Metapopulation dynamics of multiple species in a heterogeneous landscape

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1   **Running head**: Metapopulations of multiple species

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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*

47

INTRODUCTION

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.

5

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**).

7

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

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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 km^2) and Marie-Galante (170.5 km^2) 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 $p = \frac{(\Sigma_{i=1}^{M} x_{i,t-1})}{M}$, 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 $c_D = 0$

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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_t.

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×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    $\ln(\varphi)$ (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

17

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   logit(φ_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

19

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   <mark>(data, JAGS code, and R code for the model with covariates are in Data S2).</mark>

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

Spatial variation: site-specific persistence

437

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 ($P_{ap} = 1 \mid$ 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,

24

528   highlighting results for the most frequent taxa (i.e. observed in more than 150 of the 3429 total

529   site × 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 $d_W = 0.23 ± 0.21$;

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 ±

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 ≤

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. kuhniana*,

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. kuhniana*, *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. kuhniana* despite their similar range of expected

594   stationary occupancy values ($p^* = 0.07$-0.3l; 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, $p_{visit,t}$ $d_W w$) 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, $\varphi_W = 0.76 \pm 0.14$

605   (0.71 ± 0.12 when considering the most frequent taxa), $c_W = 0.19 \pm 0.19$ (0.27 ± 0.23), $\varphi_D = 0.57$

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_t; 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_t; 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_t), 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_t) 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

31

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

34

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

36

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. kuhniana* 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 Caenogastopods 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

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

1018

1019 LITERATURE CITED

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

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

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

Figure legends

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

Figure 2. Metapopulation extinction and colonization rates. The ratio of extinction over colonization (log-transformed; with 2.5% and 97.5% CI) for all taxa from the model without covariates is shown. Black points are values calculated using e_W/c_W and white points are values calculated using $(e_W w + e_D (1-w)) / (c_W w)$. 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 $\leq$ 50 or $\leq$ 150 instances, or 1.46% and 4.37% respectively, of the total 3429 observation instances possible) are highlighted with grey coloring.

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

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

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

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

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

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

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

(green), or considering only covariates where SVSS support equaled or exceeded 0.6 (grey).

Plots for all species are given in Appendix S1: Figure S6. Instances where a scenario has no

colored density plot indicates that the species went extinct before year 1000 in that scenario

(Appendix S1: Table S8).
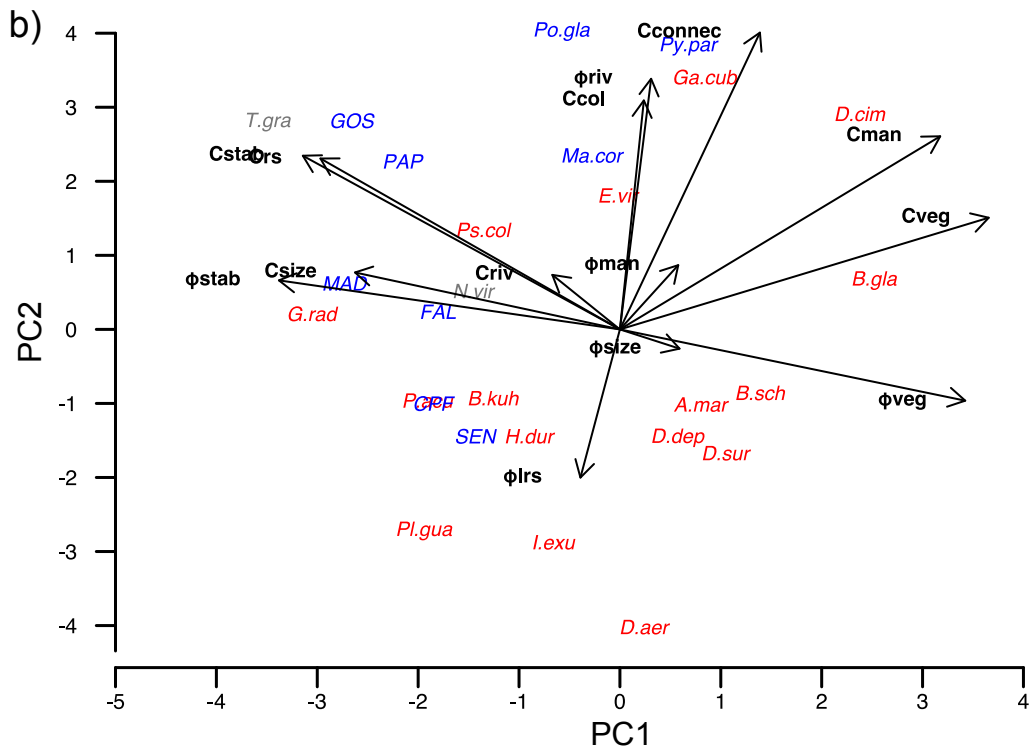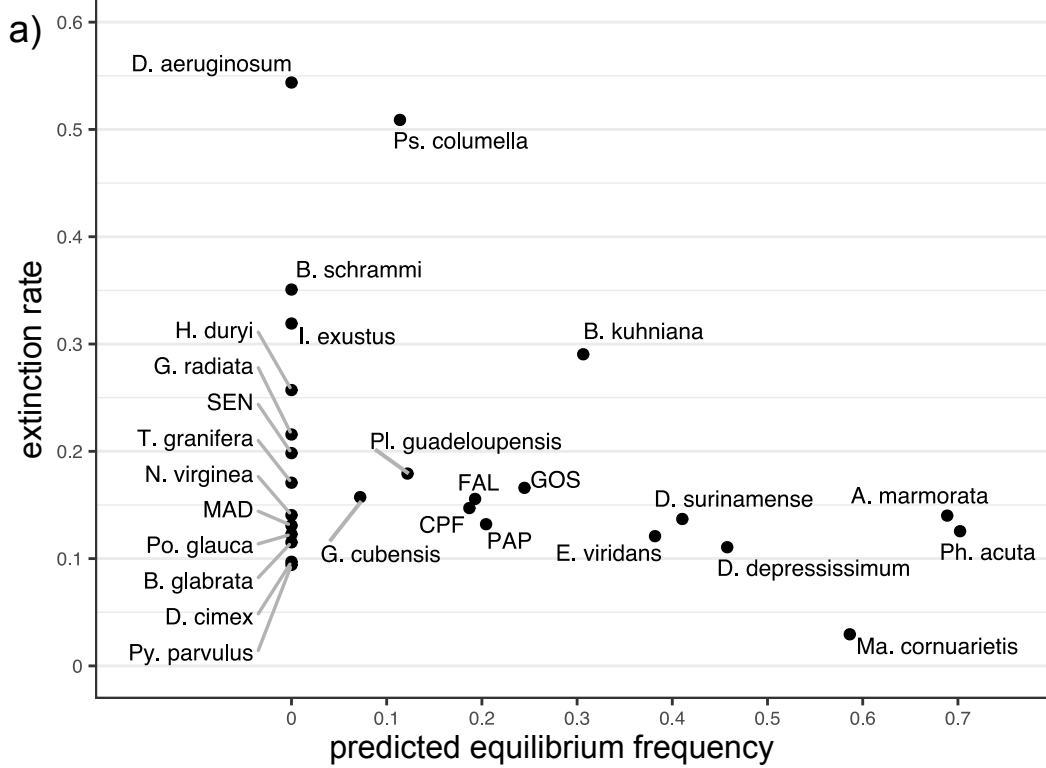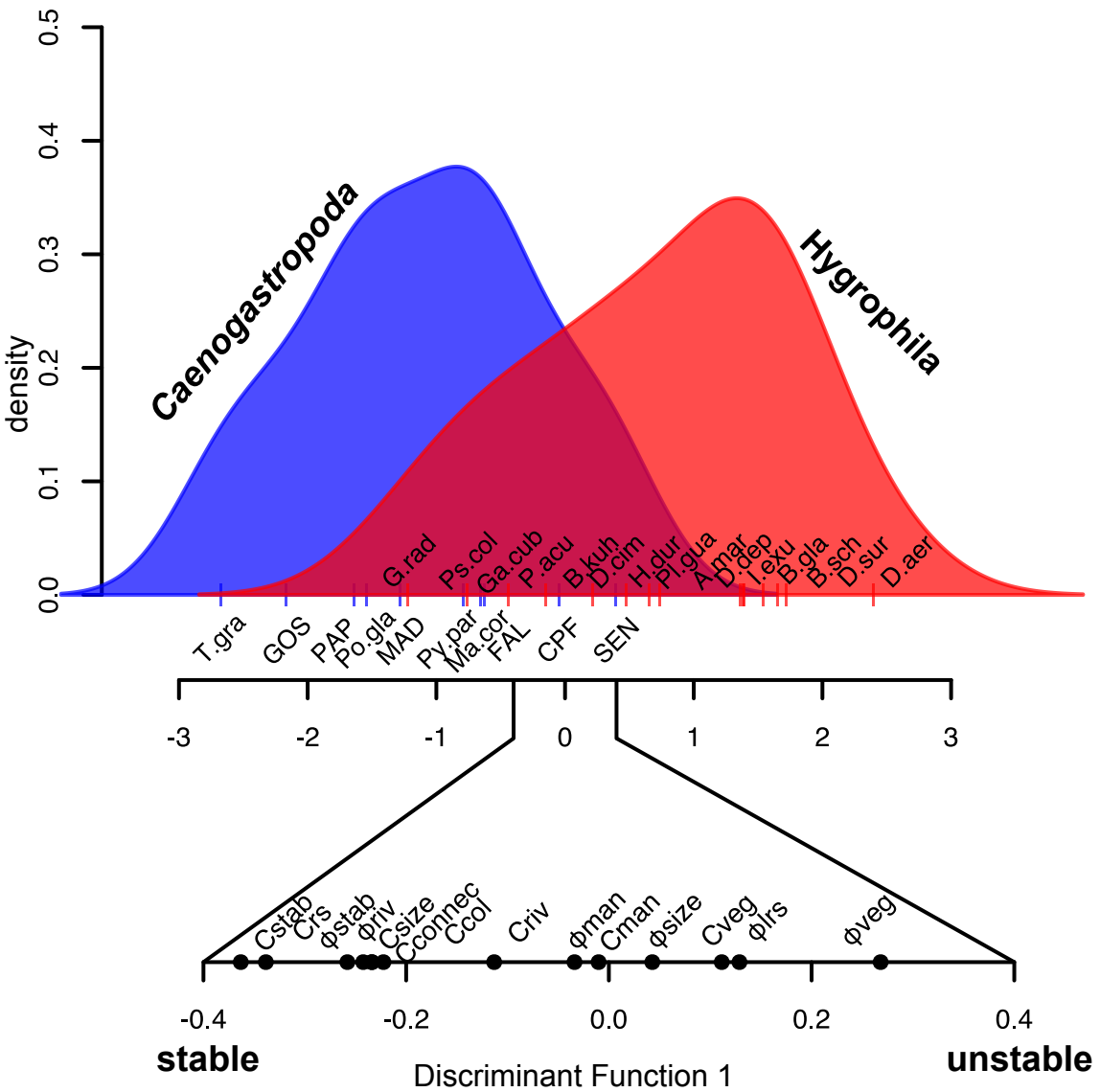
a) *A. marmorata* — without covariates / with covariates
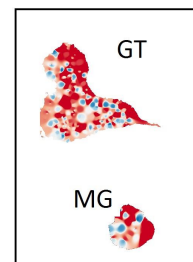
b) *Ph. acuta*

c) *B. glabrata*

d) *Ma. cornuarietis*

e) *Me. tuberculata PAP*

e) *Me. tuberculata GOS*

$p_{t,obs}$
p_t
$p_{visit,t}dWw$

proportion of sites occupied

year

without covariates

a) without covariates

Introduced ●
Native ○

observed detection frequency (y-axis)
expected detection frequency (x-axis)

A. marmorata, D. depressissimum, B. kuhniana, D. surinamense, Ps. columella, PAP, Ph. acuta, Ma. cornuarietis, B. glabrata, Py. parvulus, D. cimex, Po. glauca, B. schrammi, G. radiata, G. cubensis, T. granifera, D. aeruginosum, MAD, E. viridans, GOS, N. virginea, I. exustus, Pl. guadeloupensis, SEN, H. duryi, CPF, FAL

b) with covariates

observed detection frequency (y-axis)
expected detection frequency (x-axis)

A. marmorata, D. depressissimum, D. surinamense, B. kuhniana, PAP, Ps. columella, Ph. acuta, Ma. cornuarietis, Po. glauca, E. viridans, B. schrammi, B. glabrata, D. aeruginosum, G. radiata, G. cubensis, GOS, N. virginea, I. exustus, Py. parvulus, T. granifera, SEN, FAL, H. duryi, D. cimex, MAD, CPF, Pl. guadeloupensis

a) Scatter plot of extinction rate versus predicted equilibrium frequency. Species labels include: D. aeruginosum, Ps. columella, B. schrammi, H. duryi, I. exustus, B. kuhniana, G. radiata, SEN, T. granifera, Pl. guadeloupensis, N. virginea, FAL, GOS, D. surinamense, A. marmorata, MAD, CPF, PAP, E. viridans, Po. glauca, G. cubensis, B. glabrata, D. depressissimum, Ph. acuta, D. cimex, Py. parvulus, Ma. cornuarietis.

b) PCA biplot with axes PC1 (horizontal) and PC2 (vertical). Labels include: Po.gla, Cconnec, Py.par, φriv, Ga.cub, Ccol, D.cim, T.gra, GOS, Cman, PAP, Ma.cor, Cveg, Ps.col, E.vir, Crstab, Crs, B.gla, φman, Criv, φstab, Csize, MAD, N.vir, G.rad, FAL, φsize, φveg, B.kuh, A.mar, B.sch, PCPF, CPF, SEN, H.dur, D.dep, D.sur, φlrs, Pl.gua, I.exu, D.aer.

a) *A. marmorata*

c) *B. glabrata*
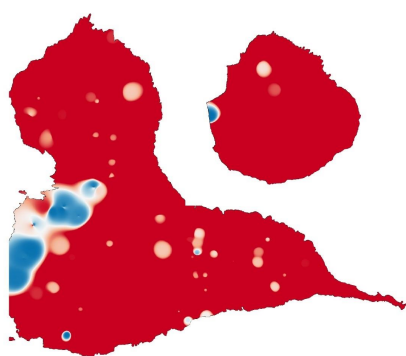
e) *Me. tuberculata* PAP
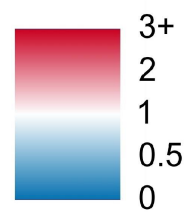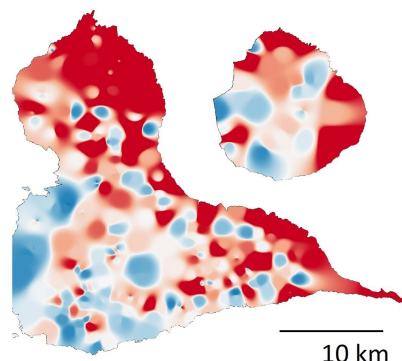
b) *Ph. acuta*
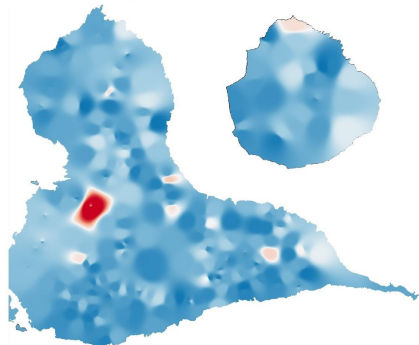
d) *Ma. cornuarietis*

f) *Me. tuberculata* GOS
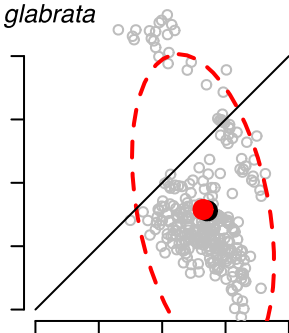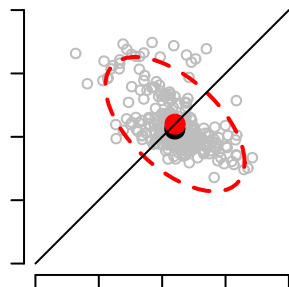
3+
2
1
0.5
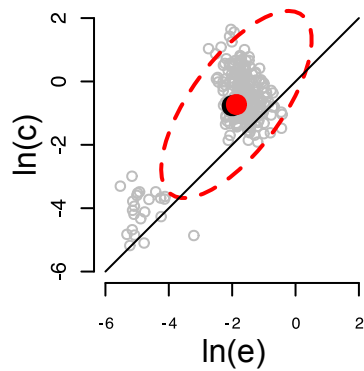0

10 km
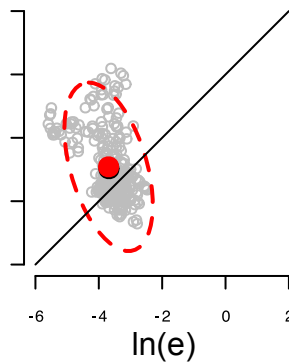
GT

MG
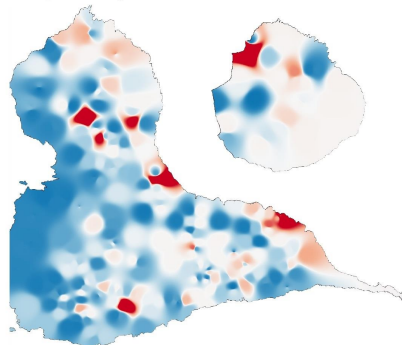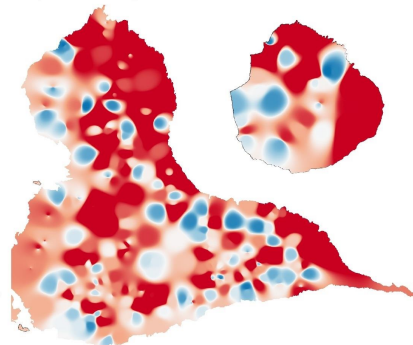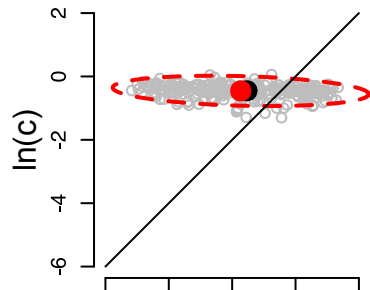
A. marmorata *B. glabrata* *Me. tuberculata PAP*

Ph. acuta *Ma. cornuarietis* *Me. tuberculata GOS*

Pr(simulations)

p1000

1) no covariates
2) covariates, intercept
3) covariates
4) covariates, reduced sites
5) covariates, $\alpha_p \geq 0.6$