MOLECULAR ECOLOGY

Molecular Ecology (2013) **22**, 4445–4456 doi: 10.1111/mec.12399

Variation in habitat connectivity generates positive correlations between species and genetic diversity in a metacommunity

T. LAMY,*† P. JARNE,*‡ F. LAROCHE,* J.-P. POINTIER,† G. HUTH,*§¶ A. SEGARD* and P. DAVID*

Centre d'Ecologie Fonctionnelle et Evolutive—UMR 5175, Campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France, †USR 3278 CNRS-EPHE, 52, avenue Paul Alduy, 66860 Perpignan Cedex, France, ‡AgroParisTech, 19 avenue du Maine, 75732 Paris Cedex 15, France, §Université Montpellier 2—UMR AMAP, TA A-51/PS2, Boulevard de la Lironde, 34398 Montpellier, France, ¶Laboratoire Charles Coulomb—UMR 5221, Université Montpellier 2, 34095 Montpellier, France

Abstract

An increasing number of studies are simultaneously investigating species diversity (SD) and genetic diversity (GD) in the same systems, looking for 'species– genetic diversity correlations' (SGDCs). From negative to positive SGDCs have been reported, but studies have generally not quantified the processes underlying these correlations. They were also mostly conducted at large biogeographical scales or in recently degraded habitats. Such correlations have not been looked for in natural networks of connected habitat fragments (metacommunities), and the underlying processes remain elusive in most systems. We investigated these issues by studying freshwater snails in a pond network in Guadeloupe (Lesser Antilles). We recorded SD and habitat characteristics in 232 ponds and assessed GD in 75 populations of two species. Strongly significant and positive SGDCs were detected in both species. Based on a decomposition of SGDC as a function of variance–covariance of habitat characteristics, we showed that connectivity (opportunity of water flow between a site and the nearest watershed during the rainy season) has the strongest contribution on SGDCs. More connective sites received both more alleles and more species through immigration resulting in both higher GD and higher SD. Other habitat characteristics did not contribute, or contributed negatively, to SGDCs. This is true of the desiccation frequency of ponds during the dry season, presumably because species markedly differ in their ability to tolerate desiccation. Our study shows that variation in environmental characteristics of habitat patches can promote SGDCs at metacommunity scale when the studied species respond homogeneously to these environmental characteristics.

Keywords: *Aplexa marmorata*, biodiversity, *Drepanotrema depressissimum*, freshwater snail, immigration, species–genetic diversity correlation

Received 11 February 2013; revision received 14 May 2013; accepted 23 May 2013

Introduction

The similarities between processes shaping genetic diversity (GD) within species and species diversity (SD) within communities have been stressed for several decades (Antonovics 1976; and see review in Vellend & Geber 2005). It has been hypothesized that some ecological and evolutionary processes, mediated through local characteristics of habitats, may similarly affect genetic and SD, leading to positive 'species– genetic diversity correlations' (SGDCs; Vellend 2003, 2004; Vellend & Geber 2005). An increasing number of empirical studies have indeed simultaneously investigated both diversity levels, revealing positive (Vellend 2003, 2004; Cleary *et al*. 2006; Papadopoulou *et al*. 2011; Struebig *et al*.

Correspondence and Present address: Thomas Lamy, Département de Sciences Biologiques, Université de Montréal, Montréal, Québec, Canada, Fax: 514-343-2293; E-mail: thomas.lamy27@gmail.com

2011; Blum *et al.* 2012; Wei & Jiang 2012), nonsignificant (Odat *et al.* 2004; Derry *et al.* 2009; Silvertown *et al.* 2009; Taberlet *et al.* 2012; Wei & Jiang 2012) or negative (Wehenkel *et al.* 2006; Puşcaş *et al.* 2008) SGDCs. This suggests that genetic and species diversities may not always be regulated by processes acting similarly at both organizational scales. Pinpointing these processes and evaluating their quantitative influence on SGDCs remains an essentially open question. Most empirical studies so far could not adequately address this issue, probably because of sampling designs involving a too limited number of populations (generally less than 10; e.g. Vellend 2003; Cleary *et al.* 2006; Evanno *et al.* 2009; Odat *et al.* 2004; Silvertown *et al.* 2009) or of too low numbers of individuals to properly estimate local diversity (Struebig *et al.* 2011; Taberlet *et al.* 2012; see critics in Nazareno and Jump 2012). Together with limited ecological characterization of habitat patches, these limitations made it difficult to decompose SGDCs into contributions of habitat characteristics (see, however, Vellend 2003, 2004).

In addition, empirical studies have mostly been conducted, either at biogeographical scale (e.g. archipelago, Vellend 2003; Papadopoulou *et al.* 2011; mountain ranges, Puşcaş *et al.* 2008; Taberlet *et al.* 2012) or in disturbed systems (e.g. continuous habitats that have recently been fragmented due to logging or plantation development, Vellend 2004; Cleary *et al.* 2006; Struebig *et al.* 2011; habitats disturbed by human activities, Wei & Jiang 2012; Blum *et al.* 2012). From a conceptual point of view, SGDCs might also arise at landscape scale, in naturally fragmented systems of local communities/populations, submitted to steady extinction–colonization dynamics and connected by individual dispersal (metacommunities/metapopulations). Given the importance of such systems in both ecology and evolutionary biology (Hanski & Gaggiotti 2004; Leibold *et al.* 2004; Hanski 2011), evaluating whether SGDCs are actually detected at this scale and which habitat characteristics cause these patterns is of prime importance.

At landscape scale, GD within habitat patches depends on the immigration of new alleles, genetic drift, natural selection and possibly mutation depending on the timescale considered (Hartl & Clark 2007). Some of these processes are affected by habitat characteristics. Some can alter GD without favouring or disfavouring any particular allele on average (neutral effects), while others affect particular alleles in a consistent way (hereafter, allele-specific effects). As an example of neutral effects, habitat disturbance may wholly extirpate a local population irrespective of its genetic makeup (Wade & McCauley 1988), and changes in carrying capacity (and subsequently, in local population size) determine the intensity of genetic drift for all alleles (Hartl & Clark 2007). On the other hand, allele-specific effects depend on particular allele–habitat interactions. A typical example are alleles involved in local adaptation, such as those conferring insecticide resistance, which are favoured in habitats sprayed with insecticides, and deleterious elsewhere (Lenormand *et al.* 1999). In most SGDC studies, however, GD is measured using loci with no known phenotypic effects, such as microsatellites (e.g. Struebig *et al.* 2011), allozymes (e.g. Sei *et al.* 2009) or AFLPs (e.g. Odat *et al.* 2004). Although a given marker may occasionally deviate from neutrality or be in linkage disequilibrium with a gene under selection, it is unlikely that the diversity measured at a whole set of markers will be influenced by some habitat-specific selection regime. Consequently, local GD in most SGDC studies is expected to predominantly reflect neutral effects that act on all genetic variants.

Species diversity within local communities similarly experiences effects which can, or not, be species-specific. However, different species do usually have different phenotypes, possibly resulting in specific species–habitat interactions (Rosenzweig 1995; Morin 2011). When different species tend to perceive habitat characteristics in the same way (i.e. weak species–habitat interactions), SD is shaped by the same effects as GD at neutral markers within species, resulting in positive SGDCs (Vellend 2005; Vellend & Geber 2005). On the other hand, species-specific effects resulting from strong species–habitat interactions can erode positive SGDCs, possibly generating negative SGDCs (Vellend 2005). For example, if some species favour specific habitats that are very different from those favoured by other species (niche effect), they may thrive and accumulate neutral GD in these particular habitats (e.g. Derry *et al.* 2009). This can produce cases of large genetic variability associated with limited SD therefore decreasing SGDCs. Importantly, SGDCs are most likely to arise when variation in site characteristics is high and carrying capacity not too low on average, otherwise the local abundance of a species may be positively correlated with its GD but negatively correlated with the abundance of other species. This competition for space within habitat patches would then promote negative SGDCs (Vellend 2005; Wehenkel *et al.* 2006; Odat *et al.* 2010).

The important aspect is therefore whether habitat patches vary in their long-term characteristics and whether species respond homogeneously to this variation. Three main characteristics should act in a similar way on both diversities at metacommunity scale when all species perceive them in a sufficiently similar way: (i) patch size—the size of habitat patches can simultaneously affect population size of the focal species and species richness. Larger sites can harbour larger

populations that are more resistant to the random loss of alleles within local populations by genetic drift. They may also harbour more species because they are less sensitive to the random loss of species through ecological drift and because the diversity of subhabitats within a patch increases with its size (Vellend 2003), and so does the probability that each species finds its preferred habitat. Note that in the latter case, species are heterogeneous for their ecological preferences for subhabitats within a patch, but the overall result is a homogeneous response to patch-level characteristics (species are all more likely to occur in large patches). All these processes should be directly related to the carrying capacity of habitat patches; (ii) patch perturbation regime—temporary destruction or perturbation of habitat patches can also cause extinction of alleles and species irrespectively of their identities. This process should be related to local perturbation regime; and (iii) patch connectivity—contacts between habitat patches can contribute simultaneously to the arrival of new alleles and new species into a patch by immigration. This process should be related to local connectivity of patches.

In this study, we focused on a metacommunity of snails inhabiting a network of freshwater ponds in the Grande-Terre Island (Guadeloupe) and propose a way to assess the relative contribution of processes, acting both at metapopulation and at metacommunity scales, underpinning SGDC patterns. We estimated GD in two focal species and SD at metacommunity scale to estimate SGDCs based on a large number of sites. We then decomposed these two SGDCs into the contribution of four habitat characteristics (size, vegetation, perturbation regime and connectivity) representative of the three processes (drift, extinction and immigration) describe above.

Materials and methods

Study system—the freshwater snail metacommunity of Guadeloupe (Lesser Antilles)

The Guadeloupe archipelago, located in the Lesser Antilles (French West Indies), is composed of (i) a main island divided into two geological structures, a recent volcanic island (Basse-Terre) connected to an older limestone plateau (Grande-Terre); and (ii) several smaller islands: Marie Galante, Les Saintes and La Désirade. Grande-Terre (about 570 km^2) harbours different types of freshwater habitats, including mainly many ponds (*c.* 2000) but also a few small gullies (which consist of succession of ponds occasionally connected by water flow) and swamp grasslands connected to mangroves (Bruyere & Questel 2001; Pointier & David 2004; Lamy *et al.* 2012a,b, 2013). Some of these sites are permanent, but many ponds completely dry out, either yearly or more irregularly, during the dry season (i.e. from December to March). Those sites can remain dry for up to several months until the beginning of the following rainy season. Rainfall during the rainy season causes overflow of many of these freshwater environments, inducing transient aquatic connection of sites belonging to the same catchment area.

Freshwater snails are common in these environments and compose the most important part of the macrobenthos. Their distribution and ecology have been well studied in Guadeloupe for about 40 years (e.g. Pointier 1974; Leveque & Pointier 1976; Pointier & Combes 1976; Pointier *et al.* 1977; Pointier & David 2004; Lamy *et al.* 2012a, 2013), and a yearly extensive survey has been initiated in 2001. Twenty-nine mollusc species (Table S1, Supporting information; Pointier 2008) have been recorded in Guadeloupe, essentially belonging to two major clades, the Pulmonates and the Caenogastropods. Pulmonates are represented by the Basommatophoran order (Dayrat *et al.* 2011), which includes simultaneous hermaphroditic species exhibiting short life cycles and occupying a wide variety of habitats, from very unstable ponds to large stable rivers and lakes. On the other hand, Caenogastropods exhibit longer life cycles and are considered less tolerant to large variation in ecological characteristics, especially with regard to water availability (see Brown 1994; Dillon 2000).

Yearly survey of the metacommunity

From 2001 to 2011, 232 freshwater sites distributed over the whole Grande-Terre were surveyed annually (Fig. 1; Lamy *et al.* 2012a, 2013) at the beginning of the dry season (January–February). Mollusc densities are high at that time of the year and snail communities expand. During each survey, each site was explored by at least three persons for 10–15 min. Snails were caught using a scoop (0.5 m) that allowed foraging both the sediment and the various plant strata. All freshwater mollusc species were recorded as present or absent. A set of ecological characteristics was also recorded per site, including size (pond diameter) and the proportion of the area harbouring aquatic vegetation (both log-transformed in further analyses). We also assessed the desiccation likelihood on a 5-level scale (i.e. hydrological regime: from fully permanent to highly likely to dry out during the dry season)—this provides an indication on whether the pond was likely (or not) to desiccate later on during the dry season. This score was estimated based on the 40-year field experience of the samplers, the visual aspect of water margins and topographical characteristics.

Fig. 1 Location of the 232 sites surveyed from 2001 to 2011 (in January and February). The 57 sites sampled for the genetic analysis are pictured as grey squares.

Habitat characteristics

We focused on long-term characteristics of sites that may explain differences in species and GD: vegetation cover, size, connectivity and perturbation regime. For vegetation cover (*V*) and habitat size (*S*i), we used arithmetic averages over the whole temporal series. We included *V* because the amount of useful habitat might be better reflected by the vegetated area (which usually harbours more snails) than by habitat size.

Connectivity was estimated for each site in order to reflect the potential to receive immigrants from the rest of the metacommunity as a whole. We considered two sources of information: the first is a GIS-based estimate of pond density in a circular area centred on the focal pond (*G*: assuming a radius of 2 km). The second (*C*) takes into account the local topography and our historical knowledge. Briefly, we classified each pond into one of four categories: 0 (completely isolated by topography; several metres of increase in water levels would be needed to connect the pond with any other water body during the rainy season); 1 (can be occasionally connected during severe floods, e.g. through flooded grasslands, but has no natural outlet); 2 (natural outlet active during the rainy season and interrupted during the dry season, which connect the pond to at least one permanent or temporary water body); and 3 (natural outlet which is usually active even during the dry season). As explained below (see Results), we focused on *C* rather than *G* because the latter never explained any significant variance in genetic or SD (Table S2, Supporting information). Moreover, GIS-based estimates of pond density have no effect on colonization and extinction probabilities in a demographic model of metapopulation dynamics in our system (Lamy *et al*. 2012a, 2013).

We quantified site stability (*St*) as an indicator of desiccation risk during the dry season, based on several parameters: (i) the proportion of visits during which the site was dry over the 2001–2011 period; (ii) the temporal variance in size of the water body and in the percentage of vegetation cover during the same period; and (iii) the 5-level scale index of the likelihood of desiccation described above recorded at each visit and averaged over all visits. These three parameters were highly correlated. *St* was defined as site coordinate on the first axis (56% of total variance) of a principal component analysis (PCA; negative values indicate habitats prone to desiccation; positive ones indicate permanent water bodies).

Because the habitat characteristics (*Si*,*V*,*C* and *St*) were intercorrelated (Table S3, Supporting information), sites were also characterized by their coordinates (*F*1, *F*2, *F*3 and *F*4) on the four axes of a PCA (Table S4, Supporting information) on *Si*, *V*, *C* and *St*.

Genetic diversity in Drepanotrema depressissimum and Aplexa marmorata

We assessed GD in 57 sites (Fig. 1), in at least one of the two most represented snail species of the metacommunity, *D. depressissimum* and *A. marmorata*. Both are native Basommatophoran species. *A. marmorata* (Gastropoda: Basommatophora: Physidae) is the most represented species in the metacommunity (mean site occupancy over the 11 surveyed years: 71%) and mostly reproduces through selfing (Dubois *et al.* 2008; Escobar *et al.* 2011). *D. depressissimum* (Gastropoda: Basommatophora: Planorbidae) is the second most represented species in the metacommunity (mean site occupancy: 58%) and mostly reproduces through outcrossing (Nicot *et al.* 2009; Lamy *et al.* 2012b). At each site, eight to 32 snails (mean = 21.77 ± 7.78) were collected corresponding to a total of 1633 individuals (902 and 731 in 32 and 43 sites in *D. depressissimum* and *A. marmorata,* respectively; previous rarefaction analysis suggested that sampling ten to 15 individuals per population for both species allows to capture difference in GD). Snails were killed in 80 °C water for one min and preserved in 95 ° ethanol prior to genetic analysis. Genetic diversity was assessed at ten and eight microsatellite markers in *D. depressissimum* and *A. marmorata,* respectively (Dubois *et al.* 2008; Nicot *et al.* 2009). DNA was extracted using a Chelex® method (Bio-Rad). PCR were based on multiplex amplifications and conditions were as in Nicot *et al.* (2009) for *D. depressissimum* and as in Dubois *et al.* (2008) for *A. marmorata*.

Genetic diversity was estimated as allelic richness (R_A, Petit *et al.* 1998) and gene diversity (H_E, Nei 1987) averaged over loci using F_{STAT} 2.9.3 (Goudet 2001). Selfing species typically exhibit many repeated homozygous genotypes along with a few heterozygous genotypes (i.e. genotypes including at least one heterozygous locus). We therefore also estimated the genotypic diversity (R_G) in *A. marmorata*. Indeed, different loci represent independent realizations of colonization and drift processes in an outcrossing species such as *D. depressissimum*. In contrast, predominant self-fertilization in *A. marmorata* results in strong allelic associations and loci cannot be considered as independent (they tend to behave as a single locus). We used the rarefaction method of Petit *et al.* (1998) to estimate the number of repeated genotypes for a minimum sample size of seven. The GD used in the main text is R_A in *D. depressissimum* and R_G in *A. marmorata* (Tables S5 and S6, Supporting information). R_A, H_E and R_G were highly correlated with *A. marmorata* (see Table S7, Supporting information), and similar results were obtained with R_A and H_E in *D. depressissimum*. For *D. depressissimum*, we can also estimate R_A repeatability because a subset ($N = 12$) of surveyed sites has been genotyped in two or three different years in another study (Lamy *et al.* 2012a): the site effect explains 67.59% of the variance in R_A, which therefore represents the repeatability of the measure based on one temporal sample (used in the present study; see Falconer 1989). Such temporal data are unfortunately not available to assess R_G repeatability in *A. marmorata*.

Species diversity in the metacommunity

α-species richness was estimated per site as the average number of species (over the eleven years) found per sampling visit. Averaging over years increases the precision of the long-term estimation of species richness. This is the traditional approach in SGDC studies, in which temporal variation in both diversities has never been assessed (see Discussion)—this aspect will be the object of a future study. We cannot use rarefaction method to assess the robustness of yearly estimates of species richness per site because we do not have absolute abundance data for each species (as is the case in many SGDC studies). However, the 'site' effect (random) explains 42.43% of the variance in the number of species observed per site and visit (linear mixed model) so the repeatability of the site SD estimate (averaged over 11 visits) is 86.72%. We also computed separately the mean number of Pulmonates and Caenogastropods species.

Statistical analysis

The association between SD and GD was tested in the two species using Pearson's product moment correlation coefficient r. Its significance was tested, assuming that r follows a t distribution with N-2 d.f. (with N the sample size). When visual inspection of distributions suggested non-normality, we also tested the correlations using the nonparametric Spearman's ρ.

The effect of habitat characteristics on both levels of diversity was assessed using multiple regressions on GD and SD as:

$$GD = \alpha_1 V + \alpha_2 Si + \alpha_3 C + \alpha_4 St + \varepsilon_G \quad (1)$$

$$SD = \beta_1 V + \beta_2 Si + \beta_3 C + \beta_4 St + \varepsilon_S \quad (2)$$

where α_i and β_i are regression coefficients. All α_i and β_i were kept for subsequent analyses, and their significance was tested using nested model simplification and ANOVA for model comparisons (i.e. by stepwise removal of the covariate coefficient with the largest P-value until only significant covariate coefficients remain in the model). As SD, GD and habitat characteristics were all standardized, α_i and β_i correspond to standardized regression coefficients.

To investigate how habitat characteristics contribute to the SGDC, we decomposed the covariance between SD and GD as follows:

$$\begin{aligned} r_{SD,GD} = SGDC &= \frac{cov(SD, GD)}{\sigma_{SD}\sigma_{GD}} \\ &= cov\left(\frac{SD - \overline{SD}}{\sigma_{SD}}, \frac{GD - \overline{GD}}{\sigma_{GD}}\right) = cov(\widetilde{SD}, \widetilde{GD}) \end{aligned} \quad (3)$$

with $cov(\widetilde{SD}, \widetilde{GD})$ the covariance between standardized SD and GD; σ_{SD} and σ_{GD} their standard deviations; and $\overline{SD}$ and $\overline{GD}$ their means. Using the α_i and β_i from eqns (1) and (2), we obtained:

$$\begin{aligned} SGDC = cov(\widetilde{SD}, \widetilde{GD}) &= \alpha_1\beta_1 Var(V) + \alpha_2\beta_2 Var(Si) + \alpha_3\beta_3 Var(C) \\ &+ \alpha_4\beta_4 Var(St) + (\alpha_1\beta_2 + \alpha_2\beta_1) Cov(V, Si) \\ &+ (\alpha_1\beta_3 + \alpha_3\beta_1) Cov(V, C) \\ &+ (\alpha_1\beta_4 + \alpha_4\beta_1) Cov(V, St) \\ &+ (\alpha_2\beta_3 + \alpha_3\beta_2) Cov(Si, C) \\ &+ (\alpha_2\beta_4 + \alpha_4\beta_2) Cov(Si, St) \\ &+ (\alpha_3\beta_4 + \alpha_4\beta_3) Cov(St, C) + Cov(\varepsilon_G, \varepsilon_S) \end{aligned} \quad (4)$$

These terms identify the habitat characteristics, if any, contributing to the SGDC. The first four terms represent the direct effects of site characteristics. For example, $\alpha_1\beta_1 Var(V)$ represents the fraction of covariance between $\widetilde{SD}$ and $\widetilde{GD}$ that is due to parallel effects of vegetation cover on $\widetilde{SD}$ and $\widetilde{GD}$. If vegetation cover turns out to have opposite effects on $\widetilde{SD}$ and $\widetilde{GD}$, this covariance component will be negative, otherwise it will be positive. The fifth to tenth terms are the components of the

SGDC due to covariance between pairs of habitat characteristics, which can either reinforce or weaken the direct effects of these characteristics. For example, a negative covariance between size and connectivity ($Cov(Si, C) < 0$), both of which have positive effects on $\widetilde{SD}$ and $\widetilde{GD}$, results in a negative component of covariance between $\widetilde{SD}$ and $\widetilde{GD}$. The last term describes the covariance between the residuals of $\widetilde{SD}$ and $\widetilde{GD}$ that are not explained, that is, the effect of either unmeasured habitat characteristics or of deterministic processes such as competition between the focal species and the rest of the community. Its significance was assessed using Pearson's correlation coefficient between the two residuals of the multiple regressions on standardized SD ($\widetilde{SD}$) and on standardized genetic diversity ($\widetilde{GD}$).

To test whether the 32 and 43 sites sampled for the genetic analysis of *D. depressissimum* and *A. marmorata*, respectively, were representative of all sites, we compared the distributions of both SD and the four habitat characteristics (*V*, *Si*, *C* and *St*) between each of the two subsamples and the 232 sites of the metacommunity using nonparametric Mann–Whitney–Wilcoxon tests. All statistical analyses were performed using R 2.13.1 (R Development Core Team 2011).

Results

Genetic diversity, measured as allelic richness (R_A; standardized for a sample size of 14 individuals) in *D. depressissimum* and as genotypic diversity (R_G; standardized for a sample size of seven individuals) in *A. marmorata*, was highly variable among localities, ranging from 6.26 to 14.16 alleles per locus in *D. depressissimum* (Fig. 2a and Table S5, Supporting information) and ranging from 1 to 6.45 multilocus genotypes per site in *A. marmorata* (Fig. 2b and Table S6, Supporting information). Species richness was also highly variable among localities, ranging from 0 to 8.20 species per site over years among the 232 metacommunity sites and from 1.67 to 7.73 (respectively 1.18–8.20) species per site over years among sites in which the GD of *D. depressissimum* (respectively *A. marmorata*) was measured (Fig. 2). The sites in which the genetic samples were collected had essentially the same distribution of connectivity and SD as the other sites (connectivity: $W = 2949$, $P = 0.465$ and $W = 3791$, $P = 0.483$; SD: $W = 3665$, $P = 0.187$ and $W = 4613$, $P = 0.167$ for *D. depressissimum* and *A. marmorata*, respectively). However, they exhibited slightly more vegetation cover than the others ($W = 4212$, $P = 0.004$ and $W = 5554$, $P = 0.0001$ for *D. depressissimum* and *A. marmorata*, respectively), and *D. depressissimum* also tended to be sampled in relatively more unstable sites ($W = 2233$, $P = 0.006$).

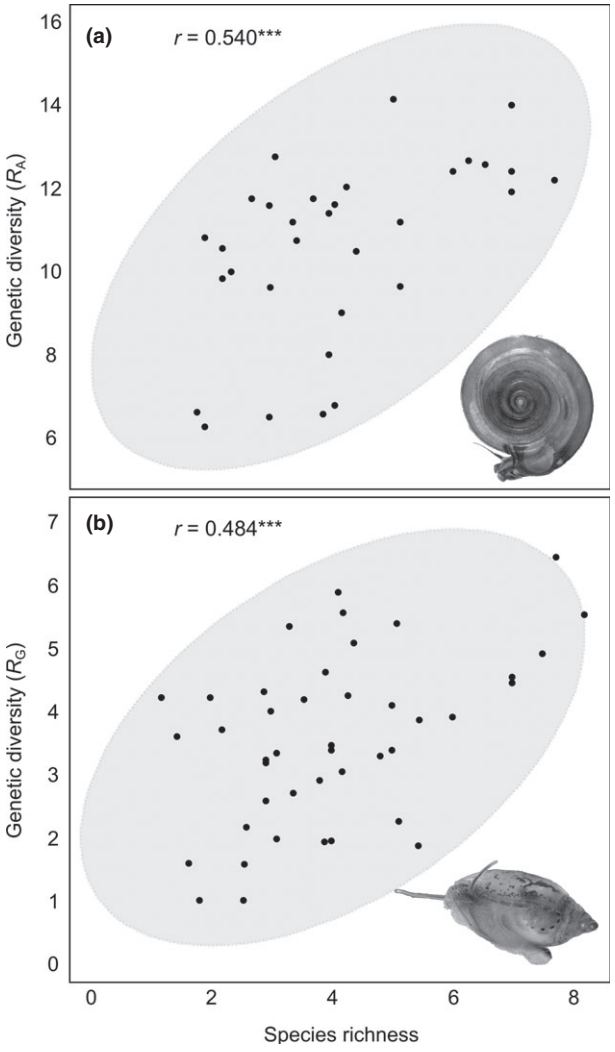

Fig. 2 Correlations between species richness and genetic diversity in (a) 32 populations of *Drepanotrema depressissimum* and (b) 43 populations of *Aplexa marmorata*. *r* is Pearson's correlation coefficient (*** $P < 0.001$; similar results were obtained using Spearman rank order correlation coefficient: $\rho = 0.752$, $P = 0.0006$ and $\rho = 0.449$, $P = 0.002$, respectively). Grey ellipsoids are 95% confidence regions. Genetic diversity was measured as the average allelic richness per locus in *D. depressissimum* and as the average multilocus genotypic richness in *A. marmorata*. However, the correlations remain significant in both species when using other indicators of genetic diversity [allelic richness, genotypic richness or expected heterozygosity; Table S7 (Supporting information)].

We detected strongly significant positive correlations between species richness and GD in both *D. depressissimum* (Fig. 2a; $r = 0.540$, $P = 0.0014$) and *A. marmorata* (Fig. 2b; $r = 0.484$, $P = 0.001$). SGDCs were similar when Pulmonates and Caenogastropods were accounted for separately (Pulmonates, *D. depressissimum*: $r = 0.436$, $P = 0.012$; *A. marmorata*: $r = 0.359$,

$P = 0.018$; Caenogastropods, *D. depressissimum*: $r = 0.471$, $P = 0.006$; *A. marmorata*: $r = 0.454$, $P = 0.002$).

Genetic diversity in both *D. depressissimum* and *A. marmorata* was positively affected by connectivity (Table 1). Pond size also had a positive effect on *A. marmorata* GD. Species richness was positively affected by all habitat characteristics (Table 1). Regressions restricted to those sites sampled for genetic analysis returned essentially the same results for connectivity, although they were more variable for other habitat characteristics (Table 1). This might be due to a smaller number of sites and the difficulty to disentangle the effects of stability, size and vegetation, which are highly positively correlated (Table S3, Supporting information). Using independent synthetic habitat variables obtained by PCA on the four habitat characteristics, two factors had large positive effects on SD irrespective of the set of sites considered: *F*1, which represents the joint effect of size, vegetation and stability, and *F*2, which represents connectivity (Table S4, Supporting information).

Table 1 Effects of habitat characteristics on genetic diversity and species diversity

	Vegetation	Size	Connectivity	Stability
Genetic diversity				
Drepanotrema depressissimum	0.10	0.29	0.52**	−0.16
Aplexa marmorata	0.04	0.32*	0.37*	0.02
Species diversity				
All sites	0.27***	0.27***	0.52***	0.19***
D. depressissimum sites	0.12	0.10	0.75***	0.26**
A. marmorata sites	0.24*	0.29**	0.77***	−0.01

Partial standardized regression coefficients are displayed together with their significance levels (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). For species diversity, regressions were performed both on all sites ($n = 232$) and on subsamples restricted to sites in which the genetic diversity of *Drepanotrema depressissimum* ($n = 32$) or *Aplexa marmorata* ($n = 43$) was estimated. Residuals from all linear models did not deviate significantly from normality (all $P > 0.01$).

Covariance decomposition indicated that differences in connectivity among ponds had the strongest incidence on SGDC in both species (accounting for 71% of the correlation in *D. depressissimum* and 59% in *A. marmorata*, Fig. 3). In both species, all other components had much weaker contributions. Essentially the same results were obtained using PCA scores instead of habitat characteristics, as the second principal component (*F*2), which was mainly driven by variation in connectivity, accounted for most of the correlation (Fig. S1, Supporting information). Importantly, the residual covariance between genetic and SD was not significant in both *D. depressissimum* and *A. marmorata*, indicating that our habitat characteristics captured most of the covariation. Interestingly, the only measure of connectivity that had a significant effect was the water connectivity index, *C*. The GIS-based estimate of pond density, *G*, had almost no effect explaining 6.56% and 1.21% of the SGDCs only (Table S2, Supporting information).

Discussion

SGDCs at metacommunity scale

In line with previous studies (Vellend 2003, 2004; Cleary *et al.* 2006; Papadopoulou *et al.* 2011; Struebig

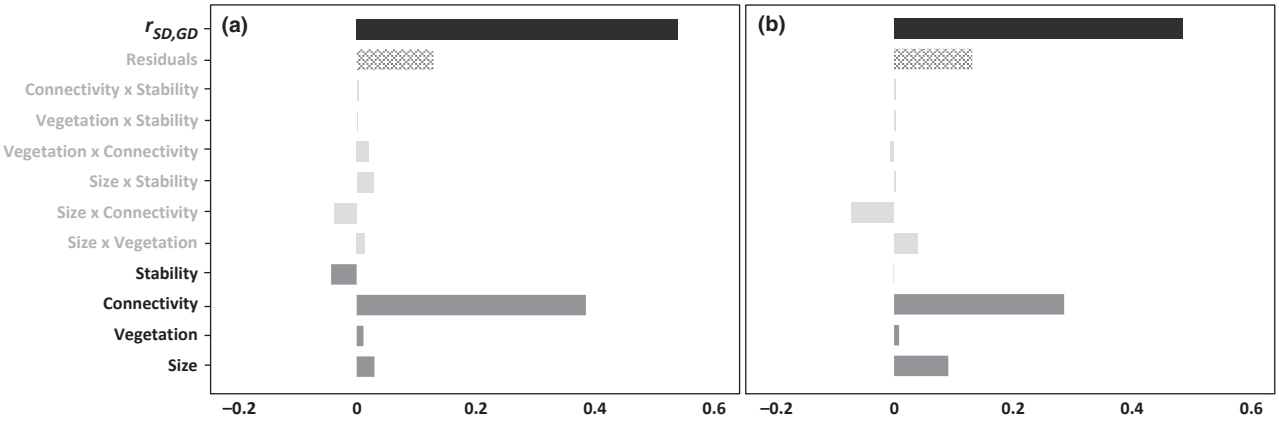

Fig. 3 Decomposition of the correlation between species and genetic diversity (SGDC; $r_{SD,GD}$) in (a) *D. depressissimum* and (b) *A. marmorata*. Black bars are the total SGDC ($r_{SD,GD}$). Dark and light grey bars represent the respective contributions of habitat characteristics and of correlations between pairs of habitat characteristics to total SGDC. Dashed grey bars are residual correlations, that is, the fraction of SGDC which is not explained by the habitat characteristics considered here (not significant in both species). The black bar is the algebraic sum of all other (negative and positive) components.

et al. 2011; Blum *et al.* 2012; Wei & Jiang 2012), our results show that a positive correlation between SD and GD can arise. However, these studies were conducted at large biogeographical scales (e.g. islands in an archipelago, Vellend 2003; Papadopoulou *et al.* 2011) or in artificial or anthropized systems (e.g. Vellend 2004; Cleary *et al.* 2006; Struebig *et al.* 2011; Blum *et al.* 2012; Wei & Jiang 2012). Our study therefore extends the scope of SGDCs analyses to a network of naturally fragmented habitats (metacommunity) and is the first to quantitatively assess the importance of different habitat characteristics in either promoting or impeding SGDCs at this scale.

Processes underlying SGDCs

Importantly, our results bring new insights into the nature of the factors underlying SGDCs. Overall, connectivity (defined as *C* or *F*2) stood out as the habitat characteristic showing a significant effect in all analyses of both genetic and species diversities taken separately, suggesting a potential role of this habitat characteristic in generating the observed SGDCs in both focal species. In addition, large sample size allowed us to quantify the effect of habitat characteristics using SGDC decomposition into variances and covariances of these characteristics and to confirm that variation in water connectivity among sites underlies the positive SGDCs found in both species. This general method (e.g. Lynch & Walsh 1998) has never been used to our knowledge to break down SGDCs, but should prove useful in future studies, pending that both species and GD exhibit high variance among sites and that enough sites are sampled to precisely estimate these variances and covariances.

Water connectivity here means the existence of water flow during the rainy season that may consequently connect neighbouring sites and temporary streams to the focal sites. This property affects the flow of individuals among habitat patches and therefore the inflow of both new alleles and new species from the metacommunity into the focal site. The predominant role of connectivity on the two SGDCs means that all species are sufficiently similar in their migration modes to perceive the same sites as easily accessible (i.e. connected). Note that the density of surrounding ponds in a given radius (*G*) did not explain any significant variation in both genetic and SD, suggesting that nearby sites do not contribute more to immigration than sites further away in Guadeloupe, unless they are connected to the same catchment area than the focal site during the rainy season.

Our study also revealed that other habitat characteristics than connectivity (or their interactions) contributed little to SGDCs. For instance, the weak contribution of habitat stability to the SGDC found in *A. marmorata* or its negative contribution to the SGDC found in *D. depressissimum* suggests that species respond in different ways to pond desiccation. This is not surprising because *D. depressissimum* seems to favour unstable sites where individuals are able to aestivate during desiccation, whereas other species are wiped out (Lamy *et al.* 2012a, 2013). Habitat size also contributed substantially to SGDC found in *A. marmorata*. However, the negative covariance between this habitat characteristic and connectivity resulted in a negative contribution to SGDC.

Choosing focal species for genetic analysis and species guild delimitation

SGDCs can be affected by the choice of both the focal species and the species guild used to estimate SD. The identity of the focal species is important because specialized or rare species are likely to have a distribution differing from other species in the metacommunity; for example, specialized species may be abundant and exhibit high GD in sites where other species are rare hence weakening SGDC (Vellend 2005). As a consequence, the subset of sites in which reasonable samples of a specialized species can be collected could be ecologically very distinct from other sites of the metacommunity. In our study, we selected the two most prevalent species of the metacommunity, which occupy a large range of habitats. The sites sampled for estimating GD had essentially the same distribution of connectivity and SD as the other sites. This indicates that the choice of focal species did not affect the main component of SGDC. However, the sites sampled for both species had slightly more vegetation cover than the others, and *D. depressissimum* was also sampled in relatively more unstable sites. This suggests that the focal species were not randomly distributed with regard to these habitat characteristics; however, these characteristics did not happen to contribute significantly to SGDCs.

The other possible source of variation in SGDC is the phylogenetic or functional extent of the species assemblage used to assess SD. More homogeneous guilds, in terms of life history traits or functional attributes, offer more favourable situations for detecting SGDCs (Taberlet *et al.* 2012). Freshwater snails from the Guadeloupe metacommunity belong to two ecologically, phenotypically and phylogenetically contrasted groups: the Pulmonates and the Caenogastropods (Brown 1994; Dillon 2000). Although the two focal species studied for GD belong to the Pulmonates, SGDCs were similar whether all species, Pulmonates or Caenogastropods were accounted for in SD. The robustness of SGDC to

the species guild used to measure SD suggests that life history differences between these two groups, although important, did not alter the observed SGDC because both groups respond in a similar way to the variation in connectivity among sites. Conversely, SGDC provides an indirect way to assess the ecological homogeneity of guilds.

What can SGDCs tell us about metacommunity assembly?

The importance of species differences in generating patterns of SD within natural systems is an open question in ecology. Tenants of the neutral theory suggest that the main features of the distribution of SD could emerge in neutral assemblages without any biological difference among species, a hotly debated issue (Hubbell 2001; Gravel *et al.* 2006; McGill 2010; Vellend 2010). The SGDC approach is a way to link patterns of SD within guilds to neutral references provided by GD at noncoding markers. A positive SGDC emerges when species respond in a similar way to variation in habitat characteristics despite their life history differences, as in this study. On the contrary, one could expect negative SGDC when the focal species tends to respond in a way opposite to the rest of the community, while null SGDC are expected when all species have purely idiosyncratic behaviours (Vellend 2005). In addition, SGDC can be further decomposed to assess which habitat characteristics are perceived similarly by most species. For instance, connectivity largely contributed here to SGDCs, presumably because most species probably rely on water flow to disperse. Conversely, species respond in a very different way to habitat stability because some species developed specific strategies to overcome long periods of drought (Lamy *et al.* 2012a, 2013). In this context, the SGDC approach allows to distinguish aspects of biodiversity patterns that depend on species life history differences.

SGDCs at metacommunity scale vs. larger spatial and temporal scales

In this study, we assumed that both metapopulation dynamics of alleles and metacommunity dynamics of species were at steady state, meaning that local species and genetic diversities essentially depend on processes that operated during the short timescale investigated (Hanski & Gaggiotti 2004; Hartl & Clark 2007). This actually contrasts with studies that investigated SGDCs at larger spatial and temporal scales, in systems that have not yet reach equilibrium and in which processes underlying both species and genetic diversities also result from historical events that small-scale habitat characteristics may not capture (Puşcaş *et al.* 2008; Taberlet *et al.* 2012). Although migration and drift are major processes operating at both diversity levels at biogeographical scale, they frequently have contrasting effects on different species (e.g. past climatic oscillations left contrasting footprints on the GD of species; Hewitt 2000), making the identification of putative parallel processes underlying SGDCs more challenging (Puşcaş *et al.* 2008; Taberlet *et al.* 2012). Additional processes, such as speciation, can also substantially increase SD at such a scale (Losos & Schluter 2000). Hence, different processes and hypothesis should be considered when investigating larger spatial and temporal scales (Vellend 2003; Puşcaş *et al.* 2008; Papadopoulou *et al.* 2011; Taberlet *et al.* 2012), and caution is needed when trying to generalize SGDCs across scales.

It follows that genetic markers should be chosen according to the investigation scale. At metacommunity scale, microsatellites are well suited as they are commonly assumed to be neutral and their high mutation rate allows tracking recent demographic events (Jarne & Lagoda 1996; Goldstein & Schlotterer 1999). Microsatellites have been properly used in some SGDC studies (e.g. Cleary *et al.* 2006; Struebig *et al.* 2011; Blum *et al.* 2012; Wei & Jiang 2012). Other markers have also been used, including AFLP (e.g. Odat *et al.* 2004; Puşcaş *et al.* 2008; Evanno *et al.* 2009; Silvertown *et al.* 2009; Taberlet *et al.* 2012), allozymes (e.g. Vellend 2003, 2004; Wehenkel *et al.* 2006) or mitochondrial DNA (mtDNA, e.g. Derry *et al.* 2009; Papadopoulou *et al.* 2011). These markers, however, do not provide the same information as their mutation rates is either much lower (e.g. mtDNA) or unknown (e.g. AFLP). Sequence data are relevant at biogeographical scale, because they allow to infer phylogenetic relationships and the nature of the historical processes that first shaped divergence between different genetic lineages, sometimes millions of years ago (Avise 2000). Still, processes inferred from mtDNA frequently differ from those inferred using nuclear DNA due to recurrent selective sweeps or introgression between species (Ballard & Whitlock 2004).

Finally, space and timescale also matter for the sampling strategy, because some of the variation measured will reflect either noise or signal depending on the processes underlying SGDCs. We focused on SGDC among sites in a metacommunity and on the effect of long-term habitat characteristics. As a consequence, year-to-year variation in genetic or SD within sites represents noise, while long-term differences among sites are signal. The ratio of signal (among-site variance) to noise (within-site temporal variance) determines the repeatability of diversity measures that set an upper bound to SGDC. In our case, we could estimate the repeatability of SD

(r_{SD} = 87%) and of allelic richness for *D. depressissimum* (r_{GD} = 68%). The observed correlation between the two measures ($r = 0.54$) is expected to underestimate the true correlation between long-term averages of SD and GD in such a way that an approximate upper bound for our correlation is $\sqrt{r_{SD} \times r_{GD}} = 0.766$ (Text S1, Supporting information). We therefore suspect that SGDCs in our study were even stronger than the estimated correlations. This assumes that year-to-year variation in specific and allelic diversity within sites are uncorrelated, which we could not test here, but can in principle be tested. Such a test would measure temporal (not spatial) SGDC, reflecting responses of species to recent historical events within patches (recent perturbation, succession dynamics, priority effects etc.) rather than to long-term characteristics; however, it requires a different sampling scheme, with temporal replicates for both genetic and allelic diversity (Cleary *et al.* 2006; Evanno *et al.* 2009). More generally, it seems important for future SGDC studies to focus on the temporal and spatial scales of the processes under study and evaluate repeatability accordingly if possible. While the issue of sample size and resulting bias of diversity estimates has already been raised (Nazareno and Jump 2012), similar problems may emerge from temporal variance in diversity, which cannot be solved by increasing sample size. This is especially an issue in systems that are not at steady state, such as recently degraded habitats (Vellend 2004; Cleary *et al.* 2006; Evanno *et al.* 2009; Struebig *et al.* 2011; Blum *et al.* 2012; Wei & Jiang 2012), in which SD and allelic diversity might not necessarily respond at the same rate.

Conclusion

SGDCs outline the similarities between those processes controlling species and genetic diversities. This has been an important driver for empirical studies since the founding papers of Vellend and co-workers (Vellend 2003, 2004, 2005; Vellend & Geber 2005). It has been, however, more difficult to characterize these processes and to quantify their influence. A major goal for future studies should be to progress in this direction whatever the sign and magnitude of SGDCs. We provided an example at metacommunity scale in which positive SGDCs emerge from the parallel influence of connectivity on both species and allelic diversities. Although theoretical work is clearly needed to better understand the conditions under which such patterns may arise, our approach can be widely applied to other systems.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

This manuscript was improved by comments from J.R. Auld. The authors thank the SMGE at CEFE and the environmental genomics platform of the 'Montpellier Environnement Biodiversité' Research Federation for help with genotyping. T. Lamy was supported by a fellowship from the French Ministry of Research. This work was supported by grants from the CNRS, ANR AFFAIRS (BioAdapt program), the Ecosystèmes Tropicaux program and a 'Chercheurs d'Avenir' Grant to P. David from the Région Languedoc-Roussillon.

References

Antonovics J (1976) The input from population genetics: "the new ecological genetics". *Systematic Botany*, **1**, 233–245.

Avise JC (2000) *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, Massachusetts.

Ballard JWO, Whitlock MC (2004) The incomplete natural history of mitochondria. *Molecular Ecology*, **13**, 729–744.

Blum MJ, Bagley MJ, Walters DM *et al.* (2012) Genetic diversity and species diversity of stream fishes covary across a land-use gradient. *Oecologia*, **168**, 83–95.

Brown D (1994) *Freshwater Snails of Africa and their Medical Importance*, 2nd edn. Taylor and Francis Ltd, London.

Bruyere F, Questel Y (2001) *Etude De Recensement Des Mares Et Des Canaux En Guadeloupe Basse-Terre*. DIREN Guadeloupe, Basse-Terre.

Cleary DFR, Fauvelot C, Genner MJ, Menken SBJ, Mooers AØ (2006) Parallel responses of species and genetic diversity to El Niño Southern Oscillation-induced environmental destruction. *Ecology Letters*, **9**, 304–310.

Dayrat B, Conrad M, Balayan S *et al.* (2011) Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): new insights from increased taxon sampling. *Molecular Phylogenetics and Evolution*, **59**, 425–437.

Derry AM, Arnott SE, Shead JA, Hebert PDN, Boag PT (2009) Ecological linkages between community and genetic diversity in zooplankton among boreal shield lakes. *Ecology*, **90**, 2275–2286.

Dillon RT (2000) *The Ecology of Freshwater Molluscs*. Cambridge University Press, Cambridge.

Dubois M-P, Nicot A, Jarne P, David P (2008) Characterization of 15 polymorphic microsatellite markers in the freshwater snail *Aplexa marmorata* (Mollusca Gastropoda). *Molecular Ecology Resources*, **8**, 1062–1064.

Escobar JS, Auld JR, Correa AC *et al.* (2011) Patterns of mating-system evolution in hermaphroditic animals: correlations among selfing rate inbreeding depression and the timing of reproduction. *Evolution*, **65**, 1233–1253.

Evanno G, Castella E, Antoine C, Paillat G, Goudet J (2009) Parallel changes in genetic diversity and species diversity following a natural disturbance. *Molecular Ecology*, **18**, 1137–1144.

Falconer DS (1989) *Introduction to Quantitative Genetics*. Longman, New York.

Goldstein D, Schlotterer C (1999) *Microsatellites: Evolution and Applications*. Oxford University Press, Oxford.

Goudet J (2001) *FSTAT, a program to estimate and test gene diversities and fixation indices* (version 2.9.3).

Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters*, **9**, 399–409.

Hanski I (2011) Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 14397–14404.

Hanski I, Gaggiotti OE (2004) *Ecology Genetics and Evolution of Metapopulations*. Elsevier Academic Press, San Diego, CA.

Hartl DL, Clark AG (2007) *Principles of Population Genetics*. Sinauer Associates, Sunderland.

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907–913.

Hubbell SP (2001). *The Unified Neutral Theory of Biogeography and Biodiversity*. Princeton University Press Princeton, Princeton.

Jarne P, Lagoda PJL (1996) Microsatellites, from molecules to populations and back. *Trends in Ecology & Evolution*, **11**, 424–429.

Lamy T, Pointier J-P, Jarne P, David P (2012a) Testing metapopulation dynamics using genetic demographic and ecological data. *Molecular Ecology*, **21**, 1394–1410.

Lamy T, Lévy L, Pointier J-P, Jarne P, David P (2012b) Does life in unstable environments favour facultative selfing? A case study in the freshwater snail *Drepanotrema depressissimum* (Basommatophora: Planorbidae). *Evolutionary Ecology*, **26**, 639–655.

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

Leibold MA, Holyoak M, Mouquet N *et al.* (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Lenormand T, Bourguet D, Guillemaud T, Raymond M (1999) Tracking the evolution of insecticide resistance in the mosquito *Culex pipiens*. *Nature*, **400**, 861–864.

Leveque C, Pointier J-P (1976) Study of growth of *Biomphalaria-Glabrata* (Say) and other Planorbidae in Guadeloupe (West-Indies). *Annals of Tropical Medicine and Parasitology*, **70**, 199–204.

Losos JB, Schluter D (2000) Analysis of an evolutionary species-area relationship. *Nature*, **408**, 847–850.

Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Sunderland.

McGill BJ (2010) Towards a unification of unified theories of biodiversity. *Ecology Letters*, **13**, 627–642.

Morin PJ (2011) *Community Ecology*. Wiley-Blackwell, Oxford.

Nazareno AG, Jump AS (2012) Species–genetic diversity correlations in habitat fragmentation can be biased by small sample sizes. *Molecular Ecology*, **21**, 2847–2849.

Nei M (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New-York.

Nicot A, Jarne P, David P (2009) Development of polymorphic microsatellite loci in the hermaphroditic freshwater snails *Drepanotrema surinamense* and *D. depressissimum*. *Molecular Ecology Resources*, **9**, 897–902.

Odat N, Jetschke G, Hellwig FH (2004) Genetic diversity of *Ranunculus acris L.* (Ranunculaceae) populations in relation to species diversity and habitat type in grassland communities. *Molecular Ecology*, **13**, 1251–1257.

Odat N, Hellwig FH, Jetschke G, Fischer M (2010) On the relationship between plant species diversity and genetic diversity of *Plantago lanceolata* (Plantaginaceae) within and between grassland communities. *Journal of Plant Ecology*, **3**, 41–48.

Papadopoulou A, Anastasiou I, Spagopoulou F *et al.* (2011) Testing the species–genetic diversity correlation in the Aegean archipelago: toward a haplotype-based macroecology? *The American Naturalist*, **178**, 241–255.

Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. *Conservation Biology*, **12**, 844–855.

Pointier J-P (1974) Faune malacologique dulçaquicole de l'île de la Guadeloupe (Antilles françaises). *Bulletin du muséum national d'histoire naturelle*, **235**, 905–933.

Pointier J-P (2008) *Guide to the Freshwater Molluscs of the Lesser Antilles*. ConchBooks, Hackenheim.

Pointier J-P, Combes C (1976) La saison sèche en Guadeloupe et ses conséquences sur la démographie des mollusques dans les biotopes à *Biomphalaria glabrata* (Say 1818) vecteur de la bilharziose intestinale. *La Terre et la Vie*, **30**, 121–147.

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

Pointier J-P, Salvat B, Delplanque A, Golvan Y (1977) Principaux facteurs régissant la densité des populations de *Biomphalaria glabrata* (Say 1818) mollusque vecteur de la Schistosome en Guadeloupe (Antilles françaises). *Annales de Parasitologie*, **52**, 277–323.

Puşcaş M, Taberlet P, Choler P (2008) No positive correlation between species and genetic diversity in European alpine grasslands dominated by *Carex curvula*. *Diversity and Distributions*, **14**, 852–861.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press Cambridge, Cambridge.

Sei M, Lang BK, Berg DJ (2009) Genetic and community similarities are correlated in endemic-rich springs of the northern Chihuahuan Desert. *Global Ecology and Biogeography*, **18**, 192–201.

Silvertown J, Biss PM, Freeland J (2009) Community genetics: resource addition has opposing effects on genetic and species diversity in a 150-year experiment. *Ecology letters*, **12**, 165–170.

Struebig MJ, Kingston T, Petit EJ *et al.* (2011) Parallel declines in species and genetic diversity in tropical forest fragments. *Ecology Letters*, **14**, 582–590.

Taberlet P, Zimmermann NE, Englisch T *et al.* (2012) Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. *Ecology Letters*, **15**, 1439–1448.

Vellend M (2003) Island biogeography of genes and species. *The American Naturalist*, **162**, 358–365.

Vellend M (2004) Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology*, **85**, 3043–3055.

Vellend M (2005) Species diversity and genetic diversity: parallel processes and correlated patterns. *The American Naturalist*, **166**, 199–215.

Vellend M (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, **85**, 183–206.
Vellend M, Geber MA (2005) Connections between species diversity and genetic diversity. *Ecology Letters*, **8**, 767–781.
Wade MJ, McCauley DE (1988) Extinction and recolonization: their effects on the genetic differentiation of local populations. *Evolution*, **42**, 995–1005.
Wehenkel C, Bergmann F, Gregorius H-R (2006) Is there a trade-off between species diversity and genetic diversity in forest tree communities? *Plant Ecology*, **185**, 151–161.
Wei X, Jiang M (2012) Contrasting relationships between species diversity and genetic diversity in natural and disturbed forest tree communities. *New Phytologist*, **193**, 779–786.

T.L., P.J. and P.D. developed the concepts, T.L., P.J., J-P.P. and P.D. collected the data, T.L., A.S. and G.H. genotyped the different individuals. T.L., F.L., G.H. and P.D. analyzed the data, and T.L., P.J., F.L. and P.D. wrote the manuscript.

Data accessibility

Microsatellite genotypes, habitat characteristics and sampling locations: Dryad doi:10.5061/dryad.52c2h.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Decomposition of the correlation between species and genetic diversity using PCA scores instead of habitat variables.

Table S1 List of the 29 species of the freshwater snail metacommunity of Guadeloupe.

Table S2 Summary of the analysis using the GIS-based index of connectivity, *G*.

Table S3 Pearson' scorrelation coefficient between ecological characteristics.

Table S4 SGDC decomposition using PCA scores instead of habitat variables.

Table S5 Information on the 32 populations of *Drepanotrema depressissimum* sampled in Grande-Terre.

Table S6 Information on the 43 populations of *Aplexa marmorata* sampled in Grande-Terre.

Table S7 Pearson's correlation coefficient between the genetic diversity indicators in the two species studied.

Text S1 Estimation of a SGDC upper bound.