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Connectivity and selfing drives population genetic structure in a patchy landscape: a comparative approach of four co-occurring freshwater snail species

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1 **Connectivity and selfing drives population genetic structure in a patchy landscape:**
2 **a comparative approach of four co-occurring freshwater snail species**

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25

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34

35 **Abstract** (291 words)

36 The distribution of neutral genetic variation in subdivided populations is driven by the interplay
37 between genetic drift, migration and extinction / colonization. The influence of environmental
38 and demographic factors has also been increasingly examined in empirical studies, but
39 generally focusing on a single species. An open question is whether these factors will similarly,
40 or idiosyncratically, affect a guild of species occupying the same geographical space and
41 exhibiting different traits, mating systems and histories. We addressed it by comparing the
42 population genetic structure of the four most common species of hermaphroditic freshwater
43 snails in Guadeloupe (Lesser Antilles), which occupy a network of patchily distributed sites
44 experiencing temporal variation in water availability. We analyzed microsatellite variability in
45 21 to 43 populations per species, and built predictions on how several environmental and
46 demographic variables, quantified from a long-term annual survey, as well as species traits,
47 may affect the distribution of genetic variation. These species displayed similarities, such as
48 fairly high levels of variation, but with marked differences among sites, as well strong genetic
49 differentiation and limited isolation by distance, which can be explained by passive dispersal
50 (strong role of site connectivity), extinction/colonization dynamics and variation in local
51 population size. They also exhibit differences, largely due to the mating system with less genetic
52 diversity and more genetic differentiation in the two selfing species when compared to the two
53 outcrossing ones. These differences can also be attributed to interspecific interactions resulting
54 from the ongoing invasion of Guadeloupe by one of the species studied, which affects the
55 demography of other species, and, to a limited extent, to local environmental factors. Our
56 comparative approach shows both differences and uniqueness in the way species occupy the
57 same landscape, and provides a possible entry to interspecific interactions in community
58 assembly.

59

60 **Introduction**

61 The evolutionary dynamics of species occupying patchily distributed habitats has been
62 the subject of a large body of both experimental and theoretical work (Hanski & Gaggiotti,
63 2004; Bell, 2008; Charlesworth & Charlesworth, 2010), highlighting the role of finite size of
64 populations and migration, and of their spatial and temporal variation. Metapopulation
65 approaches also consider the role of population extinction and colonization, which roles depend
66 particularly from the origin of the propagule pool (Levins, 1969; Whitlock & Barton, 1997;
67 Hanski & Gaggiotti, 2004). These demographic processes may also occur at the scale of whole
68 metapopulations, for example in situations of biological invasions (e.g., Davis, 2008; Facon &
69 David, 2006), with possible variation loss at migration front due to founder effects. Other
70 factors, such as the mating system or environmental parameters (e.g., through local adaptation),
71 should also be considered (e.g., Pannell, 2002; Hanski & Gaggiotti, 2004; Foll & Gaggiotti,
72 2006).

73 In this context, we will analyze here how the spatial distribution of neutral variation in
74 a patchy landscape is affected by the following factors: (i) environmental factors, especially
75 local ones, (ii) invasion dynamics, and (iii) traits, especially mating systems. (i) Variation in
76 population size, as well as extinction / colonization dynamics, may affect the strength of both
77 genetic drift and gene flow, and therefore genetic variation (Barton & Whitlock, 1997; Hanski
78 & Gaggiotti, 2004). Both processes may depend on environmental variables and their temporal
79 variation (Hanski & Gaggiotti, 2004; Lamy et al., 2013a). The role of local factors is
80 increasingly accounted for in analyses of population genetic structure (e.g., Foll & Gaggiotti,
81 2006; Frichot, Mathieu, Trouillon, Bouchard, & François, 2014). An example of local factor is
82 site size, which affects both population demography and migration (large sites can harbor larger
83 populations and are larger targets for migrants). At larger scale, the connectivity of local sites
84 to the whole network impacts gene flow and colonization. Connectivity can be evaluated based

85 on local features of accessibility, but also through some form of geographic distance, possibly
86 taking into account landscape elements modulating dispersal (Barton & Whitlock, 1997;
87 Rousset, 1997; Balkenhol, Cushman, Storfer, & Waits, 2015; Manel & Holderegger, 2013). (ii)
88 Extinction and colonization may also occur at metapopulation scale in situations of regional
89 invasion or extinction, both leaving traces in the distribution of genetic variability. For example,
90 invasion is often associated with founder effect and variation loss at invasion front (Roman &
91 Darling, 2007; Pannell, 2015), with increased frequencies of some alleles through genetic drift
92 (Excoffier & Ray, 2008). (iii) Mating systems can vary widely among species, even closely
93 related ones, or even within species, which affects the distribution of genetic variability, as they
94 interact in a complex manner with both environmental factors and demography (see e.g.
95 Charlesworth & Charlesworth, 2010). Self-fertilization is a striking example, on one hand
96 decreasing the effective population size, and thus modulating the impact of demography on
97 genetic diversity and population structure (see Charlesworth, 2003; Jarne, 1995). On the other
98 hand, it may affect population demography itself (Abu Awad & Billiard, 2017), and increased
99 selfing rates may be a way to cope with lack of partners / pollinators, protecting from local
100 extinction and giving an advantage in colonizing situations (Jarne, 1995; Pannell, 2015). Other
101 specific traits might be considered, such as the capacity to withstand bad conditions (e.g.,
102 escaping dryness through aestivation or seed banks), modulating the extinction dynamics
103 (Lamy et al., 2013a; Fréville et al., 2013).

104 An important point in the perspective presented above is that the distribution of diversity
105 is considered within species, and most studies of population focus on single species (see e.g. in
106 Bell, 2008; Charlesworth & Charlesworth, 2010). We may wonder to what extent different
107 species occupying the same landscape differ with respect to genetic diversity within and among
108 populations, since they can both be differentially be affected by local and regional factors and
109 exhibit different traits. This issue can be addressed through a comparative analysis of a species

110 set occupying the same landscape. The taxonomic range of the species set matters, since species
111 belonging to very different groups (e.g., arthropods, gastropods and amphibians in freshwater
112 habitats) are usually so different, for example with regard to migration, that even the
113 delimitation of local populations strongly differs. The issue is much less trivial when
114 considering closely related species (e.g., within arthropods, or gastropods, or amphibians). We
115 report in Table S1 the few examples of multispecies studies analyzing genetic diversity at small
116 geographic scale that we were able to find, which, incidentally, includes mostly studies
117 conducted in freshwater organisms. These comparative analyses evaluated whether the
118 environmental parameters mentioned above (e.g., affecting local population demography) are
119 more important than species traits such as the mating system (e.g., monogamous *vs.*
120 polygamous reproduction) in shaping population genetic structure. For example, connectivity
121 and habitat patchiness play a role in structuring population structure in orthopterans from
122 central Spain (Ortego, Garcia-Navas, Nogueras, & Cordero, 2015), while turtle species
123 studied in the USA were sensitive to water availability (Reid, Mladenoff, & Peery, 2017; see
124 Table S1). Note that a fraction only of these studies considers closely related species, and, even
125 fewer, species sets occupying the same landscape.

126 We here conduct such a multispecies (comparative) analysis of population genetic
127 structure in a guild of freshwater pulmonate snails (*Hydrophila*) occupying a patchy landscape
128 in Guadeloupe (Lesser Antilles). Freshwater habitats, especially lentic ones (e.g., ponds), are
129 appropriate systems for such a purpose, because the available habitats are clearly delimited
130 from the inhospitable matrix and a wide variety of environmental parameters can be considered
131 (see references in Table S1). In a pond network, snails disperse essentially passively through
132 either more or less temporary waterways connecting sites, or aerial vectors such as birds (Jarne
133 & Delay, 1991; Figuerola & Green, 2002; Kappes & Haase, 2012; Van Leeuwen et al., 2013).
134 Importantly, our sampling covers the whole space occupied by freshwater snails from Grande-

135 Terre of Guadeloupe, meaning that migration takes place essentially at this scale, with limited
136 ‘natural’ input from outside Grande-Terre, except through occasional introductions, essentially
137 through aquarium trade or birds (see e.g. Duggan, 2010). Moreover, we focused on the four
138 most common snail species in this landscape, with reasonably similar occupancy at
139 metapopulation scale (50-70% of occupied sites), certainly because sampling is easier, but also
140 because genetic and demographic parameters can more precisely be estimated than in rare
141 species (Heino et al., 2015). The Guadeloupe system has been well characterized through a
142 long-term survey of snail distribution on an island scale, as well as population genetics,
143 demographic and ecological studies (Chapuis et al., 2017; Dubart et al., 2019; Lamy et al., 2012;
144 Lamy et al., 2013a; Pantel et al., submitted).

145 We characterized microsatellite variation in 21 to 43 populations in these four species.
146 They experience the same variation in environmental parameters, such as site size and
147 connectivity, which may influence the distribution of genetic variation (Lamy et al., 2012). This
148 variation may however be affected by differences among species (see Chapuis et al., 2017;
149 Dubart et al., 2019; Lamy et al., 2012; Lamy et al., 2013a; Pantel et al., submitted). First, they
150 exhibit demographic differences, for example in extinction and colonization rates, but also
151 similarities (e.g., similar metapopulation occupancy, as mentioned above). Second, two of them
152 are mainly outcrossing, while the remaining two are mainly self-fertilizing. They also differ in
153 their aestivation capacity in dry sites. Third, one of them (*Physa acuta*) is an introduced species
154 in the process of rapidly invading the whole Grande-Terre, while the other three are native and
155 rather stable in terms of metapopulation occupancy. Our objective is to quantify genetic
156 variation within and among populations within species in order to characterize the factors and
157 processes to which these species react similarly vs. idiosyncratically (a comparative approach).
158 We consider the role of mating systems and traits, population demography, and several
159 environmental and landscape characteristics, building predictions on their influence (e.g., site

160 size should be associated with larger or more accessible populations and therefore more
161 variation). Four species is certainly not a sufficient number to draw conclusions on the factors
162 driving species differences in genetic structure in general. However, we suggest conducting
163 more comparative studies, up to now rather rare, to evaluate the generality of these factors. We
164 also discuss how such a comparative approach should help to progress towards a more
165 integrated eco-evolutionary perspective on community building and species interaction
166 (Hendry, 2017; Vellend, 2016).

167

168 **Materials and Methods**

169 *Long-term survey of snail communities*

170 The biological system, surveys and species studied have been described in papers spanning the
171 last five decades (see Pointier & Combes, 1976; Pointier & David, 2004; Pointier, 2008;
172 Chapuis et al., 2017; Dubart et al., 2019; Lamy et al., 2012; Lamy et al., 2013a; Pantel et al.,
173 submitted), and we provide here the relevant information for the current analysis. We initiated
174 in 2001 a long-term yearly study of the guild of freshwater snails from the geographically close
175 islands of Grande-Terre and Marie-Galante (Guadeloupe archipelago, Lesser Antilles). Grande-
176 Terre is a plateau of about 800 km² harboring a network of ponds (*ca.* 2000) of various sizes,
177 and a few small rivers (mostly temporary) and swamp grasslands connected to mangroves
178 (back-mangroves). Marie-Galante is a smaller island (160 km²) with a similar topography and
179 pond network. Water availability varies widely in time with the highest water level at the end
180 of the rainy season (August to November or December). A fraction of sites completely dry out
181 either yearly, or more irregularly, and stay dry for up to several months.

182 This long-term survey includes almost 280 sites, 245 of which are in Grande-Terre
183 (Lamy et al., 2012; Lamy et al., 2013a). Field sampling takes place in January-February when
184 these communities peak in abundance. They include 24 mollusc species, which makes up the

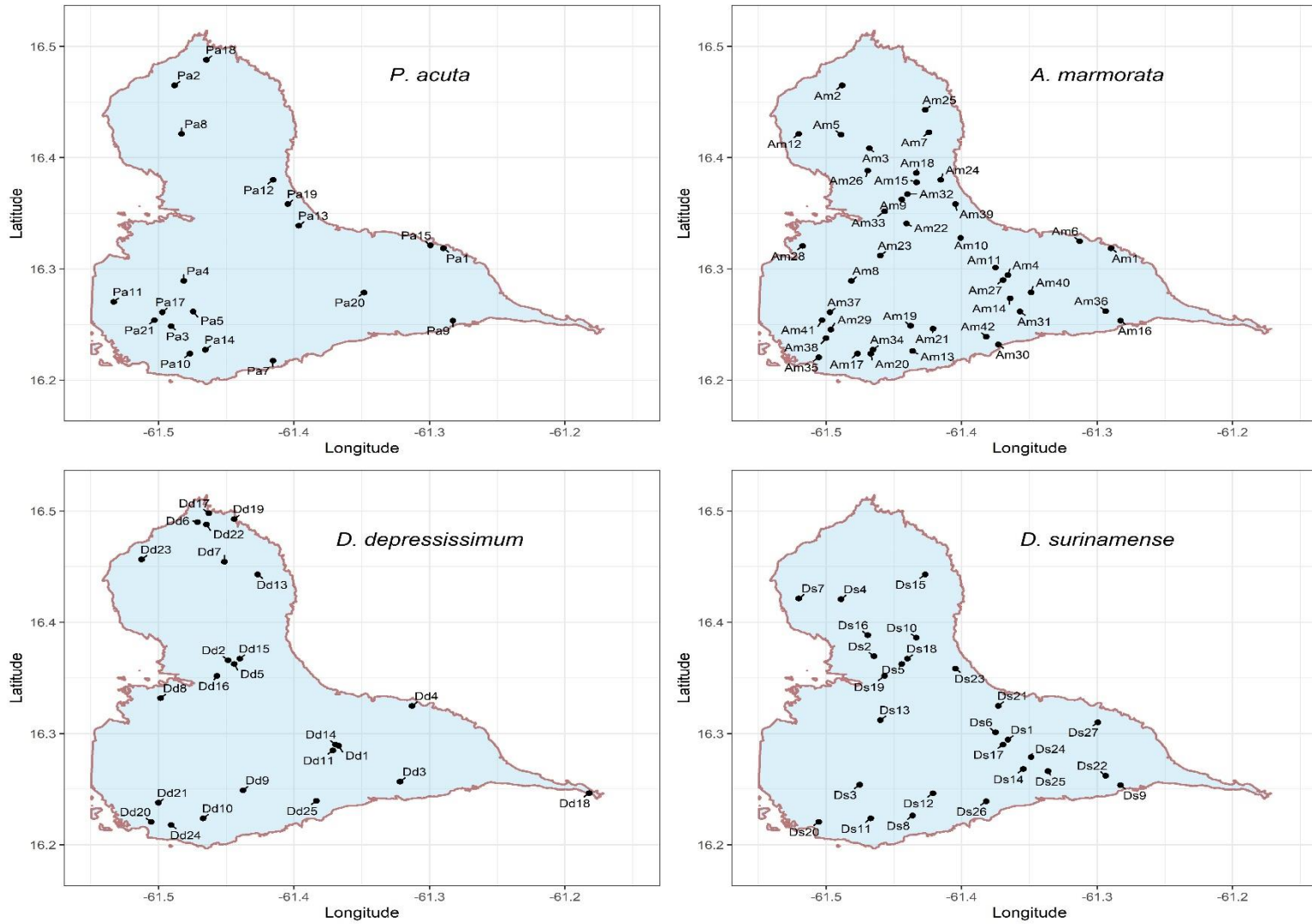
185 major part of the macrobenthos. Each site was explored by three persons for at least 15 min at
186 each visit (total searching time: 45 min). The presence and density of snails were estimated by
187 foraging both the sediment and plant strata using a scoop, and rock surfaces or floating debris
188 were visually surveyed. Snail density was estimated on a semi-log scale (no individuals, < 1
189 ind. / m², 1 to 5 ind. / m², 5 to 10 ind. / m² ...). Several environmental parameters were
190 characterized per site (detailed in Table S2) including size, aquatic vegetation cover, water
191 connectivity to neighboring watersheds, hydrological regime, and density of favorable habitats.
192 Site stability was defined based on the first four variables. From snail density and site size, we
193 built a demographic parameter called 'long-term population size'.

194

195 *The species studied and population sampling*

196 Our analysis bears on two pairs of closely related species (Morgan et al., 2002; Wethington and
197 Lydeard, 2007): *P. acuta* and *Aplexa marmorata* from the Physidae family, and *Drepanotrema*
198 *depressissimum* and *Drepanotrema surinamense* from the Planorbidae family. In each pair,
199 species are ecologically and morphologically similar, but do not hybridize. *Physa acuta* and *D.*
200 *depressissimum* are outcrossers, while *A. marmorata* and *D. surinamense* are selfers (Escobar
201 et al., 2011). These four species are the most common ones in the Guadeloupe metacommunity,
202 occupying *ca.* 50-70% of sites on average, and co-occur in a large number of sites (Dubart et
203 al., 2019; Pantel et al., submitted; Pointier & David, 2004). *Physa acuta* originates from the
204 Eastern-central USA and has markedly increased its range over the last two centuries to now
205 be cosmopolitan (Bousset et al., 2014; Ebbs, Loker, & Brant, 2018; Vinarsky, 2017). We
206 observed it in two sites from Grande-Terre in 2001, but this figure increased to *ca.* 60% of sites
207 in 2017. The three other species are neotropical and are considered native in the Lesser Antilles
208 (Pointier 2008). The two Physid species have been shown to interact in Guadeloupe, most likely
209 through direct reciprocal competition, with a depressing effect of *P. acuta* on the demography

210 **Figure 1.** Distribution of the sites studied in Guadeloupe (Grande Terre). Species name is indicated for each panel, and population acronyms are
 211 provided in Table S3. The four sites sampled in Basse Terre of Guadeloupe and Marie-Galante (Table S3) are not represented.
 212



214 **Table 1.** Predictions on the influence of mating system, site (environmental) characteristics and demographic factors on population genetic diversity
 215 and structure in the four species studied. The rationale for these predictions is given in the main text. Although predictions for several characteristics
 216 are identical (e.g., size and connectivity), they are presented separately for the sake of clarity. The effects are given on genetic diversity within
 217 populations (Div) and differentiation among populations (Diff). Predicted effect: positive (+), negative (-), limited, and unclear (?).
 218
 219

Characteristics	<i>Physa acuta</i> (outcrosser)		<i>Aplexa marmorata</i> (selfer)		<i>Drepanotrema depressissimum</i> (outcrosser)		<i>Drepanotrema surinamense</i> (selfer)	
	Div	Diff	Div	Diff	Div	Diff	Div	Diff
Mating system	High	Weak	Low	Strong	High	Weak	Low	Strong
Effect of site characteristics								
Size	+	-	+	-	+	-	+	-
Vegetation cover	-	+	+	-	+	-	+	-
Connectivity	+	-	+	-	+	-	+	-
Stability	+	-	+	-	Limited	Limited	Limited	Limited
Density of favourable habitats	+	-	+	-	+	-	+	-
Effect of demographic factors								
Invasion age / years since <i>P. acuta</i> invasion	+	-	-	+	?	?	?	?
Long-term population size	+	-	+	-	+	-	+	-

221 of *A. marmorata*, but a predicted stable co-existence (Dubart et al., 2019) and a character
222 displacement (life-history traits) towards more 'r-strategy' in *A. marmorata* within sites,
223 following the arrival of *P. acuta* (Chapuis et al., 2017). The two *Drepanotrema* species also
224 resist better in dry sites than the two Physids, aestivating under rocks or vegetation (Pointier &
225 Combes, 1976). This invasion allowed to introduce a second demographic variable in our
226 analyses, the time in years since the first detection of the invasive *P. acuta* - referred to as
227 'invasion age' in this species and 'time since *P. acuta* invasion' in the other species (Table S2).
228 We considered two classes, not or recently invaded by *P. acuta* vs. invaded for more than two
229 years, as in Chapuis et al. (2017). In *A. marmorata* and *Drepanotrema* spp., populations of the
230 first class are unlikely to show a detectable evolutionary response to the presence of *P. acuta*
231 because of the limited number of generations (Chapuis et al., 2017).

232 The four species were sampled in Grande-Terre during the yearly field surveys in 74
233 sites in which one to three of the four species were co-occurring (Figure 1, Tables S3 and S4;
234 1.57 species per site). Four sites from Basse-Terre and Marie-Galante were also considered in
235 the study of *P. acuta* (three sites) and *A. marmorata* (one site). *Physa acuta*, *A. marmorata*, *D.*
236 *depressissimum* and *D. surinamense* were sampled in 21, 43, 25 and 27 sites respectively, from
237 2007 to 2010. Individuals were killed just after sampling in 80°C water for 1 minute and
238 preserved in 95° ethanol. The genetic analysis was conducted on at least 10 individuals per
239 population for a total of 459 individuals in *P. acuta* (mean per population \pm s.d.: 21.86 ± 5.51),
240 781 in *A. marmorata* (18.14 ± 6.42 s.d.), 749 in *D. depressissimum* (29.96 ± 2.73 s.d.), and 365
241 in *D. surinamense* (13.52 ± 6.3). Less than 10 individuals were available in three populations
242 (Table S4).

243 Note that the population genetic data used in this paper have partly been published: a
244 full analysis of population structure in *D. depressissimum* in Guadeloupe is reported in Lamy
245 et al. (2012) and population genetic richness of both *D. depressissimum* and *A. marmorata* is

246 used in Lamy et al. (2013b). However, we will present all the genetic data for the sake of clarity,
247 and refer to previous work when required.

248

249 *Microsatellite characterization*

250 DNA extraction and allele characterization have been described in Sourrouille et al. (2003),
251 Bousset, Henry, Sourrouille, & Jarne (2004), and Escobar, Nicot, & David (2008) for *P. acuta*,
252 in Dubois, Nicot, Jarne, & David (2008) for *A. marmorata* and in Nicot, Jarne, & David (2009)
253 and Lamy et al. (2012) for *D. surinamense* and *D. depressissimum*. Briefly, DNA was extracted
254 using a Chelex method (Bio-Rad). Genotypes were obtained at polymorphic microsatellite loci
255 giving reproducible results, seven in *P. acuta* (Pac1, Pac2, Pac5, Sourrouille et al. 2003;
256 AF108762, AF108764, Monsutti & Perrin, 1999; Pasu1-11, Pasu1-2, Escobar et al., 2008),
257 eight in *A. marmorata* (Ama1, Ama4, Ama7, Ama9, Ama10, Ama12, Ama13, Ama14, Dubois
258 et al., 2008), 10 in *D. depressissimum* (DDE03, DDE04, DDE06, DDE09, DDE12, DDE14,
259 DDE16, DDE20, DDE22, DDE23, Lamy et al., 2012), and 12 in *D. surinamense* (DSU01,
260 DSU02, DSU04, DSU05, DSU07, DSU09, DSU11, DSU12, DSU13, DSU14, DSU15, DSU16,
261 Nicot et al., 2009). Allele reading was performed independently by two persons.

262

263 *Genetic diversity and differentiation*

264 The analyses were conducted in the same way in the four species, except when otherwise stated.
265 We computed the number of polymorphic loci, allelic richness (rarefied to the smallest sample
266 size per species (R_A , Petit, El Mousadik, & Pons, 1998; 8, 10, 14 and 7 diploid individuals in *P.*
267 *acuta*, *A. marmorata*, *D. surinamense* and *D. depressissimum* respectively) per population and
268 species using FSTAT 2.9.3.2 (Goudet, 2001). Gene diversity (unbiased H_e ; Nei, 1987) and
269 genotypic disequilibrium for locus pairs (Weir, 1996) were computed using GENEPOP 4.4
270 (Rousset, 2008). In the two selfing species (*A. marmorata* and *D. surinamense*), we also

271 estimated the genotypic diversity (R_G ; i.e. the number of genotypes) rarified to sample size of
272 10 and 7 respectively. We calculated the correlation between R_A and H_e in each species, as well
273 as with R_G in the selfing species, using Pearson's correlation coefficient.

274 Deviations from Hardy-Weinberg equilibrium (HWE) were tested at each locus using
275 exact tests (Raymond & Rousset, 1995), and a global P -value for all loci was obtained using
276 Fisher's exact test and Markov Chain algorithm with GENEPOP 4.4. A multilocus estimate of
277 Wright's inbreeding coefficient (F_{IS}) was estimated following Weir and Cockerham (1984). The
278 selfing rate (S) was calculated based on David, Pujol, Viard, Castella, & Goudet (2007)'s
279 method, which is insensitive to null alleles, an acute issue in outcrossing species, and less of a
280 problem in selfing species since null alleles are readily detected when occurring in the
281 homozygous state (see Jarne & David, 2008). S was here derived from the g_2 method using
282 RMES (David et al., 2007).

283 Genetic differentiation between population pairs and overall differentiation was
284 assessed in each species based on exact tests using GENEPOP 4.4, and their magnitude was
285 estimated based on the estimator θ of F_{ST} , which was calculated following Weir and Cockerham
286 (1984). Hereafter, we refer to the estimates between populations pairs as pairwise F_{ST} . We also
287 estimated the genetic differentiation between each local population and all other sampled
288 populations, hereafter site-specific F_{ST} , using the Bayesian method implemented in GESTE 2.0
289 (Foll & Gaggiotti, 2006). We calculated Pearson's correlation coefficient between site-specific
290 F_{ST} and genetic diversity (H_e) in each species. The geographic distribution of genetic diversity
291 was evaluated first by testing for isolation by distance in each species based on pairwise
292 distance matrices (linear geographical distance and $F_{ST}/(1-F_{ST})$) using a Mantel test (1000
293 permutations) in *Vegan* R package (Oksanen et al., 2015; R Development Core Team, 2005
294 version 3.6.3). We also examined visually the pairwise F_{ST} matrix after they have been
295 restructured based on a seriation approach implemented with *seriation* in R (R Development

296 Core Team, 2005) – the occurrence of population clusters would be evidenced by population
297 blocks with lower intra-block F_{ST} than with other populations. This also allows building
298 cladograms to better visualize population relationships using the “complete” method of *hclust*
299 (R Development Core Team, 2005). We also used a more formal clustering approach, sNMF,
300 proposed by Frichot et al. (2014). This method reconstitutes population clusters based on
301 ancestry coefficients. This method is not sensitive to strong inbreeding, and was previously
302 successfully used in the highly selfing snail *Biomphalaria pfeifferi* (Tian-Bi et al., 2019) – this
303 is the reason why we preferred it to popular approaches such as STRUCTURE (Pritchard et al.,
304 2000). sNMF was implemented using the R package *LEA* (Frichot & François, 2015 ; R
305 Development Core Team, 2005). We used a target number of clusters varying from 1 to 10, a
306 regularization parameter of 50, 50 runs were performed per analysis, and several analyses were
307 performed per species. Based on the optimal number of clusters, we drew barplots of average
308 ancestry coefficients per population, and reported these values as piecharts on the Grande-Terre
309 maps using the *gdal* R package (R Development Core Team, 2005).

310

311 *Environmental and demographic drivers of genetic diversity*

312 We assessed the influence of several site characteristics and demographic factors (described
313 above; see Table S2) on allelic richness (R_A) and on genetic differentiation (site-specific F_{ST}) in
314 the four species, but also on genotypic richness (R_G) in the selfing *A. marmorata* and *D.*
315 *surinamense*. The site characteristics were size, vegetation cover, connectivity, stability and
316 density of favorable habitats, and the demographic factors were invasion age and long-term
317 population size. Given that our first genetic sampling was performed in 2007, we used the value
318 per site of these variables over the 2001-2007 period (averaged for those variables for which
319 we got a value per year; Table S5). Because environmental data were missing, the following
320 populations were excluded from the analyses: Sainte Rose (Basse-Terre) for *P. acuta*, Ravine

321 Vinty (Basse-Terre) for *A. marmorata* and Pointe des Chateaux (Grande-Terre) for *D.*
322 *depressissimum*.

323 We built general predictions on genetic diversity and structure, based on (i) the mating
324 system, (ii) environmental parameters, and (iii) demographic parameters (Table 1). (i) We
325 expect less diversity and more divergence in selfing than in outcrossing populations, as detailed
326 in Introduction. (ii) The predictions depend on the model of population genetic structure
327 underlying species dynamics, especially on how the environmental variables are affected by the
328 demography and traits of species. However, we expect that site size, site connectivity, and
329 density of favorable habitats should contribute positively to intrapopulation variability and
330 negatively to differentiation among populations, because they positively affect effective
331 population size and gene flow. Stability might have the same effect than the first three
332 parameters in the two physids. The two *Drepanotrema* species are dwelling well in unstable
333 sites, because of their aestivating capacity (Pointier & Combes, 1976), which should limit
334 (perhaps annihilate) the effect. These predictions can be refined on the basis of previously
335 obtained estimates of extinction and colonization rates at metapopulation scale per species
336 (Dubart et al., 2019; Pantel et al., submitted). In most cases, these environmental parameters
337 did not affect these rates, and when they did, this was in the direction of the predictions above
338 (Table S6). For example, site size positively affect colonization in three species, which should
339 contribute positively to genetic diversity. Vegetation cover should also have the same effect in
340 *A. marmorata* and the two *Drepanotrema* species, but the reverse one in *P. acuta*, given its
341 incidence on extinction and colonization (Table S6). (iii) Invasion age is predicted to affect the
342 two *Physa* species. In the invasive *P. acuta*, young populations should be less diverse than old
343 ones reflecting temporary founder effects at the colonization front. Both demographic
344 population size and colonization rates are negatively affected in *A. marmorata* by the
345 competition with *P. acuta* (Chapuis et al., 2017; Dubart et al., 2019), which should depress

346 diversity in sites that have been invaded by the latter for a longer time. The expectation is less
347 clear in the two *Drepanotrema* species, since the arrival of *P. acuta* only slightly affects their
348 density ($P = 0.051$ and 0.038 respectively vs. $1.2 \cdot 10^{-4}$ in *A. marmorata*; see Chapuis et al., 2017
349 for details). Long-term population size should have the same effect as site size.

350 We compared size, vegetation cover, connectivity and stability over all sites studied
351 between the 2001-2007 and 2008-2015 periods using a paired *t*-test to check for temporal
352 homogeneity. The other variables were not considered, either because they do not vary in time
353 (density of favorable habitats), or because the comparison is irrelevant (e.g., invasion age). All
354 variables were compared between the populations studied for genetic variation and all other
355 populations from the long-term survey using linear models. We evaluated the effect of
356 environmental and site variables on genetic variability (R_A in *P. acuta* and *D. depressissimum*
357 and both R_A and R_G in *A. marmorata* and *D. surinamense*) using linear models. We first built
358 models with the five site variables (size, vegetation cover, connectivity, stability and density of
359 favorable habitats), and then added invasion age and long-term population size in turn in order
360 to avoid considering too many variables compared to the number of data points. The most
361 parsimonious combination of explanatory variables was retained based on AIC (Akaike, 1974).
362 Explanatory and response variables were standardized in order to obtain comparable regression
363 coefficients in the linear models. All statistical analyses were performed using R (R
364 Development Core Team, 2005).

365

366 **Results**

367 *Genetic diversity within populations and species*

368 Summary results on genetic diversity in the four species are reported in Table 2, and full results
369 in Table S4. Much more variation was detected in the two outcrossing species (especially in *D.*
370 *depressissimum*, due to highly variable tetranucleotide loci), with all loci polymorphic in all

371 populations, than in the two selfing species. Some populations of these two species even showed
 372 no variation at all, i.e. exhibited a single, fully homozygous, multilocus genotype. The average
 373 allelic richness (R_A) per population was 3.287 (minimum 1.982 / maximum 4.426), 1.588 (1.000
 374 / 2.555), 11.052 (6.260 / 14.160) and 2.039 (1.000 / 3.193) in *P. acuta*, *A. marmorata*, *D.*
 375 *depressissimum* and *D. surinamense* respectively. As a comparison, the mean number of alleles,
 376 averaged over loci, was 9.29, 6.00, 37.20, and 9.08 respectively. Genotypic diversity ranged
 377 from 1.000 to 8.816 in *A. marmorata*, and from 1.000 to 7.000 in *D. surinamense*. The average
 378 gene diversity (H_e) was 0.530 (minimum 0.311/ maximum 0.658) in *P. acuta*, 0.169 (0.0 / 0.504)
 379 in *A. marmorata*, 0.865 (0.736 / 0.921) in *D. depressissimum*, and 0.271 (0.00 / 0.471) in *D.*
 380 *surinamense*.

381 Significant deviations from HWE ($P < 0.05$) were observed in most populations of *P.*
 382 *acuta* (18 out of 21), and heterozygote deficiencies were low to moderate (mean $F_{IS} = 0.159$;
 383 Tables 2 and S4A). However, the selfing rates estimated with RMES were not significantly
 384 different from zero (mean $S(g_2) = 0.030$), suggesting that the significant heterozygote
 385 deficiencies are due to null alleles, as reported previously in this species (Bousset et al., 2004,
 386 2014; Escobar et al., 2008). The selfing rates estimated with RMES were similarly very low in
 387 *D. depressissimum* (mean $S(g_2) = 0.012$), significantly departing from zero in a single
 388 population out of 25 (Table S4C). This corresponds to low F_{IS} values (mean = 0.036) with only
 389 four populations in which Hardy-Weinberg proportions were rejected at $P < 10^{-3}$ (Lamy et al.,
 390 2012). The situation was very different in the other two species: most tests of departures from
 391 Hardy-Weinberg equilibrium were highly significant (Tables S4B and S4D). The estimates of
 392 F_{IS} were accordingly very high (0.970 in *A. marmorata* and 0.922 in *D. surinamense*; Table 2),
 393 and the selfing rates as well (0.984 and 0.950 respectively). The selfing rates estimated with
 394 RMES were high and significantly different from zero in the subsets of populations of *A.*
 395 *marmorata* and *D. surinamense* in which it was possible to successfully run the analysis (Tables

396 S4B and S4D). Exceptions are one population for each of these two species in which a selfing
 397 rate estimated with F_{IS} matched with an absence of selfing with the RMES approach.

398

399 *Population genetic differentiation*

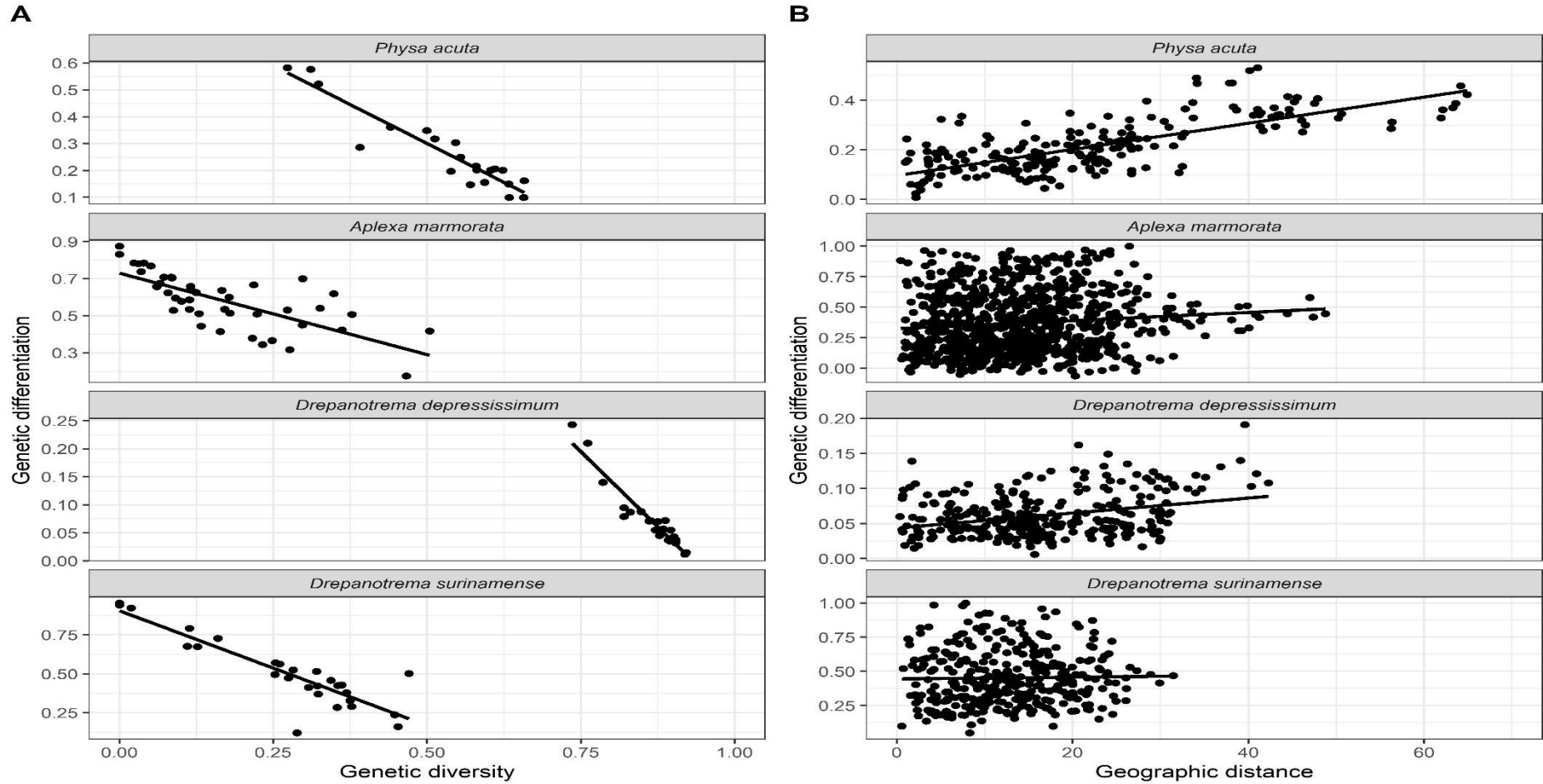
400 Highly significant genetic differentiation was detected between most population pairs in *P.*
 401 *acuta* and the two *Drepanotrema* species (Table S7). In both *P. acuta* and *D. surinamense*, a
 402 single P -value was higher than 0.01, and none in *D. depressissimum*. The situation is somewhat
 403 different in *A. marmorata* with 142 tests out of 841 with $P > 0.05$ (Table S7). Fourteen
 404 populations out of 43 were involved in more than 10 such tests (out of 42 per population),
 405 especially Favreau, Grand Maison, and Sainte Rose Est (18, 22, and 17 such results).
 406 Interestingly, eight of these fourteen populations are located in the Eastern part of Grande-Terre
 407 (Figure 1). The average estimate of pairwise genetic differentiation (θ) between *P. acuta*
 408 populations was 0.213 (range: 0.007 / 0.533; Table 2). The two populations from Marie-Galante
 409 contributed significantly to this differentiation, since it went down to 0.170 when excluding
 410 them. The same estimates were 0.371 (0.000 / 1.000) in *A. marmorata*, 0.062 (0.006 / 0.191) in
 411 *D. depressissimum*, and 0.453 (0.049 / 1.000) in *D. surinamense*. Matrices of pairwise F_{ST}
 412 estimates in the four species are reported in Table S7. The average site-specific F_{ST} was 0.249
 413 (range: 0.100 / 0.562) in *P. acuta*, 0.547 (0.215 / 0.872) in *A. marmorata*, 0.071 (0.012 / 0.243)
 414 in *D. depressissimum*, and 0.506 (0.121 / 0.954) in *D. surinamense*, and are not very different
 415 from the mean pairwise values. The average genetic diversity predicted quite accurately the
 416 site-specific differentiation, with more scattered data in *A. marmorata* than in the other species
 417 (Table 2, Figure 2).

418 Mantel test revealed isolation by distance in *P. acuta* populations ($r = 0.710$, $P = 0.001$;
 419 Figure 2), even when populations from Marie-Galante were excluded ($r = 0.301$, $P = 0.011$).
 420 Mantel test was significant in *D. depressissimum* ($r = 0.318$, $P = 0.020$), but neither in *A.*

Table 2. Mean values (range) of population genetic parameters in the four species studied. N_{pop} and N_{loc} are the number of populations and microsatellite loci studied. Other parameters are mean values across populations (minimum / maximum): n is the number of individuals, R_A the allelic richness, R_G the genotypic richness (in selfing species only), H_e the gene diversity, F_{IS} Wright's inbreeding coefficient, S the estimate of the selfing rate based on F_{IS} , $S(g_2)$ the estimate of the selfing rate based on David et al. (2007)'s method, and the population-pairwise F_{ST} . Negative values of F_{IS} were set to 0 when estimating the average S value, and negative values of F_{ST} were set to 0 when estimating the average F_{ST} . NC: not calculated because the values can be estimated in too few populations.

Parameter	<i>Physa acuta</i>	<i>Aplexa marmorata</i>	<i>Drepanotrema depressissimum</i>	<i>Drepanotrema surinamense</i>
N_{pop}	21	43	25	27
N_{loc}	7	8	10	12
n	21.86 (8 / 32)	18.14 (10 / 31)	29.96 (22 / 32)	13.52 (7 / 32)
R_A	3.287 (1.982 / 4.426)	1.588 (1.000 / 2.555)	11.052 (6.260 / 14.160)	2.039 (1.000 / 3.193)
R_G	-	4.336 (1.000 / 8.815)	-	4.662 (0.233 / 7.000)
H_e	0.530 (0.273 / 0.658)	0.169 (0.000 / 0.504)	0.865 (0.736 / 0.921)	0.271 (0.000 / 0.470)
F_{IS}	0.159 (-0.050 / 0.253)	0.970 (0.783 / 1.000)	0.036 (-0.003 / 0.096)	0.922 (0.483 / 1.000)
S	0.266 (0.000 / 0.404)	0.984 (0.878 / 1.000)	0.070 (0.000 / 0.075)	0.955 (0.651 / 1.000)
$S(g_2)$	0.030 (0.000 / 0.206)	NC	0.012 (0.000 / 0.168)	NC
F_{ST}	0.213 (0.007 / 0.533)	0.371 (0.000 / 1.000)	0.062 (0.006 / 0.191)	0.453 (0.049 / 1.000)

Figure 2. Genetic diversity, genetic differentiation, and spatial distance in the four species studied. A. Genetic differentiation (population-centered F_{ST}) as a function of genetic diversity (H_e). B. Genetic differentiation (pairwise-population F_{ST}) as a function of geographical (Euclidean) distance between population pairs. The black lines represent linear regression lines. Note that the y-scale differs among species.



1 *marmorata* ($r = 0.037$, $P = 0.236$; $r = 0.074$, $P = 0.130$ when excluding the single population
2 outside Grande-Terre), nor in *D. surinamense* ($r = -0.077$, $P = 0.857$; Figure 2). The seriation
3 and clustering approach did not allow detecting clear patterns of population differentiation
4 (results not shown). The few indications are consistent with the results of the more quantitative
5 sNMF approach, and we therefore rely on the latter, considering each species in turn. In *P.*
6 *acuta*, the optimal number of ancestral populations is four (Figure S1A). The two populations
7 from Marie-Galante belong to a single cluster (V2). One cluster (V1) is largely represented in
8 the North of Grande-Terre, and one (V3) in the South-West, while V4 is widespread. A lower
9 optimal number of clusters was detected in *A. marmorata* ($K = 2$; Figure S1B), with the smallest
10 cluster rather distributed in the South-West of Grande-Terre, but not only. A single cluster was
11 detected in *D. depressissimum*, suggestive, together with the limited isolation by distance, of
12 an even distribution of genetic diversity at Grande-Terre scale. The pattern is much more
13 complex in *D. surinamense* with eight clusters (Figure S1C), few populations (e.g., Belin or
14 Poucet) belonging to a single cluster and no obvious population structure. Moreover, this
15 analysis did not suggest common geographic patterns of clustering among species. Even when
16 enforcing a fixed number of clusters for all species (e.g., $K = 2$, as in *A. marmorata*), no
17 common pattern emerged (data not shown).

18

19 *Environmental and demographic drivers of genetic diversity*

20 The mean values of site characteristics (Table S4) for the 2001-2007 period did not differ
21 significantly from those of the 2008-2015 period in the same set of sites (Table S8), suggesting
22 temporal stability over our survey. It should be added that no temporal variation in cumulative
23 rainfall over both the rainy season and the little rainy season has been detected over the same
24 period (Pantel et al., submitted). We also compared values for these sites with those of all other
25 sites in our survey over the 2001-2007 period, and detected no difference, except for stability:

26 the genotyped populations were in more stable sites than the others (Table S8), presumably
27 because unstable sites are often dry by definition, limiting the possibility of sampling. With this
28 exception, the sites in which genetic analyses were conducted therefore seem representative of
29 all sites in our survey. We conducted the same two series of tests for each species separately.
30 No differences were detected (all $P > 0.05$; results not shown), except when comparing the sites
31 studied in *A. marmorata* and *D. depressissimum* and all other sites for vegetation cover ($t = -$
32 3.039 , $P = 0.004$ and $t = -4.009$, $P = 3 \cdot 10^{-3}$ respectively): the sites sampled for genetic analyses
33 showed less vegetation cover. We detected correlations between some of these variables when
34 considering all genotyped populations (Table S9). Unsurprisingly, stability was positively
35 correlated with size and vegetation cover, and connectivity was positively correlated with
36 invasion age. It is less expected to find a negative correlation between size and connectivity and
37 a positive one between stability and density of favorable habitats.

38 In both *P. acuta* and *D. depressissimum*, all descriptors of genetic diversity and
39 differentiation (R_A , H_E and site-specific F_{ST}) were highly correlated, F_{ST} being negatively
40 correlated to the other two descriptors (R^2 of linear regression of F_{ST} on H_E was 0.882 in *P.*
41 *acuta*, and 0.909 in *D. depressissimum*, and the corresponding value for the regression of F_{ST}
42 on R_A was 0.926 and 0.910; Figure 2 and Table S10). The same was true for R_G , H_E and F_{ST} in
43 *A. marmorata* and *D. surinamense* (R^2 of F_{ST} on H_E was 0.529 in *A. marmorata*, and 0.784 in
44 *D. surinamense*, and the corresponding value for the regression of F_{ST} on R_G was 0.539 and
45 0.530; Figure 2 and Table S10). When two species co-occurred in a large-enough number of
46 populations, we tested for correlations between species pairs for these descriptors: the only
47 significant correlation was found for *P. acuta* and *A. marmorata* (R^2 was between 0.300 and
48 0.326 for the three descriptors; $N = 11$ sites). We analyzed how genetic diversity and
49 differentiation was affected by the environmental and population variables (Table S2) using
50 linear models (results in Tables 3 and S11). The results were not qualitatively affected by

51 considering, or not, the populations outside Grande-Terre in *P. acuta* and *A. marmorata*. The
52 most influential variable was connectivity with a positive effect on genetic diversity in three
53 species (marginally significant for R_A in *P. acuta*; Figure 3), except *D. surinamense*. Similarly,
54 connectivity affected negatively population differentiation in *A. marmorata* and *D.*
55 *depressissimum*. Vegetation cover had a significant positive effect on diversity, and a negative
56 one, on differentiation in *D. depressissimum*. Long-term population size had the same effect in
57 *D. depressissimum*, but that on differentiation was no more significant when vegetation cover
58 and connectivity were included in the model. More surprisingly, this factor also had a positive
59 effect on differentiation in *A. marmorata*. Allelic and genotypic diversity were higher in *A.*
60 *marmorata* populations recently or never invaded by *P. acuta* than in those that have been
61 invaded for longer. However, invasion age had no effect on *P. acuta* itself. These results can be
62 compared to the expectations proposed in Table 1, and most were not fulfilled with a majority
63 of non-significant effects. However, significant effects (15 situations) went in the expected
64 direction, except that of long-term population size on differentiation in *A. marmorata*.

65

66 **Discussion**

67 *A comparative multispecies approach to population genetic structure*

68 The most classical approach for deciphering the neutral population genetic structure has been,
69 and remains, to study several populations of a single species sampled at a given time, and to
70 infer population processes based on signatures in molecular markers (Charlesworth &
71 Charlesworth, 2010; Lewontin, 1974). These signatures have been in many cases related to
72 traits, for example the mating system, sex or dispersal, but also to population demography,
73 spatial distribution and environmental variables, using more and more sophisticated statistical
74 approaches (Hanski & Gaggiotti, 2004; Foll & Gaggiotti, 2006; Balkenhol et al., 2015; Manel
75 & Holderegger, 2013). We here analyzed genetic variation in several species at once, a

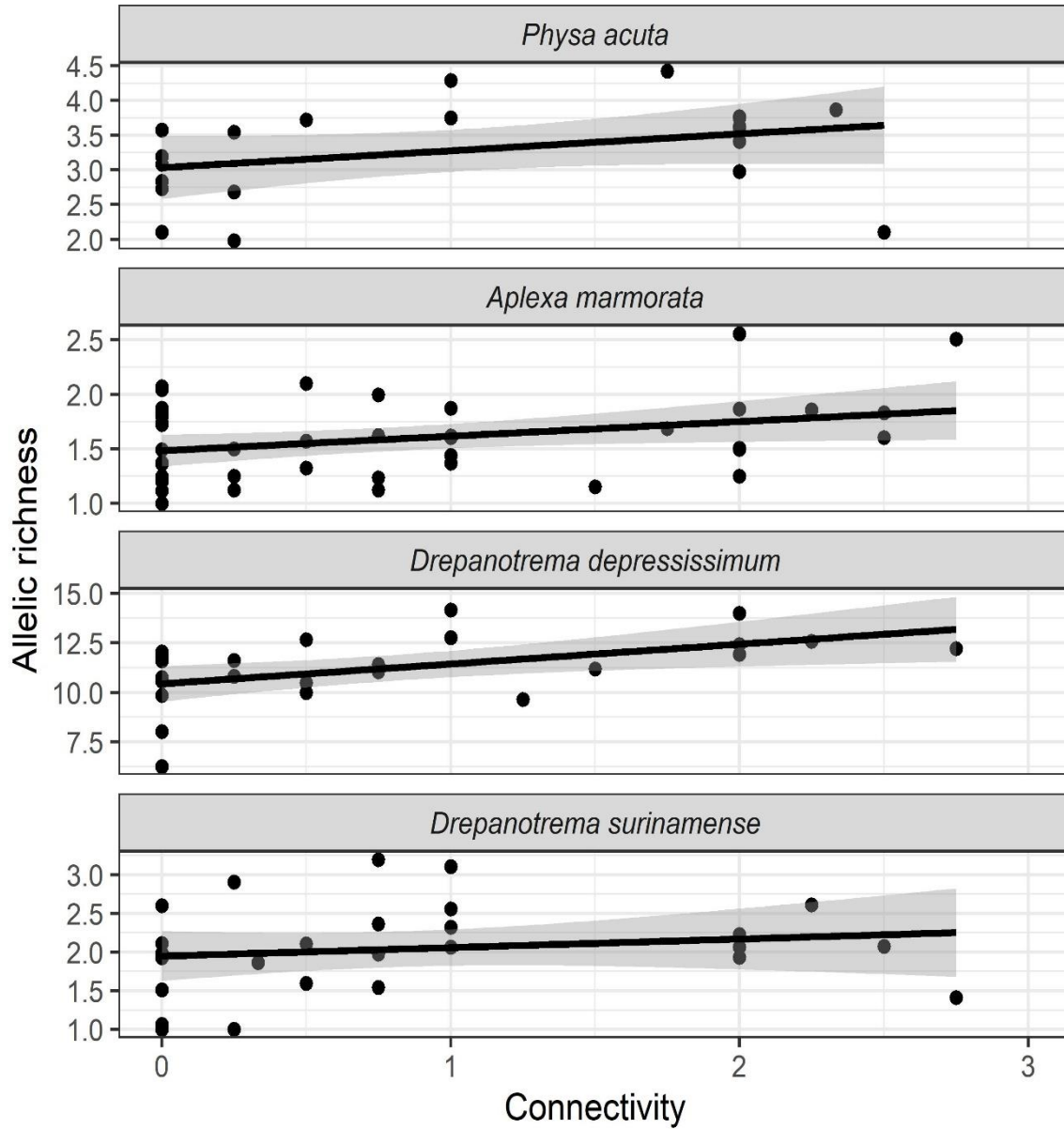
76 **Table 3.** Effect of environmental and population variables on genetic diversity and
77 differentiation in the four species studied. Results are reported for R_A and site-specific F_{ST} in *P.*
78 *acuta* and *D. depressissimum*, and for R_A , R_G and F_{ST} in *A. marmorata* and *D. surinamense*.
79 Results are from linear models (see text for explanation), and the best models were evaluated
80 based on Akaike Information Criterion. The significant (positive or negative) effects are
81 indicated by + or - ($P < 0.05$), and by ++ or -- ($P < 0.01$). NS indicates no effect. The P -value
82 for connectivity in *P. acuta* was indeed 0.08, and 0.07 for invasion age in *A. marmorata*. Full
83 models and effect sizes are reported in Appendix Table S11. All significant effects were in the
84 Direction predicted in Table 1, except the effect of invasion in *D. surinamense* for which we
85 had no specific prediction.

86
87

Variable	<i>Physa acuta</i>	<i>Aplexa marmorata</i>	<i>Drepanotrema depressissimum</i>	<i>Drepanotrema surinamense</i>
Size	NS/NS	NS/NS/NS	NS/NS	NS/NS/NS
Vegetation cover	NS/NS	NS/NS/NS	+/--	NS/NS/NS
Connectivity	+/NS	++/++/-	++/-	NS/NS/NS
Stability	NS/NS	NS/NS/NS	NS/NS	NS/NS/NS
Density of favorable habitats	NS/NS	NS/NS/NS	NS/NS	NS/NS/NS
Invasion age	NS/NS	-/-/+	NS/NS	NS/+/NS
Long-term population size	NS/NS	NS/NS/+	+/-	NS/NS/NS

88

89 **Figure 3.** Relationship between allelic richness and connectivity in the four species studied.
90 Each point is a population. The black lines are simple linear regressions (with 95% SE as grey
91 overlay). Connectivity is measured on an increasing scale (from 0 to 3).
92



94 comparative approach that remains relatively rare (Table S1). The four species studied display
95 rather high levels of genetic variation within populations, but with strong variance among
96 populations, suggesting a variable effect of genetic drift within sites, as already observed at
97 similar spatial scale in *P. acuta* (Bousset et al., 2004; Escobar et al., 2008). The extremely high
98 variation in *D. depressissimum* is largely due to highly variable (tetranucleotide) loci (Lamy et
99 al. 2012). In the two remaining species, we do not know of previous studies to which our values
100 can be compared. The marked differentiation among populations was associated with no to
101 limited isolation by distance and an absence of clear geographic patterns. Moreover, most of
102 genetic differentiation, especially in the two selfing species, is due to differences in within-
103 population diversity, irrespective of geographic position, and therefore probably driven by
104 population-specific factors. We can therefore suggest that the genetic structure of the four
105 species at Guadeloupe scale corresponds more to an asymmetric island or a metapopulation
106 model than to other models (e.g., a single panmictic population), as may be expected for
107 freshwater snails occupying ponds (Jarne & Delay, 1991; Lamy et al., 2012). In the former
108 models, we indeed expect marked variation in genetic diversity among populations and no
109 marked geographic structure. Note, however, that cautiousness is required with *P. acuta* since
110 quasi-equilibrium has probably not been reached because of its expanding dynamics. We
111 previously show that the asymmetric island model should be favored over a metapopulation
112 model in *D. depressissimum*, based on both spatial and temporal genetic data (Lamy et al. 2012).
113 Temporal data are not available in the three other species, preventing further distinction in
114 models of population structure – noting that the conditions under which the metapopulation
115 model actually applies are rather narrow (Fronhoefer et al., 2012). In our study, we also
116 observed large differences in genetic diversity and differentiation, lower and higher respectively
117 in *A. marmorata* and *D. surinamense* than in *P. acuta* and *D. depressissimum*. These similarities
118 and differences will be discussed below with regard to environmental parameters, demography

119 and the mating system.

120

121 *Connectivity is a major driver of the distribution of genetic variability*

122 We proposed in Table 1 how several environmental factors may affect genetic variation
123 following the logic of Lamy et al. (2012). We found essentially no effect in *P. acuta* and *D.*
124 *surinamense*, and two to three significant effects in the two other species. The most marked
125 effect is that of connectivity, detected in three species, affecting both genetic diversity and
126 population differentiation. Our definition of connectivity is based on local landscape structure,
127 i.e. site accessibility linked to local topography, and therefore falls in the ‘structural
128 connectivity’ category (see e.g., Storfer et al., 2007). In a comparative study of freshwater fish
129 and invertebrates from Australia, structural connectivity corresponds to realized connectivity,
130 estimated with genetic markers, in 50% of the 110 studies taken into account (Hughes, Huey,
131 & Schmidt, 2013). It can therefore be considered as a rather good indicator of the distribution
132 of genetic variation, as observed in our study. The central effect of connectivity on genetic
133 variation was already highlighted by Lamy et al. (2012) in *D. depressissimum* in Guadeloupe,
134 but also by Bousset et al. (2004) and Escobar et al. (2008) in southern France populations of *P.*
135 *acuta*. Sites with high connectivity index are indeed connected during the rainy season, and the
136 effective size of local populations is probably much enlarged by these connections. It is perhaps
137 less obvious why *D. surinamense* is not affected by connectivity. This species might disperse
138 less efficiently through flood or more actively through bird transportation. However, this should
139 apply to *D. depressissimum*, since the two species have similar ecology and aptitude to colonize
140 empty sites and an extinction/colonization dynamics driven by the same environmental factors
141 (Pantel et al., submitted). Interestingly, colonization is not affected by connectivity, except in
142 *P. acuta*, even if the colonization rate is higher in physids than in planorbids (Table S6; neither
143 is extinction with no difference among species). This suggests that the effect of connectivity is

144 not mediated by the extinction/colonization dynamics – we already noticed that the latter has
145 little influence on the distribution of genetic variability in *D. depressissimum* (Lamy et al.,
146 2012). Moreover, there was no correlation in genetic diversity among species, except between
147 the two physids. Overall, these results might be explained by the fact that dispersal is mostly
148 passive (through water currents or birds), and leads to colonization or migration events that are
149 both occasional and occurs at random with regard to both species and geographic scale.

150

151 *The impact of the mating system*

152 Our analysis confirms that the observed genetic patterns are consistent with an outcrossing
153 mating system in *P. acuta* and *D. depressissimum* and a selfing one in *A. marmorata* and *D.*
154 *surinamense*, as previously recognized (Escobar et al., 2011; Lamy et al., 2012). Genetic
155 diversity is extremely similar in the two selfers, and comparable to what has been observed in
156 other selfing snails (Charbonnel et al., 2002; Lounnas et al., 2017; Tian Bi et al., 2019). The
157 results on population structure (F_{ST}) mirror those obtained with within-population variation,
158 unsurprisingly given the strong correlations between within- and among-population variation
159 in the four species, especially in *D. depressissimum*. We observed both lower diversity and
160 higher differentiation in the two selfing than in the two outcrossing species. This was expected
161 because of reduced effective population size and increased selective interference in selfers than
162 in outcrossers (review in Jarne, 1995; Charlesworth, 2003; Ingvarsson, 2002). Interestingly, if
163 we assume a neutral island model and an effective population size divided by two in selfers
164 compared to outcrossers, based on the differentiation measured in the selfing species, F_{ST} in the
165 outcrossers should be that observed in *P. acuta* (see below the role of invasion in this species).
166 Even if this reasoning is only approximate, the mating system alone might explain this
167 difference. However, we observed strikingly large intrapopulation diversity and low
168 differentiation value in *D. depressissimum*. Both could be due to a higher mutation rate,

169 consistent with the extremely large number of alleles detected, but also to a higher regional
170 demographic size. This latter can be estimated as the product of the number of occupied sites
171 multiplied by the number of individuals per site. The first does not differ markedly among the
172 four species with 50-70% of occupied sites per species (Pantel et al., submitted). The second
173 can be approximated through long-term population size (Table S2), which, however, was lower
174 in *D. depressissimum* than in the other species. Demographic size therefore does not seem to
175 be an explanation to the higher diversity / lower differentiation, except if the ‘genetic size /
176 demographic size’ ratio is much higher in *D. depressissimum*. One cause might be aestivation
177 since this species survives very well in dry sites (Lamy et al., 2013a), but this is also true of *D.*
178 *surinamense* (Pantel et al., submitted). We also note that long-term population size did not
179 affect genetic variation within species, suggesting that this estimator of demographic size does
180 not capture adequately effective population size. As mentioned above, the four species differ in
181 their colonization rate (not in extinction rates), but the difference is between the two families,
182 not between selfers and outcrossers (Pantel et al., submitted). Since the difference is not
183 between the two taxonomic families, it is likely that demographic extinction and colonization
184 do not affect genetic variation strongly, as already shown in *D. depressissimum* (Lamy et al.,
185 2012), but rather modulate the influence of the mating system. Overall, this latter seems to
186 strongly influence genetic variation in the four species studied, due to its effects on effective
187 population size.

188

189 *Which other factors affect genetic variation?*

190 We tested the influence of other factors than the mating system and connectivity with
191 mostly identical expectations in the four species (Table 1). Most are not fulfilled (no effect),
192 but when they are, it is generally in the right direction (Table 3). Vegetation cover shows the
193 expected effect in *D. depressissimum* only. It should in principle favors large population size;

194 it indeed favors both population permanence in all species, except *P. acuta* (no effect; Pantel et
195 al., submitted), and colonization in *D. surinamense*. A possible explanation is that the
196 ‘vegetation cover’ variable aggregates several plant and algae species (Pantel et al., submitted),
197 and that the four species react to different types of vegetation. It is also somewhat unexpected
198 that site size, site stability and the density of favorable habitats did not affect genetic variation,
199 all the more that stability is positively correlated with both site size and density of favorable
200 habitats. Site size might be a poor indicator of population size, as suggested by the fact that
201 long-term population size, which beyond size also includes population density, is connected to
202 genetic variation in two species. Stability is perhaps of limited impact, because the three native
203 species studied might have developed strategies allowing coping with drought (Pointier &
204 Combes, 1976; Lamy et al., 2013a). The absence of effect of density of favorable habitats is
205 suggestive of a limited role for passive dispersal through birds compared to passive dispersal
206 through water flow, given the strong effect of connectivity (the two variables are not correlated).
207 More generally, our work indicates that both common and idiosyncratic effects of the
208 environment, space and interspecific interactions on genetic variability can be detected, calling
209 for detailed studies. For example, Haag, Riek, Hottinger, Pajunen, & Ebert (2005) showed that
210 genotypic richness increases with population age in two *Daphnia* species, but that other factors
211 (e.g., presence of competitor species) did not. Other examples are mentioned in Introduction
212 and can be found in Table S1.

213 The distribution of genetic variation may also be affected by species invasion, especially
214 in the invasive species *P. acuta*. In terms of site occupancy at landscape scale, *P. acuta* has
215 been spreading since our first survey in 2000, and still shows an invasive dynamics in Grande-
216 Terre (Dubart et al., 2019; Pantel et al., submitted). This dynamics might be associated with
217 variation loss (Dlugosch & Parker 2008; Estoup et al., 2016; Wares, Hughes, & Grosberg,
218 2005;), but limited loss has been observed in invasive populations of this species at worldwide

219 scale (Bousset et al., 2014; Ebbs et al., 2018). Moreover, the average variability of Guadeloupe
220 populations (e.g., $H_e = 0.530$) is similar to that observed in the two studies conducted at similar
221 scale (Bousset et al., 2004; Escobar et al., 2008). It therefore seems that the invasion of *P. acuta*
222 in Guadeloupe is ancient enough – the species presence has been noted in some restricted areas
223 since the early 1970's (JP Pointier, pers. obs.), and involved a large number of propagules as
224 perhaps the result of several invasion origins. Theory also predicts a loss of variation at invasion
225 front as a consequence of bottlenecks (Excoffier & Ray, 2008; Nei, 1975). However, we did
226 not detect an effect of invasion age on genetic variability (except perhaps in the two populations
227 of Marie-Galante, which are poorly variable), suggesting that site colonization involves large
228 number of propagules.

229 A last point is whether this invasion may affect genetic variation in native species. The
230 two physid species indeed showed competitive interactions through modified extinction and
231 colonization when the other species is present (Dubart et al., 2019). Moreover, Chapuis et al.
232 (2017) showed that, although the number of sites occupied by *A. marmorata* is stable,
233 population density has strongly been affected by the invasion of *P. acuta*. Moreover, this study
234 highlighted an evolution of life-history traits in *A. marmorata* in response to this invasion. This
235 was mirrored in the present study by a loss of neutral genetic variation in *A. marmorata*. Such
236 an effect was not detected in the two *Drepanotrema* species, although their population density
237 is slightly affected by the invasion of *P. acuta*. This suggests that the effect might occur in
238 *Drepanotrema* with some delay. Invasive species may have a negative effect on population
239 densities of native species in introduction areas, which in turn may affect the dynamics of genes
240 and induce rapid evolution (e.g., Strauss, Lau, & Carroll, 2006; Stuart et al., 2014). A rapid
241 shift in life-history traits has previously been documented in *A. marmorata* as a result of the
242 invasion of *P. acuta* (Chapuis et al., 2017). Whether the reduction in neutral genetic variation
243 documented here is related to this shift remains an open question, but documenting such

244 decreases in other bioinvasions might be a first approach to analyzing their evolutionary impact.

245

246 **Conclusion and perspectives**

247 The comparative approach developed here leads towards a more general perspective on
248 population genetic structure than proposed in studies focusing on single species. Indeed, it
249 allows detecting common and idiosyncratic effects of the environment, space and interspecific
250 interactions on the distribution of genetic variation in sets of species occupying the same space
251 with limited migration from outside. The four species studied here displayed striking
252 similarities in genetic structure, with marked variation in genetic diversity among sites and
253 strong genetic differentiation, due to passive dispersal, extinction/colonization dynamics and
254 erratic variation in local population size. Differences are due to the mating system that amplifies
255 local drift in selfing populations, interspecific interactions, and to a very limited extent local
256 environmental factors. We also detected little geographic coherence in the distribution of
257 genetic variation among species. In studies conducted at the same (not too large) geographic
258 scale (Table S1), the effect of traits on genetic variation was detected in some cases (e.g.,
259 lifespan in Reid et al., 2017), but landscape structure (e.g., habitat fragmentation in Ortego et
260 al., 2015) and demographic factors (e.g., population age in Haag et al., 2006) also play a role.
261 However, none of these studies, with the possible exception of the last two studies cited, carry
262 out a comparative analysis to detect common genetic patterns and the role of idiosyncratic vs.
263 common influences among species. We suggest extending these comparative approaches,
264 moving towards comparative landscape genetics (see e.g. Burkhart et al., 2016; Ortego et al.,
265 2015).

266 We also suggest to include in such studies the impact of interspecific interactions, as we
267 did here and in previous genetic and demographic studies (Chapuis et al., 2017; Dubart et al.,
268 2019; Lamy et al., 2013a). Our approach constitutes a first entry into the processes shaping

269 these interactions, i.e. upscaling from population ecology to community ecology. The similarity
270 between forces acting at species and community level has long been recognized (e.g. Bell, 2001;
271 Hubbell, 2001), particularly when considering reasonably similar species occupying the same
272 matrix (i.e. a metacommunity), and is at the heart of community genetics (Agrawal, 2003;
273 Vellend, 2010; Vellend & Geber, 2005). Studying the relationships between species and genetic
274 diversity and assessing how they are affected by environmental parameters and space is one
275 way of highlighting these similarities (Lamy et al., 2017; Vellend & Geber, 2005). In the meta-
276 community of Guadeloupe, this approach highlighted (again) the influence of connectivity
277 (Lamy et al., 2013b; Lamy, Laroche, David, Massol, & Jarne, 2017). Taking into account eco-
278 evolutionary dynamics would be an alternative path - at this stage they have essentially been
279 studied at the intraspecific level (Hendry, 2017). The evolution of life-history traits and the
280 demographic decline of *A. marmorata* following the invasion by *P. acuta* is an example of such
281 eco-evolutionary dynamics (Chapuis et al., 2017). Integrative approaches, including long-term
282 genetic, demographic and ecological studies, have been carried out in other species groups,
283 such as guppies (Bassar, Simon, Roberts, Travis, & Reznick, 2017) or anoles (Pringle et al.,
284 2019) in the Caribbean, to name just a few well-known examples, thus providing an insight into
285 the links between population biology and community ecology. They should be continued and
286 generalized to other model systems, including more complex communities.

287

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297

298 **Contributions**

299 PJ and PD framed the study and supervised all analyses. TL, EC, MD, JPP, PD and PJ did field
300 sampling and were involved in the long-term monitoring in Guadeloupe. TL, EC, AS, and EC
301 did the genetic analyses. PJ, ALdC, TL, and MD ran the statistical analyses. PJ wrote the
302 manuscript with input from all other authors, especially PD, at all stages of writing.

303

304 **Data accessibility**

305 The Zenodo archive (<https://zenodo.org/; 10.5281/zenodo.4534421>) contains all information
306 analyzed in this paper (microsatellite genotypes of the four species, environmental and
307 demographic data).

308

309 **Conflict of interest**

310 The authors of this article declare that they have no financial conflict of interest with the content
311 of this article.

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