent site-specific probabilities when considering a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

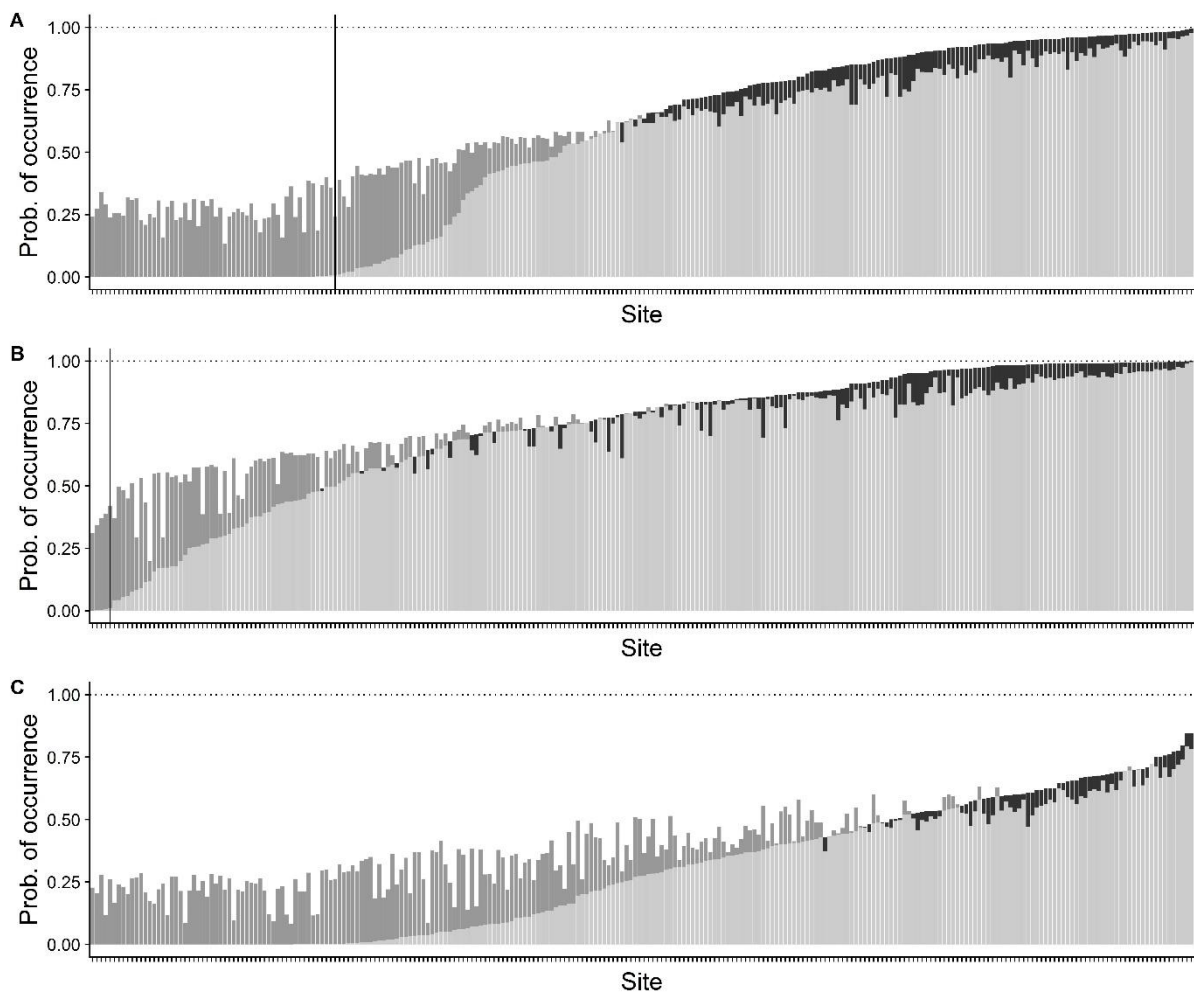
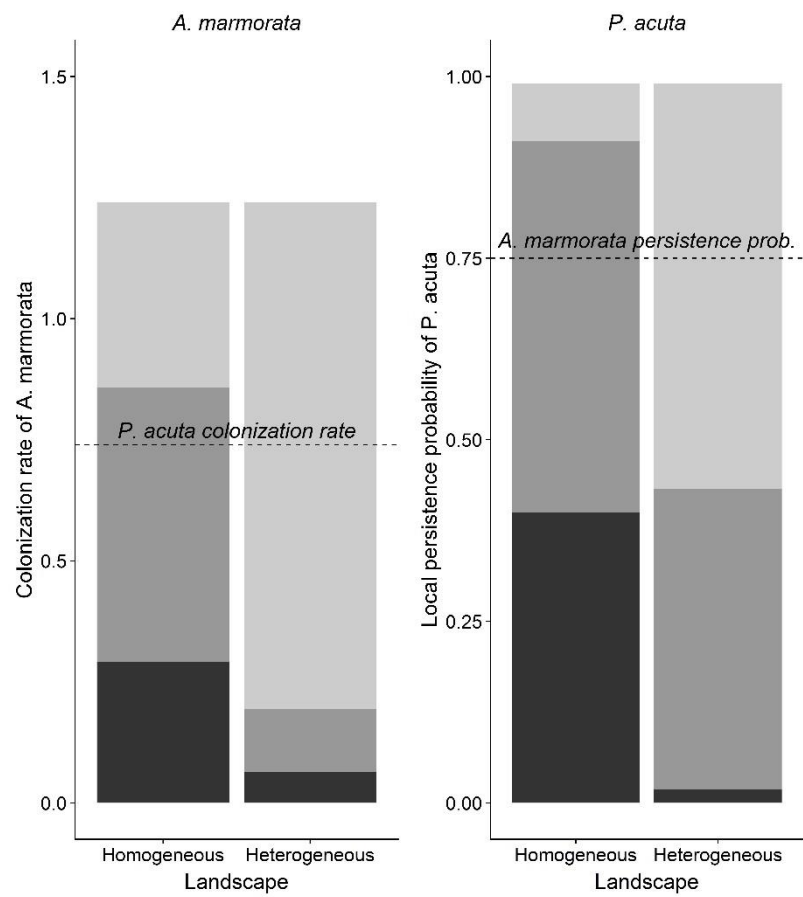


FIGURE S8. Comparison of persistence thresholds in the mean environment (homogeneous landscape) vs. in the whole environment (heterogeneous landscape), with or without competitive effects, based on simulations of a range of colonization rates (*A. marmorata*) and local persistence rate (*P. acuta*).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



1024 LITERATURE CITED

1025 Lamy, T., J. P. Pointier, P. Jarne, and P. David. 2012. Testing metapopulation dynamics using
1026 genetic, demographic and ecological data. *Molecular Ecology* 21:1394–1410.

1027 Gelman, A., and D. B. Rubin. 1992. Inference from Iterative Simulation Using Multiple
1028 Sequences. *Statistical Science* 7:457–511.

1029 Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative
1030 simulations. *Journal of Computational and Graphical statistics* 7:434–455.

1031

1032

1033

1034

1035

1036

1037

1038

1039

1040

1041

1042

1043

1044

1045

1046

1047

1048

1049

1050

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

Appendix S2 – Mathematical formulation of the model.

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

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

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

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

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

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

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

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

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

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

Where subscript W and D stand for rate/probability in wet and dry sites respectively. $X_{i,t}$ is an 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 $c_D = 0$.

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

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 :

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

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

1087
 1088
 1089