Metapopulation dynamics of multiple species in a heterogeneous landscape

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Abstract. Characterizing the diversity of demographic strategies among species can inform research in topics such as trait syndromes, community stability, coexistence and ecological succession. However, this diversity can depend on the spatial scale considered: at the landscape scale, species often form metapopulations, i.e. sets of local, sometimes short- lived, populations, inhabiting discrete habitat patches. Metapopulation dynamics are most frequently analyzed in individual species or pairs of interacting species because of the large amount of data required for multiple species, and because species vary in their perceptions of what constitutes a favorable or unfavorable habitat. Here we evaluate, using a case study, whether a metapopulation model can be used to generate accurate estimates of demographic parameters and to describe the diversity of dynamics, responses to environment, and prospects of long- term persistence in a guild of species inhabiting a common fragmented landscape. We apply this approach to a guild of 22 mollusc species that inhabit freshwater habitats on two islands of Guadeloupe, to compare metapopulation dynamics among species. We analyzed a fifteen-year time series of occupancy records for 278 sites using a multistate occupancy model that estimates colonization and extinction rates as a function of site- and year specific environmental covariates, then used model results to simulate future island metapopulation dynamics. Despite the diverse array of metapopulation trajectories - a mix of species with either stable, increasing, declining, or fluctuating metapopulations - and the inherent challenges associated with such data (e.g., imperfect detection, spatial and temporal heterogeneity), our model accurately captures among-patch variation in suitability for many mollusc taxa. The dynamics of rare species or species with habitat preferences not fully captured by the retained set of covariates were less well described. For several species, we detected a negative correlation between extinction and colonization. This variation in habitat suitability created species-specific extinction-resistant pockets in the landscape. Our comparative analysis also revealed that species had distinct strategies for metapopulation dynamics, such as ‘fast turnover’ species with both a high proportion of occupied sites and a high rate of site extinction in the landscape.

Key words: *biological invasions; comparative demography; environmental variability; extinction / colonization; freshwater snails; metapopulations; predicted dynamics*

INTRODUCTION

The metapopulation approach, which describes the dynamics of groups of local populations as discrete spatial entities that exchange migrants and are experiencing extinction and colonization dynamics (**Hanski 1999**; **Hanski & Gaggiotti 2004**), is a theoretical construction that proved useful to describe and predict species occupancy patterns (e.g., **Hanski et al. 1995**; **Lawes et al. 2000**; **Vergara et al. 2016**). It has also guided biocontrol and conservation efforts for diverse groups of species (e.g., **Marsh and Trenham 2001**; **Johst & Schöps 2003**; **Pointier & David 2004**; **Ladin et al. 2016**; but see **Smith & Green 2005** and **Fronhofer et al. 2012** for a critical assessment of when to consider species in patchy habitats as metapopulations). However, the overwhelming majority of metapopulation studies have been conducted on individual species or on pairs of interacting species (**Nee et al. 1997**; **Bull et al. 2006**). In patchy landscapes where guilds of phylogenetically or functionally similar species overlap, species may perceive the same landscape in distinct ways. Species may vary in their colonization and extinction rates, as well as whether they have stable metapopulation dynamics or are instead transiently present and expected to become extinct. Comparing metapopulation rates and dynamics across multiple species can be used to associate species' properties with their colonization and extinction rates (e.g., **Johansson et al. 2012**), to assess the consequences of the spread of introduced species on communities (**Pointier & David 2004**; **Svenning et al. 2014**), to optimize conservation planning to decrease extinction risk for multiple species (**Nicholson et al. 2006**), and more generally to better inform current and expected biodiversity patterns. Our purpose here is to evaluate, using a case study, whether a metapopulation model can be used to generate accurate estimates of demographic parameters and to describe the diversity of dynamics, responses to environment, and prospects of long-term persistence in a guild of species inhabiting a common fragmented landscape. We present a first multi-species (> 3 species), comparative metapopulation study, where estimates of demographic parameters and the environmental covariates that influence extinction and colonization are evaluated for many species together. Our approach is novel in its focus on more than 1-3 species, since we consider an entire guild with more than 20 species, as well as in its ability both to estimate metapopulation equilibrium expectations for species that are not at an equilibrium occupancy and to make predictions about future occupancy and extinction dynamics.

A metapopulation approach is appropriate when populations are spatially structured into local populations and when migration among these allows the reestablishment of extinct populations (**Hanski & Gilpin 1997**). The current generation of metapopulation models, stochastic patch occupancy models (SPOMs; **Caswell & Etter 1993**; **Hanski 1997**; **Moilanen 1999**; **Heard et al. 2013)**, focus specifically on the presence of a population in a habitat patch and allow estimation of colonization and extinction rates and metapopulation occupancy, i.e. the constitutive parameters of the foundational **Levins (1969; 1970)** metapopulation model. SPOMs have become popular because their representation of only the occupancy state (as unoccupied or occupied) of habitat patches makes them easier to parameterize than models that require local density estimates (**Moilanen 2004**). However, some key issues must be considered in order to accurately and simultaneously apply this modeling framework to several species of a guild in real, complex, and fragmented landscapes. While solutions to these challenges – imperfect detection, among-site heterogeneity, and temporally variable metapopulation dynamics - have been developed for analysis of individual species, we describe here the characteristics of our approach that were implemented to address them at the multi-species scale.

First, knowledge of a species' presence or absence from field data is usually imperfect, because species might not be detected when actually present (**Guillera-Arroita 2017**). In some cases, species may even be known to be systematically undetected by usual survey methods, such as under stressful circumstances (desiccation, freezing) that trigger the adoption of quiescent resistant forms (Lamy et al. 2013). Imperfect detection presents a difficulty for the SPOM approach because the occupancy state of each local population depends on the occupancy state at the previous time point (**Moilanen 2004**), and as a consequence estimates of colonization and extinction may be biased (**Moilanen 2002**; **MacKenzie et al. 2003**). In order to reduce these biases, **Lamy et al. (2013)** developed an occupancy model that combined two approaches, estimation of detection probabilities from repeated surveys (**MacKenzie et al. 2003**) and the inclusion of additional, undetectable, states beyond the binary of occupied / not occupied (e.g., multistate occupancy models, **MacKenzie et al. 2009**). In this model, the different states of occupancy were associated with an active life stage in wet sites and an aestivating life stage in dry sites (individuals buried in sediment), which allows estimation of colonization, extinction, and detectability parameters in wet vs. dry sites. We use the occupancy model of **Lamy et al. (2013)** in this study in order to quantify the metapopulation dynamics of a set of species that likely vary in their detectability and in their propensity to persist in a quiescent, cryptic form.

The second challenge is to account for the species-specific heterogeneity in the contributions of patches to the overall colonization and extinction dynamics in a metapopulation. Site heterogeneity has been incorporated in some spatially implicit metapopulation models: **Hanski & Ovaskainen (2002)** accounted for the destruction of some habitat patches, and quantitative variables describing heterogeneity have also been used, mostly to account for variation in patch size (considered as a proxy for population size and thus overall extinction probability) and patch connectivity (**Hanski 1994; Moilanen 2000; Wang & Altermatt 2019)**. Other spatially realistic metapopulation models have been developed that consider patch heterogeneity in the landscape (**Chandler et al. 2015**; **Howell et al. 2018**) or a site's position in a broader spatial network structure (**Gillaranz et al. 2012**; **Holmes et al. 2020**). However, a different approach may be needed when comparing multiple species in a landscape, as the extinction and colonization probabilities for species with distinct limiting resources and dispersal modes are unlikely to be captured by a shared measure of size and connectivity. The simple delimitation of habitat from non-habitat may differ across species as well. Modelling colonization and extinction parameters as a function of site-specific environmental properties across sites for each species represents a more general approach to consider site heterogeneity (**Sjögren-Gulve & Ray 1996**; **Lamy et al. 2013; van der Merwe et al. 2016; Rodhouse et al. 2018**). This has previously only been applied to individual metapopulations, but it can account for the fact that each species may perceive habitat patch quality in its own way. In an assemblage of species, effects of covariates on colonization and extinction may give rise to species-specific spatial variation in observed and expected occupancy patterns. Thus, the success of this approach can be evaluated by its ability to reproduce and provide reasonable understanding of the diversity of species occupancy maps in the landscape. Additionally, for each species site heterogeneity is important for its average dynamics at the landscape scale because variance and covariance among sites in estimates of colonization and extinction rates may alter the predicted mean time until extinction (**Frank & Wissel 2002**), the weighted fraction of occupied patches (**Ovaskainen 2002**), or have other significant impacts on metapopulation dynamics (**Sutherland et al. 2012**, **Dubart et al. 2019**).

The third challenge of metapopulation models is to correctly account for temporal variation, which can arise from three main sources. First, colonization and extinction may vary temporally because the environment changes in time (**Ovaskainen 2002; Perry & Lee 2019**). This can be addressed for example by taking time series of an appropriate length to adequately sample this temporal variation, by considering time-varying covariates for extinction and colonization rates (e.g. **Rodhouse et al. 2018**), or by considering dynamic models of stochastic patch occupancy that explicitly incorporate this temporal variation (e.g. **Bertassello et al. 2020**). Second, the absolute colonization rate (the rate at which an empty site becomes occupied) varies in time due to changes in the proportion of occupied sites in the metapopulation, which act as sources of colonists. This relationship is captured by metapopulation models that express colonization rates on a per-occupied-site basis (i.e. relative colonization rates; **Levins 1969**) in the same way that birth rates are expressed as per-capita in standard population growth models. However, many empirical studies instead estimate absolute colonization rates (e.g., **Mackenzie et al. 2003**). These estimates may be problematic especially for invading or declining species, as projections will not account for natural feedbacks of occupancy on colonization and may fail to adequately predict the long-term dynamics of the metapopulation (**Hanski 1994**). This leads to the third source of temporal variation, which is non-stationarity. Models vary in whether or not the study system is assumed to be at quasi-equilibrium (not the eventual state of extinction expected for all systems, but instead the quasi-steady state the system converges to before this point; see **Hanski 1994**). Parameterizing a model that assumes quasi-equilibrium (e.g., in early instances of the incidence function model; **Hanski 1994**) when the population is not truly at equilibrium can produce unreliable estimates. For systems away from quasi-equilibrium, long time-series with state transitions between successive time points are needed to sample representative distributions of colonization and extinction events (**Moilanen 2000**). In this study, we model a time-series of metapopulation occupancy dynamics that addresses these temporal considerations in four ways. (i) We use a long time-series, decreasing the chance that colonization and extinction measures are drawn from a non-representative sample; (ii) our model estimates relative colonization rates (i.e. per occupied site) rather than absolute ones, which conforms with Levins' original formulation; (iii) these rates are purely estimated from temporal turnover data, which removes the need for any equilibrium assumption and accounts for temporal variation in occupancy dynamics among species at the landscape scale; and (iv) we included both spatial and temporal covariates to capture environmental effects on colonization and extinction rates in our model. The framework of **Lamy et al. (2013)** allows implementation of all these features except (ii), and so we modified its formulation to allow for this (see Methods).

We applied this spatially implicit metapopulation modeling framework to the guild of snail species that inhabit freshwater habitats of two islands (Grande-Terre and Marie-Galante) in the Guadeloupe archipelago, Lesser Antilles. These islands harbor over 3000 freshwater habitats that are connected to one another to various degrees, especially during the rainy season. Many sites are dry for several months, but some species can aestivate in the sediment for several weeks or more (**Pointier 1976**). We collected occupancy records of 22 mollusc taxa in 278 sites sampled annually from 2001 to 2015. We analyzed this time series using a modeling framework adapted from **Lamy et al. (2013)**, a multistate occupancy model that estimates colonization and extinction rates as a function of site- and year-specific environmental covariates. We provide estimates of these rates, determine how they vary over time and across sites, and use them in simulations to predict either the equilibrium proportion of occupied sites or the time until extinction, while taking uncertainty in parameter estimation into account. We use our results to address five main questions: (i) How do snail taxa vary in their colonization and extinction rates, and in their likelihood to persist, increase, or decrease at the landscape scale, and can we use our models to characterize different types of metapopulation behaviors reflecting the phylogenetic and life history diversity in this guild? (ii) Are colonization and extinction rates sensitive to year- and site-specific environmental properties, do these sensitivities vary among species, and can we adequately measure these sensitivities and use them to model species differences in habitat use and spatial distribution in the landscape? (iii) Can a comparative analysis of metapopulation parameters across multiple species reveal general patterns of life history strategies at the landscape scale? (iv) Does the inclusion of habitat-dependent variation alter predictions regarding persistence and global occupancy in the landscape, and for which species? (v) What are the methodological limits to our approach?

METHODS

Study system

The islands of Grande-Terre (639 km^2) and Marie-Galante (170.5 km^2) lie in the Guadeloupe archipelago in the Lesser Antilles (see **Pointier 2008**, **Lamy et al. 2013**, **Chapuis et al. 2017** for a description of the system). The islands are geographically and geomorphologically similar to one another and distinct from other nearby islands, which is why we consider their snail populations together. They harbor diverse types of freshwater habitats, including ponds, small rivers, and swamp grasslands connected to mangroves (subsequently referred to as back-mangrove), all of which vary dynamically in water levels and connectivity. Our study focuses on 27 taxa of freshwater molluscs (Appendix S1: Table S1) that occupy these habitats and constitute the major part of the macrobenthos. These taxa mainly belong to two groups: pulmonate snails belonging to the order Hygrophila (subclass *Heterobranchia*, 15 taxa in three families), and operculate snails of the subclass *Caenogastropoda* (10 taxa), belonging to three families (*Ampullaridae, Cochliopidae, Thiaridae* each in a different order). In addition one gastropod of subclass Neritimorpha, and one bivalve (family *Sphaeridae)* are represented. We considered six morphotypes of the caenogastropod *Melanoides tuberculata* and treated them as separate metapopulations because they reproduce parthenogenetically, and each of them represents a morphological and genetic clone with its own invasion history in the islands (**Facon et al. 2003**; **2008**). Prior to the 1970s, the archipelago harbored a relatively stable number of native snail species, but invasive species have appeared and settled since then (**Pointier 1976**; **Pointier & Augustin 1999; Pointier & Jarne 2011**). Native and invasive species differ in whether or not their metapopulation dynamics have stabilized and invasive species are also in different stages of their invasion sequence. Overall, we have a mix of species with either stable, increasing, declining, or fluctuating metapopulations. The metapopulation dynamics of one of the most common species, *Drepanotrema depressissimum*, was evaluated in **Lamy et al. 2013**, showing higher colonization and persistence in dry than in wet sites (as a consequence of aestivation in dry sites) and a marked influence of some environmental parameters (e.g., positive effect of connectivity on colonization in wet sites).

Multistate occupancy model

Based on **Lamy et al. (2013)**, we utilized a state-space model with a state process capturing transitions between site states (occupied / not occupied) and an observation process linking the data (detected / not detected) to the underlying states, to take into account imperfect species detection. The model estimates extinction and colonization probabilities as well as detection probability (the probability that a species is successfully detected during a site visit), and accounts for the existence of aestivating snails that may persist (unseen) in the ground of dry sites. Our model differed slightly from that of **Lamy et al. (2013)** in a few ways. First, instead of estimating as a single parameter the absolute colonization probability (that is equal to $c{*}p$), which depends on the proportion of occupied sites p (that can act as sources of propagules for colonization) and the colonization rate per empty patch c, we modeled the true relative colonization rate c. This rate determines the transition probability that an un-occupied site becomes occupied the next year, through: $P(0 \rightarrow 1|0) = 1 - e^{-cp}$, where $p = \frac{(\sum_{i=1}^{M} x_{i,t-1})}{M}$, M is the number of sites, and $x_{i,t-1}$ is the true occupancy status of site i at occasion t-1. This formulation reflects colonization as a continuous process in time, where e^{-cp} is the probability that a site has not been colonized by any propagule in one unit of time. The occupancy dynamics of a site thus can be modeled as:

Eq. 1: $x_{i,t} = x_{i,t-1}[\varphi + (1 - \varphi)(1-e^{-cp})] + [1 - x_{i,t-1}](1 - e^{-cp})$,

where φ is the probability of persistence from one occasion to the next. Following Lamy et al. (2013), the φ and c values used depend on the wet or dry state of the site at times t-1 and t. The probability of persistence in a wet site (φ_W) is used when the site is wet at t-1, and φ_D (dry site) when the site is dry at t-1. c_W (respectively c_D) is used when the site is wet (respectively dry) at time t. c_D is likely a very small value as the time window during which colonization can occur is reduced in dry sites. Given the very low precision of c_D estimates in initial runs of the models, we preferred to reduce the number of parameters and set colonization rate of dry sites to $c_D = 0$

(our results did not differ qualitatively when c_D was estimated). This implementation of the model estimated the probability of detecting a species in a wet site (d_W; referred to as p_W in Lamy et al. 2013) with the detectability set to 0 in dry sites. The model requires turnover data (changes in species detection over years within sites) and uses repeatability data (replicated visits of the same site within each annual sampling period; the time between sampling and resampling was short enough to preclude colonization and extinction) to estimate colonization and extinction rates and detectability, but does not make an equilibrium assumption. The initial occupancy of the metapopulation at the first sampled occasion is therefore estimated as an additional parameter Ψ (rather than deduced from other parameters or equilibrium assumptions).

Fitting of the model to data was conducted using a Bayesian procedure in JAGS (Just Another Gibbs Sampler, which implements Monte Carlo Markov Chain sampling; **Plummer 2003**), implemented in R (version 3.3.3, 2017) using the base package, the 'coda' package (**Plummer et al. 2006**), and the 'rjags' package (**Plummer 2016**). The prior distribution of d_W, φ_W, φ_D, and c_W were U(0,1), a uniform distribution over the interval [0, 1]. Initial occupancy probabilities for sites on the two islands (Grande-Terre and Marie-Galante), Ψ_{GT} and Ψ_{MG}, were estimated separately, both with prior distributions U(0,1), and each island had an island-specific mean occupancy probability each year p_t.

Data

We used records of 27 taxa (22 species, with six genetically distinct morphotypes of one species; Appendix S1: Table S1) that were surveyed in 278 sites (250 sites in Guadeloupe, 28 sites in Marie-Galante) annually from 2001 to 2015. Some species did not occur in the metapopulation until after 2001 and not all sites were sampled in all years (total number of site visits = 3593, mean and standard deviation of number of site visits per year = 222 ± 59). Sampling during the year 2012 had to be reduced to 57 sites for financial reasons, and those sites were chosen non-randomly as sites where *Physa acuta* had never been observed (this was crucial information for another study to document the invasion progression of this species) and as sites with risk of drying (from our own experience) to determine their dry or wet status. The 2012 survey data is therefore biased for low presence of *Ph. acuta* and of species that are not drought tolerant. Further sampling details are given in **Lamy et al. (2012, 2013)**, **Chapuis et al. (2017)**, and **Dubart et al. (2019)**.

To determine occupancy in this survey, each site was explored by three persons for approximately 15 min at each visit (total searching time: 45 min). The presence of snails was assessed by foraging the sediment and plants using a scoop, and rock surfaces or floating debris were visually surveyed as well. A randomly chosen subset of ~30 sites was revisited to evaluate species detection or non-detection. For each year and site, we recorded the detection or non-detection of each taxon, and a series of environmental properties including the dry state (whether a site was dry or not; species cannot be detected in dry sites), size (pond diameter or river width in m), percent vegetation cover (included taxa are given in Appendix S1: Table S2), water connectivity to neighboring freshwater habitats (four levels of never, occasionally, often, and always connected; measures structural connectivity of sites), and overall hydrological regime (five levels, from fully permanent to frequently dry during the dry season). Connectivity, vegetation cover, and site hydrology were visually assessed (Appendix S1: Table S3). Sites were also characterized as ponds, rivers or back-mangroves (Appendix S1: Table S3). A small subset of sites had no observation of dry/wet state in some years (69 of 3593 total observations). In these instances, this state was replaced with a probability of that site (i) being dry in that year (t):

$dry_{i,t} = 1-w_{i,t}$ (where $w_{i,t}$ is the probability of site *i* being wet in year *t*). This probability was estimated by fitting a generalized linear mixed-effects model (GLMM) with site and year as random effects and a binomial error structure (implemented in R using the ‘lme4’ package, **Bates et al. 2014**) to all sample occasions where dry/wet state was observed.

Model without covariates

For each species, we fitted the multistate occupancy model to the data using a Bayesian framework to generate estimates of φ_W, φ_D, and c_W. Colonization of dry sites c_D was assumed to be zero (data, JAGS code, and R code for the model without covariates are in Data S1). The model was run with 20,000 iterations, the first 10,000 of which were discarded as a burn-in period, with three parallel chains (initial values of d_W, Ψ_{GT}, Ψ_{MG}, φ_W, φ_D, and $c_W = 0.1$ for chain 1, 0.5 for chain 2, and 0.9 for chain 3). Model fit to observed data was assessed by comparing the mean and 95% credibility interval (C.I.) of the posterior distribution for model-estimated proportion of occupied sites with the observed proportion each year (a posterior predictive check; **Rubin 1984**; **Gabry et al. 2019**). The observed values (per year, $p_{t,obs}$) were calculated by dividing the number of sites a species was observed in (or observed in either visit, for sites visited twice) by the number of sites visited. Since the model generates posterior distributions for occupancy values in site×year instances that were not observed in our dataset, we report model predictions for each year both as the predicted proportion of occupied sites (p_t) and as the probability of observing a given taxon that year, i.e. the proportion of wet sites that were occupied multiplied by the detection probability in wet sites and by the proportion of wet sites w ($p_{visit,t}\, d_W\, w$). This measure is most directly comparable to observed data.

Metapopulations are expected to persist if the ratio of the extinction rate to the colonization rate is less than one (**Levins 1969**). To compare our results to this persistence threshold, we converted φ to the instantaneous extinction rate e (the same as e in the Levins model) using $e = -\ln(\varphi)$ (this arises from considering that extinction occurs as a continuous process and the probability of not being extinct in one unit time is exp(-e)). To evaluate the influence of considering snail aestivation in dry sites for persistence, we compared two ways of calculating e/c: e_W/c_W (considering wet sites only) and $\left[\frac{(e_W)*w+(e_D)*(1-w)}{c_W*w}\right]$ (averaging rates over wet and dry sites). Here w is the overall probability of a site being wet, estimated as the average of all fitted values obtained from the GLMM of the observed dry state data described previously (that produced $w_{i,t}$ values). We also calculated posterior distributions for the predicted equilibrium frequency according to the Levin's model ($p^*=1-e/c$), multiplied by detection probability (d_W). Multiplication of model-expected values for p by d_W allows comparison to field observed data, which underrepresents true occupancy because of imperfect species detection. These estimates were compared across species and also between native and introduced species.

Model with covariates

For each species, we ran a second model incorporating factors that may influence demographic parameters (see **Lamy et al. 2013**, **Dubart et al. 2019**). Site-specific environmental variables (i.e. with one value per site that does not vary across years) were site size (S_i), vegetation cover (V_i), water connectivity (C_i), site stability (Stab_i), back-mangrove (m_i), and river (r_i). The values of S_i and V_i were $\log_{10}(1+X)$ transformed to better approximate a normal distribution, and the S_i, V_i, and C_i values were averaged over the 15 survey years (Appendix S1: Table S3). We chose to average these values and thus only consider them as site covariates because, although some sites show strong temporal variation, our annual measure is unlikely to capture the relevant weekly to monthly differences expected in small semi-permanent or temporary ponds. Our averaging of the annual measures instead captures a snapshot of site features at a common point in time, the beginning of the dry season.

To contrast between smaller, more variable semi-permanent or temporary sites and larger, more permanent sites, we developed a composite measure of among-year variability, Stab_i. Stab_i was computed as the first axis (explaining 65% of total variance) of a principal component analysis including the average hydrological regime (across years), the proportion of visits during which the site was dry over the 2001-2015 period, and the temporal variances of the $\log_{10}(1+X)$-transformed values of site size and vegetation cover. Year-specific environmental variables (i.e. identical for all sites within a year) included cumulative rainfall during the little rainy season (LRS_t, mm, from March 1 to May 31) and the rainy season (RS_t, mm, from July 1 to December 31) of the year preceding the sampling campaign. Rainfall covariates were taken as the average value from five weather stations (data gathered from Météo-France; information about each station in Appendix S1: Table S4, imputation of missing data points, and the choice of dates for RS_t are explained in Appendix S1: Section S1).

We also used an index of local propagule pressure per site i and year t, $D_{i,t}$. We estimated $D_{i,t}$ as $D_{i,t} = N_i P_{i,t}$, where N_i is the total number of freshwater habitats occurring within a 4-km radius circle around site i (visited or not) and $P_{i,t}$ is the proportion of occupied sites at time t among the surveyed sites within that circle (see **Lamy et al. 2013** for further detail). The 4-km distance was chosen based on practical considerations such as having a reasonable number of surveyed sites to estimate $P_{i,t}$ around each site and having circles that were still relatively small compared to the entire island. The lists and maps of all freshwater sites on Grande-Terre and

Marie-Galante were generated as described in Appendix S1: Section S2. This covariate is not a spatially-explicit dispersal kernel, which requires exhaustive sampling of all potential habitats to sum the separate contributions of all occupied sites to the propagule pressure on each empty site. As our main focus was not on dispersal kernels, we instead used $D_{i,t}$ as a correction for potential spatial variation in the local density of occupied sites.

Persistence probabilities in wet sites for each species were modeled as linear-logistic functions of six environmental variables (see **Lamy et al. 2013** for explanation of model construction):

Eq. 2: $\mathrm{logit}(\varphi_W) = \alpha_1 + \beta_1 S_i + \beta_2 V_i + \beta_3 \mathrm{Stab}_i + \beta_4 \mathrm{LRS}_t + \beta_5 m_i + \beta_6 r_i$,

where α is the intercept and each β is a regression coefficient to be estimated. We did not estimate the effects of covariates on persistence rates in dry sites, so we only estimated the intercept for φ_D as:

Eq. 3: $\mathrm{logit}(\varphi_D) = \alpha_2$.

Colonization rates in wet sites for each species were modeled as log-linear functions of eight environmental variables:

Eq. 4: $\log(c_W) = \alpha_3 + \beta_7 S_i + \beta_8 V_i + \beta_9 \mathrm{Stab}_i + \beta_{10} C_i + \beta_{11} \mathrm{RS}_t + \beta_{12} D_{i,t} + \beta_{13} m_i + \beta_{14} r_i$.

Choices for inclusion of model covariates are described in **Lamy et al. (2013)**: connectivity and local propagule pressure were expected to act only on colonization, the rainy season variable (RS_t) is likely to only impact colonization because this is when floods and water connections among sites occur, and the little rainy season (LRS_t) is likely to influence persistence as this is when sites tend to shrink in size or sometimes desiccate. Colonization rates of dry sites were assumed to be 0. We chose to construct models with various subsets of the covariates both to limit overfitting and to reflect hypotheses about expected relationships. We did not use covariates for φ_D because it was unrealistic to fit them correctly given the low number of instances of dry sites in the data. All the covariates were centered and reduced to obtain the β values on a standardized scale. The intercepts (α values) thus represent the expected value of $\text{logit}(\varphi_W)$ or $\log(c_W)$ in a site and year with average covariate values. We assessed inclusion or exclusion of environmental covariates using stochastic search variable selection (SSVS; **George and McCulloch 1993**; **O'Hara and Sillanpää 2009**), where in each iteration of the model, each regression parameter was either estimated or set to 0. The prior distribution of each regression parameter was the same as in **Lamy et al. (2013)** - in this model with covariates, the prior distribution for the intercept terms of φ_W, φ_D, and c_W was N(0, 10). We assessed inclusion of model covariates by evaluating the posterior of α_p, which is a binary indicator variable used in SSVS that is set to either 0 or 1. A covariate was considered to have a credible posterior estimate of effect size β if the proportion of posterior models that included a given covariate ($P_{\alpha p} = 1 \mid$ data) was ≥ 0.6. This value was chosen to ensure that posterior ($P_{\alpha p} = 1 \mid$ data) values were not simply reflecting the prior mean of α_p, which was 0.5. The model was run with 20,000 iterations, the first 10,000 of which were discarded as a burn-in period, with three parallel chains. Initial values of d_W, Ψ_{GT}, and $\Psi_{MG} = 0.1$ for chain 1, 0.5 for chain 2, and 0.9 for chain 3, while initial values of α_1, α_2, α_3, and each β parameter = -0.2 for chain 1, 0 for chain 2, and 0.2 for chain 3 (data, JAGS code, and R code for the model with covariates are in Data S2).

We generally expected positive effects of connectivity, local propagule pressure, and rainy season for colonization and variable effects of little rainy season for persistence depending on whether a species is harmed or aided by site desiccation. We also expected site stability to positively influence persistence for most species. Mangrove and river covariates were expected to be significant with a positive influence for species known to prefer these habitats (e.g., mangrove: *Biomphalaria glabrata* and *Drepanotrema cimex*; river: *Neritina virginea*) and not important for species without this habitat preference. Finally, we also expected an overall positive influence of site size on persistence and colonization in accordance with this general assumption in models of island biogeography (**MacArthur & Wilson 1967**) and in metapopulation models as well (**Hanski 1994**; **Moilanen & Hanski 1998**).

We compared the effects of covariates for colonization and persistence across all taxa in two ways. First, we ran a principal component analysis using the posterior mean value for each of the 14 β coefficients estimated from the model (including those for colonization and persistence for the seven environmental variables in the same analysis; calculated as the singular value decomposition of the centered and scaled matrix of coefficients). Second, we evaluated whether principal component scores differed for pulmonate (Hygrophila) and Caenogastropod taxa using a discriminant analysis of principal components (DAPC, implemented using R package ‘adegenet’, **Jombart 2008**; **Jombart & Ahmed 2011**; the analysis thus excluded *N. virginea* and *Eupera viridans*, two rare species that belong to neither of these two groups), and determining the percent of species successfully reassigned to their taxonomic grouping using the a single discriminant axis to describe the first two PC axes.

Spatial variation: site-specific persistence

Significant environmental covariates suggest there is no single colonization and extinction rate for each species, but rather that site-specific properties influence a species' ability to colonize and persist in a particular site. We plotted each site's model-estimated value of extinction rate divided by colonization rate (e_i/c_i), averaged across all years. This was done by taking the mean posterior estimate of $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$ for each site and each year obtained when all covariates were taken into account, then weighing these values by the probability a given site was wet, then averaging these values across all years. In this formulation, $\frac{e_i}{c_i} = \frac{\sum_{t=1}^{T}[(e_{D(i,t)})(1-w_{i,t})+(e_{W(i,t)})(w_{i,t})]/c_{W(i,t)}*w_{i,t}}{T}$, where T is the total number of years of observations (15 for this dataset) and $w_{i,t}$ is the probability a given site is wet in a given year. $w_{i,t}$ was estimated from the observed dry state data using the GLMM described previously.

Heterogeneity among sites may alter expectations for metapopulation occupancy and long-term persistence because favorable sites can provide extinction-resistant pockets even if many other sites are unfavorable (**Frank & Wissel 2002**; **Ovaskainen 2002**; we also present a simplified derivation of the effects of variance and covariance in colonization and extinction in a spatially implicit metapopulation model, which is the case in this analysis, in Appendix S3: Section S1). The use of covariates is a first way to account for this heterogeneity, but it is also possible that some species are completely unable to live in some sites, for example if they are specialized on a particular resource or condition that is not captured by our covariates. In that case, fitting the model on the entire set of sites might represent an overly pessimistic view of their possibility to persist as a metapopulation. An optimistic view would be to consider only those sites in which the species has been detected at least once, which demonstrates its ability to colonize or persist in that site. To better understand how site-specific covariates modify our expectations for species persistence, we calculated e_i and c_i using (i) only the model intercept value (and therefore using the same value for $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$ for each site), (ii) using all covariates, and (iii) using all covariates but only considering sites where the species was observed at least once during our survey (we also report results in appendices using only covariates that were retained by the SSVS procedure in ≥ 60% of the Bayesian model iterations, but this did not qualitatively change the main results). For scenario (iii), we did not re-fit the entire model using this subset of sites but instead used the values obtained for these sites from the overall model with covariates (Equations 2-4). The variance, covariance, and Pearson's correlation coefficient for all e_i and c_i values were calculated as well.

Temporal analysis: metapopulation persistence expectations

To provide expectations for how long each species would be expected to persist on the islands and what proportion of sites would be occupied each year based on the results of our model-estimated colonization and extinction parameters, we simulated occupancy dynamics (annual transition between occupied and un-occupied states) on a 1000-site landscape for 999 years (or until the species went extinct) using a combination of model-estimated parameters and observed site and year properties. We chose to simulate dynamics on a landscape with more sites than we have data available for because our sampled sites represent only a subset of the total number of sites on the islands. The simulation model considered both among-site and among-year variation in e_i and c_i to provide an expectation for metapopulation dynamics. We repeated the simulations 999 times to generate confidence intervals for the estimate of proportion of sites occupied (or time until extinction) by each species. To initialize the simulation, each of the 1000 simulated sites was randomly assigned the identity and associated values of one of the 278 observed sites. These properties are (i) the site- and year-specific $w_{i,t}$ (estimated from the GLMM described previously), (ii) the model-estimated site-specific average occupancy x_i (this is the posterior mean of the average occupancy for each site across all 15 years), which was used as the initial occupancy probability $x_{i,0}$ in the simulation, and (iii) the site- and year-specific model-estimated values of $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$. The initial occupancy of each simulated site was obtained by a draw from a Bernoulli distribution with probability $x_{i,0}$ and the initial dry state $w_{i,0}$ was obtained by a draw from a Bernoulli distribution with a probability $w_{i,t}$ where t was randomly chosen from 1-15. For each of the 999 years of the simulation, one of the 15 years of the observed data was chosen at random, and the characteristics (climatic covariates and proportion of dry sites) of the observed data for that observed year were used in the simulated year. We randomly assigned the dry state to each site each year with probability $w_{i,t}$ and the new occupancy state for that simulated year was drawn at random based on the previous occupancy, the dry state, and the appropriate transition probability matrices incorporating $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$ (Equation 1). The main goal was to simulate the expected proportion of occupied sites (p_t, estimated by p_{1000}, the proportion of occupied sites in year 1000 of the simulation) or the time until population extinction.

To illustrate how site-specific covariates modify our expectations for species persistence in this simulated model, we utilized five estimates of $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$: (i) estimates from the model with no covariates, (ii) estimates using only the intercept values from the model with covariates, (iii) estimates including all covariates, (iv) estimates from the model with all covariates but only including sites where the species was observed at least once during our survey, and (v) estimates using only covariates where SVSS support ($P_{\alpha p} = 1$ | data) equaled or exceeded 0.6. To compare the frequency of observation of species at each site in the metapopulation ($p_{i,obs}$) with the occupancy expectation at quasi-equilibrium generated by the simulation model (p_i*), we calculated $p_{i,obs}$ as the number of times the species was detected at a site divided by the number of visits to that site and we calculated $p_i* = d_W[c_i p* / (c_i p* + e_i)]$, where $p*$ was taken as the proportion of sites occupied by the species in year 1000 of the simulation that used all covariates (assumed to be our best estimate of quasi-equilibrium metapopulation occupancy). Here, c_i and e_i were calculated as described previously (i.e. taking $w_{i,t}$ into account), and d_W was the posterior mean detection probability obtained from the Bayesian model with covariates.

RESULTS

Overview

The freshwater snails of Guadeloupe were observed to be diverse in several ways. Some native species (*Aplexa marmorata*, *D. depressissimum*, *Drepanotrema surinamense*) and some invasive species (*Biomphalaria kuhniana*, *Ph. acuta*, *Pseudosuccinea columella*) were observed frequently (> 30% of the 3429 total site×year visits of wet sites) in many sites (> 74% of the 278 sites in the study; Appendix S1: Table S1). Other species (*Marisa cornuarietis*, *Pomacea glauca*, *E. viridans*) were observed consistently (in ~12-24% of visits) but at a more limited number of sites (~31-43% of sites). Many (15) of the taxa were rare, observed in < 5% of the total visits to wet sites, but some of these were found consistently in habitats with particular characteristics. For example, *D. cimex* and *Pyrgophorus parvulus* were detected in 28 and 30 sites respectively, 15 and 11 of which are in back-mangrove. We subsequently give results for all 27 taxa, highlighting results for the most frequent taxa (i.e. observed in more than 150 of the 3429 total site × year visits to wet sites; Appendix S1: Table S1).

The taxa also varied substantially in their metapopulation occupancy dynamics over the course of the 15 year survey (Figure 1, Appendix S2: Figures S1 and S2). Some were declining (*B. glabrata*, *Biomphalaria schrammi*) and some were stable or slowly decreasing with a degree of fluctuation (*A. marmorata*, *D. depressissimum*, *D. surinamense*). Some introduced species were observed to be spreading, at either a rapid (*Ph. acuta*) or slow (*Ma. cornuarietis*, *Tarebia granifera*) pace, while other introduced species remained restricted to a few sites (*Indoplanorbis exustus*, *Helisoma duryi*).

Model without covariates

The model provided estimates that fit well with the observed data (Figure 1, left column; Appendix S2: Figure S1; see Appendix S1: Table S10 for a list of Tables and Figures that allow comparison of results for models without and with covariates), especially when comparing the model-estimated probability of observing a taxa in a given survey year ($p_{visit,t}\, d_W\, w$; blue points in Figure 1) with the observed occupancy data ($p_{t,obs}$; orange points in Figure 1). The mean detection probabilities over all snail taxa was 0.59, with some variation among taxa (standard deviation ± 0.18; Table 1). This becomes 0.67 (± 0.12) when considering the most frequent taxa (≥ 150 total occurrences in the data set). This illustrates the variation in estimate uncertainty for taxa that appear at various frequencies in the dataset (Tables 1 and Appendix S1: Table S1). Detection probabilities were generally estimated with a high degree of certainty using our site re-visit procedure (average width of the 95% C.I. of the posterior distribution for d_W = 0.23 ± 0.21; 0.10 ± 0.05 for the most frequent taxa). On average, the 27 snail taxa experienced high persistence (φ_W: 0.86 ± 0.09; 0.85 ± 0.09 for the most frequent taxa) and colonization (c_W: 0.21 ± 0.14; 0.26 ± 0.17 for the most frequent taxa) rates in wet sites. Persistence in dry sites was both lower and more variable among taxa (φ_D: 0.59 ± 0.22; 0.72 ± 0.23 for the most frequent taxa). This parameter was estimated with a relatively low degree of certainty (average width of the 95% C.I. of φ_D posterior distribution = 0.66 ± 0.28; 0.46 ± 0.22 for the most frequent taxa), likely due to the relative dearth of dry sites (164 out of 3593 total observations across all sites and all years) and the fact that species that are very rare or occur only in stable sites will thus not have any survey records that allow estimating dry persistence. For example, for species with $\leq$ 50 total occurrences in the dataset, the estimates reflected the uniform prior distribution (i.e. posterior mean close to 0.5 and C.I. close to 0.025-0.975; Table 1). Nevertheless, some species (e.g., *A. marmorata*, *D. depressissimum*, *D. lucidum*, *B. straminea*, *Ma. cornuarietis*) did have both high and reliable estimates for φ_D. The 95% C.I. of the posterior distributions for φ_W, φ_D, c_W, and d_W are given in Table 1.

Some taxa would be projected to persist (as opposed to decline to extinction) under a Levins equilibrium assumption that populations persist when colonization rates exceed extinction rates ($e/c < 1$; Figure 2). The inclusion of dry sites and φ_D estimates did influence the persistence threshold estimates, decreasing the prospects of persistence for some species (Figure 2, white points). Seven species are expected to persist with high confidence (i.e. the 95% C.I. for $\log(e/c)$ is entirely below 0): *D. surinamense*, *D. depressissimum*, *A. marmorata*, *Ph. acuta*, *B. kuhniana*, *Ma. cornuarietis*, and *E. viridans*. Five species are expected to be extinct with high confidence (*Po. glauca*, *B. glabrata*, *B. schrammi*, *Gundlachia radiata*, and *D. aeruginosum*). Seven taxa are expected to persist but the 95% C.I. crosses the extinction threshold (*Ps. columella*, *Galba cubensis*, *Plesiophysa guadeloupensis*, *Me. tuberculata* PAP, *Me. tuberculata* GOS, *Me.*

tuberculata FAL, and *Me. tuberculata* CPF) and eight taxa are expected to be extinct but have 95% C.I. that span the persistence threshold (*Py. parvulus*, *D. cimex*, *T. granifera*, *Me. tuberculata* MAD, *N. virginea*, *I. exustus*, *Me. tuberculata* SEN, and *H. duryi*). The predicted equilibrium frequency according to the Levins model ($p^*=1-e/c$), after multiplying by detection probability (d_W), can be plotted against the frequency of detection of each species observed from the data (averaged over years; Figure 3a). This plot shows whether species are expected to decline (observed > expected, above the 1:1 line in Figure 3a) or increase (expected > observed, below the 1:1 line in Figure 3a) in the long term. Both declining and increasing trends are predicted for some native and introduced species, indicating that not all introduced species are experiencing a continued successful invasion process. However, some introduced species (*Ph. acuta*, *Ma. cornuarietis*) are clearly still spreading (Figures 1 and 3a).

The extinction rate parameter e represents the relative rate of turnover in occupied sites when considered in the long term, since at equilibrium the colonization of new sites exactly replaces extinct sites. The snail taxa can thus be broadly classified as fast turnover (*D. aeruginosum*, *Ps. columella*, *B. kuhniana*, *B. schrammi*, and *I. exustus* – but note from Figure 2 that only some of these species are expected to persist in the long term), slow turnover (*Ma. cornuarietis*), and intermediate turnover (all other species; Figure 4a). Some species have similar expected equilibrium occupancies (p^*), but differ in extinction rate. For example, the two most common *Me. tuberculata* morphs (GOS and PAP), as well as *Ga. cubensis*, have a much lower turnover (e) rate than *Ps. columella* and *B. kuhniana* despite their similar range of expected stationary occupancy values ($p^* = 0.07\text{-}0.31$; Figure 4a).

Model with covariates

The model provided estimates of proportion of sites occupied for each year in the study period (p_t, $p_{visit,t}d_{W}W$) that fit well with the observed data ($p_{t,obs}$; Figure 1 and Appendix S2: Figure S2). Including covariates slightly improved the match between the observed proportion of occupied sites (p) and the model-predicted proportion of occupied sites at equilibrium (p^*), as indicated by more species being closer to the 1:1 line in Figure 3b than in Figure 3a (Pearson correlation between p and p^* for model without covariates = 0.81, for model with covariates = 0.82). Consideration of site and year covariates shifted the posterior distributions of estimated parameters from the model without covariates. On average across all 27 taxa, $\varphi_W = 0.76 \pm 0.14$ (0.71 ± 0.12 when considering the most frequent taxa), $c_W = 0.19 \pm 0.19$ (0.27 ± 0.23), $\varphi_D = 0.57 \pm 0.24$ (0.61 ± 0.28), and $d_W = 0.61 \pm 0.20$ (0.61 ± 0.21) (Table 1) based on intercepts of the models given in Equations 2-4 - most of these values, especially persistence rates, were slightly lower than when covariates were not considered. Some of the covariates influenced colonization and extinction (the posterior 95% C.I. did not include zero and $P_{\alpha p} \geq 0.6$ - the proportion of Bayesian posterior samples where SSVS included the covariate; details in Appendix S1: Tables S5 and S6 and plotted in Appendix S1: Figures S1 and S2; posterior means are given only including iterations where $\alpha_p = 1$). Each covariate strongly influenced φ_W or c_W (i.e. $\alpha_p \geq 0.6$) for at least three of the 27 taxa and on average taxa were strongly influenced ($\alpha_p \geq 0.6$) by 4.11 ± 2.68 of the 14 covariates. Some species were particularly influenced by environment. For example, *Ph. acuta* persistence in wet sites (φ_W) was positively influenced by rainfall in the little rainy season (posterior mean and 95% C.I. of β_{LRS}: $0.34 \leq 0.76 \leq 1.24$, $\alpha_p = 0.99$) and was higher in back-mangrove sites (β_m: $0.37 \leq 1.14 \leq 2.38$, $\alpha_p = 1.00$), while its colonization rate in wet sites was positively influenced by size (β_S: $0.23 \leq 0.40 \leq 0.56$, $\alpha_p = 1.00$) and connectivity (β_C: $0.29 \leq 0.50 \leq 0.75$, $\alpha_p = 1.00$) and negatively influenced by vegetation (β_V: $-0.74 \leq -0.60 \leq -0.45$, $\alpha_p =$

1.00), rainfall in the rainy season (β_{RS}: $-0.56 \leq -0.34 \leq -0.14$, $\alpha_p = 0.96$), and the back-mangrove habitat (β_m: $-1.71 \leq -1.12 \leq -0.73$, $\alpha_p = 1.00$). On the other hand, *A. marmorata* was influenced by only one covariate, i.e. vegetation cover increased persistence in wet sites (β_V: $1.58 \leq 2.09 \leq 2.63$, $\alpha_p = 1.00$).

The PCA of posterior mean β coefficients for covariates highlighted additional properties of species metapopulation demography. The first two axes explained 37% of the variation. PC axis 1 oriented some species that had higher colonization and persistence rates in unstable sites with high vegetation cover (V_i), in mangrove sites (m_i), and when rainfall in the rainy season is low (RS_t; e.g. *B. glabrata*, *B. schrammi*), against other species that thrived in stable sites with little vegetation (V_i) and that colonized more efficiently when rainfall in the rainy season was high (RS_t; e.g. *T. granifera*, *Gu. radiata*; Figure 4b). Positive values on PC axis 2 were associated with species that had high persistence in riverine sites (r_i) and also with colonization rates that depended on connectivity (C_i) and local propagule pressure ($D_{i,t}$; *Ga. cubensis, Po. glauca, Py. parvulus*; Figure 4b).

The clustering of species by their taxonomic group (Caenogastropods or pulmonates) in PC space was reflected in the discriminant function analysis. The linear discriminant function of the PC scores for model covariate coefficients was successful in sorting snail taxa into the two taxonomic groups, successfully re-assigning 80% of taxa to their correct classification (12 of 15 pulmonate snails and 8 of 10 *Caenogastropoda*; Figure 5). The position of covariate regression parameters (β_i) along the discriminant function axis indicates that taxonomic groups are broadly described by the effects of stability. The association of strong positive effect sizes for site stability (Stab_i), rainfall in the rainy season (RS_t), site size (S_i), local propagule pressure ($D_{i,t}$), and site connectivity (C_i) for colonization and for site stability (Stab_i) and riverine sites (r_i) for persistence indicate that Caenogastropods are more likely to colonize and persist at sites that are large, stable, and highly connected to other sites. Pulmonate snails were associated with strong positive effect sizes of vegetation (V_i) and rainfall in the little rainy season (LRS_t) for persistence and of vegetation (V_i) for colonization. For these taxa, site stability was less important for colonization and persistence (Figures 4b and 5). Some taxa do not conform to these broad patterns, such as *Gu. radiata* (which has a strong positive effect of stability and size for colonization) and *Ga. cubensis* (which has a strong positive effect of propagule pressure and connectivity for colonization).

Site-specific colonization and extinction

Our visualization of among-site habitat suitability across the islands of Grand-Terre and Marie-Galante indicates that for most species, sites vary in whether they are metapopulation "sources" ($e_i/c_i > 1$) or "sinks" ($e_i/c_i < 1$). For some species, the sources greatly outnumber the sinks throughout the islands (Figures 6a, b, d). Depending on species, source sites are spatially scattered (Figure 6f), or clustered (Figures 6c, and 6e; maps for all taxa are given in Appendix S2: Figure S3). Plots of each site's estimated e_i and c_i values from the model with covariates are given in Figure 7, while plots using different subsets of data (i.e. using only the model intercept value, all covariates, or all covariates but only for sites where the species was observed at least once) are provided in Appendix S1: Figure S3 (Appendix S1: Figure S4 includes results when considering only covariates that were retained by the SSVS procedure in ≥ 0.6 of the Bayesian model iterations, but this did not qualitatively change the results). These plots indicate that while the model intercepts are helpful in summarizing the overall persistence expectation, sites varied substantially in their e_i and c_i values when covariates were taken into account. The effect of covariates on extinction and colonization is expected to result in negative correlations between e_i and c_i across sites in most species (Appendix S1: Table S7; Appendix S1: Figure S5), which is important because it indicates that extinction-prone sites are less likely to be colonized and suitable sites are more likely to be colonized.

Metapopulation persistence expectations

Model predictions obtained by simulation suggest that metapopulation persistence and stationary state can depend on covariates. For the most frequent taxa, the difference is a small variation in the proportion of occupied sites (Figure 8). However, for species of low to moderate frequency, considering covariates can substantially alter the expectations (Figures 6 and Appendix S1: Figure S6; Table S8). Many species that would go extinct in the model using only the intercept values for φ_W, φ_D, c_W instead persist (*Me. tuberculata* PAP, GOS, FAL, MAD, *Po. glauca*, *B. glabrata*, *Ga. cubensis*, *Gu. radiata*, *Py. parvulus*, *D. cimex*, *T. granifera*, and *Pl. guadeloupensis*) or go extinct at a much later time in the simulations (*B. schrammi*, *D. aeruginosum*, *N. virginea*). None of the species expected to persist using only the intercept went extinct when covariates were taken into account. For most of the species expected to persist in the three scenarios (no covariates, intercept from model with covariates, and all covariates), the expected p_{1000} was higher when covariates were taken into account. The opposite pattern was however observed in *A. marmorata*, *Ph. acuta*, *Ma. cornuarietis*, and *E. viridans*. In these cases the decrease in p_{1000} was small, except for *Ma. cornuarietis*, which has a posterior mean p_{1000} of 0.63 without covariates and 0.49 with covariates. The simulation results differed in some instances when the metapopulation was modelled excluding (i.e. considering as non-habitat) the sites where the species was never observed (Appendix S1: Figure S6, Table S8). This assumption resulted in large decreases in p_{1000} for *Ph. acuta, Ma. cornuarietis*, *Me. tuberculata* GOS, and *T. granifera*, four species that are experiencing ongoing invasions. This suggests that these species have not yet encountered potentially favorable sites, and excluding these sites provides an underestimate of favorable habitats. The only species with expected extinction in all scenarios except the reduced sites scenario was *B. schrammi*.

We compared the observed site-specific occupancy $p_{i,obs}$ with the simulation model expectation of p_i*. We first evaluated these deviations averaged across all 278 sites. For many species, the deviations of the expected p_i* from $p_{i,obs}$ were relatively small (the average deviation across all 27 taxa, across all 278 sites = -0.031 ± 0.198), and the observed frequency matched the predicted values more closely than the model without covariates (i.e. comparing Figures 3a and 3b). The taxa with observed frequencies below the expected value were primarily introduced taxa such as *Ph. acuta* and *Ma. cornuarietis* that experienced an increase in the number of sites occupied over the survey period. These taxa are predicted to reach equilibrium occupancy at much higher values than their average past occupancy, irrespective of whether covariates are included or not in the model. We also evaluated site-specific variation in the deviation between observed and simulated occupancy values. Deviations across sites were relatively small for most of the most frequently observed taxa, with most average deviation values < 0.1 and a largely positive correlation between predicted and observed site-specific occupancies (Appendix S1: Table S9; Appendix S2: Figure S4). The species with the largest deviations again include recently invasive species (*i.e. Ph. acuta, Ma. cornuarietis*, *T. granifera*) for which the model indicates more favorable sites than the species has been observed in during the study period. Sites with p_i* values that greatly exceeded $p_{i,obs}$ values are locations where the invasive species are expected to expand their range.

DISCUSSION

Metapopulation models have successfully been used to describe the dynamics of single species in fragmented landscapes. We generalized this approach to a guild of 27 mollusc taxa occupying freshwater habitats on the islands of Grand-Terre and Marie-Galante and used simulations to explore their dynamics in the landscape. Importantly, these taxa were quite diverse in terms of current dynamics, prevalence, spatial distributions, and their ease of detection during field surveys. We subsequently address the five main questions raised in the Introduction based on the findings of our study.

A high diversity of metapopulation dynamics in a guild of taxa inhabiting the same landscape

The first issue was to characterize the diversity of demographic rates and future dynamics in the landscape, and this was first performed using a mean-field approximation treating all sites and years as identical, i.e. using models without covariates. These models already fit the observed data remarkably well (Figure 1 and Appendix S2: Figure S1). This fit is noteworthy given the diversity of observed trajectories, including introduced taxa that were invading the system slowly (*Ma. cornuarietis*, *Me. tuberculata* GOS) or rapidly (*Ph. acuta*) and local species that were slowly declining (*B. schrammi*, *B. glabrata*, *Po. glauca*) or fluctuating around stationary occupancies at various levels (high in *A. marmorata* and *D. depressissimum*; low in *E. viridans*).

Demography within populations is usually characterized through time-independent parameters (carrying capacity) and per-capita temporal rates (birth, death and growth rates)

(**Verhulst 1838**). These notions have inspired well-known classifications of strategies such as the *r*-*K* continuum (**MacArthur & Wilson 1967**; **Pianka 1970**; **Reznick & Bashey 2002**), the Grime CSR triangle (**Grime 1977**; but see **Silvertown et al. 1992**), and the fast-slow continuum (**Stearns 1983**; **Franco & Silvertown 1996**; **Oli 2004**), all of which attempt to relate trait syndromes (especially life-history traits) to demography. These approaches could be applied to the landscape scale using metapopulation equivalents of carrying capacity and temporal rates derived from Levins' *e* and *c* parameters, provided these metapopulation parameters are measured for several species in a landscape. Our results provide such information and illustrate the diversity of metapopulation strategies in the studied guild. A first way to characterize strategies is with the metapopulation equivalent of the carrying capacity, the theoretical stationary occupancy (proportion of sites occupied at stationary state, $p^* = 1 - e/c$; **Amarasekare 1998**), which in our study ranges from 0% (species predicted to go extinct) to 70% of sites for *A. marmorata* and *Ph. acuta* (Figures 2 and 4a). For native species, these stationary occupancies are usually close to those observed during our survey (Figure 3a). Differences arise for multiple reasons. Predicted values are lower than observed ones for some native species such as *B. glabrata* and *Po. glauca* that are declining and may become extinct. Predicted occupancies tend to be higher for introduced species experiencing the invasion process (*Ph. acuta, Me. tuberculata* morphs, *T. granifera*), especially for slow invaders such as *Ma. cornuarietis*.

The second way to characterize taxa is using the Levins model *e* parameter, which represents the metapopulation turnover rate. For any given stationary occupancy p^*, *e* is also proportional to the metapopulation growth rate which is $\left(\frac{p^*}{1-p^*}\right) e$, equivalent to the *r* in a population (**Amarasekare 1998**). We found that taxa with similar expected stationary occupancy

(p^*) may experience very different turnover rates. For example, *Ps. columella* and the most abundant morphs of *Me. tuberculata* (PAP and GOS) are introduced taxa with similar expected occupancy, but in this stationary state approximately half of the occupied sites change every year for *Ps. columella* while only around 15% change for the *Me. tuberculata* morphs (Figure 4a). Among species sharing a given stationary occupancy, high-turnover ones are also theoretically expected to reach this stationary state more rapidly and to be more prone to stochastic fluctuation than low-turnover ones.

Despite their simplicity, the mean field models (without covariates) perform remarkably well in capturing past dynamics of species inhabiting a common landscape. While it is not yet possible to determine how well simulations will fit future occupancy dynamics, their fit to past observed dynamics represent useful starting points to predict the fate of the mollusc community on the scale of a few years to a decade, provided the environment remains similar and no new invaders with large effects are introduced. The validity of any model projection depends on the quality and abundance of data, and taxa in our dataset varied in their frequency of appearance. Larger confidence intervals for model parameters were obtained for taxa that were rare in the dataset, which means their predicted dynamics are uncertain. Importantly, these species turn out to belong to two categories with very different implications for conservation. The first category includes species that may be able to occupy potentially more habitats than they now occupy but are currently declining (this is the case for *B. glabrata*, which was formerly very common on the island; **Pointier 1976; Pointier & David 2004**). The second category includes taxa that may be stable but restricted to particular types of habitats representing a small fraction of the total sites (known specialists of brackish sites or back-mangroves such as *N. virginea*, *D. cimex* or *Py.*

parvulus; **Pointier 1976; 2008**). For the latter, the predictions should therefore be improved by including among-site variation in extinction and colonization rates.

Environmental variation in metapopulation parameters and the diversity in habitat use in a metacommunity

Although the incidence function model introduced by **Hanski (1994)** considers patch variation in patch area and isolation, these properties are not always sufficient to predict metapopulation or occupancy dynamics (e.g. **Prugh et al. 2008**). Instead, an increasing number of studies consider variation in properties beyond patch size or isolation (**Fleishman et al. 2002**; **Heard et al. 2015**; **Howell et al. 2018**). Studies that considered environmental properties directly, not just via their impact on patch area and isolation, have demonstrated the importance of environmental features to predict occupancy (**Sjögren-Gulve & Ray 1996**; **Fleishman et al. 2002**; **Schooley & Branch 2009**; **Heard et al. 2015**) and thus that patches likely vary in their values of the metapopulation parameters that influence occupancy.

In addition, theoretical metapopulation studies that consider how colonization varies among sites usually focus on among-patch variation in contribution to the propagule pool and do not explicitly consider the variation in the capacity of a site to receive propagules. The latter may vary because of positional effects in spatially explicit models, but are not usually modelled as a function of site-specific habitat variables (e.g., **Moilanen & Hanski 1998**; **Hanski & Ovaskainen 2000**). However such responses to local habitat properties may be likely in natural landscapes, such as if local topography affects the receptive area for colonization. In this study we tried to capture these effects through our connectivity measure, which had positive effects for colonization rate in many taxa, confirming its importance. More generally, we modelled the effects of site characteristics on the probability to be colonized and to be extinct, while leaving aside other potential effects such as variation in site contribution to the propagule pool and spatial distance effects (the relatively weak effects of our local propagule pressure covariate suggest that potential improvements by relaxing these assumptions may be limited, but this requires further studies to be confirmed). This allowed us to quantify the responses of site-specific colonization rates and extinction rates to different sets of local habitat characteristics and also the variance and covariance among these rates emerging from such effects.

Our results confirmed that many site- and year-specific covariates, including (but not only) patch size and isolation, had substantial and taxon-specific effects on colonization and extinction rates (Appendix S1: Figures S1 and S2), and the model with covariates accurately reflected the observed occupancy dynamics and known habitat preferences of taxa (e.g., the back-mangrove specialists *Py. parvulus* and *D. cimex*, the riverine *N. virginea*, and species such as *D. depressissimum* and *B. schrammi* known for their ability to successfully colonize unstable habitats; Figure 6; Appendix S1: Figures S1 and S2). In addition, the predicted equilibrium occupancies matched the observed ones more closely than those of the mean-field model (Figures 3a vs. 3b). These results suggest that covariates register important information in the dataset. However, the dynamics of some species, especially rare ones, remained difficult to capture. Our approach does not capture potential specialization of particular taxa to habitat types that are not reflected in our list of covariates. For example, *Gu. radiata*, a small limpet-like pulmonate, is often found attached to dead leaves (**Pointier 2008**), and no variable in our list represents this resource.

The inclusion of covariates allowed us to map spatial variation in site suitability and compare it to spatial patterns of species occurrence. From the site-specific e_i and c_i values, we can evaluate whether the metapopulation would persist (e_i/c_i <1) or not (e_i/c_i >1) if all sites were identical to that particular site, and determine which sites act as sources of colonization or sinks of extinction in the metapopulation. This characterization of sites is not the same as the formal definition of source and sink populations (**Pulliam 1988**; **Runge et al. 2006**), which considers site-specific birth and death rates. We rather evaluate sites from a metapopulation perspective, using colonization and extinction rates. For our metapopulation analysis, these e_i/c_i values highlight the diversity of habitat use among taxa at the landscape scale (Figure 6 and Appendix S2: Figure S3). Taxa vary substantially in the overall distribution of source vs. sink habitats, both in their relative frequency and in their geographic proximity. For some species, the sources greatly outnumber the sinks throughout the islands (e.g., *A. marmorata*, *Ph. acuta*, *D. depressissimum*, and *Ma. cornuarietis*). For some species, a subset of spatially scattered habitats are sources (e.g., *Me. tuberculata* GOS), while for other species these sources are spatially clustered (e.g., *Po. glauca*, *Me. tuberculata* PAP), and in one instance reduced to a small patch of back-mangrove sites (*B. glabrata*).

For abundant taxa, model-estimated site-specific stationary occupancy (p_i*) matched quite well with the proportion of times a species was observed at a site (Appendix S2: Figure S4, Appendix S1: Table S9), suggesting a good fit of the model. The match was weaker for some rare taxa (see above the example of *Gu. radiata*) and for some recently introduced species. For the latter, the model thus identifies potentially favorable habitats not yet reached when our survey began. Our approach at a landscape scale thus compares to distribution models and ecological niche models at a regional scale, i.e. modelling environmental preferences as a function of observed occurrences or abundance (**Phillips et al. 2006**; **Elith & Leathwick 2009**; **Warren & Seifert 2011**; **Norberg et al. 2019**). The dependency on presence-only data and lack of consideration for sites where species are absent is a well-documented feature of these models, and is one way our modeling approach differs (see **Guisan & Zimmermann 2000** and **Kéry et al. 2013** for discussion of species distribution models including presence-absence data and **Warren 2012** for a discussion on the application of presence-only models). Expectations for occupancy and persistence can shift when only sites where the species was ever observed are considered, especially for invasive species because their potential habitat is not taken into account (Figure 8 and Appendix S1: Figure S6), and so our model's combination of including many freshwater sites and site-specific covariates can identify these potential sites for future expansion. Our modelling approach is also mechanistic rather than purely correlative, as it explicitly considers underlying demographic rates at the landscape scale and how they are tied to theoretical expectations for metapopulation persistence. However, we did not (yet) incorporate a detailed dispersal modelling and within-population demographic modelling as seen in other approaches (e.g., **Bocedi et al 2014**; see **Normand et al. 2014** for a review).

Comparative analysis of metapopulation dynamics across multiple species

One advantage of fitting the metapopulation model to data for 27 taxa is that we can compare results across taxa, and determine whether particular groups of species have similar or distinct strategies in their occupancy of the landscape. We distinguished between pulmonates and Caenogastropods, and found that fast-turnover species (based on e) were primarily pulmonate snails (Figure 4a). We observed that many of these species showed visible fluctuations around their expected equilibrium occupancy (the native *D. depressissimum* and *D. surinamense,* the introduced *B. kuhniana* and *Ps. columella*, see Figure 1, Figure 4a, Appendix S2: Figure S1, and Appendix S2: Figure S2) or rapidly increased towards their expected equilibrium (*Ph. acuta*). On the other hand, low-turnover species which include most Caenogastropods show slow, regular trends over the entire sampling period (Figure 1, Appendix S2: Figure S1, and Appendix S2: Figure S2). This gradual and regular trend was observed both for declining (the native *Po. glauca*) and increasing (*Me. tuberculata* GOS, *T. granifera*, *Ma. cornuarietis*) taxa.

The different metapopulation behaviors between pulmonates and Caenogastopods likely reflect their life-history characteristics. Pulmonates are generally small-sized, light-shelled and short-lived compared to Caenogastropods. They have shorter generation times and are known for their ability to rapidly proliferate (**Davis 1982**; **Taylor 1988**; **Dillon 2000**), and they are hermaphrodites capable of self-fertilization, which can be an advantage for colonization (**Jarne & Charlesworth 1993**; **Escobar et al. 2011**). They also have lungs and spend time breathing air at the surface, while most Caenogastropods dwell on the bottom. This lifestyle is likely why pulmonates easily attach to water birds (**Rees 1965**; **Malone 1965**; **van Leeuwen & van der Velde 2012**) and are usually the first snails to colonize new ponds (**Davis 1982**; **Barnes 1983**; **Kappes & Haase 2012**). We found that comparing the effects of covariates across taxa and also evaluating whether covariate effect sizes can discriminate between the two taxonomic groups provided insights beyond descriptions of each species independently. Pulmonates broadly depended on colonization and persistence at sites with high vegetation cover, while Caenogastropods were instead better able to colonize large, stable sites, with colonization that was more strongly dependent on rainfall during the rainy season. They also experienced higher persistence at more stable, connected sites. These trends are observed in both multivariate analyses (Figures 4b and 5). However, we detected exceptions such as the pulmonate *Gu. radiata* that tended to colonize stable sites and whose persistence was negatively influenced by site size and vegetation cover (Figures 4b, 5, Appendix S1: Figures S1 and S2). Metapopulation parameters may thus be related to trait syndromes to some extent, although this requires support from more comparative metapopulation studies with precise trait measurements for more taxa.

The role of among-site variation for metapopulation persistence and occupancy

An important goal of the study was to understand how expected metapopulation occupancy and persistence can be influenced by variance and covariance in colonization and extinction rates induced by habitat characteristics (**Frank & Wissel 2002**; **Ovaskainen 2002**). While including among-patch heterogeneity in size and position does not modify the general behaviour of the Levins metapopulation model (**Gyllenberg & Hanski 1997**; **Etienne 2002**), **Frank & Wissel (2002)** showed that among-patch heterogeneity in colonization and extinction rates, including spatially correlated extinctions, can influence the mean lifetime of a metapopulation. Temporal synchrony among sites in colonization and extinction is the focus of other studies that consider patch heterogeneity as well (e.g., **Ovaskainen 2002**; **Sutherland et al. 2012**).

Among-site variation in e and c as well as their negative covariance can increase equilibrium occupancy or prolong metapopulation persistence over time (**Frank & Wissel 2002**; **Ovaskainen 2002**; **Sutherland et al. 2012**; see also Appendix S3: Section S1 for a simplified derivation to illustrate this). In our study, the effects of covariates generated non negligible amounts of variance and negative correlations between e_i and c_i (Appendix S1: Table S7; Appendix S1: Figure S5). Incorporating habitat-driven variability in colonization and extinction indeed seemed to improve prospects of persistence for several taxa in the landscape, compared to simulation results derived from the mean-field model without covariates, or using only model intercepts (i.e. scenarios with the same c and e for all sites). This was especially true for many species with low frequency in the dataset (e.g., *B. glabrata, Ga. cubensis, Gu. radiata*; Figure 8 and Appendix S1: Figure S6; Appendix S1: Table S8).

Site size is a classic example of a source of negative covariance between *e* and *c* (**Hanski 1994**), as large sites can harbor large, extinction-resistant populations and attract more colonists at the same time. In our study, while site size has a generally positive effect on colonization, it has inconsistent effects on persistence (Appendix S1: Figures S1 and S2). Instead, descriptors of site quality such as vegetation cover, hydrological stability, and habitat type (mangrove or river) seem to be important drivers of variance and covariance among sites depending on species. This is especially true of species concentrated in particular habitats (back-mangrove: *B. glabrata* and *D. cimex*; riverine: *N. virginea*; unstable habitats: *D. depressissimum* and *B. schrammi*), some of which are predicted to go extinct in the simulation models using the mean-field or intercept parameter estimates but persist when covariates are considered. Overall, our results suggest that the diversity in site characteristics in the Guadeloupe landscape generally plays a protective role for metapopulation persistence, and that accounting for this variation through the use of covariates improves predictions, especially for rare or specialized species.

Limits of our approach

Although our method generally succeeded in capturing the diversity of uses of a common landscape by different species, often in line with field observations of habitat use, it also has some limitations to consider for future applications. First, our methodology, like any other, requires sufficient data to make accurate inferences. The validity of model inference may be questionable for fugitive species (species that may occasionally found locally abundant populations with a short half-life; e.g., *D. aeruginosum*), for species recently introduced in one or a few sites that are still at an uncertain initial invasion stage (e.g., *H. duryi*, *I. exustus*), or for species that are abundant in particular types of sites that are only marginally represented in the dataset (e.g., *N. virginea*). The potential consequences of surveying several species in a common set of sites highlight the importance of a careful study design where species with overlapping ranges of possible habitats that are reasonably represented in the sample are considered. The validity of model predictions also necessarily depends on our choice of covariates and not overlooking crucially important variables, a general issue in ecology.

Another limitation for long-term predictions is the assumption that features of the environment, including the quantity and quality of available habitat, are not also directionally changing with time. In fact, the freshwater habitats on the island of Guadeloupe are far from static. Ponds are sometimes lost to urbanization or land use changes. Although our rainfall variables did not indicate climatic tendencies over the 15 years of the study, on the long term, Caribbean islands are expected to experience a 2-5 °C increase in annual mean temperature, decreased overall rainfall and increased variability in rainfall, increase in cyclone activity, and sea level rise that can further exacerbate freshwater habitat loss (**Neelin et al. 2006**; **Karmalkar et al. 2013**). In addition, colonization and extinction parameters that depend on habitat quality may be time-dependent as well (**ter Braak et al. 1998**; **Moilanen 1999**; **Pellet et al. 2009; van der Merwe et al. 2016**), and temporal variation in habitat quality and associated colonization and extinction rates can influence metapopulation extinction risk (**Ranius 2007**). Our modeling approach focused on the use of environmental covariates to distinguish patch use among species, and we thus did not attempt to detect temporal trends in estimates of e_i and c_i (other than related to rainfall) for the multiple species considered in this study. Future simulation models can take into account the loss of freshwater habitat as well as environmental shifts expected under climate change scenarios.

An additional feature that our model currently does not take into account is interactions among species. For example, one species, *B. glabrata* (Figure 6c), seems restricted to a favorable subset of sites that overlap with the distribution of another species, *Ma. cornuarietis* (Figure 6d). *Biomphalaria glabrata* was previously much more widespread in Guadeloupe (**Pointier 1976**; **Noya et al. 2015**), but its range has contracted (mostly before our survey began) after the introduction of *Ma. cornuarietis*, a voracious grazer that greatly reduces the plant used as a substrate by *B. glabrata* for laying eggs (**Pointier & David 2004**). In this instance, though *Ma. cornuarietis* presence is not used as a covariate for *B. glabrata*, vegetation is used and had a positive influence on both its persistence (Appendix S1: Figure S1) and colonization (Appendix S1: Figure S2). Our model thus indirectly captures the impact of *Ma. cornuarietis* presence on *B. glabrata* through the vegetation covariate. Our model also successfully predicted the divergent spatial distributions of two morphs of *M. tuberculata*, PAP (Figure 6e) and GOS (Figure 6f), that are suspected to compete strongly with one another. In this way, our comparative metapopulation model may capture competitive interactions without explicitly modeling them. Nevertheless, interactions not reflected in the measured environmental covariates are likely, especially for species that have not reached their potential range expansions. For example, the future spread of invasive species such as *Ma. cornuarietis* may impact colonization and extinction of various local species and come to act as a source of environmental degradation in those habitats. Our projections may thus be improved by explicitly considering competitive interactions (see **Dubart et al. 2019** for consideration of model predictions for a pair of competing species in this system).

CONCLUSION

We conducted a comparative analysis of metapopulation dynamics in a guild of species inhabiting the same area and general habitat (freshwater bodies). This approach proved useful for characterizing colonization and extinction rates and their dependence on site- and year-specific environmental properties, and to project future dynamics. An important aspect of our model system is that it is disconnected from the continent and from other Caribbean islands, which means that colonization from outside can be disregarded as a contributor to metapopulation dynamics, although it explains the occasional arrival of new species. This approach can certainly be improved by considering competition among species and future shifts in climate with subsequent effects on the environmental variables considered here. Importantly our comparative approach could be considered as a first step to link metapopulation approaches that focus on single species in patchy environments (as studied by Hanski and others; see references above) to metacommunity approaches (e.g., **Leibold et al. 2004**; **Vellend 2010**) that describe collective features of guilds. It is also complementary to (joint) species-distribution models (e.g., **Little & Altermatt 2018**; **Norberg et al. 2019**), which can potentially include environmental covariables and can consider more complex guilds with more diverse types of species interactions, but which also provide less detailed knowledge on demographic dynamics. Our approach provides insight on demographic strategies at the metapopulation level such as low- and high-turnover species dynamics that reflect life-history properties. It can thus complement classic metapopulation, metacommunity, and species distribution models to better understand how species respond to environmental variation.

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Table 1. Persistence (φ), colonization (*c*) and detection probability (*d*) at the metapopulation scale for the 22 species studied (and clones in *Me. tuberculata*) for models without (no cov.) and with covariates (cov.). We provide the mean values and 95% credible intervals derived from posterior distributions. Values are given for species in descending order of number of appearances in the dataset (Detection$_{\mathrm{tot}}$ in Appendix S1: Table S1). The subscripts *W* and *D* indicate wet and dry sites respectively.

Species	φ_W		φ_D		c_W		d_W	
	no cov.	cov.	no cov.	cov.	no cov.	cov.	no cov.	cov.
A. marmorata	0.87 (0.83, 0.9)	0.8 (0.74, 0.85)	0.85 (0.67,0.99)	0.92 (0.71, 1)	0.47 (0.38, 0.57)	0.67 (0.57, 0.78)	0.82 (0.8, 0.84)	0.84 (0.82, 0.86)
D. depressissimum	0.89 (0.86, 0.92)	0.8 (0.75, 0.85)	0.97 (0.9, 1)	0.95 (0.77, 1)	0.22 (0.15, 0.29)	0.33 (0.22, 0.43)	0.7 (0.67, 0.73)	0.75 (0.71, 0.78)
B. kuhniana	0.75 (0.69, 0.8)	0.66 (0.55, 0.73)	0.76 (0.49, 0.97)	0.77 (0.39, 1)	0.44 (0.36, 0.52)	0.48 (0.4, 0.56)	0.74 (0.71, 0.78)	0.75 (0.71, 0.79)
D. surinamense	0.87 (0.82, 0.91)	0.66 (0.57, 0.73)	0.98 (0.92, 1)	0.94 (0.73, 1)	0.25 (0.17, 0.33)	0.44 (0.3, 0.57)	0.61 (0.57, 0.65)	0.69 (0.65, 0.73)
Ph. acuta	0.89 (0.85, 0.92)	0.88 (0.82, 0.93)	0.76 (0.46, 0.98)	0.85 (0.48, 1)	0.44 (0.37, 0.52)	0.49 (0.39, 0.59)	0.73 (0.7, 0.76)	0.74 (0.71, 0.77)
Ps. columella	0.66 (0.59, 0.73)	0.49 (0.38, 0.58)	0.16 (0.01, 0.48)	0.27 (0, 0.98)	0.6 (0.51, 0.7)	0.61 (0.52, 0.72)	0.73 (0.68, 0.78)	0.74 (0.7, 0.79)
Me. tuberculata PAP	0.89 (0.87, 0.92)	0.82 (0.74, 0.87)	0.6 (0.32, 0.89)	0.78 (0.29, 1)	0.18 (0.14, 0.22)	0.18 (0.13, 0.25)	0.74 (0.71, 0.78)	0.76 (0.73, 0.79)
Ma. cornuarietis	0.98 (0.97, 0.99)	0.98 (0.96, 0.99)	0.83 (0.61, 0.97)	0.87 (0.64, 1)	0.08 (0.05, 0.1)	0.05 (0.03, 0.08)	0.86 (0.84, 0.88)	0.86 (0.84, 0.89)
Po. glauca	0.92 (0.89, 0.94)	0.84 (0.73, 0.91)	0.45 (0.17, 0.8)	0.51 (0.03, 0.99)	0.07 (0.05, 0.11)	0.07 (0.04, 0.1)	0.7 (0.65, 0.74)	0.73 (0.69, 0.78)
E. viridans	0.89 (0.85, 0.93)	0.85 (0.77, 0.92)	0.79 (0.45, 0.99)	0.9 (0.56, 1)	0.21 (0.15, 0.27)	0.21 (0.15, 0.29)	0.51 (0.46, 0.57)	0.55 (0.48, 0.61)
B. glabrata	0.9 (0.87, 0.94)	0.62 (0.4, 0.81)	0.68 (0.35, 0.97)	0.28 (0, 0.96)	0.06 (0.03, 0.1)	0.06 (0.03, 0.1)	0.71 (0.65, 0.77)	0.77 (0.69, 0.84)
Me. tuberculata GOS	0.88 (0.82, 0.93)	0.8 (0.68, 0.9)	0.48 (0.04, 0.96)	0.52 (0, 1)	0.23 (0.17, 0.31)	0.18 (0.11, 0.26)	0.64 (0.57, 0.72)	0.68 (0.6, 0.75)
Ga. cubensis	0.86	0.8	0.8	0.73	0.18	0.07	0.48	0.56

	(0.79, 0.92)	(0.56, 0.94)	(0.48, 0.99)	(0.06, 1)	(0.12, 0.26)	(0.03, 0.13)	(0.4, 0.57)	(0.46, 0.67)
B. schrammi	0.7	0.61	0.93	0.77	0.21	0.18	0.45	0.49
	(0.57, 0.8)	(0.34, 0.83)	(0.74, 1)	(0.18, 1)	(0.11, 0.35)	(0.06, 0.36)	(0.35, 0.57)	(0.35, 0.68)
Gu. radiata	0.88	0.78	0.22	0.15	0.12	0.11	0.23	0.25
	(0.8, 0.94)	(0.6, 0.91)	(0.01, 0.64)	(0, 0.71)	(0.05, 0.21)	(0.04, 0.21)	(0.17, 0.31)	(0.18, 0.33)
Py. parvulus	0.96	0.59	0.43	0.37	0.08	0.03	0.52	0.68
	(0.92, 0.99)	(0.25, 0.89)	(0.04, 0.93)	(0, 1)	(0.04, 0.14)	(0, 0.07)	(0.45, 0.6)	(0.58, 0.78)
D. cimex	0.94	0.52	0.49	0.43	0.05	0.03	0.52	0.55
	(0.89, 0.98)	(0.16, 0.9)	(0.16, 0.87)	(0, 0.99)	(0.02, 0.1)	(0, 0.08)	(0.43, 0.6)	(0.44, 0.67)
T. granifera	0.89	0.87	0.43	0.41	0.17	0.08	0.81	0.83
	(0.82, 0.95)	(0.69, 0.97)	(0.02, 0.96)	(0, 1)	(0.1, 0.27)	(0.03, 0.15)	(0.73, 0.89)	(0.75, 0.91)
D. aeruginosum	0.62	0.64	0.72	0.62	0.28	0.13	0.1	0.1
	(0.15, 0.85)	(0.09, 0.94)	(0.2, 0.99)	(0.01, 1)	(0.03, 0.8)	(0, 0.51)	(0.05, 0.19)	(0.05, 0.22)
Me. tuberculata FAL	0.9	0.85	0.44	0.45	0.22	0.15	0.66	0.66
	(0.8, 0.97)	(0.59, 0.98)	(0.02, 0.96)	(0, 1)	(0.1, 0.38)	(0.04, 0.3)	(0.5, 0.79)	(0.5, 0.8)
Me. tuberculata MAD	0.93	0.93	0.44	0.43	0.12	0.04	0.62	0.65
	(0.81, 0.99)	(0.75, 1)	(0.02, 0.96)	(0, 1)	(0.02, 0.26)	(0, 0.14)	(0.45, 0.8)	(0.48, 0.81)
Pl. guadeloupensis	0.89	0.79	0.42	0.35	0.23	0.13	0.54	0.61
	(0.7, 0.99)	(0.37, 0.99)	(0.02, 0.95)	(0, 0.99)	(0.08, 0.47)	(0.02, 0.33)	(0.35, 0.81)	(0.35, 0.97)
N. virginea	0.91	0.49	0.46	0.46	0.05	0.02	0.54	0.5
	(0.77, 0.99)	(0.02, 0.99)	(0.02, 0.97)	(0, 1)	(0, 0.19)	(0, 0.08)	(0.34, 0.73)	(0.3, 0.7)
Me. tuberculata CPF	0.91	0.94	0.46	0.4	0.22	0.1	0.4	0.35
	(0.72, 1)	(0.57, 1)	(0.02, 0.97)	(0, 1)	(0.06, 0.46)	(0, 0.33)	(0.19, 0.73)	(0.15, 0.78)
I. exustus	0.77	0.8	0.45	0.4	0.23	0.1	0.75	0.75
	(0.53, 0.95)	(0.42, 0.98)	(0.02, 0.96)	(0, 1)	(0.06, 0.52)	(0.01, 0.3)	(0.34, 0.99)	(0.32, 0.99)
Me. tuberculata SEN	0.86	0.9	0.47	0.45	0.14	0.04	0.62	0.45
	(0.62, 0.99)	(0.53, 1)	(0.02, 0.97)	(0, 1)	(0.01, 0.42)	(0, 0.17)	(0.14, 0.99)	(0.11, 0.97)
H. duryi	0.82	0.75	0.49	0.48	0.2	0.05	0.27	0.24
	(0.46, 0.99)	(0.1, 1)	(0.02, 0.97)	(0, 1)	(0.01, 0.66)	(0, 0.27)	(0.06, 0.61)	(0.05, 0.52)

Figure legends

Figure 1. Observed and model-estimated proportion of occupied sites across the study years 2001-2015 for models without (left panels) and with (right panels) environmental covariates. Shown are six of the 27 taxa included in the study (a: *A. marmorata*, b: *Ph. acuta*, c: *B. glabrata*, d: *Ma. cornuarietis*, e: *Me. tuberculata* PAP, and f: *Me. tuberculata* GOS), which represent a range of metapopulation occupancy dynamics: species are increasing, decreasing, common and rare. The full set of species is represented in Appendix S2: Figures S1 and S2.The figures show the proportion of occupied sites that were observed from the data collected at 278 sites ($p_{t,obs}$; orange points), that were estimated by the model (p_t; gray points), and that were estimated by the model but restricted to include only site×year instances where the site was actually visited (since not all sites were visited each year) and where the site was observed to be wet (3170 out of 3593 total observations) modified by the detection probability ($p_{visit,t}\, d_W\, w$; blue points). The points represent the mean of the posterior distribution sampled from the Bayesian model, and the error bars are the 95% C.I. values. The survey year 2012 was anomalous, with only 57 sites visited (see Methods).

Figure 2. Metapopulation extinction and colonization rates. The ratio of extinction over colonization (log-transformed; with 2.5% and 97.5% CI) for all taxa from the model without covariates is shown. Black points are values calculated using e_W/c_W and white points are values calculated using $(e_W w + e_D (1\text{-}w)) / (c_W w)$. Values below 0 (black vertical dashed line) indicate the species is expected to persist according to the equilibrium expectation (p*: grey vertical lines) of the model of Levins (1969). The taxa are arranged in descending order by their

decreasing frequency of observations in the dataset (Appendix S1: Table S1). Species that appeared frequently in the dataset (in > 150 of the 3429 total instances where it was possible to observe the species, i.e. the total number of site-by-year visits where the site was observed to be wet) are shown in white, and species that appeared infrequently in the dataset (in ≤ 50 or ≤ 150 instances, or 1.46% and 4.37% respectively, of the total 3429 observation instances possible) are highlighted with grey coloring.

Figure 3. Metapopulation observed and equilibrium occupancy for all taxa. (a) Comparison of observed proportion of occupied sites and the model-predicted proportion of occupied sites at equilibrium for the model with no covariates. The *x*-axis is the average value from the posterior distribution of the model expected p^* value ($1-e/c$) multiplied by the model-estimated detection probability (d_W). The *y*-axis is the observed detection frequency p (number of sites a species was observed in each year divided by the number of sites visited that year, averaged across years). The shaded part of the plot (below the 1:1 line) indicates species that were detected at frequencies below their equilibrium expectation and the unshaded proportion indicates species above their expected frequency. Introduced species are black points and native species are white points. (b) Same as (a) for the model with covariates. In this instance, the *x*-axis is p_i^*, the occupancy expectation at quasi-equilibrium generated by the simulation model. This value was calculated as $p_i^* = d_W[c_i p^* / (c_i p^* + e_i)]$, where p^* was taken as the proportion of sites occupied by the species in year 1000 of the simulation that used all covariates. The c_i and e_i values were calculated taking $w_{i,t}$ into account, and d_W was the posterior mean detection probability obtained from the Bayesian model with covariates. The *y*-axis is the same as in (a).

Figure 4. Comparison of metapopulation demographic properties across the 27 snail taxa inhabiting the ponds of Guadeloupe. (a) Comparison of the posterior means for model-estimated equilibrium proportion of occupied sites (p^*, x-axis) and extinction rate (e, y-axis; calculated using $e_W w + e_D (1-w)$), for the model without covariates. The comparison indicates the expected site turnover (given by e) or change in occupied sites for species when at their equilibrium occupancy (p^*). (b) Biplot of the first two axes from a principal component analysis (PCA) of the posterior mean of coefficients for covariates influencing persistence (φ) and colonization (c) rates. PC1 and 2 are on the first two PCA axes. Arrows (and black labels) correspond to each coefficient's alignment with PCA axes (for persistence rate at wet sites, φ, and for colonization at wet sites, C; size refers to S_i, veg refers to V_i, stab refers to $Stab_i$, lrs refers to LRS_t, man refers to m_i, riv refers to r_i, connec refers to C_i, rs refers to RS_t, and col refers to $D_{i,t}$). A label for each species indicates their scores along each PC axis - pulmonate snails are labeled in red, Caenogastropods in blue, and the two additional species in grey.

Figure 5. Discriminant analysis of metapopulation demographic properties. A density plot of species associations with a single linear discriminant function (DF1) that separates Caenogastropods from pulmonates is shown. The density of Caenogastropods (blue) and Hygrophila (pulmonates; red) are depicted, as well as the position of coefficients for site and year covariates along the DF1 axis.

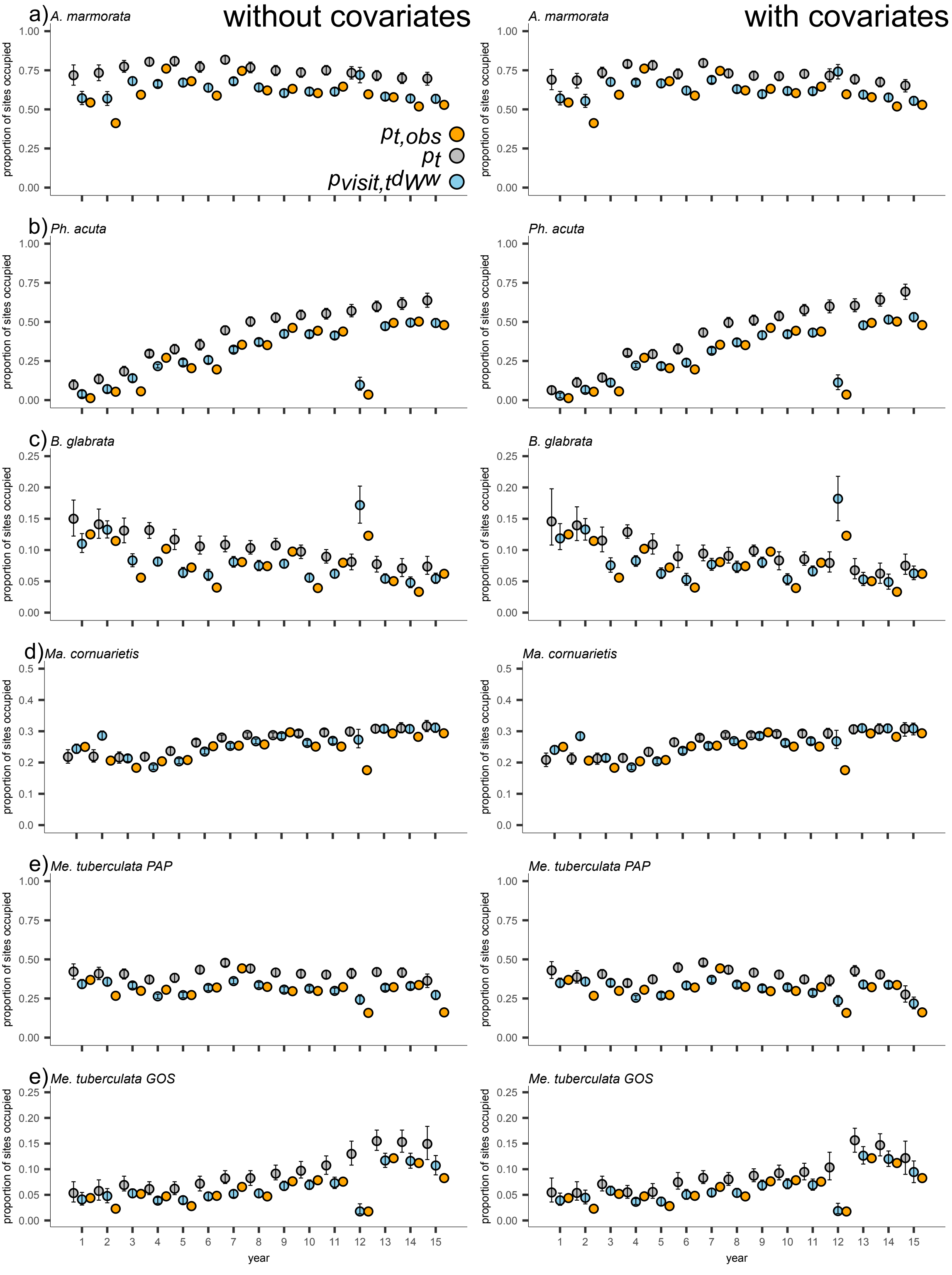
Figure 6. Map of extinction / colonization ratio per site (e_i/c_i) for six species in Grande-Terre (GT, larger island) and Marie-Galante (MG, smaller island), when taking into account all site-specific covariates. Continuous plots were constructed using Inverse Distance Weighting of

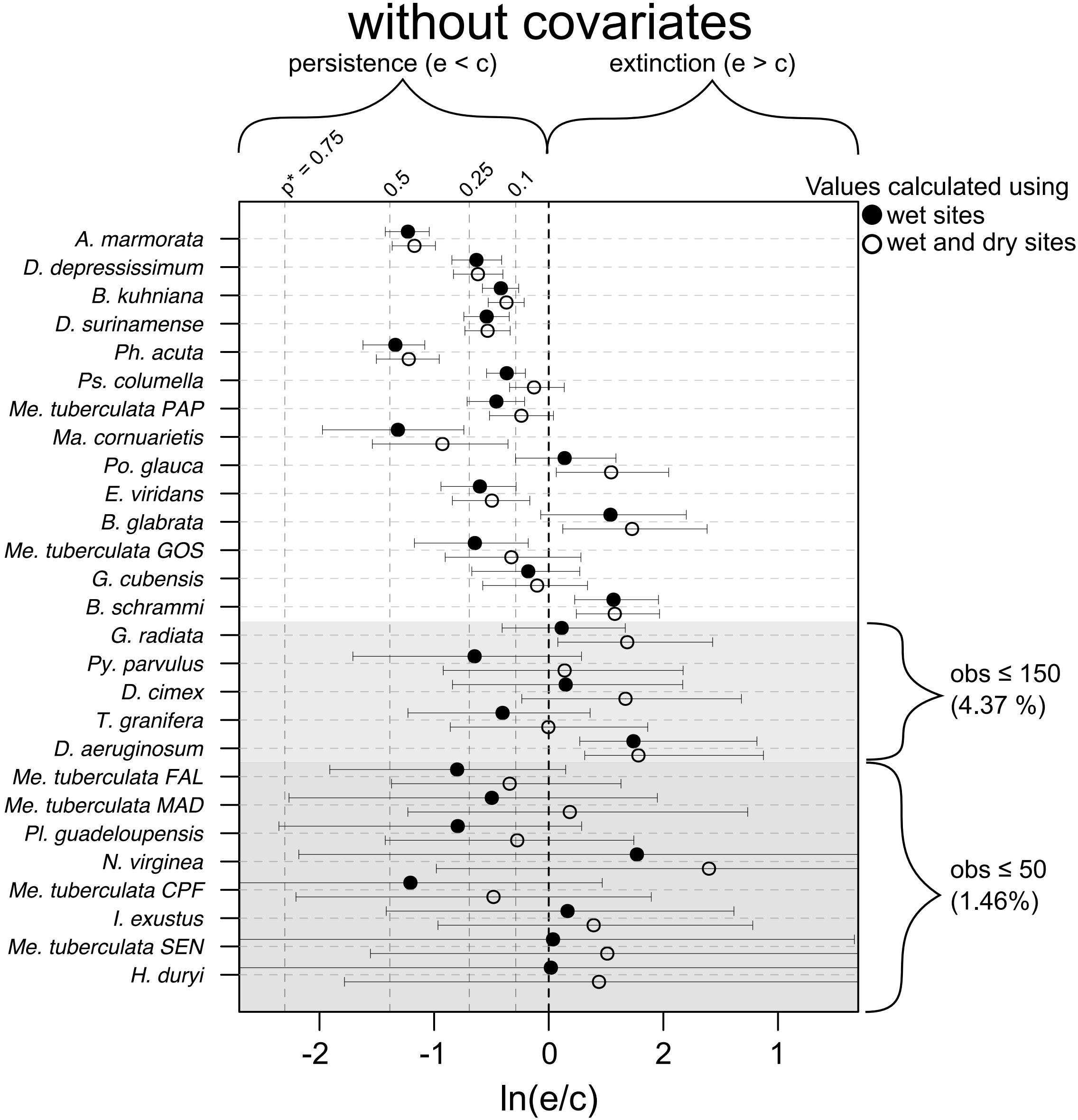
model-estimated e_i/c_i values with a distance coefficient of 5. Taxa included are (a) *A. marmorata*, (b) *Ph. acuta*, (c) *B. glabrata*, (d) *Ma. cornuarietis*, (e) *Me. tuberculata* PAP, and (f) *Me. tuberculata* GOS. The e_i/c_i values above 1 (indicating that location acts as a metapopulation sink) are colored red and values below 1 (metapopulation source) are colored in blue. The two islands are shown to scale, but their relative positions have been modified for easier visualization; the small framed map in the last panel shows their true relative positions. Maps for all species are given in Appendix S2: Figure S3.

Figure 7. Colonization (c_i) and extinction (e_i) values (ln of values are shown) predicted from the model with covariates for six mollusc taxa. Gray points represent the model-estimated values at each site (the posterior mean value when all covariates are taken into account). Red ellipses are the 95% confidence ellipse, which defines the region that contains 95% of all samples that can be drawn from the underlying Gaussian distribution (estimated using function dataEllipse in R package 'car'; Fox & Weisberg 2011) and red dots are the centroids of the values. The black dots indicate the posterior mean of the intercepts of the model.

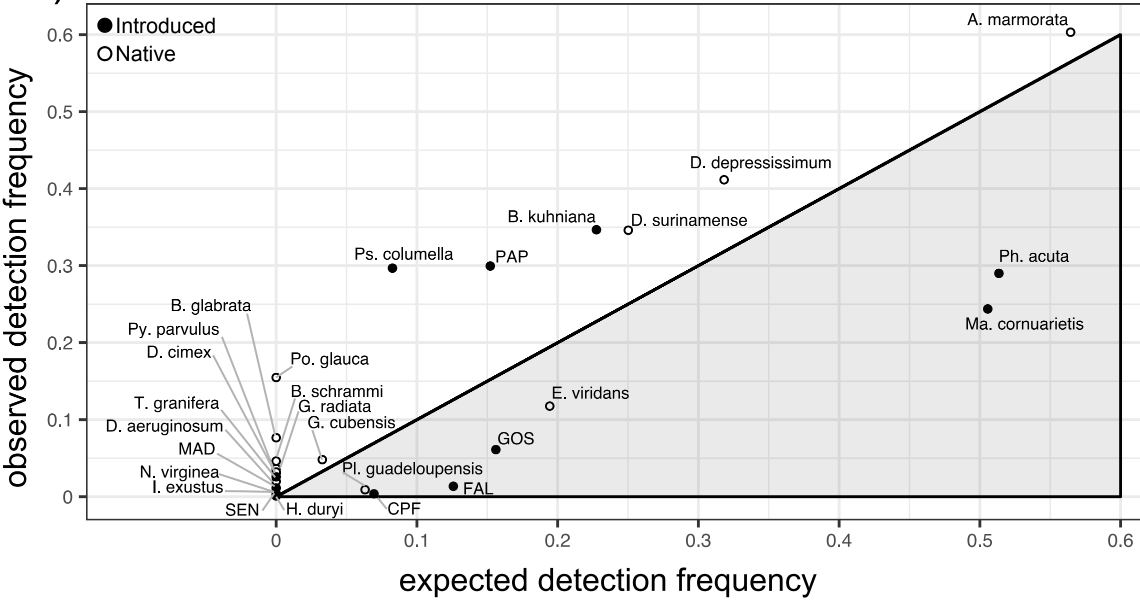
Figure 8. Distribution of occupancy (proportion of sites where species persists, *x*-axis) in year 1000 of a simulated 1000-site metapopulation for (a) *A. marmorata*, (b) *Ph. acuta*, (c) *B. glabrata*, (d) *Ma. cornuarietis*, (e) *Me. tuberculata* PAP, and (f) *Me. tuberculata* GOS. Density plots give the relative density (*y*-axis) of p_{1000} values for 1000 runs of the simulation model, for five scenarios that differ in the data used for the $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$ estimates: model with no covariates (black), intercept values for the model with covariates (red), using all covariates (blue), using all covariates with sites restricted to those where the species was ever observed

(green), or considering only covariates where SVSS support equaled or exceeded 0.6 (grey). Plots for all species are given in Appendix S1: Figure S6. Instances where a scenario has no colored density plot indicates that the species went extinct before year 1000 in that scenario (Appendix S1: Table S8).

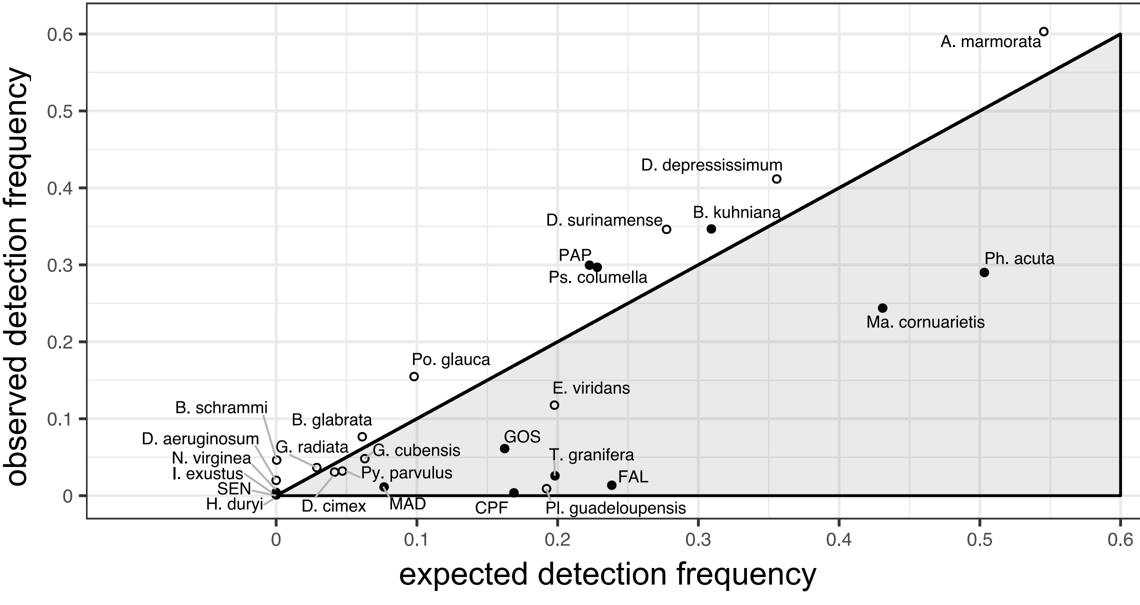

without covariates
with covariates
a)
A. marmorata
A. marmorata
$p_{t,obs}$
p_t
$p_{visit,t}d^{W^w}$
b)
Ph. acuta
Ph. acuta
c)
B. glabrata
B. glabrata
d)
Ma. cornuarietis
Ma. cornuarietis
e)
Me. tuberculata PAP
Me. tuberculata PAP
e)
Me. tuberculata GOS
Me. tuberculata GOS
proportion of sites occupied
0.00
0.25
0.50
0.75
1.00
0.05
0.10
0.15
0.20
0.0
0.1
0.2
0.3
0.4
0.5
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
year

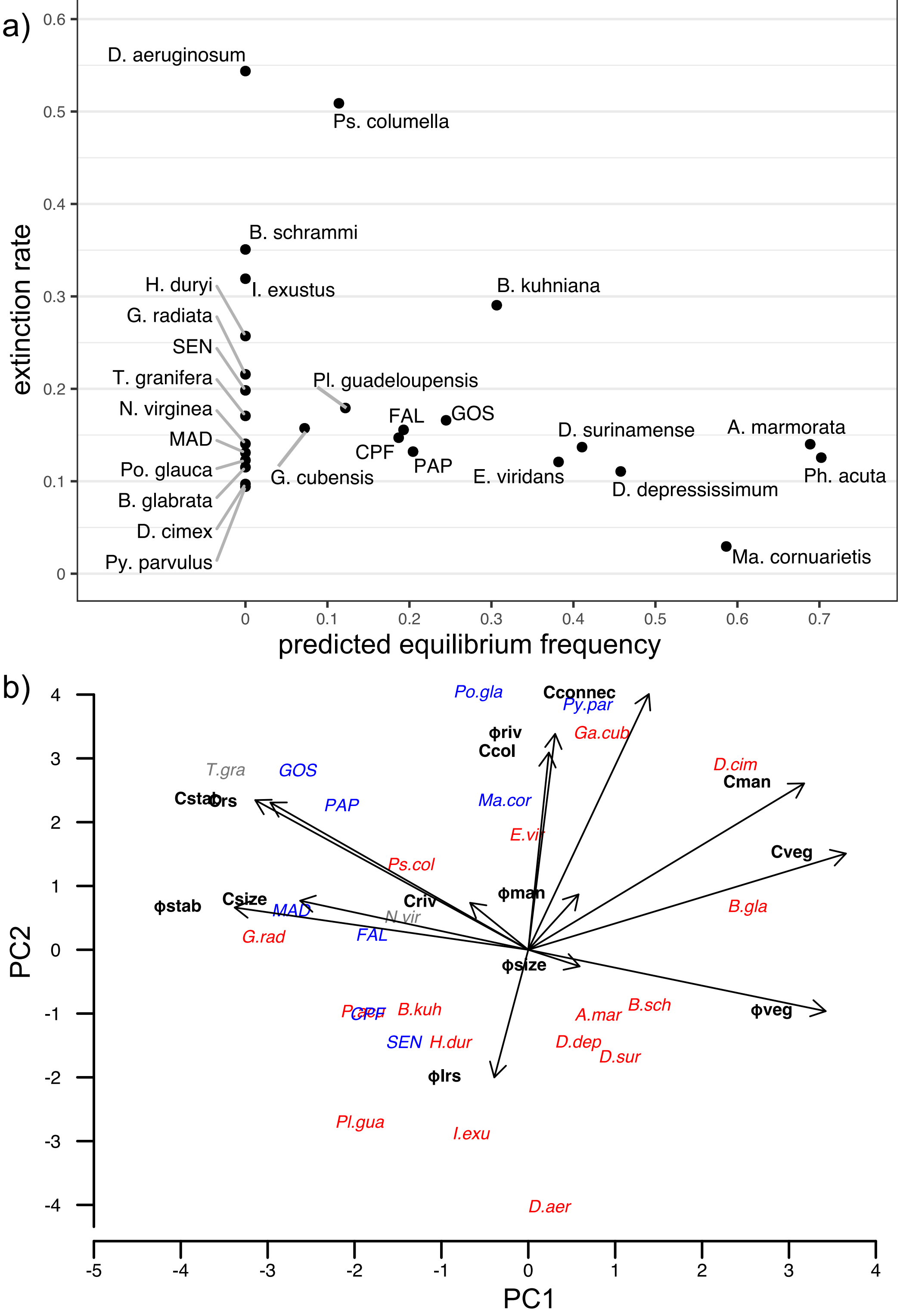

without covariates
persistence (e < c)
extinction (e > c)
p* = 0.75
0.5
0.25
0.1
Values calculated using
● wet sites
○ wet and dry sites
A. marmorata
D. depressissimum
B. kuhniana
D. surinamense
Ph. acuta
Ps. columella
Me. tuberculata PAP
Ma. cornuarietis
Po. glauca
E. viridans
B. glabrata
Me. tuberculata GOS
G. cubensis
B. schrammi
G. radiata
Py. parvulus
D. cimex
T. granifera
D. aeruginosum
Me. tuberculata FAL
Me. tuberculata MAD
Pl. guadeloupensis
N. virginea
Me. tuberculata CPF
I. exustus
Me. tuberculata SEN
H. duryi
obs ≤ 150
(4.37 %)
obs ≤ 50
(1.46%)
-2
-1
0
2
1
ln(e/c)

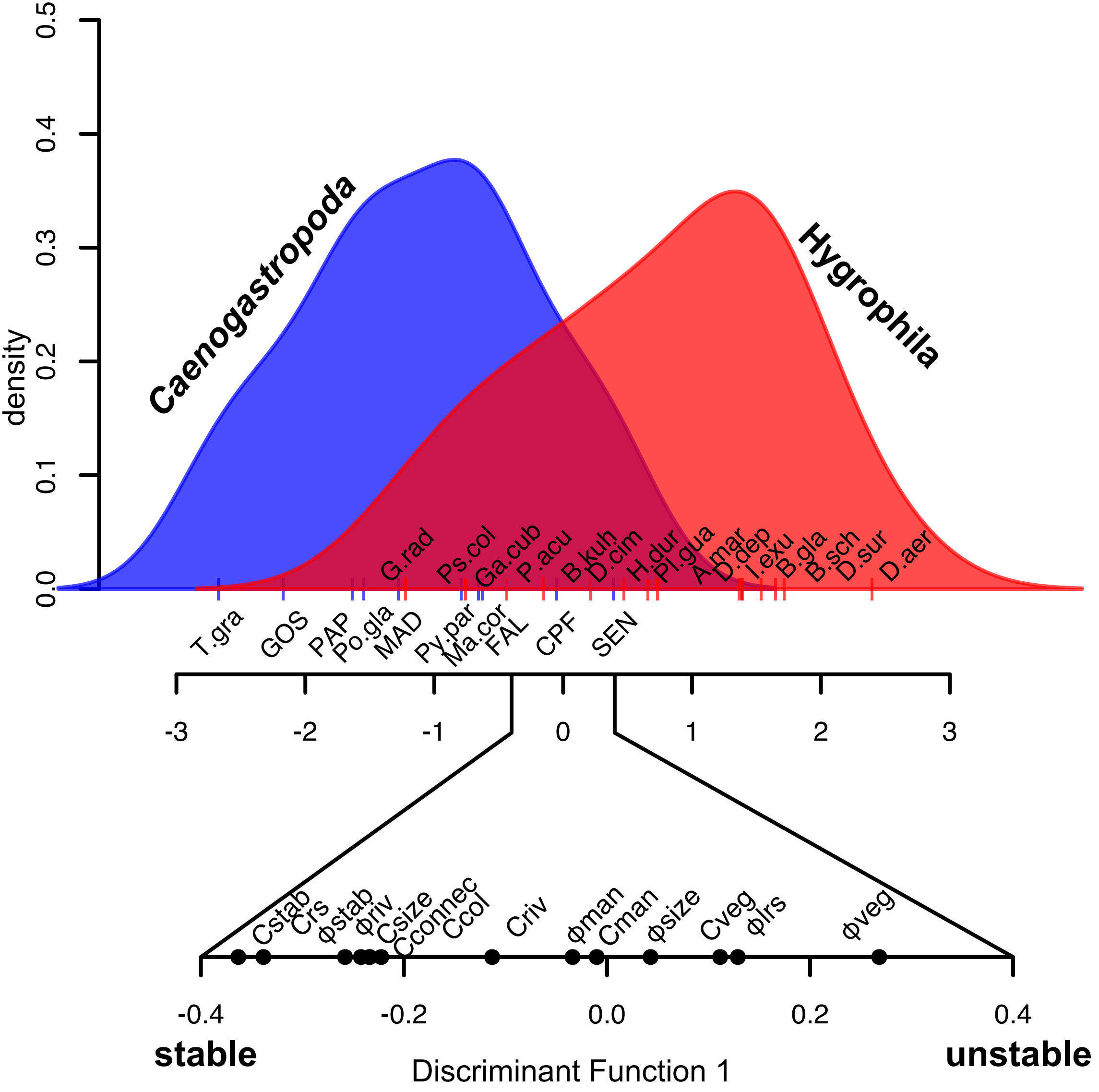
a) without covariates

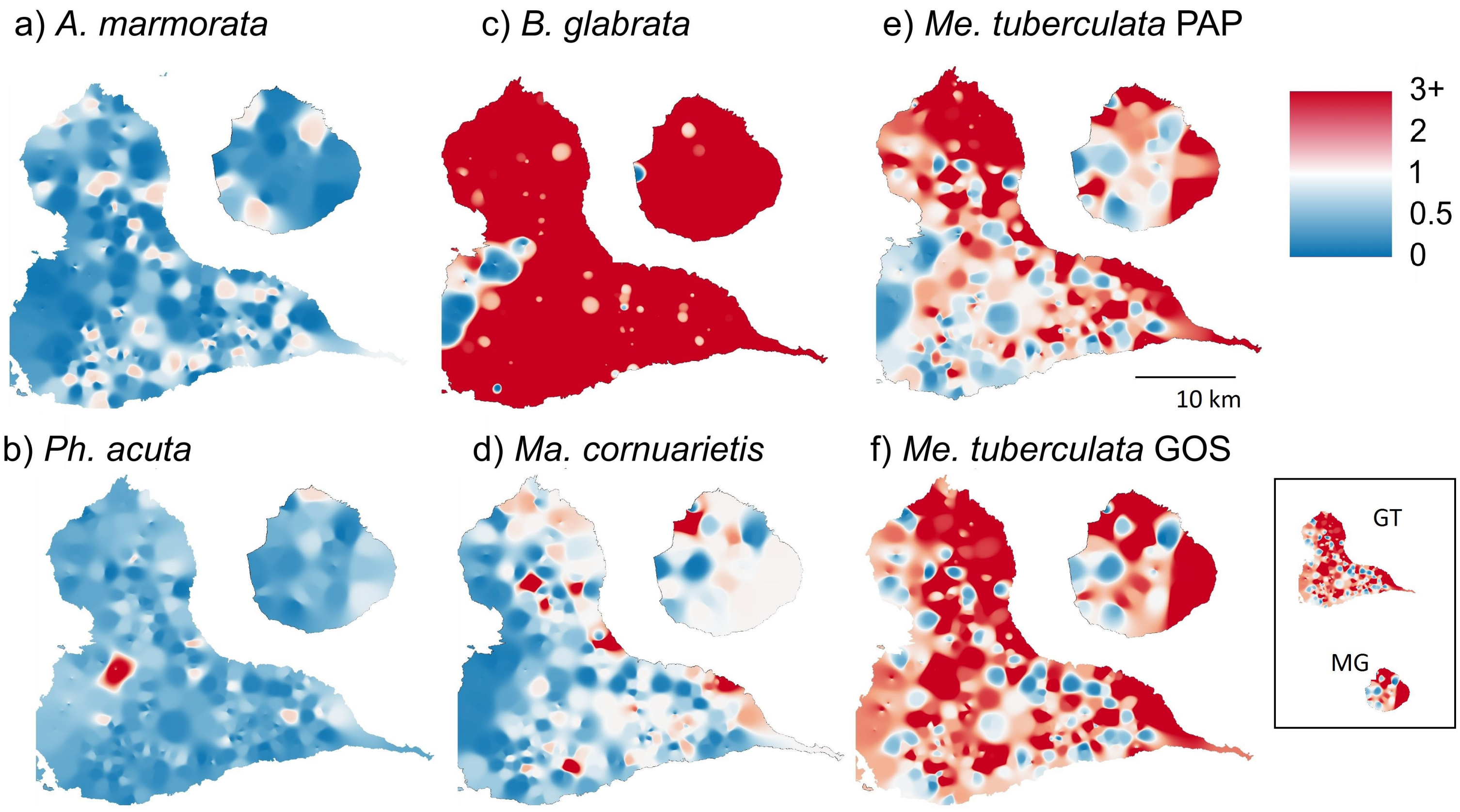


b) with covariates




a)
extinction rate
predicted equilibrium frequency
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
D. aeruginosum
Ps. columella
B. schrammi
I. exustus
H. duryi
G. radiata
SEN
T. granifera
N. virginea
MAD
Po. glauca
B. glabrata
D. cimex
Py. parvulus
B. kuhniana
Pl. guadeloupensis
G. cubensis
FAL
GOS
CPF
PAP
E. viridans
D. surinamense
D. depressissimum
A. marmorata
Ph. acuta
Ma. cornuarietis
b)
PC1
PC2
-5
-4
-3
-2
-1
0
1
2
3
4
Po.gla
Cconnec
Py.par
φriv
Ccol
Ga.cub
T.gra
GOS
D.cim
Cman
Cstab
Φrs
PAP
Ma.cor
E.vir
Cveg
Ps.col
φstab
Csize
MAD
Criv
φman
B.gla
N.vir
G.rad
FAL
φsize
P.acu
CPF
B.kuh
A.mar
B.sch
φveg
SEN
H.dur
D.dep
D.sur
φlrs
Pl.gua
I.exu
D.aer


Caenogastropoda
Hygrophila
density
0.0
0.1
0.2
0.3
0.4
0.5
G.rad
Ps.col
Ga.cub
P.acu
B.kuh
D.cim
H.dur
Pl.gua
A.mar
D.dep
I.exu
B.gla
B.sch
D.sur
D.aer
T.gra
GOS
PAP
Po.gla
MAD
Py.par
Ma.cor
FAL
CPF
SEN
-3
-2
-1
0
1
2
3
Cstab
Crs
φstab
φriv
Csize
Cconnec
Ccol
Criv
φman
Cman
φsize
Cveg
φlrs
φveg
-0.4
-0.2
0.0
0.2
0.4
stable
unstable
Discriminant Function 1



a) *A. marmorata*

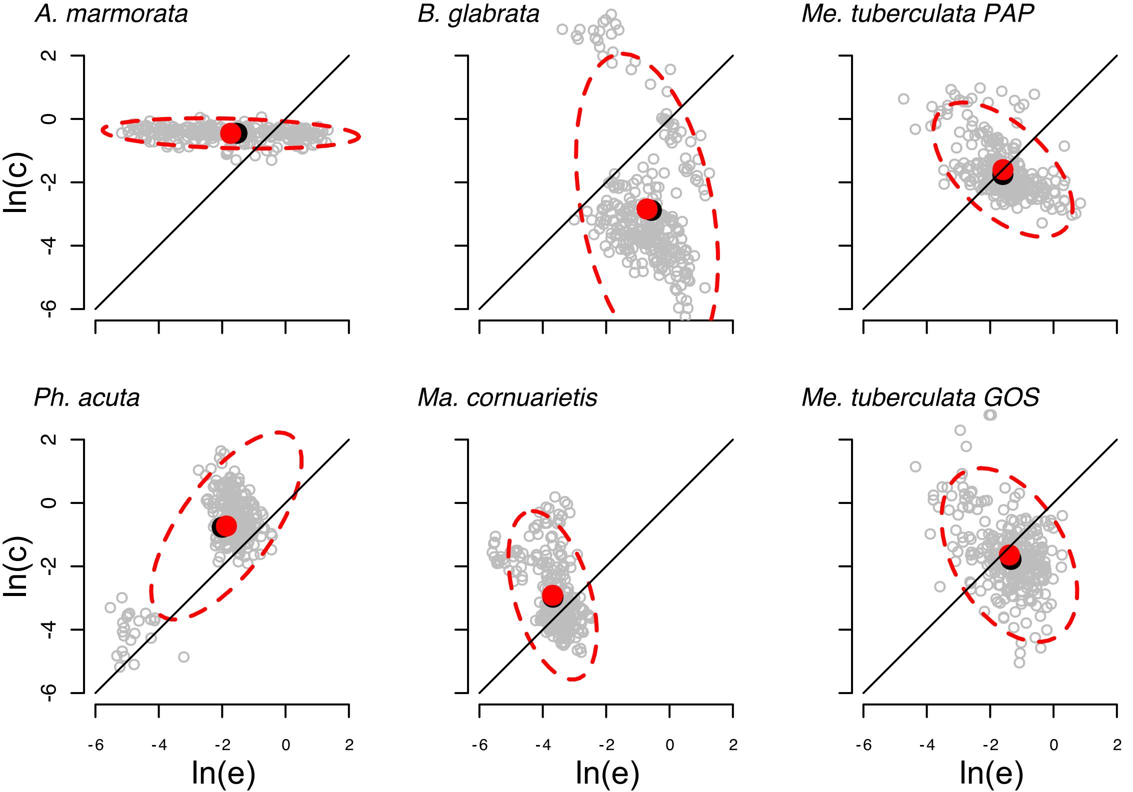
c) *B. glabrata*

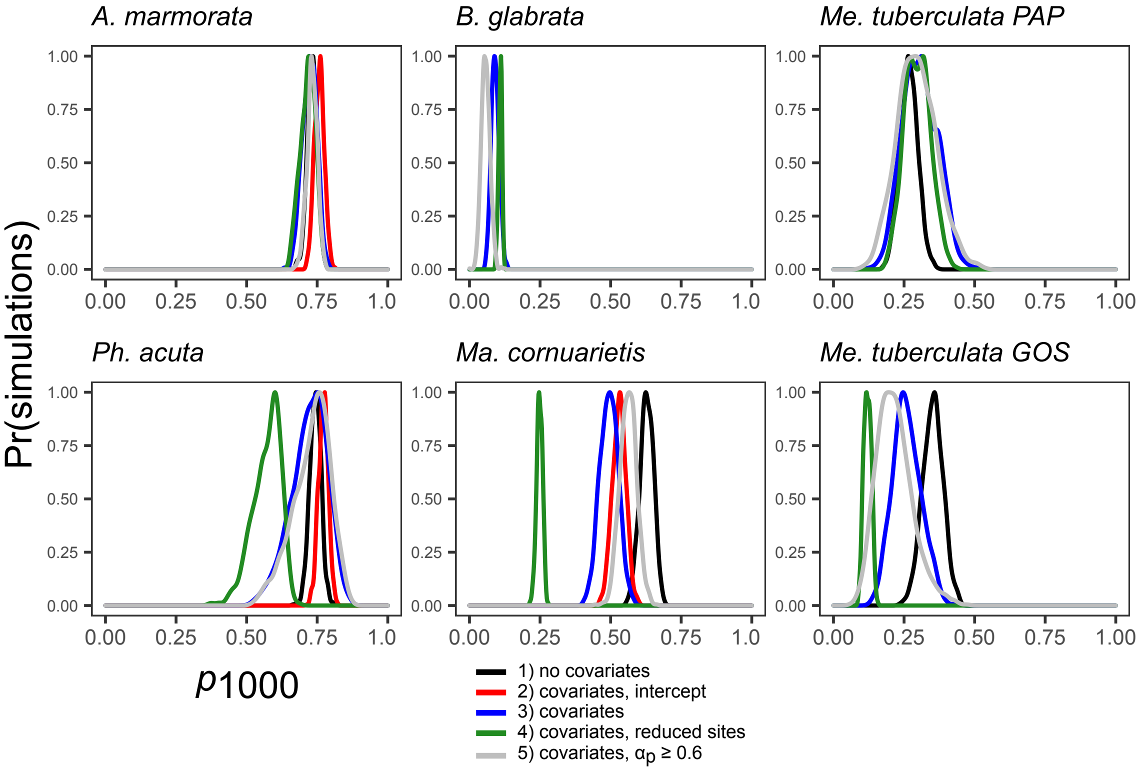
e) *Me. tuberculata* PAP

b) *Ph. acuta*

d) *Ma. cornuarietis*

f) *Me. tuberculata* GOS


A. marmorata
B. glabrata
Me. tuberculata PAP
Ph. acuta
Ma. cornuarietis
Me. tuberculata GOS
ln(c)
ln(c)
ln(e)
ln(e)
ln(e)
2
0
-2
-4
-6
-6
-4
-2
0
2


A. marmorata
B. glabrata
Me. tuberculata PAP
Ph. acuta
Ma. cornuarietis
Me. tuberculata GOS
Pr(simulations)
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.0
1.00
p_{1000}
1) no covariates
2) covariates, intercept
3) covariates
4) covariates, reduced sites
5) covariates, $\alpha_p \geq 0.6$