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17

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

41 landscape. Our comparative analysis also revealed that species had distinct strategies for
42 metapopulation dynamics, such as ‘fast turnover’ species with both a high proportion of
43 occupied sites and a high rate of site extinction in the landscape.

44

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

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49

50 The metapopulation approach, which describes the dynamics of groups of local
51 populations as discrete spatial entities that exchange migrants and are experiencing extinction
52 and colonization dynamics (**Hanski 1999; Hanski & Gaggiotti 2004**), is a theoretical
53 construction that proved useful to describe and predict species occupancy patterns (e.g., **Hanski**
54 **et al. 1995; Lawes et al. 2000; Vergara et al. 2016**). It has also guided biocontrol and
55 conservation efforts for diverse groups of species (e.g., **Marsh and Trenham 2001; Johst &**
56 **Schöps 2003; Pointier & David 2004; Ladin et al. 2016**; but see **Smith & Green 2005** and
57 **Fronhofer et al. 2012** for a critical assessment of when to consider species in patchy habitats as
58 metapopulations). However, the overwhelming majority of metapopulation studies have been
59 conducted on individual species or on pairs of interacting species (**Nee et al. 1997; Bull et al.**
60 **2006**). In patchy landscapes where guilds of phylogenetically or functionally similar species
61 overlap, species may perceive the same landscape in distinct ways. Species may vary in their
62 colonization and extinction rates, as well as whether they have stable metapopulation dynamics
63 or are instead transiently present and expected to become extinct. Comparing metapopulation
64 rates and dynamics across multiple species can be used to associate species' properties with their
65 colonization and extinction rates (e.g., **Johansson et al. 2012**), to assess the consequences of the
66 spread of introduced species on communities (**Pointier & David 2004; Svenning et al. 2014**), to
67 optimize conservation planning to decrease extinction risk for multiple species (**Nicholson et al.**
68 **2006**), and more generally to better inform current and expected biodiversity patterns. Our
69 purpose here is to evaluate, using a case study, whether a metapopulation model can be used to
70 generate accurate estimates of demographic parameters and to describe the diversity of

71 dynamics, responses to environment, and prospects of long-term persistence in a guild of species
72 inhabiting a common fragmented landscape. We present a first multi-species (> 3 species),
73 comparative metapopulation study, where estimates of demographic parameters and the
74 environmental covariates that influence extinction and colonization are evaluated for many
75 species together. Our approach is novel in its focus on more than 1-3 species, since we consider
76 an entire guild with more than 20 species, as well as in its ability both to estimate metapopulation
77 equilibrium expectations for species that are not at an equilibrium occupancy and to make
78 predictions about future occupancy and extinction dynamics.

79 A metapopulation approach is appropriate when populations are spatially structured into
80 local populations and when migration among these allows the reestablishment of extinct
81 populations (**Hanski & Gilpin 1997**). The current generation of metapopulation models,
82 stochastic patch occupancy models (SPOMs; **Caswell & Etter 1993**; **Hanski 1997**; **Moilanen**
83 **1999**; **Heard et al. 2013**), focus specifically on the presence of a population in a habitat patch
84 and allow estimation of colonization and extinction rates and metapopulation occupancy, i.e. the
85 constitutive parameters of the foundational **Levins (1969; 1970)** metapopulation model. SPOMs
86 have become popular because their representation of only the occupancy state (as unoccupied or
87 occupied) of habitat patches makes them easier to parameterize than models that require local
88 density estimates (**Moilanen 2004**). However, some key issues must be considered in order to
89 accurately and simultaneously apply this modeling framework to several species of a guild in
90 real, complex, and fragmented landscapes. While solutions to these challenges – imperfect
91 detection, among-site heterogeneity, and temporally variable metapopulation dynamics - have
92 been developed for analysis of individual species, we describe here the characteristics of our
93 approach that were implemented to address them at the multi-species scale.

94 First, knowledge of a species' presence or absence from field data is usually imperfect,
95 because species might not be detected when actually present (**Guillera-Arroita 2017**). In some
96 cases, species may even be known to be systematically undetected by usual survey methods,
97 such as under stressful circumstances (desiccation, freezing) that trigger the adoption of
98 quiescent resistant forms (Lamy et al. 2013). Imperfect detection presents a difficulty for the
99 SPOM approach because the occupancy state of each local population depends on the occupancy
100 state at the previous time point (**Moilanen 2004**), and as a consequence estimates of colonization
101 and extinction may be biased (**Moilanen 2002; MacKenzie et al. 2003**). In order to reduce these
102 biases, **Lamy et al. (2013)** developed an occupancy model that combined two approaches,
103 estimation of detection probabilities from repeated surveys (**MacKenzie et al. 2003**) and the
104 inclusion of additional, undetectable, states beyond the binary of occupied / not occupied (e.g.,
105 multistate occupancy models, **MacKenzie et al. 2009**). In this model, the different states of
106 occupancy were associated with an active life stage in wet sites and an aestivating life stage in
107 dry sites (individuals buried in sediment), which allows estimation of colonization, extinction,
108 and detectability parameters in wet vs. dry sites. We use the occupancy model of **Lamy et al.**
109 **(2013)** in this study in order to quantify the metapopulation dynamics of a set of species that
110 likely vary in their detectability and in their propensity to persist in a quiescent, cryptic form.

111 The second challenge is to account for the species-specific heterogeneity in the
112 contributions of patches to the overall colonization and extinction dynamics in a metapopulation.
113 Site heterogeneity has been incorporated in some spatially implicit metapopulation models:
114 **Hanski & Ovaskainen (2002)** accounted for the destruction of some habitat patches, and
115 quantitative variables describing heterogeneity have also been used, mostly to account for
116 variation in patch size (considered as a proxy for population size and thus overall extinction

117 probability) and patch connectivity (**Hanski 1994; Moilanen 2000; Wang & Altermatt 2019**).

118 Other spatially realistic metapopulation models have been developed that consider patch

119 heterogeneity in the landscape (**Chandler et al. 2015; Howell et al. 2018**) or a site's position in

120 a broader spatial network structure (**Gillaranz et al. 2012; Holmes et al. 2020**). However, a

121 different approach may be needed when comparing multiple species in a landscape, as the

122 extinction and colonization probabilities for species with distinct limiting resources and dispersal

123 modes are unlikely to be captured by a shared measure of size and connectivity. The simple

124 delimitation of habitat from non-habitat may differ across species as well. Modelling

125 colonization and extinction parameters as a function of site-specific environmental properties

126 across sites for each species represents a more general approach to consider site heterogeneity

127 (**Sjögren-Gulve & Ray 1996; Lamy et al. 2013; van der Merwe et al. 2016; Rodhouse et al.**

128 **2018**). This has previously only been applied to individual metapopulations, but it can account

129 for the fact that each species may perceive habitat patch quality in its own way. In an assemblage

130 of species, effects of covariates on colonization and extinction may give rise to species-specific

131 spatial variation in observed and expected occupancy patterns. Thus, the success of this approach

132 can be evaluated by its ability to reproduce and provide reasonable understanding of the diversity

133 of species occupancy maps in the landscape. Additionally, for each species site heterogeneity is

134 important for its average dynamics at the landscape scale because variance and covariance

135 among sites in estimates of colonization and extinction rates may alter the predicted mean time

136 until extinction (**Frank & Wissel 2002**), the **weighted** fraction of occupied patches (**Ovaskainen**

137 **2002**), or have other significant impacts on metapopulation dynamics (**Sutherland et al. 2012,**

138 **Dubart et al. 2019**).

139 The third challenge of metapopulation models is to correctly account for temporal
140 variation, which can arise from three main sources. First, colonization and extinction may vary
141 temporally because the environment changes in time (**Ovaskainen 2002; Perry & Lee 2019**).
142 This can be addressed for example by taking time series of an appropriate length to adequately
143 sample this temporal variation, by considering time-varying covariates for extinction and
144 colonization rates (e.g. **Rodhouse et al. 2018**), or by considering dynamic models of stochastic
145 patch occupancy that explicitly incorporate this temporal variation (e.g. **Bertassello et al. 2020**).
146 Second, the absolute colonization rate (the rate at which an empty site becomes occupied) varies
147 in time due to changes in the proportion of occupied sites in the metapopulation, which act as
148 sources of colonists. This relationship is captured by metapopulation models that express
149 colonization rates on a per-occupied-site basis (i.e. relative colonization rates; **Levins 1969**) in
150 the same way that birth rates are expressed as per-capita in standard population growth models.
151 However, many empirical studies instead estimate absolute colonization rates (e.g., **Mackenzie**
152 **et al. 2003**). These estimates may be problematic especially for invading or declining species, as
153 projections will not account for natural feedbacks of occupancy on colonization and may fail to
154 adequately predict the long-term dynamics of the metapopulation (**Hanski 1994**). This leads to
155 the third source of temporal variation, which is non-stationarity. Models vary in whether or not
156 the study system is assumed to be at quasi-equilibrium (not the eventual state of extinction
157 expected for all systems, but instead the quasi-steady state the system converges to before this
158 point; see **Hanski 1994**). Parameterizing a model that assumes quasi-equilibrium (e.g., in early
159 instances of the incidence function model; **Hanski 1994**) when the population is not truly at
160 equilibrium can produce unreliable estimates. For systems away from quasi-equilibrium, long
161 time-series with state transitions between successive time points are needed to sample

162 representative distributions of colonization and extinction events (**Moilanen 2000**). In this study,
163 we model a time-series of metapopulation occupancy dynamics that addresses these temporal
164 considerations in four ways. (i) We use a long time-series, decreasing the chance that
165 colonization and extinction measures are drawn from a non-representative sample; (ii) our model
166 estimates relative colonization rates (i.e. per occupied site) rather than absolute ones, which
167 conforms with Levins' original formulation; (iii) these rates are purely estimated from temporal
168 turnover data, which removes the need for any equilibrium assumption and accounts for temporal
169 variation in occupancy dynamics among species at the landscape scale; and (iv) we included both
170 spatial and temporal covariates to capture environmental effects on colonization and extinction
171 rates in our model. The framework of **Lamy et al. (2013)** allows implementation of all these
172 features except (ii), and so we modified its formulation to allow for this (see Methods).

173 We applied this spatially implicit metapopulation modeling framework to the guild of snail
174 species that inhabit freshwater habitats of two islands (Grande-Terre and Marie-Galante) in the
175 Guadeloupe archipelago, Lesser Antilles. These islands harbor over 3000 freshwater habitats that
176 are connected to one another to various degrees, especially during the rainy season. Many sites
177 are dry for several months, but some species can aestivate in the sediment for several weeks or
178 more (**Pointier 1976**). We collected occupancy records of 22 mollusc taxa in 278 sites sampled
179 annually from 2001 to 2015. We analyzed this time series using a modeling framework adapted
180 from **Lamy et al. (2013)**, a multistate occupancy model that estimates colonization and
181 extinction rates as a function of site- and year-specific environmental covariates. We provide
182 estimates of these rates, determine how they vary over time and across sites, and use them in
183 simulations to predict either the equilibrium proportion of occupied sites or the time until
184 extinction, while taking uncertainty in parameter estimation into account. We use our results to

185 address five main questions: (i) How do snail taxa vary in their colonization and extinction rates,
186 and in their likelihood to persist, increase, or decrease at the landscape scale, and can we use our
187 models to characterize different types of metapopulation behaviors reflecting the phylogenetic
188 and life history diversity in this guild? (ii) Are colonization and extinction rates sensitive to year-
189 and site-specific environmental properties, do these sensitivities vary among species, and can we
190 adequately measure these sensitivities and use them to model species differences in habitat use
191 and spatial distribution in the landscape? (iii) Can a comparative analysis of metapopulation
192 parameters across multiple species reveal general patterns of life history strategies at the
193 landscape scale? (iv) Does the inclusion of habitat-dependent variation alter predictions
194 regarding persistence and global occupancy in the landscape, and for which species? (v) What
195 are the methodological limits to our approach?

196

197 METHODS

198

199 *Study system*

200 The islands of Grande-Terre (639 km²) and Marie-Galante (170.5 km²) lie in the
201 Guadeloupe archipelago in the Lesser Antilles (see **Pointier 2008, Lamy et al. 2013, Chapuis et**
202 **al. 2017** for a description of the system). The islands are geographically and geomorphologically
203 similar to one another and distinct from other nearby islands, which is why we consider their
204 snail populations together. They harbor diverse types of freshwater habitats, including ponds,
205 small rivers, and swamp grasslands connected to mangroves (subsequently referred to as back-
206 mangrove), all of which vary dynamically in water levels and connectivity. Our study focuses on
207 27 taxa of freshwater molluscs (Appendix S1: Table S1) that occupy these habitats and constitute

208 the major part of the macrobenthos. These taxa mainly belong to two groups: pulmonate snails
209 belonging to the order Hygrophila (subclass *Heterobranchia*, 15 taxa in three families), and
210 operculate snails of the subclass *Caenogastropoda* (10 taxa), belonging to three families
211 (*Ampullaridae*, *Cochliopidae*, *Thiaridae* each in a different order). In addition one gastropod of
212 subclass Neritimorpha, and one bivalve (family *Sphaeridae*) are represented. We considered six
213 morphotypes of the caenogastropod *Melanoides tuberculata* and treated them as separate
214 metapopulations because they reproduce parthenogenetically, and each of them represents a
215 morphological and genetic clone with its own invasion history in the islands (**Facon et al. 2003;**
216 **2008**). Prior to the 1970s, the archipelago harbored a relatively stable number of native snail
217 species, but invasive species have appeared and settled since then (**Pointier 1976; Pointier &**
218 **Augustin 1999; Pointier & Jarne 2011**). Native and invasive species differ in whether or not
219 their metapopulation dynamics have stabilized and invasive species are also in different stages of
220 their invasion sequence. Overall, we have a mix of species with either stable, increasing,
221 declining, or fluctuating metapopulations. The metapopulation dynamics of one of the most
222 common species, *Drepanotrema depressissimum*, was evaluated in **Lamy et al. 2013**, showing
223 higher colonization and persistence in dry than in wet sites (as a consequence of aestivation in
224 dry sites) and a marked influence of some environmental parameters (e.g., positive effect of
225 connectivity on colonization in wet sites).

226

227 *Multistate occupancy model*

228 Based on **Lamy et al. (2013)**, we utilized a state-space model with a state process capturing
229 transitions between site states (occupied / not occupied) and an observation process linking the
230 data (detected / not detected) to the underlying states, to take into account imperfect species

231 detection. The model estimates extinction and colonization probabilities as well as detection
 232 probability (the probability that a species is successfully detected during a site visit), and
 233 accounts for the existence of aestivating snails that may persist (unseen) in the ground of dry
 234 sites. Our model differed slightly from that of **Lamy et al. (2013)** in a few ways. First, instead of
 235 estimating as a single parameter the absolute colonization probability (that is equal to c^*p),
 236 which depends on the proportion of occupied sites p (that can act as sources of propagules for
 237 colonization) and the colonization rate per empty patch c , we modeled the true relative
 238 colonization rate c . This rate determines the transition probability that an un-occupied site
 239 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
 240 the number of sites, and $x_{i,t-1}$ is the true occupancy status of site i at occasion $t-1$. This
 241 formulation reflects colonization as a continuous process in time, where e^{-cp} is the probability
 242 that a site has not been colonized by any propagule in one unit of time. The occupancy dynamics
 243 of a site thus can be modeled as:

244

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

246

247 where φ is the probability of persistence from one occasion to the next. Following Lamy et al.
 248 (2013), the φ and c values used depend on the wet or dry state of the site at times $t-1$ and t . The
 249 probability of persistence in a wet site (φ_W) is used when the site is wet at $t-1$, and φ_D (dry site)
 250 when the site is dry at $t-1$. c_W (respectively c_D) is used when the site is wet (respectively dry) at
 251 time t . c_D is likely a very small value as the time window during which colonization can occur is
 252 reduced in dry sites. Given the very low precision of c_D estimates in initial runs of the models,
 253 we preferred to reduce the number of parameters and set colonization rate of dry sites to $c_D = 0$

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

263 Fitting of the model to data was conducted using a Bayesian procedure in JAGS (Just
264 Another Gibbs Sampler, which implements Monte Carlo Markov Chain sampling; **Plummer**
265 **2003**), implemented in R (version 3.3.3, 2017) using the base package, the ‘coda’ package
266 (**Plummer et al. 2006**), and the ‘rjags’ package (**Plummer 2016**). The prior distribution of d_W ,
267 ϕ_W , ϕ_D , and c_W were $U(0,1)$, a uniform distribution over the interval $[0, 1]$. Initial occupancy
268 probabilities for sites on the two islands (Grande-Terre and Marie-Galante), Ψ_{GT} and Ψ_{MG} , were
269 estimated separately, both with prior distributions $U(0,1)$, and each island had an island-specific
270 mean occupancy probability each year p_i .

271

272 *Data*

273 We used records of 27 taxa (22 species, with six genetically distinct morphotypes of one
274 species; Appendix S1: Table S1) that were surveyed in 278 sites (250 sites in Guadeloupe, 28
275 sites in Marie-Galante) annually from 2001 to 2015. Some species did not occur in the
276 metapopulation until after 2001 and not all sites were sampled in all years (total number of site

277 visits = 3593, mean and standard deviation of number of site visits per year = 222 ± 59).
278 Sampling during the year 2012 had to be reduced to 57 sites for financial reasons, and those sites
279 were chosen non-randomly as sites where *Physa acuta* had never been observed (this was crucial
280 information for another study to document the invasion progression of this species) and as sites
281 with risk of drying (from our own experience) to determine their dry or wet status. The 2012
282 survey data is therefore biased for low presence of *Ph. acuta* and of species that are not drought
283 tolerant. Further sampling details are given in **Lamy et al. (2012, 2013)**, **Chapuis et al. (2017)**,
284 and **Dubart et al. (2019)**.

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

300 $dry_{i,t} = 1 - w_{i,t}$ (where $w_{i,t}$ is the probability of site i being wet in year t). This probability was
301 estimated by fitting a generalized linear mixed-effects model (GLMM) with site and year as
302 random effects and a binomial error structure (implemented in R using the ‘lme4’ package,
303 **Bates et al. 2014**) to all sample occasions where dry/wet state was observed.

304

305 *Model without covariates*

306 For each species, we fitted the multistate occupancy model to the data using a Bayesian
307 framework to generate estimates of ϕ_W , ϕ_D , and c_W . Colonization of dry sites c_D was assumed to
308 be zero (data, JAGS code, and R code for the model without covariates are in Data S1). The
309 model was run with 20,000 iterations, the first 10,000 of which were discarded as a burn-in
310 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
311 1, 0.5 for chain 2, and 0.9 for chain 3). Model fit to observed data was assessed by comparing the
312 mean and 95% credibility interval (C.I.) of the posterior distribution for model-estimated
313 proportion of occupied sites with the observed proportion each year (a posterior predictive
314 check; **Rubin 1984**; **Gabry et al. 2019**). The observed values (per year, $p_{t,obs}$) were calculated by
315 dividing the number of sites a species was observed in (or observed in either visit, for sites
316 visited twice) by the number of sites visited. Since the model generates posterior distributions for
317 occupancy values in site \times year instances that were not observed in our dataset, we report model
318 predictions for each year both as the predicted proportion of occupied sites (p_t) and as the
319 probability of observing a given taxon that year, i.e. the proportion of wet sites that were
320 occupied multiplied by the detection probability in wet sites and by the proportion of wet sites w
321 ($p_{visit,t} d_W w$). This measure is most directly comparable to observed data.

322 Metapopulations are expected to persist if the ratio of the extinction rate to the colonization
323 rate is less than one (Levins 1969). To compare our results to this persistence threshold, we
324 converted ϕ to the instantaneous extinction rate e (the same as e in the Levins model) using $e = -$
325 $\ln(\phi)$ (this arises from considering that extinction occurs as a continuous process and the
326 probability of not being extinct in one unit time is $\exp(-e)$). To evaluate the influence of
327 considering snail aestivation in dry sites for persistence, we compared two ways of calculating
328 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
329 sites). Here w is the overall probability of a site being wet, estimated as the average of all fitted
330 values obtained from the GLMM of the observed dry state data described previously (that
331 produced $w_{i,t}$ values). We also calculated posterior distributions for the predicted equilibrium
332 frequency according to the Levin's model ($p^*=1-e/c$), multiplied by detection probability (d_W).
333 Multiplication of model-expected values for p by d_W allows comparison to field observed data,
334 which underrepresents true occupancy because of imperfect species detection. These estimates
335 were compared across species and also between native and introduced species.

336

337 *Model with covariates*

338 For each species, we ran a second model incorporating factors that may influence
339 demographic parameters (see Lamy et al. 2013, Dubart et al. 2019). Site-specific
340 environmental variables (i.e. with one value per site that does not vary across years) were site
341 size (S_i), vegetation cover (V_i), water connectivity (C_i), site stability ($Stab_i$), back-mangrove (m_i),
342 and river (r_i). The values of S_i and V_i were $\log_{10}(1+X)$ transformed to better approximate a
343 normal distribution, and the S_i , V_i , and C_i values were averaged over the 15 survey years
344 (Appendix S1: Table S3). We chose to average these values and thus only consider them as site

345 covariates because, although some sites show strong temporal variation, our annual measure is
346 unlikely to capture the relevant weekly to monthly differences expected in small semi-permanent
347 or temporary ponds. Our averaging of the annual measures instead captures a snapshot of site
348 features at a common point in time, the beginning of the dry season.

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

361 We also used an index of local propagule pressure per site i and year t , $D_{i,t}$. We estimated
362 $D_{i,t}$ as $D_{i,t} = N_i P_{i,t}$, where N_i is the total number of freshwater habitats occurring within a 4-km
363 radius circle around site i (visited or not) and $P_{i,t}$ is the proportion of occupied sites at time t
364 among the surveyed sites within that circle (see **Lamy et al. 2013** for further detail). The 4-km
365 distance was chosen based on practical considerations such as having a reasonable number of
366 surveyed sites to estimate $P_{i,t}$ around each site and having circles that were still relatively small
367 compared to the entire island. The lists and maps of all freshwater sites on Grande-Terre and

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

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

376

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

378

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

382

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

384

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

387

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

389

390 Choices for inclusion of model covariates are described in **Lamy et al. (2013)**:
391 connectivity and local propagule pressure were expected to act only on colonization, the rainy
392 season variable (RS_t) is likely to only impact colonization because this is when floods and water
393 connections among sites occur, and the little rainy season (LRS_t) is likely to influence
394 persistence as this is when sites tend to shrink in size or sometimes desiccate. Colonization rates
395 of dry sites were assumed to be 0. We chose to construct models with various subsets of the
396 covariates both to limit overfitting and to reflect hypotheses about expected relationships. We did
397 not use covariates for φ_D because it was unrealistic to fit them correctly given the low number of
398 instances of dry sites in the data. All the covariates were centered and reduced to obtain the β
399 values on a standardized scale. The intercepts (α values) thus represent the expected value of
400 $\text{logit}(\varphi_W)$ or $\log(c_W)$ in a site and year with average covariate values. We assessed inclusion or
401 exclusion of environmental covariates using stochastic search variable selection (SSVS; **George**
402 **and McCulloch 1993**; **O'Hara and Sillanpää 2009**), where in each iteration of the model, each
403 regression parameter was either estimated or set to 0. The prior distribution of each regression
404 parameter was the same as in **Lamy et al. (2013)** - in this model with covariates, the prior
405 distribution for the intercept terms of φ_W , φ_D , and c_W was $N(0, 10)$. We assessed inclusion of
406 model covariates by evaluating the posterior of α_p , which is a binary indicator variable used in
407 SSVS that is set to either 0 or 1. A covariate was considered to have a credible posterior estimate
408 of effect size β if the proportion of posterior models that included a given covariate ($P_{\alpha_p} = 1 \mid$
409 data) was ≥ 0.6 . This value was chosen to ensure that posterior ($P_{\alpha_p} = 1 \mid$ data) values were not
410 simply reflecting the prior mean of α_p , which was 0.5. The model was run with 20,000 iterations,
411 the first 10,000 of which were discarded as a burn-in period, with three parallel chains. Initial
412 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

413 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
414 (data, JAGS code, and R code for the model with covariates are in Data S2).

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

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

436

437 *Spatial variation: site-specific persistence*

438 Significant environmental covariates suggest there is no single colonization and extinction
439 rate for each species, but rather that site-specific properties influence a species' ability to
440 colonize and persist in a particular site. We plotted each site's model-estimated value of
441 extinction rate divided by colonization rate (e_i/c_i), averaged across all years. This was done by
442 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
443 when all covariates were taken into account, then weighing these values by the probability a
444 given site was wet, then averaging these values across all years. In this formulation, $\frac{e_i}{c_i} =$
445 $\frac{\sum_{t=1}^T [(e_{D(i,t)})(1-w_{i,t}) + (e_{W(i,t)})(w_{i,t})] / c_{W(i,t)} * w_{i,t}}{T}$, where T is the total number of years of observations
446 (15 for this dataset) and $w_{i,t}$ is the probability a given site is wet in a given year. $w_{i,t}$ was
447 estimated from the observed dry state data using the GLMM described previously.

448 Heterogeneity among sites may alter expectations for metapopulation occupancy and long-
449 term persistence because favorable sites can provide extinction-resistant pockets even if many
450 other sites are unfavorable (**Frank & Wissel 2002; Ovaskainen 2002**; we also present a
451 simplified derivation of the effects of variance and covariance in colonization and extinction in a
452 spatially implicit metapopulation model, which is the case in this analysis, in Appendix S3:
453 Section S1). The use of covariates is a first way to account for this heterogeneity, but it is also
454 possible that some species are completely unable to live in some sites, for example if they are
455 specialized on a particular resource or condition that is not captured by our covariates. In that
456 case, fitting the model on the entire set of sites might represent an overly pessimistic view of
457 their possibility to persist as a metapopulation. An optimistic view would be to consider only
458 those sites in which the species has been detected at least once, which demonstrates its ability to

459 colonize or persist in that site. To better understand how site-specific covariates modify our
460 expectations for species persistence, we calculated e_i and c_i using (i) only the model intercept
461 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
462 covariates, and (iii) using all covariates but only considering sites where the species was
463 observed at least once during our survey (we also report results in appendices using only
464 covariates that were retained by the SSVS procedure in $\geq 60\%$ of the Bayesian model iterations,
465 but this did not qualitatively change the main results). For scenario (iii), we did not re-fit the
466 entire model using this subset of sites but instead used the values obtained for these sites from
467 the overall model with covariates (Equations 2-4). The variance, covariance, and Pearson's
468 correlation coefficient for all e_i and c_i values were calculated as well.

469

470 *Temporal analysis: metapopulation persistence expectations*

471 To provide expectations for how long each species would be expected to persist on the
472 islands and what proportion of sites would be occupied each year based on the results of our
473 model-estimated colonization and extinction parameters, we simulated occupancy dynamics
474 (annual transition between occupied and un-occupied states) on a 1000-site landscape for 999
475 years (or until the species went extinct) using a combination of model-estimated parameters and
476 observed site and year properties. We chose to simulate dynamics on a landscape with more sites
477 than we have data available for because our sampled sites represent only a subset of the total
478 number of sites on the islands. The simulation model considered both among-site and among-
479 year variation in e_i and c_i to provide an expectation for metapopulation dynamics. We repeated
480 the simulations 999 times to generate confidence intervals for the estimate of proportion of sites
481 occupied (or time until extinction) by each species. To initialize the simulation, each of the 1000

482 simulated sites was randomly assigned the identity and associated values of one of the 278
483 observed sites. These properties are (i) the site- and year-specific $w_{i,t}$ (estimated from the GLMM
484 described previously), (ii) the model-estimated site-specific average occupancy x_i (this is the
485 posterior mean of the average occupancy for each site across all 15 years), which was used as the
486 initial occupancy probability $x_{i,0}$ in the simulation, and (iii) the site- and year-specific model-
487 estimated values of $e_{W(i,t)}$, $e_{D(i,t)}$, and $c_{W(i,t)}$. The initial occupancy of each simulated site was
488 obtained by a draw from a Bernoulli distribution with probability $x_{i,0}$ and the initial dry state $w_{i,0}$
489 was obtained by a draw from a Bernoulli distribution with a probability $w_{i,t}$ where t was
490 randomly chosen from 1-15. For each of the 999 years of the simulation, one of the 15 years of
491 the observed data was chosen at random, and the characteristics (climatic covariates and
492 proportion of dry sites) of the observed data for that observed year were used in the simulated
493 year. We randomly assigned the dry state to each site each year with probability $w_{i,t}$ and the new
494 occupancy state for that simulated year was drawn at random based on the previous occupancy,
495 the dry state, and the appropriate transition probability matrices incorporating $e_{W(i,t)}$, $e_{D(i,t)}$, and
496 $c_{W(i,t)}$ (Equation 1). The main goal was to simulate the expected proportion of occupied sites (p_t ,
497 estimated by p_{1000} , the proportion of occupied sites in year 1000 of the simulation) or the time
498 until population extinction.

499 To illustrate how site-specific covariates modify our expectations for species persistence in
500 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
501 model with no covariates, (ii) estimates using only the intercept values from the model with
502 covariates, (iii) estimates including all covariates, (iv) estimates from the model with all
503 covariates but only including sites where the species was observed at least once during our
504 survey, and (v) estimates using only covariates where SVSS support ($P_{ap} = 1 \mid \text{data}$) equaled or

505 exceeded 0.6. To compare the frequency of observation of species at each site in the
506 metapopulation ($p_{i,obs}$) with the occupancy expectation at quasi-equilibrium generated by the
507 simulation model (p_i^*), we calculated $p_{i,obs}$ as the number of times the species was detected at a
508 site divided by the number of visits to that site and we calculated $p_i^* = d_W[c_i p^* / (c_i p^* + e_i)]$,
509 where p^* was taken as the proportion of sites occupied by the species in year 1000 of the
510 simulation that used all covariates (assumed to be our best estimate of quasi-equilibrium
511 metapopulation occupancy). Here, c_i and e_i were calculated as described previously (i.e. taking
512 $w_{i,t}$ into account), and d_W was the posterior mean detection probability obtained from the
513 Bayesian model with covariates.

514

515 RESULTS

516

517 *Overview*

518 The freshwater snails of Guadeloupe were observed to be diverse in several ways. Some
519 native species (*Aplexa marmorata*, *D. depressissimum*, *Drepanotrema surinamense*) and some
520 invasive species (*Biomphalaria kuhniana*, *Ph. acuta*, *Pseudosuccinea columella*) were observed
521 frequently (> 30% of the 3429 total site×year visits of wet sites) in many sites (> 74% of the 278
522 sites in the study; Appendix S1: Table S1). Other species (*Marisa cornuarietis*, *Pomacea glauca*,
523 *E. viridans*) were observed consistently (in ~12-24% of visits) but at a more limited number of
524 sites (~31-43% of sites). Many (15) of the taxa were rare, observed in < 5% of the total visits to
525 wet sites, but some of these were found consistently in habitats with particular characteristics.
526 For example, *D. cimex* and *Pyrgophorus parvulus* were detected in 28 and 30 sites respectively,
527 15 and 11 of which are in back-mangrove. We subsequently give results for all 27 taxa,

528 highlighting results for the most frequent taxa (i.e. observed in more than 150 of the 3429 total
529 site \times year visits to wet sites; Appendix S1: Table S1).

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

537

538 *Model without covariates*

539 The model provided estimates that fit well with the observed data (Figure 1, left column;
540 Appendix S2: Figure S1; see Appendix S1: Table S10 for a list of Tables and Figures that allow
541 comparison of results for models without and with covariates), especially when comparing the
542 model-estimated probability of observing a taxa in a given survey year ($p_{visit,t} d_W w$; blue points in
543 Figure 1) with the observed occupancy data ($p_{t,obs}$; orange points in Figure 1). The mean
544 detection probabilities over all snail taxa was 0.59, with some variation among taxa (standard
545 deviation ± 0.18 ; Table 1). This becomes 0.67 (± 0.12) when considering the most frequent taxa
546 (≥ 150 total occurrences in the data set). This illustrates the variation in estimate uncertainty for
547 taxa that appear at various frequencies in the dataset (Tables 1 and Appendix S1: Table S1).
548 Detection probabilities were generally estimated with a high degree of certainty using our site re-
549 visit procedure (average width of the 95% C.I. of the posterior distribution for $d_W = 0.23 \pm 0.21$;
550 0.10 ± 0.05 for the most frequent taxa). On average, the 27 snail taxa experienced high

551 persistence (ϕ_W : 0.86 ± 0.09 ; 0.85 ± 0.09 for the most frequent taxa) and colonization (c_W : $0.21 \pm$
552 0.14 ; 0.26 ± 0.17 for the most frequent taxa) rates in wet sites. Persistence in dry sites was both
553 lower and more variable among taxa (ϕ_D : 0.59 ± 0.22 ; 0.72 ± 0.23 for the most frequent taxa).
554 This parameter was estimated with a relatively low degree of certainty (average width of the
555 95% C.I. of ϕ_D posterior distribution = 0.66 ± 0.28 ; 0.46 ± 0.22 for the most frequent taxa),
556 likely due to the relative dearth of dry sites (164 out of 3593 total observations across all sites
557 and all years) and the fact that species that are very rare or occur only in stable sites will thus not
558 have any survey records that allow estimating dry persistence. For example, for species with \leq
559 50 total occurrences in the dataset, the estimates reflected the uniform prior distribution (i.e.
560 posterior mean close to 0.5 and C.I. close to 0.025-0.975; Table 1). Nevertheless, some species
561 (e.g., *A. marmorata*, *D. depressissimum*, *D. lucidum*, *B. straminea*, *Ma. cornuarietis*) did have
562 both high and reliable estimates for ϕ_D . The 95% C.I. of the posterior distributions for ϕ_W , ϕ_D ,
563 c_W , and d_W are given in Table 1.

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

574 *tuberculata* FAL, and *Me. tuberculata* CPF) and eight taxa are expected to be extinct but have
575 95% C.I. that span the persistence threshold (*Py. parvulus*, *D. cimex*, *T. granifera*, *Me.*
576 *tuberculata* MAD, *N. virginea*, *I. exustus*, *Me. tuberculata* SEN, and *H. duryi*). The predicted
577 equilibrium frequency according to the Levins model ($p^*=1-e/c$), after multiplying by detection
578 probability (d_w), can be plotted against the frequency of detection of each species observed from
579 the data (averaged over years; Figure 3a). This plot shows whether species are expected to
580 decline (observed > expected, above the 1:1 line in Figure 3a) or increase (expected > observed,
581 below the 1:1 line in Figure 3a) in the long term. Both declining and increasing trends are
582 predicted for some native and introduced species, indicating that not all introduced species are
583 experiencing a continued successful invasion process. However, some introduced species (*Ph.*
584 *acuta*, *Ma. cornuarietis*) are clearly still spreading (Figures 1 and 3a).

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

595

596 *Model with covariates*

597 The model provided estimates of proportion of sites occupied for each year in the study
 598 period ($p_t, p_{visit,t}, d_{WW}$) that fit well with the observed data ($p_{t,obs}$; Figure 1 and Appendix S2:
 599 Figure S2). Including covariates slightly improved the match between the observed proportion of
 600 occupied sites (p) and the model-predicted proportion of occupied sites at equilibrium (p^*), as
 601 indicated by more species being closer to the 1:1 line in Figure 3b than in Figure 3a (Pearson
 602 correlation between p and p^* for model without covariates = 0.81, for model with covariates =
 603 0.82). Consideration of site and year covariates shifted the posterior distributions of estimated
 604 parameters from the model without covariates. On average across all 27 taxa, $\phi_W = 0.76 \pm 0.14$
 605 (0.71 ± 0.12 when considering the most frequent taxa), $c_W = 0.19 \pm 0.19$ (0.27 ± 0.23), $\phi_D = 0.57$
 606 ± 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
 607 models given in Equations 2-4 - most of these values, especially persistence rates, were slightly
 608 lower than when covariates were not considered. Some of the covariates influenced colonization
 609 and extinction (the posterior 95% C.I. did not include zero and $P_{\alpha_p} \geq 0.6$ - the proportion of
 610 Bayesian posterior samples where SSVS included the covariate; details in Appendix S1: Tables
 611 S5 and S6 and plotted in Appendix S1: Figures S1 and S2; posterior means are given only
 612 including iterations where $\alpha_p = 1$). Each covariate strongly influenced ϕ_W or c_W (i.e. $\alpha_p \geq 0.6$) for
 613 at least three of the 27 taxa and on average taxa were strongly influenced ($\alpha_p \geq 0.6$) by $4.11 \pm$
 614 2.68 of the 14 covariates. Some species were particularly influenced by environment. For
 615 example, *Ph. acuta* persistence in wet sites (ϕ_W) was positively influenced by rainfall in the little
 616 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
 617 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
 618 was positively influenced by size (β_S : $0.23 \leq 0.40 \leq 0.56$, $\alpha_p = 1.00$) and connectivity (β_C : $0.29 \leq$
 619 $0.50 \leq 0.75$, $\alpha_p = 1.00$) and negatively influenced by vegetation (β_V : $-0.74 \leq -0.60 \leq -0.45$, $\alpha_p =$

620 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
621 habitat (β_m : $-1.71 \leq -1.12 \leq -0.73$, $\alpha_p = 1.00$). On the other hand, *A. marmorata* was influenced
622 by only one covariate, i.e. vegetation cover increased persistence in wet sites (β_V : $1.58 \leq 2.09 \leq$
623 2.63 , $\alpha_p = 1.00$).

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

634 The clustering of species by their taxonomic group (Caenogastropods or pulmonates) in PC
635 space was reflected in the discriminant function analysis. The linear discriminant function of the
636 PC scores for model covariate coefficients was successful in sorting snail taxa into the two
637 taxonomic groups, successfully re-assigning 80% of taxa to their correct classification (12 of 15
638 pulmonate snails and 8 of 10 *Caenogastropoda*; Figure 5). The position of covariate regression
639 parameters (β_i) along the discriminant function axis indicates that taxonomic groups are broadly
640 described by the effects of stability. The association of strong positive effect sizes for site
641 stability ($Stab_i$), rainfall in the rainy season (RS_i), site size (S_i), local propagule pressure ($D_{i,t}$),
642 and site connectivity (C_i) for colonization and for site stability ($Stab_i$) and riverine sites (r_i) for

643 persistence indicate that Caenogastropods are more likely to colonize and persist at sites that are
644 large, stable, and highly connected to other sites. Pulmonate snails were associated with strong
645 positive effect sizes of vegetation (V_i) and rainfall in the little rainy season (LRS_i) for persistence
646 and of vegetation (V_i) for colonization. For these taxa, site stability was less important for
647 colonization and persistence (Figures 4b and 5). Some taxa do not conform to these broad
648 patterns, such as *Gu. radiata* (which has a strong positive effect of stability and size for
649 colonization) and *Ga. cubensis* (which has a strong positive effect of propagule pressure and
650 connectivity for colonization).

651

652 *Site-specific colonization and extinction*

653 Our visualization of among-site habitat suitability across the islands of Grand-Terre and
654 Marie-Galante indicates that for most species, sites vary in whether they are metapopulation
655 “sources” ($e_i/c_i > 1$) or “sinks” ($e_i/c_i < 1$). For some species, the sources greatly outnumber the
656 sinks throughout the islands (Figures 6a, b, d). Depending on species, source sites are spatially
657 scattered (Figure 6f), or clustered (Figures 6c, and 6e; maps for all taxa are given in Appendix
658 S2: Figure S3). Plots of each site’s estimated e_i and c_i values from the model with covariates are
659 given in Figure 7, while plots using different subsets of data (i.e. using only the model intercept
660 value, all covariates, or all covariates but only for sites where the species was observed at least
661 once) are provided in Appendix S1: Figure S3 (Appendix S1: Figure S4 includes results when
662 considering only covariates that were retained by the SSVS procedure in ≥ 0.6 of the Bayesian
663 model iterations, but this did not qualitatively change the results). These plots indicate that while
664 the model intercepts are helpful in summarizing the overall persistence expectation, sites varied
665 substantially in their e_i and c_i values when covariates were taken into account. The effect of

666 covariates on extinction and colonization is expected to result in negative correlations between e_i
667 and c_i across sites in most species (Appendix S1: Table S7; Appendix S1: Figure S5), which is
668 important because it indicates that extinction-prone sites are less likely to be colonized and
669 suitable sites are more likely to be colonized.

670

671 *Metapopulation persistence expectations*

672 Model predictions obtained by simulation suggest that metapopulation persistence and
673 stationary state can depend on covariates. For the most frequent taxa, the difference is a small
674 variation in the proportion of occupied sites (Figure 8). However, for species of low to moderate
675 frequency, considering covariates can substantially alter the expectations (Figures 6 and
676 Appendix S1: Figure S6; Table S8). Many species that would go extinct in the model using only
677 the intercept values for ϕ_W , ϕ_D , c_W instead persist (*Me. tuberculata* PAP, GOS, FAL, MAD, *Po.*
678 *glauca*, *B. glabrata*, *Ga. cubensis*, *Gu. radiata*, *Py. parvulus*, *D. cimex*, *T. granifera*, and *Pl.*
679 *guadeloupensis*) or go extinct at a much later time in the simulations (*B. schrammi*, *D.*
680 *aeruginosum*, *N. virginea*). None of the species expected to persist using only the intercept went
681 extinct when covariates were taken into account. For most of the species expected to persist in
682 the three scenarios (no covariates, intercept from model with covariates, and all covariates), the
683 expected p_{1000} was higher when covariates were taken into account. The opposite pattern was
684 however observed in *A. marmorata*, *Ph. acuta*, *Ma. cornuarietis*, and *E. viridans*. In these cases
685 the decrease in p_{1000} was small, except for *Ma. cornuarietis*, which has a posterior mean p_{1000} of
686 0.63 without covariates and 0.49 with covariates. The simulation results differed in some
687 instances when the metapopulation was modelled excluding (i.e. considering as non-habitat) the
688 sites where the species was never observed (Appendix S1: Figure S6, Table S8). This assumption

689 resulted in large decreases in p_{1000} for *Ph. acuta*, *Ma. cornuarietis*, *Me. tuberculata* GOS, and *T.*
690 *granifera*, four species that are experiencing ongoing invasions. This suggests that these species
691 have not yet encountered potentially favorable sites, and excluding these sites provides an
692 underestimate of favorable habitats. The only species with expected extinction in all scenarios
693 except the reduced sites scenario **was *B. schrammi***.

694 We compared the observed site-specific occupancy $p_{i,obs}$ with the simulation model
695 expectation of p_i^* . We first evaluated these deviations averaged across all 278 sites. For many
696 species, the deviations of the expected p_i^* from $p_{i,obs}$ were relatively small (the average deviation
697 across all 27 taxa, across all 278 sites = **-0.031 ± 0.198**), and the observed frequency matched the
698 predicted values more closely than the model without covariates (i.e. comparing Figures [3a](#) and
699 [3b](#)). The taxa with observed frequencies below the expected value were primarily introduced
700 taxa such as *Ph. acuta* and *Ma. cornuarietis* that experienced an increase in the number of sites
701 occupied over the survey period. These taxa are predicted to reach equilibrium occupancy at
702 much higher values than their average past occupancy, irrespective of whether covariates are
703 included or not in the model. We also evaluated site-specific variation in the deviation between
704 observed and simulated occupancy values. Deviations across sites were relatively small for most
705 of the most frequently observed taxa, with most average deviation values < 0.1 and a largely
706 positive correlation between predicted and observed site-specific occupancies (Appendix S1:
707 Table S9; Appendix S2: Figure S4). The species with the largest deviations again include
708 recently invasive species (i.e. *Ph. acuta*, *Ma. cornuarietis*, *T. granifera*) for which the model
709 indicates more favorable sites than the species has been observed in during the study period.
710 Sites with p_i^* values that greatly exceeded $p_{i,obs}$ values are locations where the invasive species
711 are expected to expand their range.

712

713 DISCUSSION

714

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

722

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

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

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

735 (Verhulst 1838). These notions have inspired well-known classifications of strategies such as
736 the r - K continuum (MacArthur & Wilson 1967; Pianka 1970; Reznick & Bashey 2002), the
737 Grime CSR triangle (Grime 1977; but see Silvertown et al. 1992), and the fast-slow continuum
738 (Stearns 1983; Franco & Silvertown 1996; Oli 2004), all of which attempt to relate trait
739 syndromes (especially life-history traits) to demography. These approaches could be applied to
740 the landscape scale using metapopulation equivalents of carrying capacity and temporal rates
741 derived from Levins' e and c parameters, provided these metapopulation parameters are
742 measured for several species in a landscape. Our results provide such information and illustrate
743 the diversity of metapopulation strategies in the studied guild. A first way to characterize
744 strategies is with the metapopulation equivalent of the carrying capacity, the theoretical
745 stationary occupancy (proportion of sites occupied at stationary state, $p^* = 1 - e/c$;
746 Amarasekare 1998), which in our study ranges from 0% (species predicted to go extinct) to
747 70% of sites for *A. marmorata* and *Ph. acuta* (Figures 2 and 4a). For native species, these
748 stationary occupancies are usually close to those observed during our survey (Figure 3a).
749 Differences arise for multiple reasons. Predicted values are lower than observed ones for some
750 native species such as *B. glabrata* and *Po. glauca* that are declining and may become extinct.
751 Predicted occupancies tend to be higher for introduced species experiencing the invasion process
752 (*Ph. acuta*, *Me. tuberculata* morphs, *T. granifera*), especially for slow invaders such as *Ma.*
753 *cornuarietis*.

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

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

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

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

782

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

785 Although the incidence function model introduced by **Hanski (1994)** considers patch
786 variation in patch area and isolation, these properties are not always sufficient to predict
787 metapopulation or occupancy dynamics (e.g. **Prugh et al. 2008**). Instead, an increasing number
788 of studies consider variation in properties beyond patch size or isolation (**Fleishman et al. 2002;**
789 **Heard et al. 2015; Howell et al. 2018**). Studies that considered environmental properties
790 directly, not just via their impact on patch area and isolation, have demonstrated the importance
791 of environmental features to predict occupancy (**Sjögren-Gulve & Ray 1996; Fleishman et al.**
792 **2002; Schooley & Branch 2009; Heard et al. 2015**) and thus that patches likely vary in their
793 values of the metapopulation parameters that influence occupancy.

794 In addition, theoretical metapopulation studies that consider how colonization varies
795 among sites usually focus on among-patch variation in contribution to the propagule pool and do
796 not explicitly consider the variation in the capacity of a site to receive propagules. The latter may
797 vary because of positional effects in spatially explicit models, but are not usually modelled as a
798 function of site-specific habitat variables (e.g., **Moilanen & Hanski 1998; Hanski &**
799 **Ovaskainen 2000**). However such responses to local habitat properties may be likely in natural
800 landscapes, such as if local topography affects the receptive area for colonization. In this study
801 we tried to capture these effects through our connectivity measure, which had positive effects for
802 colonization rate in many taxa, confirming its importance. More generally, we modelled the

803 effects of site characteristics on the probability to be colonized and to be extinct, while leaving
804 aside other potential effects such as variation in site contribution to the propagule pool and
805 spatial distance effects (the relatively weak effects of our local propagule pressure covariate
806 suggest that potential improvements by relaxing these assumptions may be limited, but this
807 requires further studies to be confirmed). This allowed us to quantify the responses of site-
808 specific colonization rates and extinction rates to different sets of local habitat characteristics and
809 also the variance and covariance among these rates emerging from such effects.

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

824 The inclusion of covariates allowed us to map spatial variation in site suitability and
825 compare it to spatial patterns of species occurrence. From the site-specific e_i and c_i values, we

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

840 For abundant taxa, model-estimated site-specific stationary occupancy (p_i^*) matched quite
841 well with the proportion of times a species was observed at a site (Appendix S2: Figure S4,
842 Appendix S1: Table S9), suggesting a good fit of the model. The match was weaker for some
843 rare taxa (see above the example of *Gu. radiata*) and for some recently introduced species. For
844 the latter, the model thus identifies potentially favorable habitats not yet reached when our
845 survey began. Our approach at a landscape scale thus compares to distribution models and
846 ecological niche models at a regional scale, i.e. modelling environmental preferences as a
847 function of observed occurrences or abundance (**Phillips et al. 2006; Elith & Leathwick 2009;**
848 **Warren & Seifert 2011; Norberg et al. 2019**). The dependency on presence-only data and lack

849 of consideration for sites where species are absent is a well-documented feature of these models,
850 and is one way our modeling approach differs (see **Guisan & Zimmermann 2000** and **Kéry et**
851 **al. 2013** for discussion of species distribution models including presence-absence data and
852 **Warren 2012** for a discussion on the application of presence-only models). Expectations for
853 occupancy and persistence can shift when only sites where the species was ever observed are
854 considered, especially for invasive species because their potential habitat is not taken into
855 account (Figure 8 and Appendix S1: Figure S6), and so our model's combination of including
856 many freshwater sites and site-specific covariates can identify these potential sites for future
857 expansion. Our modelling approach is also mechanistic rather than purely correlative, as it
858 explicitly considers underlying demographic rates at the landscape scale and how they are tied to
859 theoretical expectations for metapopulation persistence. However, we did not (yet) incorporate a
860 detailed dispersal modelling and within-population demographic modelling as seen in other
861 approaches (e.g., **Bocedi et al 2014**; see **Normand et al. 2014** for a review).

862

863 *Comparative analysis of metapopulation dynamics across multiple species*

864 One advantage of fitting the metapopulation model to data for 27 taxa is that we can
865 compare results across taxa, and determine whether particular groups of species have similar or
866 distinct strategies in their occupancy of the landscape. We distinguished between pulmonates and
867 Caenogastropods, and found that fast-turnover species (based on e) were primarily pulmonate
868 snails (Figure 4a). We observed that many of these species showed visible fluctuations around
869 their expected equilibrium occupancy (the native *D. depressissimum* and *D. surinamense*, the
870 introduced *B. kuhniiana* and *Ps. columella*, see Figure 1, Figure 4a, Appendix S2: Figure S1, and
871 Appendix S2: Figure S2) or rapidly increased towards their expected equilibrium (*Ph. acuta*). On

872 the other hand, low-turnover species which include most Caenogastropods show slow, regular
873 trends over the entire sampling period (Figure 1, Appendix S2: Figure S1, and Appendix S2:
874 Figure S2). This gradual and regular trend was observed both for declining (the native *Po.*
875 *glauca*) and increasing (*Me. tuberculata* GOS, *T. granifera*, *Ma. cornuarietis*) taxa.

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

895 parameters may thus be related to trait syndromes to some extent, although this requires support
896 from more comparative metapopulation studies with precise trait measurements for more taxa.

897

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

899 An important goal of the study was to understand how expected metapopulation occupancy
900 and persistence can be influenced by variance and covariance in colonization and extinction rates
901 induced by habitat characteristics (**Frank & Wissel 2002; Ovaskainen 2002**). While including
902 among-patch heterogeneity in size and position does not modify the general behaviour of the
903 Levins metapopulation model (**Gyllenberg & Hanski 1997; Etienne 2002**), **Frank & Wissel**
904 **(2002)** showed that among-patch heterogeneity in colonization and extinction rates, including
905 spatially correlated extinctions, can influence the mean lifetime of a metapopulation. Temporal
906 synchrony among sites in colonization and extinction is the focus of other studies that consider
907 patch heterogeneity as well (e.g., **Ovaskainen 2002; Sutherland et al. 2012**).

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

917 species with low frequency in the dataset (e.g., *B. glabrata*, *Ga. cubensis*, *Gu. radiata*; Figure 8
918 and Appendix S1: [Figure S6](#); [Appendix S1](#): Table S8).

919 Site size is a classic example of a source of negative covariance between e and c (**Hanski**
920 **1994**), as large sites can harbor large, extinction-resistant populations and attract more colonists
921 at the same time. In our study, while site size has a generally positive effect on colonization, it
922 has inconsistent effects on persistence (Appendix S1: Figures S1 and S2). Instead, descriptors of
923 site quality such as vegetation cover, hydrological stability, and habitat type (mangrove or river)
924 seem to be important drivers of variance and covariance among sites depending on species. This
925 is especially true of species concentrated in particular habitats (back-mangrove: *B. glabrata* and
926 *D. cimex*; riverine: *N. virginea*; unstable habitats: *D. depressissimum* and *B. schrammi*), some of
927 which are predicted to go extinct in the simulation models using the mean-field or intercept
928 parameter estimates but persist when covariates are considered. Overall, our results suggest that
929 the diversity in site characteristics in the Guadeloupe landscape generally plays a protective role
930 for metapopulation persistence, and that accounting for this variation through the use of
931 covariates improves predictions, especially for rare or specialized species.

932

933 *Limits of our approach*

934 Although our method generally succeeded in capturing the diversity of uses of a common
935 landscape by different species, often in line with field observations of habitat use, it also has
936 some limitations to consider for future applications. First, our methodology, like any other,
937 requires sufficient data to make accurate inferences. The validity of model inference may be
938 questionable for fugitive species (species that may occasionally found locally abundant
939 populations with a short half-life; e.g., *D. aeruginosum*), for species recently introduced in one or

940 a few sites that are still at an uncertain initial invasion stage (e.g., *H. duryi*, *I. exustus*), or for
941 species that are abundant in particular types of sites that are only marginally represented in the
942 dataset (e.g., *N. virginea*). The potential consequences of surveying several species in a common
943 set of sites highlight the importance of a careful study design where species with overlapping
944 ranges of possible habitats that are reasonably represented in the sample are considered. The
945 validity of model predictions also necessarily depends on our choice of covariates and not
946 overlooking crucially important variables, a general issue in ecology.

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

962 into account the loss of freshwater habitat as well as environmental shifts expected under climate
963 change scenarios.

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

984

985 CONCLUSION

986

987 We conducted a comparative analysis of metapopulation dynamics in a guild of species
988 inhabiting the same area and general habitat (freshwater bodies). This approach proved useful for
989 characterizing colonization and extinction rates and their dependence on site- and year-specific
990 environmental properties, and to project future dynamics. An important aspect of our model
991 system is that it is disconnected from the continent and from other Caribbean islands, which
992 means that colonization from outside can be disregarded as a contributor to metapopulation
993 dynamics, although it explains the occasional arrival of new species. This approach can certainly
994 be improved by considering competition among species and future shifts in climate with
995 subsequent effects on the environmental variables considered here. Importantly our comparative
996 approach could be considered as a first step to link metapopulation approaches that focus on
997 single species in patchy environments (as studied by Hanski and others; see references above) to
998 metacommunity approaches (e.g., **Leibold et al. 2004**; **Vellend 2010**) that describe collective
999 features of guilds. It is also complementary to (joint) species-distribution models (e.g., **Little &**
1000 **Altermatt 2018**; **Norberg et al. 2019**), which can potentially include environmental covariables
1001 and can consider more complex guilds with more diverse types of species interactions, but which
1002 also provide less detailed knowledge on demographic dynamics. Our approach provides insight
1003 on demographic strategies at the metapopulation level such as low- and high-turnover species
1004 dynamics that reflect life-history properties. It can thus complement classic metapopulation,
1005 metacommunity, and species distribution models to better understand how species respond to
1006 environmental variation.
1007

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1018

1019 LITERATURE CITED

- 1020 Amarasekare, P. 1998. Allee effects in metapopulation dynamics. *The American Naturalist*,
1021 152:298–302.
- 1022 Barnes, L. E. 1983. The colonization of ball-clay ponds by macroinvertebrates and macrophytes.
1023 *Freshwater Biology*, 13:561–578.
- 1024 Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models
1025 Using lme4. *Journal of Statistical Software*, 67:1-48.
- 1026 Bertassello, L. E., Bertuzzo, E., Botter, G., Jawitz, J. W., Aubeneau, A. F., Hoverman, J. T.,
1027 Rinaldo, A., and Rao, P. S. C. 2021. Dynamic spatio-temporal patterns of metapopulation
1028 occupancy in patchy habitats. *Royal Society Open Science*, 8:201309.
- 1029 Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K., and Travis,
1030 J. M. J. 2014. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics

1031 and species' responses to environmental changes. *Methods in Ecology and Evolution*,
1032 5:388–396.

1033 Bull, J. C., Pickup, N. J., Hassell, M. P., and Bonsall, M. B. 2006. Habitat shape, metapopulation
1034 processes and the dynamics of multispecies predator–prey interactions. *Journal of Animal*
1035 *Ecology*, 75:899–907.

1036 Caswell, H., and Etter, R. J. 1993. Ecological interactions in patchy environments, from patch
1037 occupancy models to cellular automata. *Lecture Notes in Biomathematics* 96: 93– 109.

1038 Chandler, R. B., Muths, E., Sigafus, B. H., Schwalbe, C. R., Jarchow, C. J., & Hossack, B. R.
1039 2015. Spatial occupancy models for predicting metapopulation dynamics and viability
1040 following reintroduction. *Journal of Applied Ecology*, 52(5):1325-1333.

1041 Chapuis, E., Lamy, T., Pointier, J.-P., Juillet, N., Ségard, A., Jarne, P., and David, P. 2017.
1042 Bioinvasion triggers rapid evolution of life histories in freshwater snails. *The American*
1043 *Naturalist*, 190:694–706.

1044 Davis, G. M. 1982. Historical and Ecological Factors in the Evolution, Adaptive Radiation, and
1045 Biogeography of Freshwater Mollusks. *American Zoologist*, 22:375–395.

1046 Dillon, R. T. 2000. *The Ecology of Freshwater Molluscs*. Cambridge University Press,
1047 Cambridge, UK.

1048 Dubart, M., Pantel, J. H., Pointier, J.-P., Jarne, P., and David, P. 2019. Modeling competition,
1049 niche, and coexistence between an invasive and a native species in a two-species
1050 metapopulation. *Ecology* 100: e02700.

1051 Elith, J., and Leathwick, J. R. 2009. Species Distribution Models: Ecological Explanation and
1052 Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and*
1053 *Systematics*, 40:677–697.

1054 Escobar, J. S., Auld, J. R., Correa, A. C., Alonso, J. M., Bony, Y. K., Coutellec, M.-A., Koene, J.
1055 M, Pointier, J.-P., Jarne, P., and David, P. 2011. Patterns of mating-system evolution in
1056 hermaphroditic animals: correlations among selfing rate, inbreeding depression, and the
1057 timing of reproduction. *Evolution*, 65:1233–1253.

1058 Etienne, R. S. 2002. A scrutiny of the Levins metapopulation model. *Comments on Theoretical*
1059 *Biology* 7:257–281.

1060 Facon, B. Pointier, J.-P., Glaubrecht, M., Poux, C., Jarne, P., and David, P. 2003. A molecular
1061 phylogeography approach to biological invasions of the New World by parthenogenetic
1062 Thiarid snails. *Molecular Ecology* 12:3027–3039.

1063 Facon, B., Pointier, J.-P., Jarne, P., Sarda, V. and David, P. 2008. High genetic variance in life-
1064 history strategies within invasive populations by way of multiple introductions. *Current*
1065 *Biology* 18:363–367.

1066 Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C. L. and Murphy, D. D. Assessing the roles
1067 of patch quality, area, and isolation in predicting metapopulation dynamics. 2002.
1068 *Conservation Biology* 16:706–716.

1069 Fox, J. and Weisberg, S. 2011. An {R} Companion to Applied Regression, Second Edition. Sage
1070 Publications, Thousand Oaks California, USA.

1071 Franco, M., and Silvertown, J. 1996. Life history variation in plants: an exploration of the fast-
1072 slow continuum hypothesis. *Philosophical Transactions of the Royal Society of London.*
1073 *Series B: Biological Sciences*, 351:1341–1348.

1074 Frank, K. and Wissel, C. 2002. A Formula for the Mean Lifetime of Metapopulations in
1075 Heterogeneous Landscapes. *The American Naturalist*. 159:530–552.

1076 Fronhofer, E. A., Kubisch, A., Hilker, F. M., Hovestadt, T., and Poethke, H. J. 2012. Why are
1077 metapopulations so rare? *Ecology*, 93: 1967–1978.

1078 Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in
1079 Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in*
1080 *Society)*, 182(2):389-402.

1081 George, E. I. and McCulloch, R. E. 1993. Variable selection via Gibbs sampling. *Journal of the*
1082 *American Statistical Association*. 88:881–889.

1083 Gilarranz, L. J., and J. Bascompte. 2012. Spatial network structure and metapopulation
1084 persistence. *Journal of Theoretical Biology* 297:11-16.

1085 Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its
1086 relevance to ecological and evolutionary theory. *The American Naturalist*, 111: 1169–
1087 1194.

1088 Guillera-Aroita, G. (2017). Modelling of species distributions, range dynamics and communities
1089 under imperfect detection: advances, challenges and opportunities. *Ecography*, 40:281–
1090 295.

1091 Guisan, A., and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology.
1092 *Ecological Modelling*, 135:147–186.

1093 Gyllenberg, M. and Hanski, I. 1997. Habitat deterioration, habitat destruction, and
1094 metapopulation persistence in a heterogenous landscape. *Theoretical Population Biology*
1095 52:198–215.

1096 Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology*
1097 63:151–162.

- 1098 Hanski, I. 1997. Predictive and practical metapopulation models: the incidence function
1099 approach. Pages 21–45 *in* D. Tilman and P. Kareiva, editors. *Spatial ecology*. Princeton
1100 University Press, Princeton, New Jersey, USA.
- 1101 Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- 1102 Hanski, I., Pakkala, T., Kuussaari, M. and Lei, G. 1995. Metapopulation persistence of an
1103 endangered butterfly in a fragmented landscape. *Oikos* 72:21–28 1995.
- 1104 Hanski, I., and Gilpin, M. E. 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*.
1105 Elsevier Academic Press.
- 1106 Hanski, I. and Gaggiotti, O. E. 2004. *Ecology, genetics, and evolution of metapopulations*.
1107 Elsevier Academic Press.
- 1108 Hanski, I., and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape.
1109 *Nature*, 404:755–758.
- 1110 Hanski, I., and Ovaskainen, O. 2002. Extinction Debt at Extinction Threshold. *Conservation*
1111 *Biology*, 16:666–673.
- 1112 Heard, G. W., McCarthy, M. A., Scroggie, M. P., Baumgartner, J. B., & Parris, K. M. 2013. A
1113 Bayesian model of metapopulation viability, with application to an endangered amphibian.
1114 *Diversity and Distributions*, 19(5-6):555-566.
- 1115 Heard, G. W., C. D. Thomas, J. A. Hodgson, M. P. Scroggie, D. S. L. Ramsey, and N. Clemann.
1116 2015. Refugia and connectivity sustain amphibian metapopulations afflicted by disease.
1117 *Ecology Letters* 18:853–863.
- 1118 Holmes, C. J., Rapti, Z., Pantel, J. H., Schulz, K. L., and Cáceres, C. E. 2020. Patch centrality
1119 affects metapopulation dynamics in small freshwater ponds. *Theoretical Ecology*, 13:435-
1120 448.

- 1121 Howell, P. E., Muths, E., Hossack, B. R., Sigafus, B. H., and Chandler, R. B. 2018. Increasing
1122 connectivity between metapopulation ecology and landscape ecology. *Ecology*, 99:1119–
1123 1128.
- 1124 Jarne, P., & Charlesworth, D. 1993. The evolution of the selfing rate in functionally
1125 hermaphrodite plants and animals. *Annual Review of Ecology and Systematics*, 24:441–
1126 466.
- 1127 Johansson, V., Ranius, T., and Snäll, T. 2012. Epiphyte metapopulation dynamics are explained
1128 by species traits, connectivity, and patch dynamics. *Ecology*, 93: 235–241.
- 1129 Johst, K. and Schöps, K. 2003. Persistence and conservation of a consumer--resource
1130 metapopulation with local overexploitation of resources. *Biological Conservation* 109:57–
1131 65.
- 1132 Jombart, T. 2008. adegenet: a R package for the multivariate analysis of genetic markers.
1133 *Bioinformatics*, 24:1403-1405.
- 1134 Jombart T. and Ahmed I. 2011. adegenet 1.3-1: new tools for the analysis of genome-wide SNP
1135 data. *Bioinformatics*. doi: 10.1093/bioinformatics/btr521
- 1136 Kappes, H., & Haase, P. 2012. Slow, but steady: dispersal of freshwater molluscs. *Aquatic
1137 Sciences*, 74:1–14.
- 1138 Karmalkar, A. V., Taylor, M. A., Campbell, J., and Stephenson, T. 2013. A review of observed
1139 and projected changes in climate for the islands in the Caribbean. *Atmósfera* 26 :283–309.
- 1140 Kéry, M., Guillerá-Arroita, G., and Lahoz-Monfort, J. J. 2013. Analysing and mapping species
1141 range dynamics using occupancy models. *Journal of Biogeography*, 40:1463–1474.

1142 Ladin, Z. S., D’Amico, V., Baetens, J. M., Roth, R. R. and Shriver, W. G. 2016. Predicting
1143 Metapopulation Responses to Conservation in Human-Dominated Landscapes. *Frontiers in*
1144 *Ecology and Evolution*. 4:122.

1145 Lamy, T., Pointier, J. P., Jarne, P., and David, P. 2012. Testing metapopulation dynamics using
1146 genetic, demographic and ecological data. *Molecular Ecology*, 21:1394–1410.

1147 Lamy, T., Gimenez, O., Pointier, J.-P., Jarne, P., and David, P. 2013. Metapopulation dynamics
1148 of species with cryptic life stages. *The American Naturalist*, 181:479–491.

1149 Lawes, M. J., Mealin, P. E. and Piper, S. E. 2000. Patch occupancy and potential metapopulation
1150 dynamics of three forest mammals in fragmented Afromontane forest in South Africa.
1151 *Conservation Biology*, 14:1088-1098.

1152 Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt,
1153 R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004. The
1154 metacommunity concept: a framework for multi-scale community ecology. *Ecology*
1155 *Letters*, 7:601–613.

1156 Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity
1157 for biological control. *Bulletin of the Entomological Society of America* 15:237–240.

1158 Levins, R. 1970. Extinction. In *Some mathematical problems in biology*, ed. M. Gertenhaber,
1159 75–107. American Mathematical Society, Providence, Rhode Island, USA.

1160 Little, C. J., and Altermatt, F. 2018. Do priority effects outweigh environmental filtering in a
1161 guild of dominant freshwater macroinvertebrates? *Proceedings of the Royal Society B:*
1162 *Biological Sciences*, 285:20180205.

1163 MacArthur, R. H., and Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton
1164 University Press, Princeton, New Jersey, USA.

- 1165 MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. and Franklin, A. B. 2003.
1166 Estimating site occupancy, colonization, and local extinction when a species is detected
1167 imperfectly. *Ecology* 84:2200–2207.
- 1168 Mackenzie, D. I., Nichols, J. D., Seamans, M. E. and Gutiérrez, R. J. 2009. Modeling species
1169 occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.
- 1170 Malone, C. R. 1965. Killdeer (*Charadrius vociferus* Linnaeus) as a Means of Dispersal for
1171 Aquatic Gastropods. *Ecology*, 46:551–552.
- 1172 Marsh, D. M. and Trenham, P. C. 2001. Metapopulation dynamics and amphibian conservation.
1173 *Conservation Biology* 15:40–49.
- 1174 Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter
1175 estimation using implicit statistical inference. *Ecology* 80:1031–1043.
- 1176 Moilanen, A. 2000. The equilibrium assumption in estimating the parameters of metapopulation
1177 models. *Journal of Animal Ecology* 69:143–153.
- 1178 Moilanen A. 2002. Implications of empirical data quality to metapopulation model parameter
1179 estimation and application. *Oikos* 96:516–530.
- 1180 Moilanen, A. 2004. SPOMSIM: software for stochastic patch occupancy models of
1181 metapopulation dynamics. *Ecological Modelling*, 179: 533–550.
- 1182 Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and
1183 landscape structure. *Ecology* 79:2503–2515.
- 1184 Nee, S., Hassell, M. P., and May, R. M. 1997. Two-species metapopulation models. In I. Hanski
1185 and M.E. Gilpin (Ed.), *Metapopulation Biology*. Elsevier Academic Press.

1186 Neelin, J. D., Münnich, M., Su, H., Meyerson, J. E. and Holloway, C. E. 2006. Tropical drying
1187 trends in global warming models and observations. *Proceedings of the National Academy*
1188 *of Sciences of the United States of America*. 103:6110–6115.

1189 Nicholson, E., Westphal, M. I., Frank, K., Rochester, W. A., Pressey, R. L., Lindenmayer, D. B.,
1190 and Possingham, H. P. 2006. A new method for conservation planning for the persistence
1191 of multiple species. *Ecology Letters*, 9:1049–1060.

1192 Norberg, A., Abrego, N., Blanchet, F. G., Adler, F. R., Anderson, B. J., Anttila, J., Araújo, M.
1193 B., Dallas, T., Dunson, D., Elith, J., Foster, S. D., Fox, R., Franklin, J., Godsoe, W.,
1194 Guisan, A., O'Hara, B., Hill, N. A., Holt, R. D., Hui, F. K. C., Husby, M., Kålås, J. A.,
1195 Lehtikoinen, A., Luoto, M., Mod, H. K., Newell, G., Renner, I., Roslin, T., Soininen, J.,
1196 Thuiller, W., Vanhatalo, J., Warton, D., White, M., Zimmermann, N. E., Gravel, D., and
1197 Ovaskainen, O.. 2019. A comprehensive evaluation of predictive performance of 33
1198 species distribution models at species and community levels. *Ecological Monographs*
1199 89:e01370.

1200 Normand, S., Zimmermann, N. E., Schurr, F. M., and Lischke, H. 2014. Demography as the
1201 basis for understanding and predicting range dynamics. *Ecography*, 37:1149–1154.

1202 Noya, O., Katz, N., Pointier, J. P., Theron, A. and de Noya, B. A. 2015. Schistosomiasis in
1203 América In C. Franco-Paredes & J.I. Santos-Preciado (Eds.). *Neglected Tropical Diseases-*
1204 *Latin America and the Caribbean*. Springer-Verlag, Wien, Austria.

1205 O'Hara, R. B., and Sillanpää, M. J. 2009. A review of Bayesian variable selection methods:
1206 what, how and which. *Bayesian Analysis*. 4:85–117.

1207 Oli, M. K. 2004. The fast–slow continuum and mammalian life-history patterns: an empirical
1208 evaluation. *Basic and Applied Ecology*, 5:449–463.

1209 Ovaskainen, O. 2002. The effective size of a metapopulation living in a heterogeneous patch
1210 network. *The American Naturalist* 160:612–628.

1211 Pellet, J., Fleishman, E., Dobkin, D. S., Gander, A. and Murphy, D. D. 2007. An empirical
1212 evaluation of the area and isolation paradigm of metapopulation dynamics. *Biological*
1213 *Conservation* 136:483–495.

1214 Perry, G. L., and Lee, F. 2019. How does temporal variation in habitat connectivity influence
1215 metapopulation dynamics? *Oikos*, 128:1277-1286.

1216 Phillips, S. J., Anderson, R. P., and Schapire, R. E. 2006. Maximum entropy modeling of species
1217 geographic distributions. *Ecological Modelling*, 190:231–259.

1218 Pianka, E. R. 1970. On r- and K-Selection. *The American Naturalist*, 104:592–597.

1219 Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs
1220 Sampling. in *Proceedings of the 3rd International Workshop on Distributed Statistical*
1221 *Computing* (eds. Hornik, K., Leisch, F. & Zeileis, A.).

1222 Plummer, M., Best, N., Cowles, K., and Vines, K. 2006. CODA: Convergence Diagnosis and
1223 Output Analysis for MCMC, *R News* 6:7-11.

1224 Plummer, M. 2016. rjags: Bayesian Graphical Models using MCMC. R package version 4-6.
1225 <https://CRAN.R-project.org/package=rjags>

1226 Pointier, J.-P. 1976. Répartition locale et biogéographie des mollusques dulçaquicoles de la
1227 Guadeloupe (Antilles Françaises). *Malacological Review*, 9:85–103.

1228 Pointier, J.-P. 2008. Guide to the freshwater molluscs of the Lesser Antilles. Conchbooks,
1229 Germany.

1230 Pointier, J.-P. and Augustin, D. 1999. Biological control and invading freshwater snails. A case
1231 study. *Comptes Rendus l'Académie des Sci. III-Sciences la Vie* 322:1093–1098.

1232 Pointier, J. P. and David, P. 2004. Biological control of *Biomphalaria glabrata*, the intermediate
1233 host of schistosomes, by *Marisa cornuarietis* in ponds of Guadeloupe: long-term impact on
1234 the local snail fauna and aquatic flora. *Biological Control* 29:81–89.

1235 Pointier J.-P., David, P., and Jarne, P. 2011. The biological control of the snail hosts of
1236 schistosomes: the role of competitor snails and biological invasions. In: *Biomphalaria*
1237 snails and larval trematodes. (eds. Toledo R., Fried B.). Springer-Verlag, Wien, Austria.

1238 Prugh, L. R., Hodges, K. E., Sinclair, A. R. E. and Brashares, J. S. 2008. Effect of habitat area
1239 and isolation on fragmented animal populations. *Proceedings of the National Academy of*
1240 *Sciences of the United States of America* 105:20770–20775.

1241 Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–
1242 661.

1243 Ranius, T. 2007. Extinction risks in metapopulations of a beetle inhabiting hollow trees predicted
1244 from time series. *Ecography* 30:716–726.

1245 Rees, W. J. 1965. The aerial dispersal of Mollusca. *Journal of Molluscan Studies*, 36:269–282.

1246 Reznick, D., Bryant, M. J., and Bashey, F. 2002. *r*- and *K*-selection revisited: the role of
1247 population regulation in life-history evolution. *Ecology*, 83:1509–1520.

1248 Rodhouse, Thomas J., Mackenzie R. Jeffress, Kirk R. Sherrill, Sean R. Mohren, Nancy J.
1249 Nordensten, Michael L. Magnuson, Donelle Schwalm, Jessica A. Castillo, Matthew
1250 Shinderman, and Clinton W. Epps. 2018. Geographical variation in the influence of habitat
1251 and climate on site occupancy turnover in American pika (*Ochotona princeps*). *Diversity*
1252 *and Distributions* 24:1506-1520.

1253 Rubin, D. B. 1984. Bayesianly justifiable and relevant frequency calculations for the applied
1254 statistician. *The Annals of Statistics*, 12(4):1151-1172.

1255 Runge, J. P., Runge, M. C. and Nichols, J. D. 2006. The role of local populations within a
1256 landscape context: defining and classifying sources and sinks. *The American Naturalist*
1257 167:925–938.

1258 Schooley, R. L. and Branch, L. C. 2009. Enhancing the area--isolation paradigm: habitat
1259 heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecological*
1260 *Applications* 19:1708–1722.

1261 Silvertown, J., Franco, M., and McConway, K. 1992. A demographic interpretation of Grime's
1262 triangle. *Functional Ecology*, 6:130–136.

1263 Sjögren-Gulve, P. and Ray, C. 1996. Using logistic regression to model metapopulation
1264 dynamics: large-scale forestry extirpates the pool frog. In *Metapopulations and Wildlife*
1265 *Conservation* (ed. D.R. McCullough). Island Press, Washington, D.C., USA.

1266 Smith, M. A. and Green, D. M. 2005. Dispersal and the metapopulation paradigm in amphibian
1267 ecology and conservation: are all amphibian populations metapopulations? *Ecography*
1268 28:110–128.

1269 Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-
1270 history traits in the mammals. *Oikos*, 41:173–187.

1271 Sutherland, C., Elston, D. A. and Lambin, X. 2012. Multi-scale processes in metapopulations:
1272 contributions of stage structure, rescue effect, and correlated extinctions. *Ecology*
1273 93:2465–2473.

1274 Svenning, J.-C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers,
1275 K.H., Dullinger, S., Edwards, T.C., Jr, Hickler, T., Higgins, S.I., Nabel, J.E.M.S., Pagel, J.
1276 and Normand, S. 2014. The influence of interspecific interactions on species range
1277 expansion rates. *Ecography*, 37:1198-1209.

1278 Taylor, D. W. 1988. Aspects of freshwater mollusc ecological biogeography. *Palaeogeography,*
1279 *Palaeoclimatology, Palaeoecology*, 62:511–576.

1280 ter Braak, C. J. F., Hanski, I. and Verboom, J. 1998. The incidence function approach
1281 to modelling of metapopulation dynamics. In: *Modelling spatio-temporal dynamics in*
1282 *ecology* (eds. Bascompte, J. & Solé, R. V.). Landes Biosciences, Austin, Texas, USA.

1283 van der Merwe, J., Hellgren, E. C. and Schaubert, E. M. 2016. Variation in metapopulation
1284 dynamics of a wetland mammal: The effect of hydrology. *Ecosphere* 7:e01275.

1285 van Leeuwen, C. H. A., and van der Velde, G. 2012. Prerequisites for flying snails: external
1286 transport potential of aquatic snails by waterbirds. *Freshwater Science*, 31:963–972.

1287 Vellend, M. 2010. Conceptual synthesis in community ecology. *The Quarterly Review of*
1288 *Biology*, 85:183–206.

1289 Vergara, P. M., Saravia-Zepeda, A., Castro-Reyes, N. and Simonetti, J. A. 2016. Is
1290 metapopulation patch occupancy in nature well predicted by the Levins model? *Population*
1291 *Ecology* 58:335–343.

1292 Verhulst, P.-F. 1838. Notice sur la loi que la population suit dans son accroissement.
1293 *Correspondance Mathématique et Physique*, 10:113–121.

1294 Warren, D. L., and Seifert, S. N. 2011. Ecological niche modeling in Maxent: the importance of
1295 model complexity and the performance of model selection criteria. *Ecological*
1296 *Applications*, 21:335–342.

1297 Warren, D. L. 2012. In defense of ‘niche modeling.’ *Trends in Ecology & Evolution*, 27:497–
1298 500.

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_{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.
<i>A. marmorata</i>	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)
<i>D. depressissimum</i>	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)
<i>B. kuhniiana</i>	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)
<i>D. surinamense</i>	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)
<i>Ph. acuta</i>	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)
<i>Ps. columella</i>	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)
<i>Me. tuberculata PAP</i>	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)
<i>Ma. cornuarietis</i>	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)
<i>Po. glauca</i>	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)
<i>E. viridans</i>	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)
<i>B. glabrata</i>	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)
<i>Me. tuberculata GOS</i>	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)
<i>Ga. cubensis</i>	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)
<i>B. schrammi</i>	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)
<i>Gu. radiata</i>	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)
<i>Py. parvulus</i>	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)
<i>D. cimex</i>	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)
<i>T. granifera</i>	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)
<i>D. aeruginosum</i>	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)
<i>Me. tuberculata FAL</i>	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)
<i>Me. tuberculata MAD</i>	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)
<i>Pl. guadeloupensis</i>	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)
<i>N. virginea</i>	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)
<i>Me. tuberculata CPF</i>	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>I. exustus</i>	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)
<i>Me. tuberculata SEN</i>	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)
<i>H. duryi</i>	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_i ; gray points), and that were estimated by the model but restricted to include only site \times 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 $(e_W w + e_D(1-w)) / (c_W w)$. 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^* , the occupancy expectation at quasi-equilibrium generated by the simulation model. This value was calculated as $p^* = d_E [c p^* / (c p^* + e)]$, 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_E 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_i , man refers to m_i , riv refers to r_i , connec refers to C_i , rs refers to RS_i , 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.

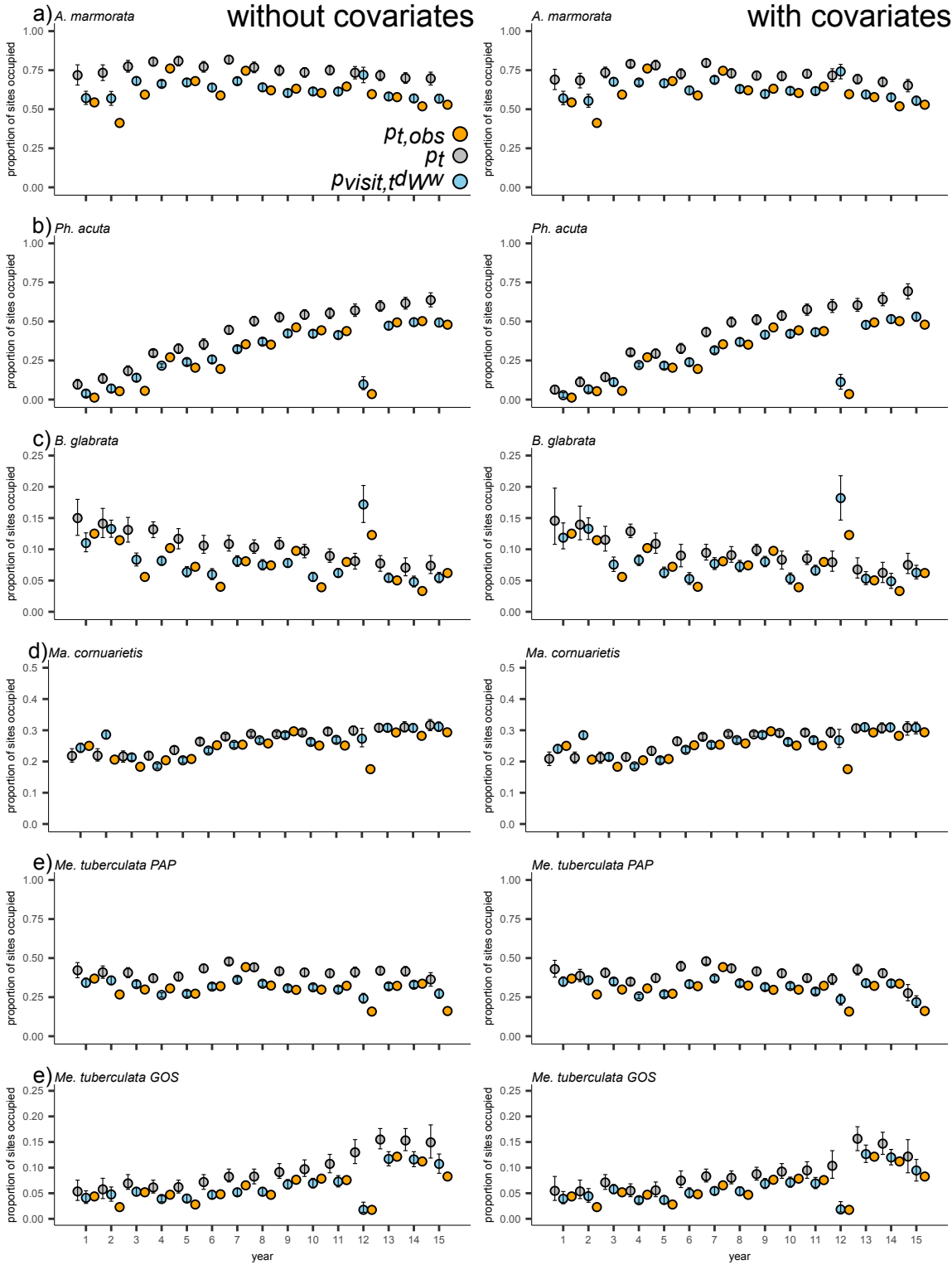
Figure 6. Map of extinction / colonization ratio per site (e_i/c_i) for six species in Grande-Terre (GT, larger island) and Marie-Galante (MG, smaller island), when taking into account all site-specific covariates. Continuous plots were constructed using Inverse Distance Weighting of

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

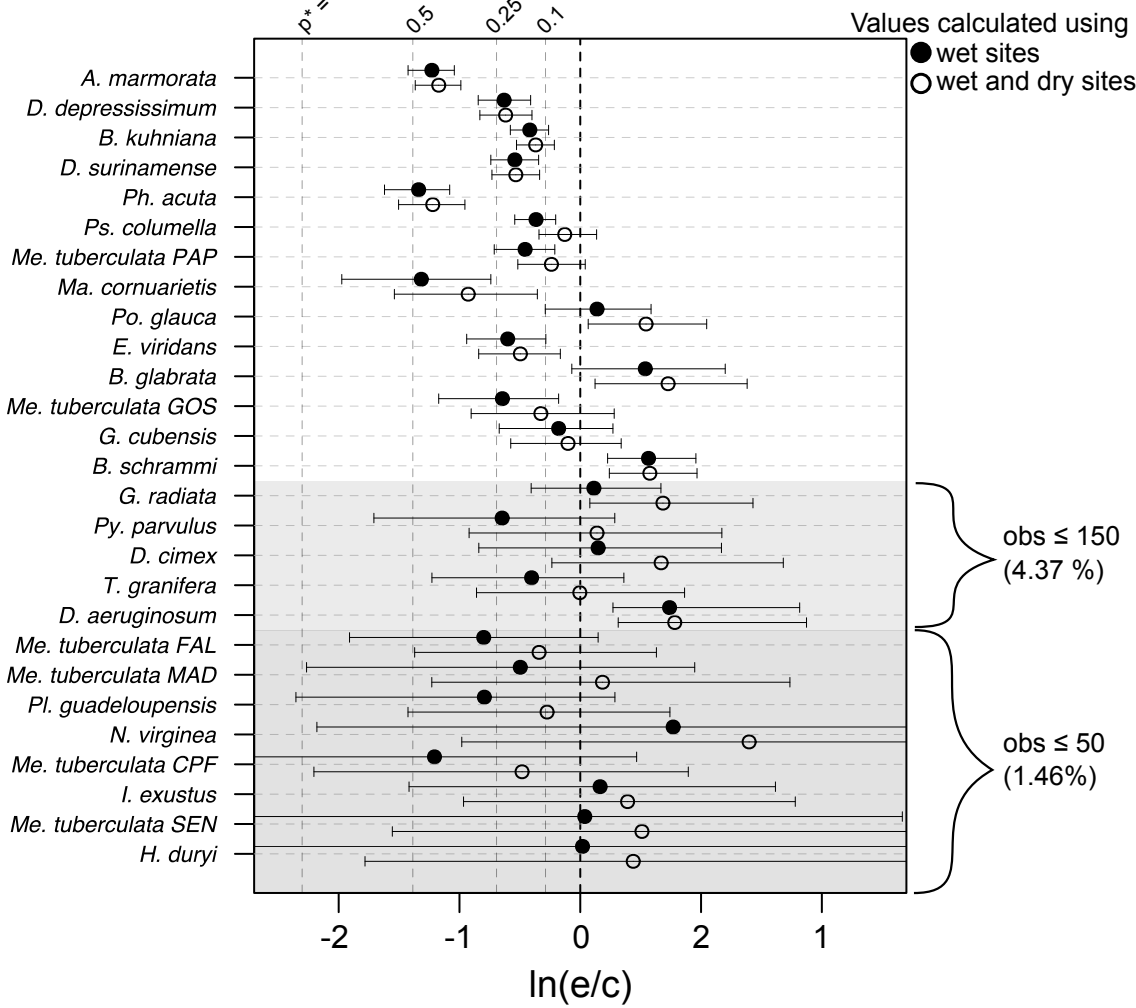
(green), or considering only covariates where SVSS support equaled or exceeded 0.6 (grey). Plots for all species are given in Appendix S1: Figure S6. Instances where a scenario has no colored density plot indicates that the species went extinct before year 1000 in that scenario (Appendix S1: Table S8).



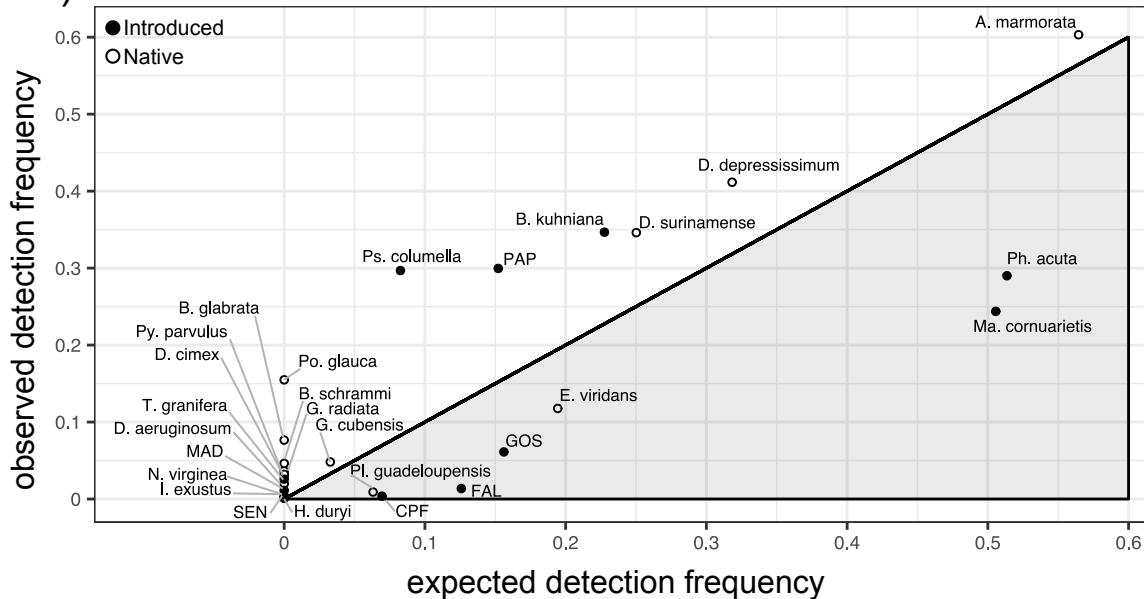
without covariates

persistence ($e < c$)

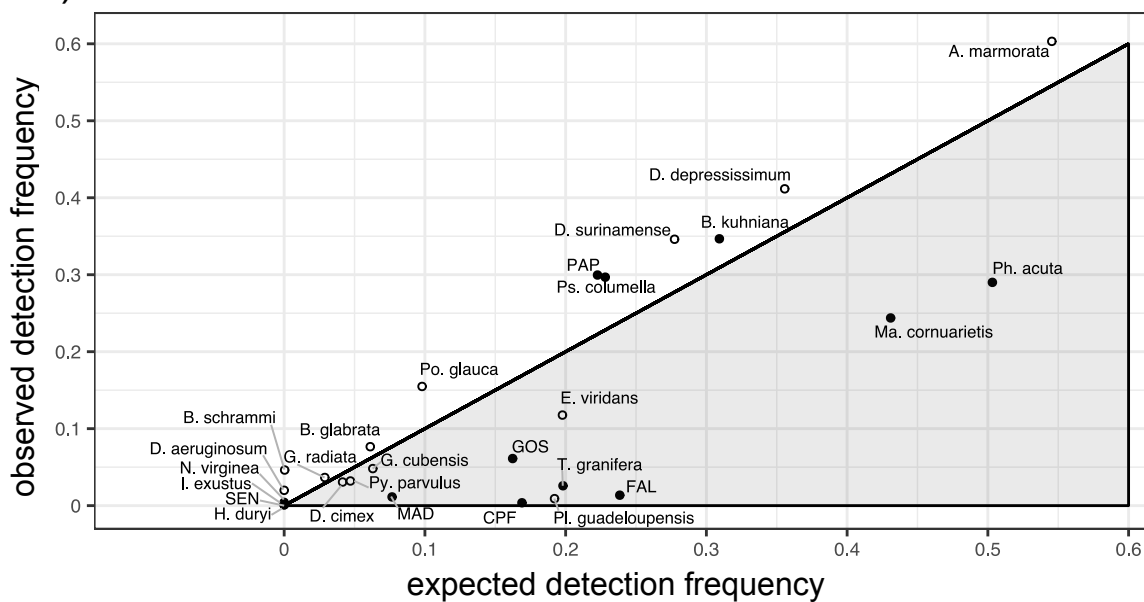
extinction ($e > c$)

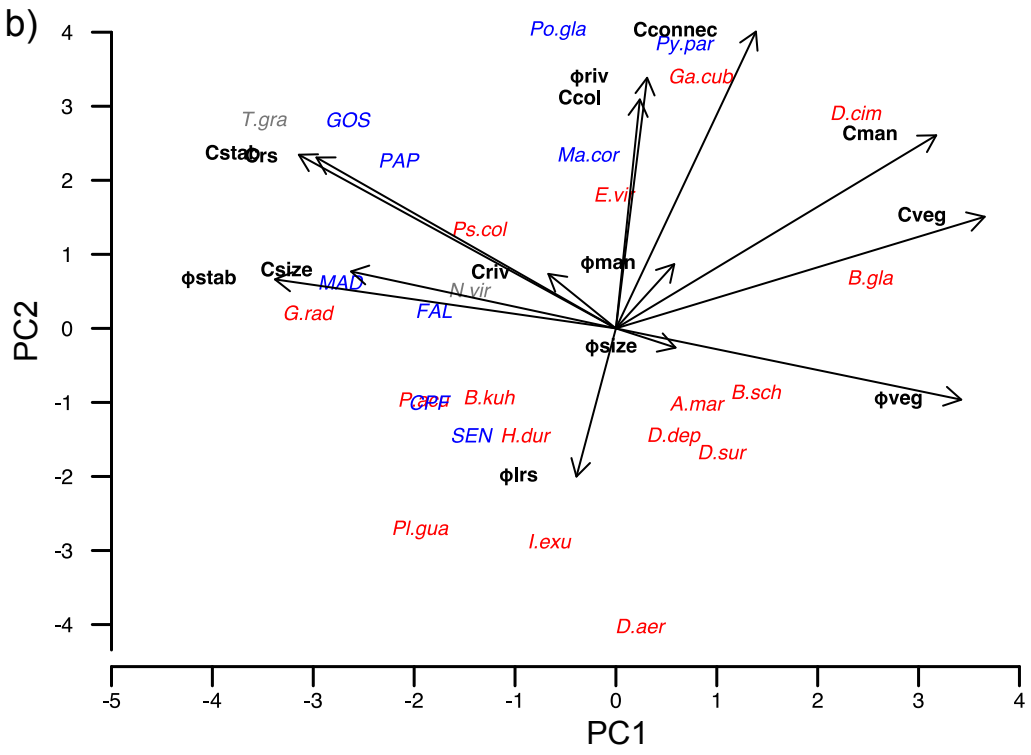
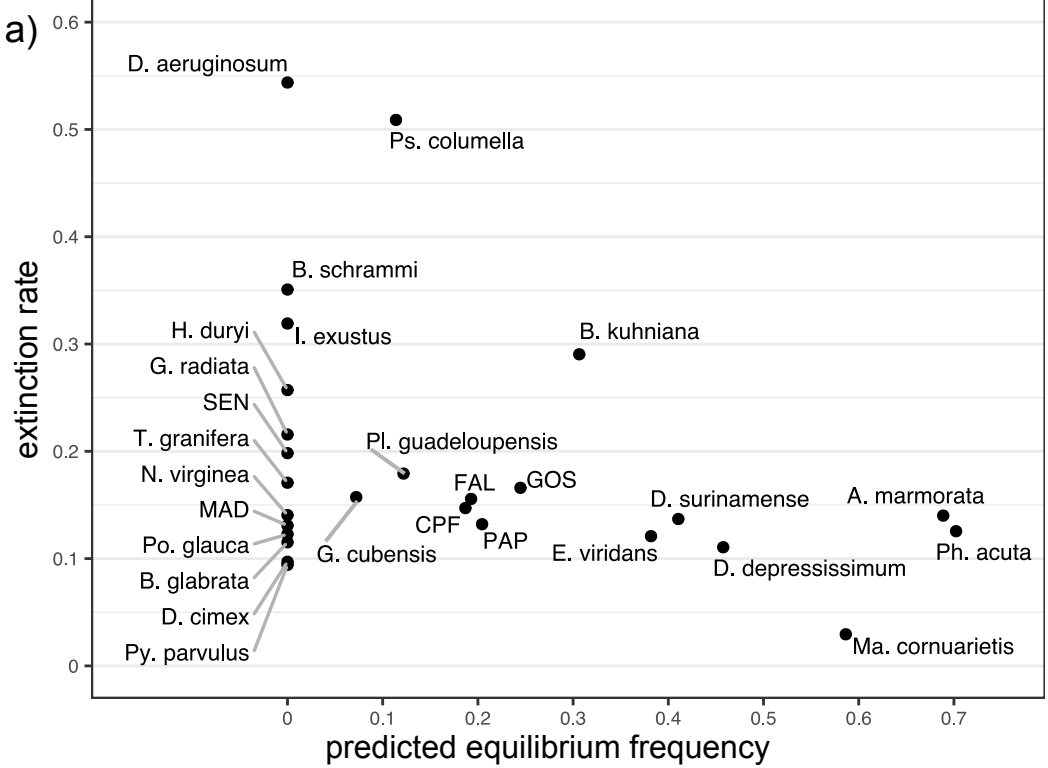


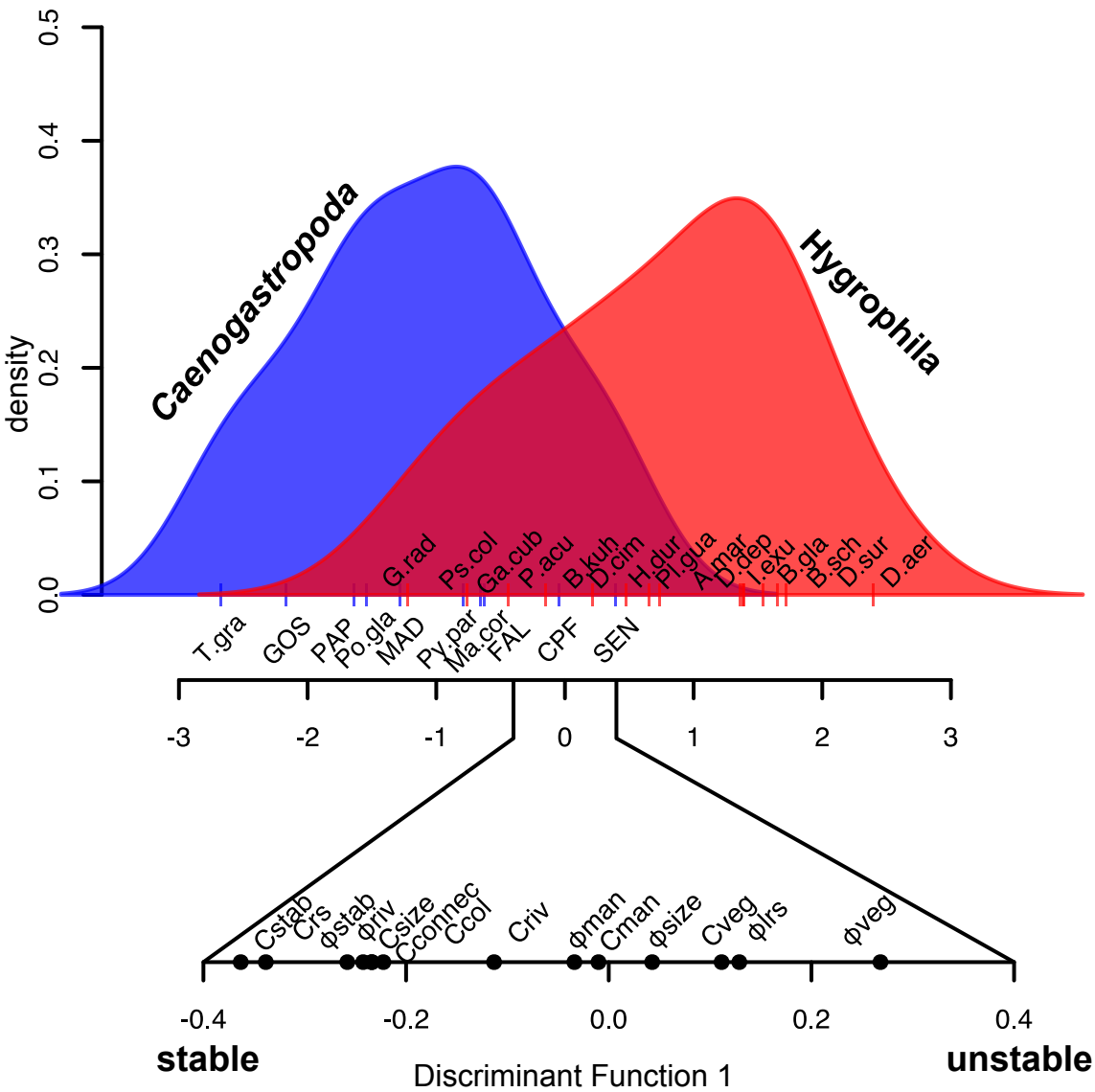
a) without covariates



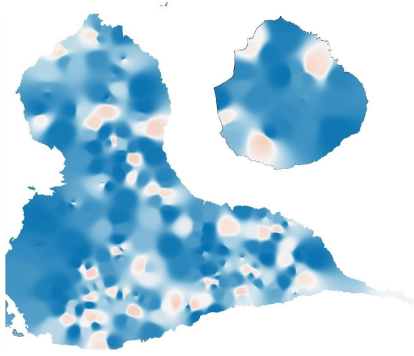
b) with covariates



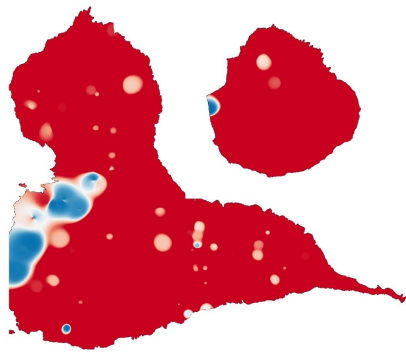




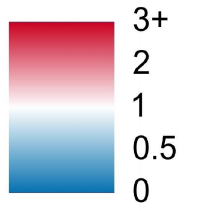
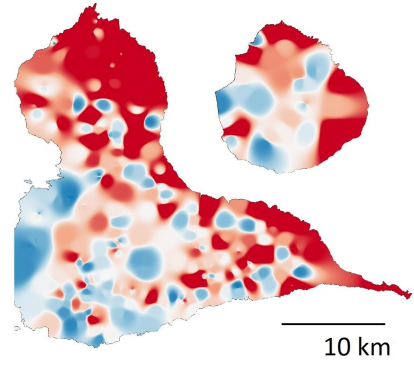
a) *A. marmorata*



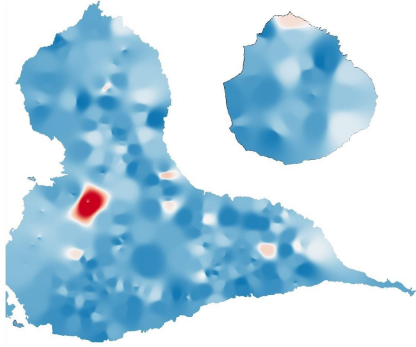
c) *B. glabrata*



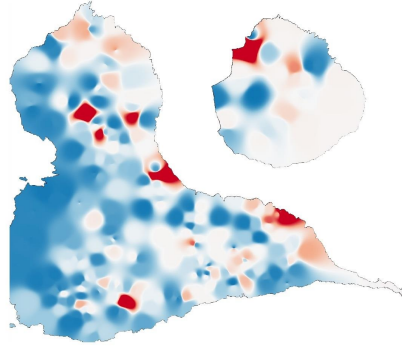
e) *Me. tuberculata* PAP



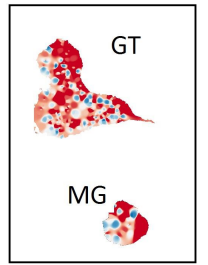
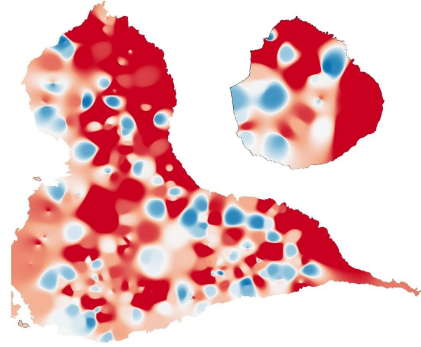
b) *Ph. acuta*



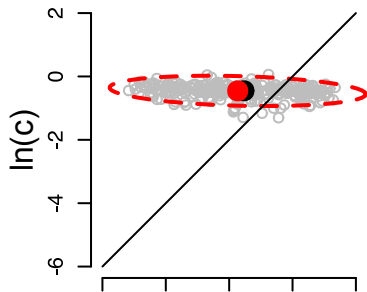
d) *Ma. cornuarietis*



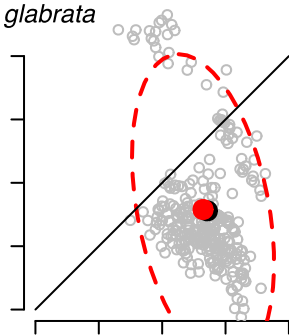
f) *Me. tuberculata* GOS



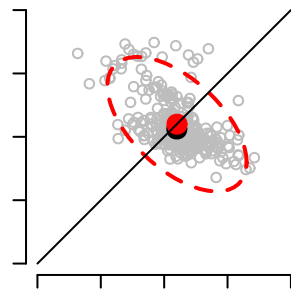
A. marmorata



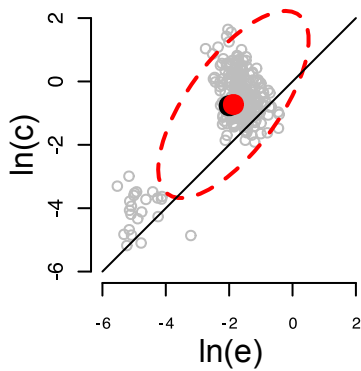
B. glabrata



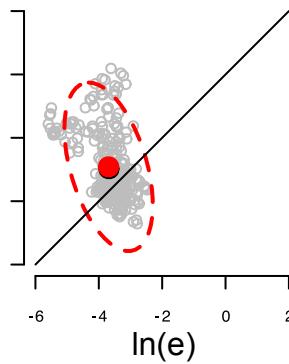
Me. tuberculata PAP



Ph. acuta



Ma. cornuarietis



Me. tuberculata GOS

