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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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21
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29 (11 tables and two figures)

30 Abstract

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

54

55 **Introduction**

56 The evolutionary dynamics of species occupying patchily distributed habitats has been
57 the subject of a large body of both experimental and theoretical work (Hanski & Gaggiotti,
58 2004; Bell, 2008; Charlesworth & Charlesworth, 2010), highlighting the role of finite size of
59 populations and migration, and of their spatial and temporal variation. Metapopulation
60 approaches additionally consider population extinction and colonization, which roles depend
61 particularly from the origin of the propagule pool (Levins, 1969; Whitlock & Barton, 1997;
62 Hanski & Gaggiotti, 2004). These demographic processes may also occur at the scale of whole
63 metapopulations, for example in situations of biological invasions (e.g., Davis, 2008; Facon &
64 David, 2006), with possible variation loss at the migration front due to founder effects. Other
65 factors, such as the mating system or environmental parameters (e.g., through local adaptation),
66 should also be considered (e.g., Pannell, 2002; Hanski & Gaggiotti, 2004; Foll & Gaggiotti,
67 2006).

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

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

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

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

121 Freshwater habitats, especially lentic ones (e.g., ponds), are appropriate systems for
122 conducting multispecies (comparative) analysis of population genetic structure, because the
123 available habitats are clearly delimited from the inhospitable matrix although temporal variation
124 occurs as a function of precipitation / drought regimes, which may affect both population size
125 and migration (Chase, 2007; Heino et al., 2015; Jarne & Delay, 1991). Whether dispersal is
126 passive or active of course also affects migration. For example, snails disperse essentially
127 passively while arthropods may disperse actively in the adult stage or as resting forms (see
128 examples in Table S1). We focus here on a guild of freshwater snails (*Hydrophila*) occupying
129 a patchy landscape in Guadeloupe, Lesser Antilles to address the influence of the three factors

130 mentioned above on population genetic structure. This biological system has been well
131 characterized through a long-term survey of snail distribution on an island scale, as well as
132 population genetics, demographic and ecological studies (Chapuis et al., 2017; Dubart et al.,
133 2019; Lamy et al., 2012; Lamy et al., 2013a; Pantel et al., submitted). Two important
134 characteristics of our study should be highlighted. First, it is conducted at the scale of the
135 Grande-Terre island, 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). Second, we focused on the four most
138 common snail species, with reasonably similar occupancy at metapopulation scale (50-70% of
139 occupied sites), certainly because sampling is easier, but also because genetic and demographic
140 parameters can more precisely be estimated than in rare species (Heino et al., 2015).

141 We focused on four species, and characterized microsatellite variation in 21 to 43
142 populations per species. This allowed us to consider the influence of the three categories of
143 factors mentioned above (environment, traits and demography), which are known to influence
144 the distribution of genetic variation in snails in general (e.g., Jarne & Delay, 1991; Escobar et
145 al., 2011; Figuerola & Green, 2002; Van Leeuwen et al., 2013), and in the Guadeloupe system
146 in particular (Chapuis et al., 2017; Lamy et al., 2012). First, the environment (and landscape)
147 was characterized based on several parameters, such as site size and connectivity, used in
148 previous studies (Lamy et al., 2012; Dubart et al., 2019; Pantel et al., submitted). Second, two
149 species are mainly outcrossing, while the two others are mainly self-fertilizing. The four species
150 also differ in their aestivation capacity when sites dry out, which occurs seasonally during the
151 dry season in a fraction of sites. Third, they exhibit demographic differences, for example in
152 extinction and colonization rates, but also similarities (e.g., similar metapopulation occupancy).
153 Moreover, *Physa acuta* is an exotic species in the process of rapidly invading the whole Grande-
154 Terre, while the other three are native and rather stable in terms of metapopulation occupancy.

155 In order to characterize how these species react similarly vs. idiosyncratically to these factors
156 (a comparative approach), we predicted how each factor should influence the distribution of
157 genetic variation (e.g., site size should be associated with larger or more accessible populations
158 and therefore more variation). Four species is certainly not a sufficient number to draw
159 conclusions on the factors driving species differences in genetic structure in general. However,
160 we suggest conducting more comparative studies, up to now rather rare, to evaluate the
161 generality of these factors. We also discuss how such a comparative approach should help to
162 progress towards a more integrated eco-evolutionary perspective on community building and
163 species interaction (Hendry, 2017; Vellend, 2016).

164

165 **Materials and Methods**

166 *Long-term survey of snail communities*

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

179 This long-term survey includes almost 280 sites, 245 of which are in Grande-Terre

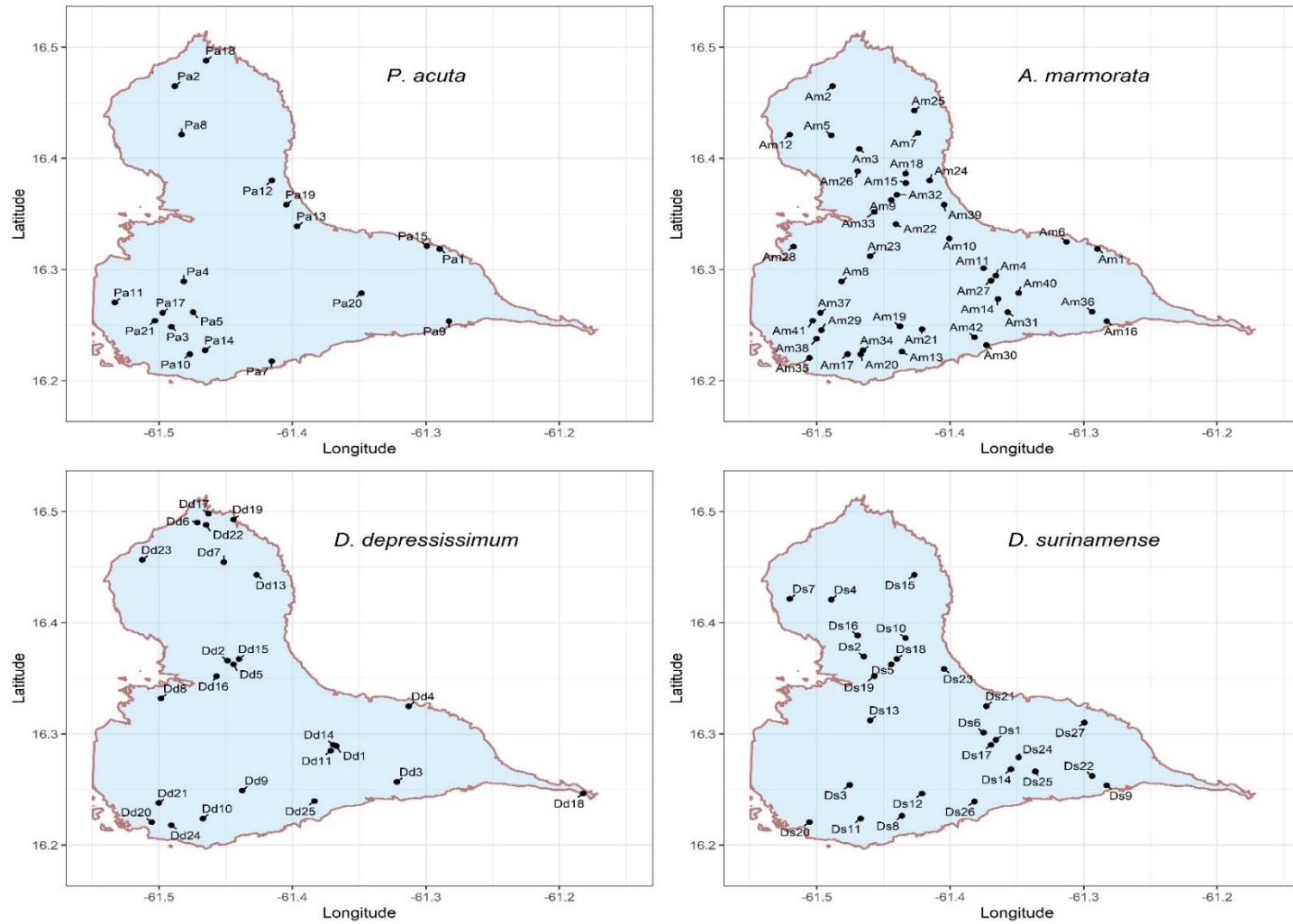
180 (Lamy et al., 2012; Lamy et al., 2013a). Field sampling took place in January-February when
181 these communities peak in abundance. They include 24 mollusc species, which makes up the
182 major part of the macrobenthos. Each site was explored by three persons for at least 15 min at
183 each visit (total searching time: 45 min). The presence and density of snails were estimated by
184 foraging both the sediment and plant strata using a scoop, and rock surfaces or floating debris
185 were visually surveyed. Snail density was estimated on a semi-log scale (no individuals, < 1
186 ind. / m², 1 to 5 ind. / m², 5 to 10 ind. / m² ...). Several environmental parameters were
187 characterized per site (detailed in Table S2) including size, aquatic vegetation cover, water
188 connectivity to neighboring watersheds, hydrological regime, and density of favorable habitats.
189 Site stability was defined based on the first four variables.

190

191 *The species studied and population sampling*

192 Our analysis bears on two pairs of closely related species: *P. acuta* and *Aplexa marmorata* from
193 the Physidae family, and *Drepanotrema depressissimum* and *Drepanotrema surinamense* from
194 the Planorbidae family (Morgan et al., 2002; Wethington and Lydeard, 2007). In each pair,
195 species are ecologically and morphologically similar, but do not hybridize. These four species
196 are the most common ones in the Guadeloupe metacommunity, occupying *ca.* 50-70% of sites
197 on average, and co-occur in a large number of sites (Dubart et al., 2019; Pantel et al., submitted;
198 Pointier & David, 2004). They differ in mating system, since *P. acuta* and *D. depressissimum*
199 are outcrossers, while *A. marmorata* and *D. surinamense* are selfers (Escobar et al., 2011). The
200 two *Drepanotrema* species also resist better in dry sites than the two Physids, aestivating under
201 rocks or vegetation (Pointier & Combes, 1976). They also exhibit demographic differences, for
202 example in rates of site colonization and extinction (Dubart et al., 2019; Pantel et al., submitted).
203 Moreover, *P. acuta* originates from the Eastern-central USA and has markedly increased its
204 range over the last two centuries to now be cosmopolitan (Bousset et al., 2014; Ebbs, Loker, &

205 **Figure 1.** Distribution of the sites studied in Guadeloupe (Grande Terre). Species name is indicated for each panel, and population acronyms are
206 provided in Table S3. The four sites sampled in Basse Terre of Guadeloupe and Marie-Galante (Table S3) are not represented. 0.1 min (geographic
207 coordinates) = ~ 10 km.
208



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

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	+	-	+	-	+	-	+	-

216

217 Brant, 2018; Vinarsky, 2017). We observed it in two sites from Grande-Terre in 2001, but this
218 figure increased to *ca.* 60% of sites in 2017. The three other species are neotropical and are
219 considered native in the Lesser Antilles (Pointier 2008). The two Physid species have been
220 shown to interact in Guadeloupe, most likely through direct reciprocal competition, with a
221 depressing effect of *P. acuta* on the demography of *A. marmorata*, but a predicted stable co-
222 existence (Dubart et al., 2019) and a character displacement (life-history traits) towards more
223 'r-strategy' in *A. marmorata* within sites, following the arrival of *P. acuta* (Chapuis et al., 2017).
224 Demography was characterized based on two parameters (Table S2). The first is 'long-term
225 population size', based on both snail density and site size. The second refers to the time in years
226 since the first detection of the invasive *P. acuta* and sampling for the genetic analysis - referred
227 to as 'invasion age' in this species and 'time since *P. acuta* invasion' in the other species (Table
228 S2). We considered two classes, not or recently invaded by *P. acuta* vs. invaded for more than
229 two years, as in Chapuis et al. (2017). In *A. marmorata* and *Drepanotrema* spp., populations of
230 the 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
233 (January-February) in 74 sites in which one to three of the four species were co-occurring
234 (Figure 1, Tables S3 and S4; 1.57 species per site). Four sites from Basse-Terre and Marie-
235 Galante were also considered in the study of *P. acuta* (three sites) and *A. marmorata* (one site).
236 *Physa acuta*, *A. marmorata*, *D. depressissimum* and *D. surinamense* were sampled in 21, 43,
237 25 and 27 sites respectively, from 2007 to 2010. Individuals were killed just after sampling in
238 80°C water for 1 minute and preserved in 95° ethanol. The genetic analysis was conducted on
239 at least 10 individuals per population for a total of 459 individuals in *P. acuta* (mean per
240 population \pm s.d.: 21.86 ± 5.51), 781 in *A. marmorata* (18.14 ± 6.42), 749 in *D. depressissimum*
241 (29.96 ± 2.73), and 365 in *D. surinamense* (13.52 ± 6.3). Less than 10 individuals were available

242 in three populations (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 a Markov Chain algorithm with GENEPOP 4.4. A multilocus estimate
277 of Wright's inbreeding coefficient (F_{IS}) was estimated following Weir and Cockerham (1984).
278 The 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 population 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 (Euclidean 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 *Drivers of genetic diversity*

312 We assessed the influence of several site characteristics, the mating system and demographic
313 factors (described above; see Table S2) on allelic richness (R_A) and on genetic differentiation
314 (site-specific F_{ST}) in the four species, but also on genotypic richness (R_G) in the selfing *A.*
315 *marmorata* and *D. surinamense*. The site characteristics were size, vegetation cover,
316 connectivity, stability and density of favorable habitats, and the demographic factors were

317 invasion age and long-term population size. Given that our first genetic sampling was
318 performed in 2007, we used the value per site of these variables over the 2001-2007 period
319 (averaged for those variables for which we got a value per year; Table S5). The spatial
320 distribution of two variables, averaged over years, is provided in Table S1. Because
321 environmental data were missing, the following populations were excluded from the analyses:
322 Sainte Rose (Basse-Terre) for *P. acuta*, Ravine Vinty (Basse-Terre) for *A. marmorata* and
323 Pointe des Chateaux (Grande-Terre) for *D. depressissimum*.

324 We built general predictions on genetic diversity and structure, based on (i)
325 environmental parameters, (ii) the mating system, and (iii) demographic parameters (Table 1).
326 These predictions are qualitative: we indeed know that the mating system should have a strong
327 effect, but the precise relationship between environmental parameters and effective population
328 size is not known. Moreover, all these parameters may interact, and the effect of each one may
329 not easily be single out (see Discussion). (i) The predictions depend on the model of population
330 genetic structure underlying species dynamics, especially on how the environmental variables
331 are connected to species demography. However, we expect that site size, site connectivity, and
332 density of favorable habitats should contribute positively to intrapopulation variability and
333 negatively to differentiation among populations, because they positively affect effective
334 population size and gene flow. Stability might have the same effect as the first three parameters
335 in the two physids. The two *Drepanotrema* species are dwelling well in unstable sites, because
336 of their aestivating capacity (Pointier & Combes, 1976), which should limit (perhaps annihilate)
337 the effect. These predictions can be refined on the basis of previously obtained estimates of
338 extinction and colonization rates per species at metapopulation scale (Dubart et al., 2019; Pantel
339 et al., submitted). In most cases, these environmental parameters did not affect these rates, and
340 when they did, this was in the direction of the predictions above (Table S6). For example, site
341 size positively affects colonization in three species, which should contribute positively to

342 genetic diversity. Vegetation cover should also have the same effect in the four species, because
343 of its negative influence on extinction and its positive influence on colonization in both *P. acuta*
344 and *D. surinamense* (Table S6). (ii) We expect less diversity and more divergence in selfing
345 than in outcrossing populations, as detailed in Introduction. Note also that given the near-
346 absence of variation in selfing rates within species, the mating system was not considered in
347 the statistical models presented below. (iii) Invasion age is predicted to affect the two *Physa*
348 species. In the invasive *P. acuta*, young populations should be less diverse than old ones
349 reflecting temporary founder effects at the colonization front. Both demographic population
350 size and colonization rates are negatively affected in *A. marmorata* by the competition with *P.*
351 *acuta* (Chapuis et al., 2017; Dubart et al., 2019), which should depress diversity in sites that
352 have been invaded by the latter for a longer time. The expectation is less clear in the two
353 *Drepanotrema* species, since the arrival of *P. acuta* only slightly affects their density ($P = 0.051$
354 and 0.038 respectively vs. $1.2 \cdot 10^{-4}$ in *A. marmorata*; see Chapuis et al., 2017 for details). Long-
355 term population size should have the same effect as site size.

356 We compared size, vegetation cover, connectivity and stability over all sites studied
357 between the 2001-2007 and 2008-2015 periods using a paired *t*-test to check for temporal
358 homogeneity. The other variables were not considered, either because they do not vary in time
359 (density of favorable habitats), or because the comparison is irrelevant (e.g., invasion age). All
360 variables were compared between the populations studied for genetic variation and all other
361 populations from the long-term survey using linear models. We calculated the correlation
362 between pairs of variables over all populations studied using Pearson's correlation coefficient.
363 We evaluated the effect of environmental and site variables on genetic variability (R_A in *P.*
364 *acuta* and *D. depressissimum* and both R_A and R_G in *A. marmorata* and *D. surinamense*) using
365 linear models. We first built models with the five site variables (size, vegetation cover,
366 connectivity, stability and density of favorable habitats), and then added invasion age and long-

367 term population size in turn in order to avoid overfitting. The most parsimonious combination
368 of explanatory variables was retained based on AIC (Akaike, 1974). We then looked for
369 interactions between these variables (when more than one was significant), but no interaction
370 was significant (see Results). Explanatory and response variables were standardized in order to
371 obtain comparable regression coefficients in the linear models. All statistical analyses were
372 performed using R (R Development Core Team, 2005).

373

374 **Results**

375 *Genetic diversity within populations and species*

376 Summary results on genetic diversity in the four species are reported in Table 2, and full results
377 in Table S4. For the sake of clarity, we tried, as much as possible, to present the results in the
378 same order: *P. acuta*, *A. marmorata*, *D. depressissimum* and *D. surinamense*. Much more
379 variation was detected in the two outcrossing species (especially in *D. depressissimum*, due to
380 highly variable tetranucleotide loci), with all loci polymorphic in all populations, than in the
381 two selfing species. Some populations of these two species even showed no variation at all, i.e.
382 exhibited a single, fully homozygous, multilocus genotype. The average allelic richness (R_A)
383 per population was 3.287 (minimum: 1.982 / maximum: 4.426), 1.588 (1.000 / 2.555), 11.052
384 (6.260 / 14.160) and 2.039 (1.000 / 3.193) in *P. acuta*, *A. marmorata*, *D. depressissimum* and
385 *D. surinamense* respectively. As a comparison, the mean number of alleles per species,
386 averaged over loci, was 9.29, 6.00, 37.20, and 9.08 respectively. Genotypic diversity ranged
387 from 1.000 to 8.816 in *A. marmorata*, and from 1.000 to 7.000 in *D. surinamense*. The average
388 gene diversity (H_e) was 0.530 (minimum: 0.311/ maximum: 0.658) in *P. acuta*, 0.169 (0.0 /
389 0.504) in *A. marmorata*, 0.865 (0.736 / 0.921) in *D. depressissimum*, and 0.271 (0.00 / 0.471)
390 in *D. surinamense*.

391 Significant deviations from HWE ($P < 0.05$) were observed in most populations of *P.*

392 *acuta* (18 out of 21), and heterozygote deficiencies were low to moderate (mean $F_{IS} = 0.159$;
393 Tables 2 and S4A). However, the selfing rates estimated with RMES were not significantly
394 different from zero (mean $S(g_2) = 0.030$), suggesting that the significant heterozygote
395 deficiencies are due to null alleles, as reported previously in this species (Bousset et al., 2004,
396 2014; Escobar et al., 2008). The situation was very different in the other Physid species, *A.*
397 *marmorata*: most tests of departures from Hardy-Weinberg equilibrium were highly significant
398 (Table S4B). The estimates of F_{IS} were accordingly very high (0.970; Table 2), and the selfing
399 rates as well (0.984). The selfing rates estimated with RMES were high and significantly
400 different from zero in the subset of populations in which it was possible to successfully run the
401 analysis (Table S4B), and similar to those derived from F_{IS} . Results in *D. depressissimum* are
402 similar to those in *P. acuta*: we detected low F_{IS} values (mean = 0.036) with only four
403 populations in which Hardy-Weinberg proportions were rejected at $P < 10^{-3}$ (Lamy et al., 2012).
404 The selfing rates estimated with RMES were similarly very low in *D. depressissimum* (mean
405 $S(g_2) = 0.012$), significantly departing from zero in a single population out of 25 (Table S4C).
406 In *D. surinamense*, as in *A. marmorata*, most tests of departures from Hardy-Weinberg
407 equilibrium were highly significant (Table S4D) and estimates of both F_{IS} and selfing rates were
408 very high (0.922 and 0.950 respectively; Table 2). The selfing rates estimated with RMES were
409 also high, and consistent, except in two populations, with those derived from F_{IS} (Table S4D).
410

411 *Population genetic differentiation*

412 Highly significant genetic differentiation was detected between most population pairs in *P.*
413 *acuta* and the two *Drepanotrema* species (Table S7). In both *P. acuta* and *D. surinamense*, a
414 single P -value was higher than 0.01, and none in *D. depressissimum*. The situation is somewhat
415 different in *A. marmorata* with 142 tests out of 841 with $P > 0.05$ (Table S7). Fourteen
416 populations out of 43 were involved in more than 10 such tests (out of 42 per population),

417 especially Favreau, Grand Maison, and Sainte Rose Est (18, 22, and 17 such results).
418 Interestingly, eight of these fourteen populations are located in the Eastern part of Grande-Terre
419 (Figure 1). The average estimate of pairwise genetic differentiation (θ) between *P. acuta*
420 populations was 0.213 (range: 0.007 / 0.533; Table 2). The two populations from Marie-Galante
421 contributed significantly to this differentiation, since it went down to 0.170 when excluding
422 them. The same estimates were 0.371 (0.000 / 1.000) in *A. marmorata*, 0.062 (0.006 / 0.191) in
423 *D. depressissimum*, and 0.453 (0.049 / 1.000) in *D. surinamense*. Matrices of pairwise F_{ST}
424 estimates in the four species are reported in Table S7. The average site-specific F_{ST} was 0.249
425 (range: 0.100 / 0.562) in *P. acuta*, 0.547 (0.215 / 0.872) in *A. marmorata*, 0.071 (0.012 / 0.243)
426 in *D. depressissimum*, and 0.506 (0.121 / 0.954) in *D. surinamense*, and are not very different
427 from the mean pairwise values. The average genetic diversity predicted quite accurately the
428 site-specific differentiation, with more scattered data in *A. marmorata* than in the other species
429 (Table 2, Figure 2).

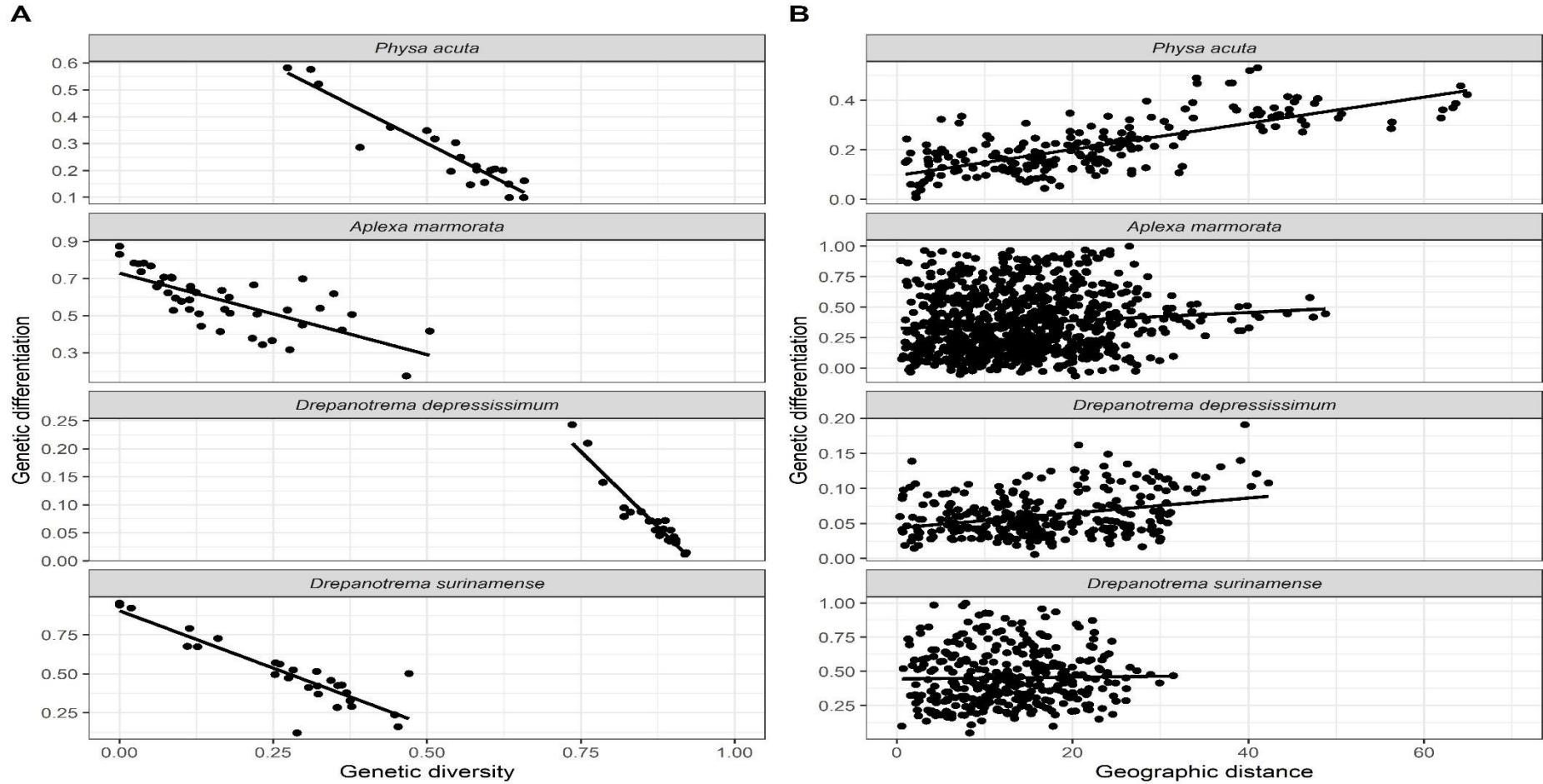
430 Mantel test revealed significant isolation by distance in *P. acuta* populations ($r = 0.710$,
431 $P = 0.001$; Figure 2), even when populations from Marie-Galante were excluded ($r = 0.301$, P
432 $= 0.011$), but not in *A. marmorata* ($r = 0.037$, $P = 0.236$; $r = 0.074$, $P = 0.130$ when excluding
433 the single population outside Grande-Terre). Mantel test was also significant in *D.*
434 *depressissimum* ($r = 0.318$, $P = 0.020$), but not in *D. surinamense* ($r = -0.077$, $P = 0.857$; Figure
435 2). The seriation and clustering approach did not allow detecting clear patterns of population
436 differentiation (results not shown). The few indications are consistent with the results of the
437 more quantitative sNMF approach, and we therefore rely on the latter, considering each species
438 in turn. In *P. acuta*, the optimal number of ancestral populations is four (Figure S2A). The two
439 populations from Marie-Galante belong to a single cluster (V2). One cluster (V1) is largely
440 represented in the North of Grande-Terre, and one (V3) in the South-West, while V4 is
441 widespread. A lower optimal number of clusters was detected in *A. marmorata* ($K = 2$; Figure

442 **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
 443 microsatellite loci studied. Other parameters are mean values across populations (minimum / maximum): n is the number of individuals, R_A the
 444 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
 445 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
 446 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
 447 calculated because the values can be estimated in too few populations.
 448
 449

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)

450

451 **Figure 2.** Genetic diversity, genetic differentiation, and spatial distance in the four species studied. A. Genetic differentiation (population-centered
 452 F_{ST}) as a function of genetic diversity (H_e). B. Genetic differentiation (pairwise-population F_{ST}) as a function of geographical (Euclidean) distance
 453 between population pairs. The black lines represent linear regression lines. Note that the y-scale differs among species.
 454



455

456 S2B), with the smallest cluster rather distributed in the South-West of Grande-Terre, but not
457 only. A single cluster was detected in *D. depressissimum*, suggestive, together with the limited
458 isolation by distance, of an even distribution of genetic diversity at Grande-Terre scale. The
459 pattern is much more complex in *D. surinamense* with eight clusters (Figure S2C), few
460 populations (e.g., Belin or Poucet) belonging to a single cluster and no obvious population
461 structure. Moreover, this analysis did not suggest common geographic patterns of clustering
462 among species. Even when enforcing a fixed number of clusters for all species (e.g., $K = 2$, as
463 in *A. marmorata*), no common pattern emerged (data not shown).

464

465 *Environmental and demographic drivers of genetic diversity*

466 The mean values of site characteristics (Table S4) for the 2001-2007 period did not differ
467 significantly from those of the 2008-2015 period in the same set of sites (Table S8), suggesting
468 temporal stability over our survey. It should be added that no temporal variation in cumulative
469 rainfall over both the rainy season and the little rainy season has been detected over the same
470 period (Pantel et al., submitted). We also compared values for these sites with those of all other
471 sites in our survey over the 2001-2007 period, and detected no difference, except for stability:
472 the genotyped populations were in more stable sites than the others (Table S8), presumably
473 because unstable sites are often dry by definition, limiting the possibility of sampling. With this
474 exception, the sites in which genetic analyses were conducted therefore seem representative of
475 all sites in our survey. We conducted the same two series of tests for each species separately.
476 No differences were detected (all $P > 0.05$; results not shown), except when comparing the sites
477 studied in *A. marmorata* and *D. depressissimum* and all other sites for vegetation cover ($t = -$
478 3.039 , $P = 0.004$ and $t = -4.009$, $P = 3 \times 10^{-3}$ respectively): the sites sampled for genetic analyses
479 showed less vegetation cover. We detected correlations between some of these variables when
480 considering all genotyped populations (Table S9). Unsurprisingly, stability was positively

481 correlated with size and vegetation cover, and connectivity was positively correlated with
482 invasion age. Two correlations were significant in cases in which we did not expect a correlation,
483 specifically, a negative correlation between size and connectivity and a positive one between
484 stability and the density of favorable habitats. Note also that none of the variables was correlated
485 to all others, suggesting that they bring partially independent information and can therefore be
486 used in the statistical models below.

487 In both *P. acuta* and *D. depressissimum* (the two outcrossing species), all descriptors of
488 genetic diversity and differentiation (R_A , H_E and site-specific F_{ST}) were highly correlated, F_{ST}
489 being negatively correlated to the other two descriptors (R^2 of linear regression of F_{ST} on H_E
490 was 0.882 in *P. acuta*, and 0.909 in *D. depressissimum*, and the corresponding value for the
491 regression of F_{ST} on R_A was 0.926 and 0.910; Figure 2 and Table S10). The same was true for
492 R_G , H_E and F_{ST} in *A. marmorata* and *D. surinamense* (R^2 of F_{ST} on H_E was 0.529 in *A.*
493 *marmorata*, and 0.784 in *D. surinamense*, and the corresponding value for the regression of F_{ST}
494 on R_G was 0.539 and 0.530; Figure 2 and Table S10). When two species co-occurred in a large-
495 enough number of populations, we tested for correlations between species pairs for these
496 descriptors: the only significant correlation was found for *P. acuta* and *A. marmorata* (R^2 was
497 between 0.300 and 0.326 for the three descriptors; $N = 11$ sites).

498 We analyzed how genetic diversity and differentiation was affected by the
499 environmental and population variables (Table S2) using linear models (results in Tables 3 and
500 S11). The results were not qualitatively affected by considering, or not, the populations outside
501 Grande-Terre in *P. acuta* and *A. marmorata*. Site size, stability and density of favorable habitats
502 had no influence. Connectivity was the most influential variable with a positive effect on
503 genetic diversity in three species (marginally significant for R_A in *P. acuta*; Figure 3), except in
504 *D. surinamense*, and a negative one on population differentiation in *A. marmorata* and *D.*
505 *depressissimum*. Vegetation cover had a significant positive effect on diversity, and a negative

506 one, on differentiation in *D. depressissimum*. Allelic and genotypic diversity were higher in *A.*
507 *marmorata* populations recently or never invaded by *P. acuta* than in those that have been
508 invaded for longer. However, invasion age had no effect on *P. acuta* itself. Long-term
509 population size had (surprisingly) a positive effect on differentiation in *A. marmorata*. It also
510 had the same effect than connectivity in *D. depressissimum*, but that on differentiation was no
511 more significant when vegetation cover and connectivity were included in the model. These
512 results can be compared to the expectations proposed in Table 1, and most were not fulfilled
513 with a majority of non-significant effects. However, significant effects (15 situations) went in
514 the expected direction, except that of long-term population size on differentiation in *A.*
515 *marmorata*.

516

517 **Discussion**

518 *A comparative multispecies approach to population genetic structure*

519 The most classical approach for deciphering the neutral population genetic structure has been,
520 and remains, to study several populations of a single species sampled at a given time, and to
521 infer population processes based on signatures in molecular markers (Charlesworth &
522 Charlesworth, 2010; Lewontin, 1974). These signatures have been in many cases related to
523 environmental variables, traits (e.g., the mating system), and to spatial distribution and
524 population demography, using more and more sophisticated statistical approaches (Hanski &
525 Gaggiotti, 2004; Foll & Gaggiotti, 2006; Balkenhol et al., 2015; Manel & Holderegger, 2013).
526 We here analyzed genetic variation in several species at once, a comparative approach that
527 remains relatively rare (Table S1). The four species studied display rather high levels of genetic
528 variation within populations, but with strong variance among populations, suggesting a variable
529 effect of genetic drift within sites, as already observed at similar spatial scale in *P. acuta*
530 (Bousset et al., 2004; Escobar et al., 2008). The extremely high variation in *D. depressissimum*

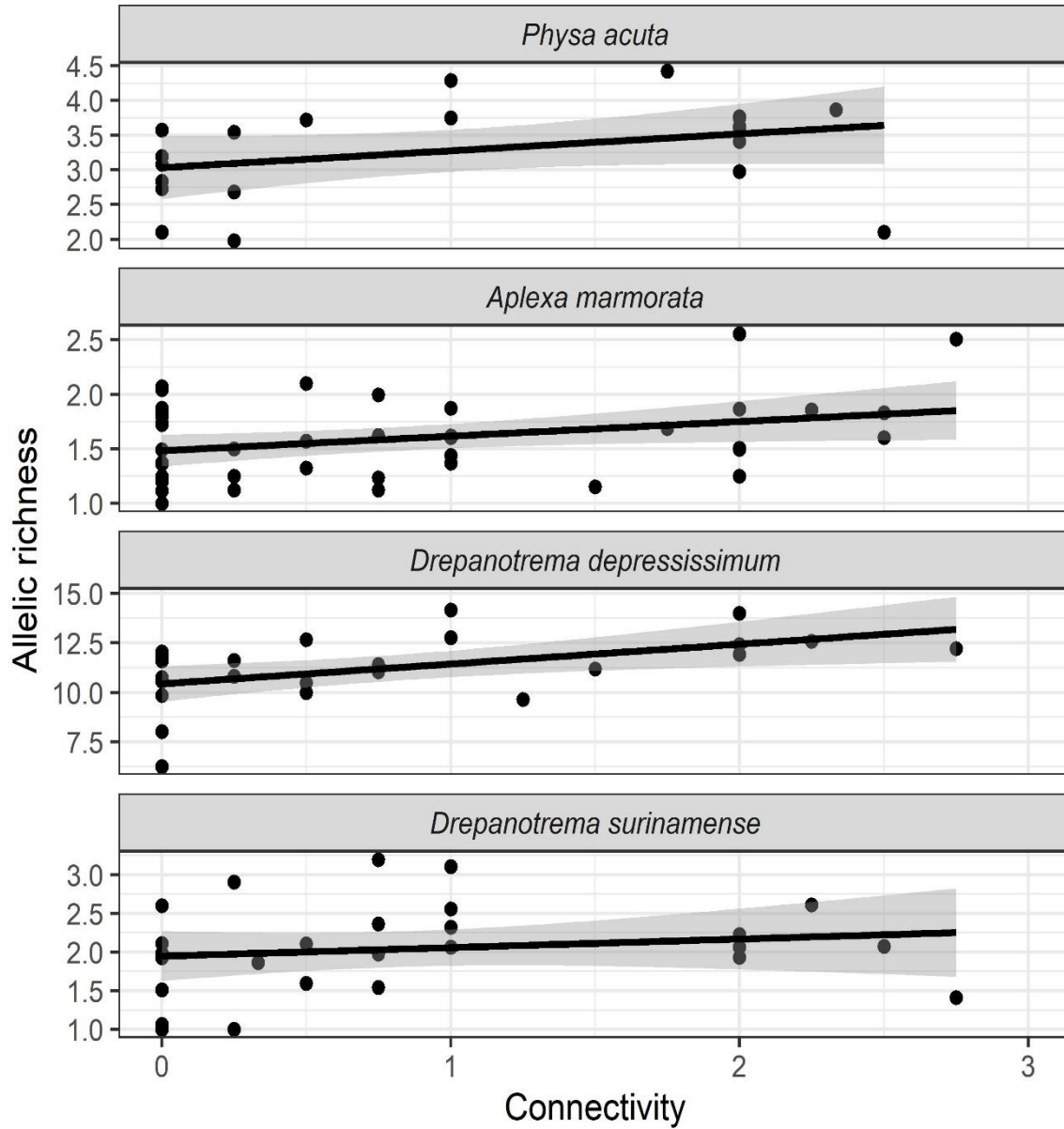
531 **Table 3.** Effect of environmental and population variables on genetic diversity and
532 differentiation in the four species studied. Results are reported for R_A and site-specific F_{ST} in *P.*
533 *acuta* and *D. depressissimum*, and for R_A , R_G and F_{ST} in *A. marmorata* and *D. surinamense*.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

541
542

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

543

544 **Figure 3.** Relationship between allelic richness and connectivity in the four species studied.
545 Each point is a population. The black lines are simple linear regressions (with 95% SE as grey
546 overlay). Connectivity is measured on an increasing scale (from 0 to 3).
547



549 is largely due to highly variable (tetranucleotide) loci (Lamy et al. 2012). In the two other
550 species, we do not know of previous studies to which our values can be compared. The marked
551 differentiation among populations is associated in the four species with no to limited isolation
552 by distance and an absence of clear geographic patterns. Moreover, most of genetic
553 differentiation, especially in the two selfing species, is due to differences in within-population
554 diversity, irrespective of geographic position, and therefore probably driven by population-
555 specific factors. We can therefore suggest that the genetic structure of the four species at
556 Guadeloupe scale corresponds more to an asymmetric island or a metapopulation model than
557 to other models (e.g., a single panmictic population), as may be expected for freshwater snails
558 occupying ponds (Jarne & Delay, 1991; Lamy et al., 2012). In the former models, we indeed
559 expect marked variation in genetic diversity among populations and no marked geographic
560 structure. Note, however, that cautiousness is required with *P. acuta* since quasi-equilibrium
561 has probably not been reached because of its expanding dynamics. We previously show that the
562 asymmetric island model should be favored over a metapopulation model in *D. depressissimum*,
563 based on both spatial and temporal genetic data (Lamy et al. 2012). Temporal data are not
564 available in the three other species, preventing further distinction in models of population
565 structure – noting that the conditions under which the metapopulation model actually applies
566 are rather narrow (Fronhofer et al., 2012). In our study, we also observed large differences in
567 genetic diversity and differentiation, lower and higher respectively in *A. marmorata* and *D.*
568 *surinamense* than in *P. acuta* and *D. depressissimum*. These similarities and differences will be
569 discussed below with regard to connectivity and the mating system, the two variables with the
570 strongest effects, and then to other environmental parameters and demography.

571

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

573 We proposed in Table 1 how several environmental factors may affect genetic variation

574 following the logic of Lamy et al. (2012). We found essentially no effect in *P. acuta* and *D.*
575 *surinamense*, and two to three significant effects in the two other species. The most marked
576 effect is that of connectivity, detected in three species, affecting both genetic diversity and
577 population differentiation. Our definition of connectivity is based on local landscape structure,
578 i.e. site accessibility linked to local topography, and therefore falls in the ‘structural
579 connectivity’ category (see e.g., Storfer et al., 2007). In a comparative study of freshwater fish
580 and invertebrates from Australia, structural connectivity corresponds to realized connectivity,
581 estimated with genetic markers, in 50% of the 110 studies considered (Hughes, Huey, &
582 Schmidt, 2013). It can therefore be considered as a rather good indicator of the distribution of
583 genetic variation, as observed in our study. The central effect of connectivity on genetic
584 variation was already highlighted by Lamy et al. (2012) in *D. depressissimum* in Guadeloupe,
585 but also by Bousset et al. (2004) and Escobar et al. (2008) in southern France populations of *P.*
586 *acuta*. Sites with high connectivity index are indeed connected during the rainy season, and the
587 effective size of local populations is probably much enlarged by these connections. It is perhaps
588 less obvious why *D. surinamense* is not affected by connectivity. This species might disperse
589 less efficiently through flood or more actively through bird transportation. However, this should
590 apply to *D. depressissimum*, since the two species have similar ecology and aptitude to colonize
591 empty sites and an extinction/colonization dynamics driven by the same environmental factors
592 (Pantel et al., submitted). Interestingly, the colonization rate is not affected by connectivity,
593 except in *P. acuta*, even if it is higher in physids than in planorbids (Table S6; neither is
594 extinction with no difference among species). This suggests that the effect of connectivity is
595 not mediated by the extinction/colonization dynamics – we already noticed that the latter has
596 little influence on the distribution of genetic variability in *D. depressissimum* (Lamy et al.,
597 2012). Moreover, there was no correlation in genetic diversity among species, except between
598 the two physids. Overall, these results might be explained by the fact that dispersal is mostly

599 passive (through water currents or birds), and leads to colonization or migration events that are
600 both occasional and occurs at random with regard to both species status and geographic scale.

601

602 *The impact of the mating system*

603 Our analysis confirms that the observed genetic patterns are consistent with an outcrossing
604 mating system in *P. acuta* and *D. depressissimum* and a selfing one in *A. marmorata* and *D.*
605 *surinamense*, with limited variation in selfing rate within species, as previously recognized
606 (Escobar et al., 2011; Lamy et al., 2012). Genetic diversity is extremely similar in the two
607 selfers, and comparable to what has been observed in other selfing snails (Charbonnel et al.,
608 2002; Lounnas et al., 2017; Tian Bi et al., 2019). The results on population structure (F_{ST}) mirror
609 those obtained with within-population variation, unsurprisingly given the strong correlations
610 between within- and among-population variation in the four species, especially in *D.*
611 *depressissimum*. We observed both lower diversity and higher differentiation in the two selfing
612 species than in the two outcrossing ones. This was expected because of reduced effective
613 population size and increased selective interference in selfers compared to outcrossers (review
614 in Charlesworth, 2003; Ingvarsson, 2002; Otto, 2021). Interestingly, if we assume a neutral
615 island model and an effective population size divided by two in selfers compared to outcrossers,
616 based on the differentiation measured in the selfing species, F_{ST} in the outcrossers should be
617 that observed in *P. acuta* (see below the role of invasion in this species). Even if this reasoning
618 is only approximate, the mating system alone might explain this difference in genetic
619 differentiation. However, we observed strikingly large intrapopulation diversity and low
620 differentiation in *D. depressissimum*. Both could be due to a higher mutation rate, consistent
621 with the extremely large number of alleles detected, but also to a higher regional demographic
622 size. This latter can be estimated as the product of the number of occupied sites multiplied by
623 the number of individuals per site. The first does not differ markedly among the four species

624 with 50-70% of occupied sites per species (Pantel et al., submitted). The second can be
625 approximated through long-term population size (Table S2), which, however, was lower in *D.*
626 *depressissimum* than in the other species. Demographic size therefore does not seem to be an
627 explanation to the higher diversity / lower differentiation, except if the ‘genetic size /
628 demographic size’ ratio is much higher in *D. depressissimum*. One cause might be aestivation
629 since this species survives very well in dry sites (Lamy et al., 2013a), but this is also true of *D.*
630 *surinamense* (Pantel et al., submitted). We also note that long-term population size did not
631 affect genetic variation within species, suggesting that this estimator of demographic size does
632 not capture adequately effective population size. As mentioned above, the four species differ in
633 their colonization rate (not in extinction rates), but the difference is between the two families,
634 not between selfers and outcrossers (Pantel et al., submitted). As a consequence, it is likely that
635 demographic extinction and colonization do not affect genetic variation strongly, as already
636 shown in *D. depressissimum* (Lamy et al., 2012), but rather modulate the influence of the
637 mating system. Overall, this latter seems to strongly influence genetic variation in the four
638 species studied, due to its effects on effective population size.

639

640 *Which other factors affect genetic variation?*

641 We tested the influence of factors other than the mating system and connectivity with
642 mostly identical expectations in the four species (Table 1). Most are not fulfilled (no effect),
643 but when they are, it is generally in the right direction (Table 3). Vegetation cover shows the
644 expected effect in *D. depressissimum* only. It should in principle favors large population size;
645 it indeed runs against population extinction in all species, except *P. acuta* (no effect; Pantel et
646 al., submitted), and favors colonization in *D. surinamense*. A possible explanation is that the
647 ‘vegetation cover’ variable aggregates several plant and algae species (Pantel et al., submitted),
648 and that the four species react to different types of vegetation. It is also somewhat unexpected

649 that site size, site stability and the density of favorable habitats did not affect genetic variation,
650 all the more that stability is positively correlated with both site size and density of favorable
651 habitats. Site size might be a poor indicator of population size, as suggested by the fact that
652 long-term population size, which beyond size also includes population density, is connected to
653 genetic variation in two species out of four. Stability is perhaps of limited impact, because the
654 three native species studied have developed strategies allowing coping with drought (Pointier
655 & Combes, 1976; Lamy et al., 2013a). The absence of effect of density of favorable habitats
656 (an indicator of possible immigration at the scale of a few km) is consistent with the weak
657 spatial patterns, both estimated through isolation by distance and the clustering analysis – *P.*
658 *acuta* is an exception, but this might be due to the invasive dynamics. Overall, this is suggestive
659 of a limited role for passive dispersal through birds compared to passive dispersal through water
660 flow, given the strong effect of connectivity (the two variables are not correlated).

661 The distribution of genetic variation may also be affected by species invasion, especially
662 in the invasive species *P. acuta*. In terms of site occupancy at landscape scale, *P. acuta* has
663 been spreading since our first survey in 2000, and still shows an invasive dynamic in Grande-
664 Terre (Dubart et al., 2019; Pantel et al., submitted). This dynamic might be associated with
665 variation loss (Dlugosch & Parker 2008; Estoup et al., 2016; Wares, Hughes, & Grosberg,
666 2005;), but limited loss has been observed in invasive populations of this species at worldwide
667 scale (Bousset et al., 2014; Ebbs et al., 2018). Moreover, the average variability of Guadeloupe
668 populations (e.g., $H_e = 0.530$) is similar to that observed in the two studies conducted at similar
669 scale (Bousset et al., 2004; Escobar et al., 2008). It therefore seems that the invasion of *P. acuta*
670 in Guadeloupe is ancient enough – the species presence has been noted in some restricted areas
671 since the early 1970's (JP Pointier, pers. obs.), and involved a large number of propagules as
672 perhaps the result of several invasion origins. Theory also predicts a loss of variation at invasion
673 front as a consequence of bottlenecks (Excoffier & Ray, 2008; Nei, 1975). However, we did

674 not detect an effect of invasion age on genetic variability (except perhaps in the two populations
675 of Marie-Galante, which are poorly variable), suggesting that site colonization involves large
676 number of propagules.

677 A last point is whether this invasion may affect genetic variation in native species. The
678 two physid species indeed showed competitive interactions through modified extinction and
679 colonization when the other species is present (Dubart et al., 2019). Moreover, Chapuis et al.
680 (2017) showed that, although the number of sites occupied by *A. marmorata* is stable,
681 population density has strongly been affected by the invasion of *P. acuta*. Moreover, this study
682 highlighted an evolution of life-history traits in *A. marmorata* in response to this invasion. This
683 was mirrored in the present study by a loss of neutral genetic variation in *A. marmorata*. Such
684 an effect was not detected in the two *Drepanotrema* species, although their population density
685 is slightly affected by the invasion of *P. acuta*. This suggests that the effect might occur in
686 *Drepanotrema* with some delay. Invasive species may have a negative effect on population
687 densities of native species in introduction areas, which in turn may affect the dynamics of genes
688 and induce rapid evolution (e.g., Strauss, Lau, & Carroll, 2006; Stuart et al., 2014). A rapid
689 shift in life-history traits has previously been documented in *A. marmorata* as a result of the
690 invasion of *P. acuta* (Chapuis et al., 2017). Whether the reduction in neutral genetic variation
691 documented here is related to this shift remains an open question, but documenting such
692 decreases in other bioinvasions might be a first approach to analyzing their evolutionary impact.

693 Overall, our work indicates that both common and idiosyncratic effects of the
694 environment, space and interspecific interactions on genetic variability can be detected, calling
695 for detailed studies. For example, Haag, Riek, Hottinger, Pajunen, & Ebert (2005) showed that
696 genotypic richness increases with population age in two *Daphnia* species, but that other factors
697 (e.g., presence of competitor species) did not. Other examples are mentioned in Introduction
698 and can be found in Table S1.

699

700 Conclusion and perspectives

701 The comparative approach developed here leads towards a more general perspective on
702 population genetic structure than proposed in studies focusing on single species. Indeed, it
703 allows detecting common and idiosyncratic effects of the environment, space and interspecific
704 interactions on the distribution of genetic variation in sets of species occupying the same space
705 with limited migration from outside. The four species studied here displayed striking
706 similarities in genetic structure, with marked variation in genetic diversity among sites and
707 strong genetic differentiation, due to passive dispersal, extinction/colonization dynamics and
708 erratic variation in local population size. Differences are due to the mating system that amplifies
709 local drift in selfing populations, interspecific interactions, and to a very limited extent local
710 environmental factors. We also detected little geographic coherence in the distribution of
711 genetic variation among species. In studies conducted at the same (not too large) geographic
712 scale (Table S1), the effect of traits on genetic variation was detected in some cases (e.g.,
713 lifespan in Reid et al., 2017), but landscape structure (e.g., habitat fragmentation in Ortego et
714 al., 2015) and demographic factors (e.g., population age in Haag et al., 2006) also play a role.
715 However, none of these studies, with the possible exception of the last two studies cited, carry
716 out a comparative analysis to detect common genetic patterns and the role of idiosyncratic vs.
717 common influences among species. We suggest extending these comparative approaches,
718 moving towards comparative landscape genetics (see e.g. Burkhart et al., 2016; Ortego et al.,
719 2015).

720 We also suggest to include in such studies the impact of interspecific interactions, as we
721 did here and in previous genetic and demographic studies (Chapuis et al., 2017; Dubart et al.,
722 2019; Lamy et al., 2013a). Our approach constitutes a first entry into the processes shaping
723 these interactions, i.e. upscaling from population ecology to community ecology. The similarity

724 between forces acting at species and community level has long been recognized (e.g. Bell, 2001;
725 Hubbell, 2001), particularly when considering reasonably similar species occupying the same
726 matrix (i.e. a metacommunity), and is at the heart of community genetics (Agrawal, 2003;
727 Vellend, 2010; Vellend & Geber, 2005). Studying the relationships between species and genetic
728 diversity and assessing how they are affected by environmental parameters and space is one
729 way of highlighting these similarities (Lamy et al., 2017; Vellend & Geber, 2005). In the meta-
730 community of Guadeloupe, this approach highlighted (again) the influence of connectivity
731 (Lamy et al., 2013b; Lamy, Laroche, David, Massol, & Jarne, 2017). Taking into account eco-
732 evolutionary dynamics would be an alternative path - at this stage they have essentially been
733 studied at the intraspecific level (Hendry, 2017). The evolution of life-history traits and the
734 demographic decline of *A. marmorata* following the invasion by *P. acuta* is an example of such
735 eco-evolutionary dynamics (Chapuis et al., 2017). Integrative approaches, including long-term
736 genetic, demographic and ecological studies, have been carried out in other species groups,
737 such as guppies (Bassar, Simon, Roberts, Travis, & Reznick, 2017) or anoles (Pringle et al.,
738 2019) in the Caribbean, to name just a few well-known examples, thus providing an insight into
739 the links between population biology and community ecology. They should be continued and
740 generalized to other model systems, including more complex communities.

741

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751

752 **Contributions**

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

757

758 **Data accessibility**

759 The Zenodo archive (<https://zenodo.org/>; 10.5281/zenodo.4534421) contains all information
760 analyzed in this paper (microsatellite genotypes of the four species, environmental and
761 demographic data). R codes have also been deposited in Zenodo (10.5281/zenodo.5119652).

762

763 **Conflict of interest**

764 The authors of this article declare that they have no financial conflict of interest with the content
765 of this article. P. Jarne is member of the group of PCI EvolBiol recommenders.

766

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