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Metacommunity structure reflects the interplay of various processes, including niche filtering, extinction/colonization and interspecific interactions. Spatial patterns of species distributions are often analyzed to infer these processes. However, such inferences rely on often unrealistic equilibrium assumptions, and remain ambiguous, as different processes can produce similar patterns. Temporal data may improve these inferences. For example, stochastic species turnover may occur in local communities, while, on the long run, temporal changes are kept within limits set by locally available niches. Our objective is to explore how the joint analysis of spatial and temporal patterns can clarify the contribution of different processes to metacommunity structure. We recorded the occurrences of 21 freshwater mollusc species, and environmental data, in 250 sites over 17 successive years in a network of ponds in Guadeloupe (Lesser Antilles). We analyzed variation in α and β-diversities in space and time, and used a joint-species distribution mode to characterize species–environment and species–species relationships. Local communities showed pronounced temporal variation reflecting both imperfect species detection and true stochastic species turnover. On the long term however, local communities were largely controlled by niche filtering along two main environmental gradients, one driven by site connectivity, the other by hydrological stability and aquatic vegetation. Two gastropod clades, caenogastropods and pulmonates, showed contrasted spatio–temporal distributions resulting from different responses to these gradients, and these distributions seemed little altered by interspecific competition. Our study illustrates the benefit of using spatiotemporal metacommunity data to discern long-term impacts of niche filtering and species interactions behind short-term stochasticity.

Keywords: dispersal, ecological niche, extinction–colonization, freshwater snails, guadeloupe, interspecific competition, species diversity

Introduction

One of the aims of community ecology is to explain patterns of species distributions in space and time (Tilman 1994, Hubbell 2001, Chase and Leibold 2003, Vellend 2016). The metacommunity framework has conceptually expanded this field by emphasizing

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the importance of interconnections among local communities through dispersal (Leibold et al. 2004). Broadly speaking, two sets of metacommunity processes are considered: 1) niche filtering (sensu lato), relying on species-specific responses to local environment and to other species (Tilman 1982, 1994, Chase and Leibold 2003), 2) regional processes depending on dispersal, recruitment limitation and stochastic extinctions. An important difference between them is that the latter can generate variation in communities even under the species equivalence assumption; for this reason, they are central in neutral models (i.e. models not considering species-specific properties), such as island biogeography (MacArthur and Wilson 1967) or the neutral theory of biodiversity (Hubbell 2001).

Empirical descriptions of metacommunities are starting to accumulate (Logue et al. 2011, Leibold and Chase 2017). These studies try to explain richness gradients (why are some local communities richer than others?), and community dissimilarity (why do sites harbor different species sets?). However, this is not a trivial task. In metacommunities, richness gradients may emerge from any source of positive spatial covariance in species presence: sites where the colonization/extinction ratio is high for many species at once, harbor richer communities at a given time. Thus, neutral models explain diversity gradients by structural properties such as site area and connectivity, assumed to affect all species positively (MacArthur and Wilson 1967, Hubbell 2001). However, niche filtering may also produce diversity gradients if some habitats are favorable to many, and others to few, species (Cilleros et al. 2017). The same dual point of view applies to dissimilarity in species composition. At one end of the conceptual continuum, a purely niche-based perspective would explain among-community dissimilarities by differences in local environments and interspecific interactions (niche filtering sensu lato), assuming no recruitment limitation (i.e. propagules of all species continuously reaching all sites). At the other end, under a purely neutral perspective, dissimilarities would arise from neutral stochastic species recruitment and extinction–colonization dynamics, as local communities at time t represent different snapshots of stochastic time-series. Of course, it is now commonplace that niche- and neutral-inspired hypotheses are not exclusive and work together (Gravel et al. 2006, Adler et al. 2007, Brown et al. 2017), leaving complex signatures in metacommunity structure. Analyzing them requires evaluating 1) how much structural variables (area, connectivity) or descriptors of the local conditions (including physicochemical features and interspecific interactions), or both, explain species (co-) occurrences, and 2) whether each variable acts equally on all species, and if not, whether it generates subgroups of species inhabiting different site types, or diversity gradients. This is our objective in our study system.

Most studies trying to quantify metacommunity processes (Logue et al. 2011, Leibold and Chase 2017) are based on spatial surveys (i.e. snapshot data: several communities at different sites at a given time). However, it is widely recognized that a given spatial pattern can be consistent with different processes (Gilbert and Bennett 2010, Smith and Lundholm 2010, Tuomisto et al. 2012). Importantly, with purely spatial data, the temporal stability of local communities is unknown (Gomes-Mello et al. 2021). Yet it matters in a few important ways. First, incorporating temporal data allows the distinction between temporal (within-site) and spatial (among-site) community dissimilarity. If neutral processes predominate, within-site dissimilarity should increase with time and reach levels similar to among-site dissimilarity, while if niche filtering predominates, within-site dissimilarities should remain below among-site dissimilarity (assuming stable environmental differences). Second, species interactions, in particular competition, are easier to detect with temporal data. Spatial covariances in species presence, once known environmental effects have been accounted for, are considered indicators of putative species interactions, but may often be obscured by undetected environmental sources of covariance (Poggiato et al. 2021). Temporal data strengthen such inferences because they can document asymmetrical interactions in time, such as competitive preemption or exclusion (when the presence of a species at time t reduces the probability of presence of another species at $t+1$). Third, repeated observations at short time intervals allow to estimate observation error (non-detection of species), a near-universal source of downward biases in species richness and upward biases in dissimilarity (Kellner and Swihart 2014, Guillera-Arroita 2017). However, only few metacommunity surveys have incorporated spatio–temporal data (Datry et al. 2016, Brown et al. 2017, Hughes et al. 2017, García-Girón et al. 2021, Gomes-Mello et al. 2021, Record et al. 2021). Here we contribute to this effort by describing species diversity and composition in both space and time in a freshwater metacommunity, and discussing the processes structuring it.

Freshwater molluscs are popular models in community ecology (Dillon 2000), studied under either a niche- or an island-biogeography perspective (Aho 1978a, Heino and Muotka 2006, Hoverman et al. 2011), and worth investigating from a metacommunity viewpoint. We here consider a long-term survey of freshwater molluscs initiated in 2001 and including ca 250 sites sampled each year in Grande-Terre of Guadeloupe (Lesser Antilles), with a wide variety of environments. All species are trophically similar (herbivorous–detritivorous), and competition occurs in some species pairs (Pointier and David 2004, Chapuis et al. 2017, Dubart et al. 2019). Importantly, high rates of extinction/colonization have been recorded at site scale in individual species (Lamy et al. 2013, Dubart et al. 2019, Pantel et al. 2022), suggesting that temporal data may matter to understand the system dynamics. Occasional airborne dispersal (by birds) allows molluscs to colonize isolated ponds (Kappes and Haase 2012, Van Leeuwen et al. 2012, 2013), but is sufficiently rare to happen irregularly, and incoming propagules are likely too few to impact the demography of already-established local populations. All in all, this system has characteristics favoring both stochastic species recruitment and niche filtering.

We describe the spatio–temporal structure of this metacommunity, based on presence/absence of species, and look for patterns reflecting niche filtering (by local environments and

species interactions) and extinction–colonization processes. In practice, we first estimated how species diversity (alpha and beta) varies in space and time and whether it depends on factors classically associated with 'neutral processes' (e.g. site size, connectivity) or 'niche processes' (other habitat features). Second, using a joint species distribution model (JSDM), we assessed how species presences vary and covary in response to habitat features and to the presence of other species in the previous year. The aim of this last part is to explore niche filtering in detail by characterizing 1) habitat–species relationships, classifying habitat features as resulting in either richness gradients or disjoint sets of species, 2) species interactions. We however acknowledge that, even using spatio–temporal data, our interpretations remain by essence hypothetical, given the observational nature of the data. A complete quantification of all processes in a metacommunity, allowing to model it fully and reproduce its spatio–temporal structure by simulation, is still out of reach, as the methodology does not yet exist (and abundance data, rather than presence/absence, may be needed – in particular, to detect among-species interactions).

Material and methods

Study area and snail metacommunity

Our system and sampling methods have previously been described (Lamy et al. 2012, 2013, Chapuis et al. 2017, Dubart et al. 2019). Briefly, the study was conducted in Grande-Terre of Guadeloupe (Lesser Antilles), a calcareous island (ca 1400 km^2) harboring a dense network of ca 2000 ponds, a few small intermittent rivers, and swamp grasslands connected to mangroves (hereafter back-mangroves) (Pointier 1974, Bruyere and Questel 2001). The nature of the ground (limestone) means that water hardness is high throughout the island, a very favorable condition for freshwater molluscs (Dillon 2000). This sub-tropical area experiences an alternation of wet (July–December) and dry season (December–June), often interrupted by a 'little rainy season' (a rainier period around April–May). Some habitats can dry out for up to several months, especially in eastern and northern Grande-Terre (Wasson et al. 2004).

Twenty-four mollusc species occupy these habitats (Pointier 2008), but only 21 were considered here, the other three being too rare (Supporting information). Seven have been introduced since the mid-20th century. Twenty species are gastropods (six caenogastropods and fourteen pulmonates), and the last one is a bivalve. Pulmonates differ from Caenogastropods by several characteristics (Dillon 2000). Pulmonates produce clutches attached to vegetation, easily moved by birds (Kappes and Haase 2012, Van Leeuwen et al. 2012, 2013) and juveniles can crawl actively onto bird's feet (Malone 1965, Rees 1965), so overland dispersal is assumed to be very efficient. In addition, Pulmonates are simultaneous hermaphrodites with fast reproduction, high fecundity and self-fertilization ability, facilitating the establishment of new populations. They are therefore considered efficient colonists (Dillon 2000). Another specificity is their aptitude to resist pond desiccation by aestivating in the ground, especially developed in flat-shelled pulmonates (*Planorbidae*) (Lamy et al. 2012, Havel et al. 2014). In contrast caenogastropods are larger-bodied and longer-lived, usually benthic, with low aestivation ability; and they have separate sexes – characteristics more favorable to exploitative competition than to colonization and tolerance to desiccation.

Study design

We used data from 250 sites surveyed yearly from 2001 to 2017 at the beginning of the dry season (January–February). Sites are mostly ponds (80%), but also small intermittent rivers (11%), and back-mangroves (9%). On average, 222.5 ± 30.5 sites were visited each year and each site was visited 14.9 times (± 3.14). A random subset of sites (ca 30) was re-sampled each year (two visits at a maximum interval of two weeks, short enough to assume no change in community composition) to estimate species detection probabilities (MacKenzie et al. 2002, Pantel et al. 2022). In sites found dry (5.8%), species were recorded as 'unknown status' rather than absent, since some survive in the ground, and are not detected. Each wet site was surveyed by three persons for 15 min, to record mollusc species and environmental characteristics (Supporting information): percentage of vegetation cover, site size and maximum depth, water quality, amount of organic debris, and a connectivity measure reflecting local accessibility. Values were averaged over years to produce long-term site-specific values. We did not include year-to-year variation in variables within each site for two reasons. First, most sites present long-term differences in environment that appear repeatable from year to year. Second, our field experience suggests that year-to-year variation is error-prone and reflect unpredictable, short-term fluctuations. Early in the dry season, most ponds are in the process of shrinking and vegetation, area, depth and water clarity vary erratically, especially in relation with recent local rains. We therefore believe that while long-term averages of these variables capture permanent differences among sites, yearly values are noisy and not meaningful to explain changes in species presences between years. However, sites differ by the stability of water level and desiccation probabilities. We therefore constructed an additional site-specific variable, site stability, representing the long-term hydrological regime (i.e. contrasting unstable sites with high probability of desiccation, to stable permanent water bodies). Finally, we included two year-specific (temporal) variables, the cumulative rainfalls during the rainy season (RS) and during the little rainy season (LRS), averaged over five Guadeloupean meteorological stations. All environmental variables were standardized, sometimes transformed, prior to analysis (Supporting information).

Environmental variables and community composition in space and time

We analyzed spatial distributions and autocorrelations of the seven spatial (site-specific) and the two temporal (year-specific) environmental variables. We calculated an environmental distance for each set of variables (Euclidean distance

in the multivariate space of standardized variables), and correlations between environmental and geographic (spatial set) or temporal (temporal set) distance. Spatial and temporal autocorrelations were represented as variograms or auto-correlograms (respectively) using the {geoR} package (Ribeiro and Diggle 2001).

We then estimated species pairwise dissimilarities (β-diversity) in space and time, including all non-empty sites, using Sorensen index (β_{sor}). As β_{sor} merges two sources of dissimilarity, species turnover and difference in species richness, we also used Simpson index (β_{sim}) that measures the turnover component alone. Species detection probabilities were estimated based on our replicated samples following Pollock's 'robust design' (Pollock 1982, MacKenzie et al. 2002, Pantel et al. 2022). We considered dissimilarity between replicated samples, which emerges purely from imperfect detection, as the minimal expected dissimilarity.

We then analyzed the relationship between pairwise dissimilarities and geographic, temporal and environmental distances. First, we tested whether dissimilarities among sites were dependent on geographic and/or environmental distances – note that some unmeasured spatially structured factors might contribute to a relationship between dissimilarities and geographic distances. Correlations between dissimilarity and both distance matrices were tested separately using Mantel tests, and jointly using partial Mantel tests, based on 999 permutations, using the {vegan} R package (Oksanen et al. 2020). Then, we repeated the analysis with dissimilarities among years (within sites), correlating them with temporal and environmental distances obtained from the two year-specific variables. Finally, we represented dissimilarities in pairs of samples from all sites and years as a function of: 1) geographic distance and time interval, 2) between-site environmental distances and time interval. The aim here was to assess the stability of community differences among sites, asking whether geographic distance or environmental contrasts were associated with differences exceeding those normally expected in two temporal samples of the same site. In addition, we investigated whether temporal variability of communities depended on particular environments: the mean lag-1 temporal β-diversity within sites (i.e. dissimilarity between a site and itself one year later, averaged over years) was regressed on site-specific environmental variables using a linear mixed-model (LMM) with spatial autocorrelation (using spaMM package, Rousset and Ferdy 2014, which implements a Matérn auto-covariance function). Significance of effects was assessed using likelihood-ratio tests.

Species richness gradients

We estimated species richness (α-richness) in all sites and years, its spatial and temporal distributions and autocorrelations. We averaged species richness over all years by site, or over all sites by year, and regressed them on respectively site- or year-specific environmental variables using LMMs with autocorrelation.

Hierarchical modelling of species communities

We used hierarchical modelling of species communities (HMSC) (Ovaskainen et al. 2017), a flexible approach that deals with both spatial and temporal data. It is complementary to the diversity analysis presented above, since it considers species specificities, not only community richness and dissimilarity. Species presence is predicted as a function of both species-specific effects of environmental variables and other species. We did not include species traits or phylogenetic information in the HSMC (Ovaskainen et al. 2017) as it was unavailable. No spatial structure was considered either as we used presence/absence data, which do not lend themselves

Table 1. Mantel and partial Mantel tests on pairwise dissimilarities. The first column indicates whether similarities were estimated between site pairs within years (averaged over years; 'spatial') or for the same site sampled in different years (averaged over sites; 'temporal'). The second column indicates Sørensen's index of β-diversity and the turnover contribution to this index (in %). In the 'model' column, a Mantel test was performed when a single variable is indicated, and a partial Mantel tests on *X* while controlling for *Y* when *X*|*Y* is indicated. We report Pearson's correlation coefficient (r) and the associated p-value computed from 999 permutations of Pearson's distribution. p-values below 0.05 are in bold characters.

	Index of β-diversity	Model	r	p
Spatial	Sørensen	Space	0.11	**0.001**
		Environment	0.39	**0.001**
		Space|Environment	0.07	**0.002**
		Environment|Space	0.38	**0.001**
	Turnover contrib. (%)	Space	0.06	**0.002**
		Environment	0.17	**0.001**
		Space|Environment	0.04	**0.016**
		Environment|Space	0.16	**0.001**
Temporal	Sørensen	Time	0.85	**0.001**
		Environment	0.18	0.098
		Time|Environment	0.86	**0.001**
		Environment|Time	0.35	**0.003**
	Turnover contrib. (%)	Time	0.66	**0.001**
		Environment	−0.08	0.726
		Time|Environment	0.66	**0.001**
		Environment|Time	−0.10	0.795

to such analysis (convergence issues). Before analysis we excluded four species, out of 21, observed in less than 2% visits (Supporting information) to avoid noisy estimations.

HSMC basically fits a generalized LMM (GLMM; probit regression) using a Bayesian MCMC approach. We used, as linear predictors, both environmental covariables and species presence/absence in the previous year in the same site. Regression coefficients thus were of two types: a 9×17 matrix of impacts of the nine environmental variables on each of the 17 species, and a 17×17 matrix of effects of species presence on each other. In the latter, diagonal coefficients are expected to be positive and represent the stability of species distribution, i.e. how the presence of a given species in year $t-1$ predicts itself in year t. Off-diagonal coefficients represent putative species interactions, negative (suggesting competition) or positive (suggesting facilitation). HMSC also returns residual spatial and temporal variance–covariance matrices (estimated through a latent variable approach, Warton et al. 2015), that reflect the unexplained variance and covariance in species presence among sites and among years. Positive and negative residual covariances provide insights into the concordant or opposite (respectively) responses of species to site (or year) characteristics that are not already captured by the covariates included in the model.

We assessed the predictive power of the model through Tjur's R^2 (Tjur 2009), an equivalent of classical R^2 for binary variables. Following Ovaskainen et al. (2017), we applied a cross-validation approach: 70% of the data were randomly chosen to fit the model, and the remaining 30% were used to compute Tjur's R^2. We ran three chains with 2 000 000 iterations, a burn-in of 1 000 000 iterations, and results were thinned every 20 steps. Estimated parameters are on probit scale and difficult to compare among species. To get comparable values, we calculated for each species the effect of each environmental variable as $\beta_{s,x}$, the relative variation in presence probability when the variable varies from -1 to $+1$ standard deviations around its mean. For species s and variable x:

$$\widetilde{\beta_{s,x}} = \left[\Phi\left(\mu_s + \beta_{s,x}\right) - \Phi\left(\mu_s - \beta_{s,x}\right)\right] / \Phi\left(\mu_s\right) \quad (1)$$

μ_s is the intercept, $\beta_{s,x}$ the estimated effect of x on probit scale, and $\Phi()$ the inverse probit function. We then summarized species responses to environmental variables using a principal component analysis (PCA) on the $\beta_{s,x}$ matrix. We expressed interspecific interaction coefficients as relative changes in the presence probability of species i in presence versus absence of species j, $[\Phi(\mu_i + \beta_{ij}) - \Phi(\mu_i)]/\Phi(\mu_i)$, with μ_i the intercept for species i and β_{ij} the effect of j on i.

Results

The distribution of environmental parameters

The spatial distributions, correlations and autocorrelations of site-specific variables are in the Supporting information. Ponds are distributed over the whole island, while backmangroves are mostly in the southwestern part. Stability, connectivity, litter, depth and to a lesser extent water quality were positively autocorrelated in space, up to a 10 km distance. Increasingly dry areas were found towards the northern and eastern parts of the island (Supporting information). Environmental distance increased slightly, but significantly, with geographical distance (Pearson $r = 0.11$, Mantel $p = 0.001$, Supporting information).

Rainfall data showed the alternation between the rainy season and the dry season, LRS showing a smaller peak during the latter (Supporting information). We did not detect trends in cumulative precipitation over the 17 years (Supporting information; year effect: $\chi^2_{df=1} = 1.30$, $p = 0.25$ for LRS, $\chi^2_{df=1} = 0.33$ $p = 0.56$ for RS). No temporal autocorrelation was detected for these two variables (Supporting information), and environmental distance did not increase with temporal distance (Pearson's $r = -0.01$, Mantel test, $p = 0.53$).

Beta diversity

The mean dissimilarity between repeated visits of a site within a year, reflecting imperfect species detection, was 0.23 ± 0.20 ($n = 482$ visits with non-zero species richness). The mean dissimilarity between two sites in a given year was 0.63 ± 0.25 with a stronger contribution of turnover than of differences in richness (66% versus 34%). Within-site lag-1 temporal dissimilarity (between two successive years) was on average 0.36 ± 0.23, (of which 40% was turnover) – increasing to 0.45 ± 0.25 between any two years.

Pairwise dissimilarity between sites (averaged over years) increased with both geographical (Supporting information, Pearson's $r = 0.11$, Mantel $p = 0.001$) and environmental (Supporting information, $r = 0.39$, $p = 0.001$) distances. In both cases the proportional contribution of turnover also increased ($r = 0.06$, $p = 0.002$ and $r = 0.17$, $p = 0.001$ respectively). The effects of spatial and environmental distances remained significant using partial Mantel tests (Table 1).

Dissimilarity among temporal samples within sites significantly increased with time lag (Supporting information, Pearson's $r = 0.85$, Mantel $p = 0.001$) and so did the turnover contribution (Pearson $r = 0.66$, $p = 0.001$). However, it did not significantly increase with environmental distance estimated from rainfall variables (Supporting information, $r = 0.18$, $p = 0.098$; and $r = -0.08$, $p = 0.726$ for the turnover fraction). When time interval and environmental distance were tested jointly using partial Mantel tests, the time effect remained significant ($r = 0.86$, $p = 0.001$), and the environmental distance effect became significant ($r = 0.35$, $p = 0.003$). The propensity of communities to change from year to year (quantified by within-site lag-1 temporal dissimilarity) varied widely among sites. It was not spatially autocorrelated (Fig. 1, linear model in Table 2), but more vegetated sites harbored less temporally variable communities (Table 2).

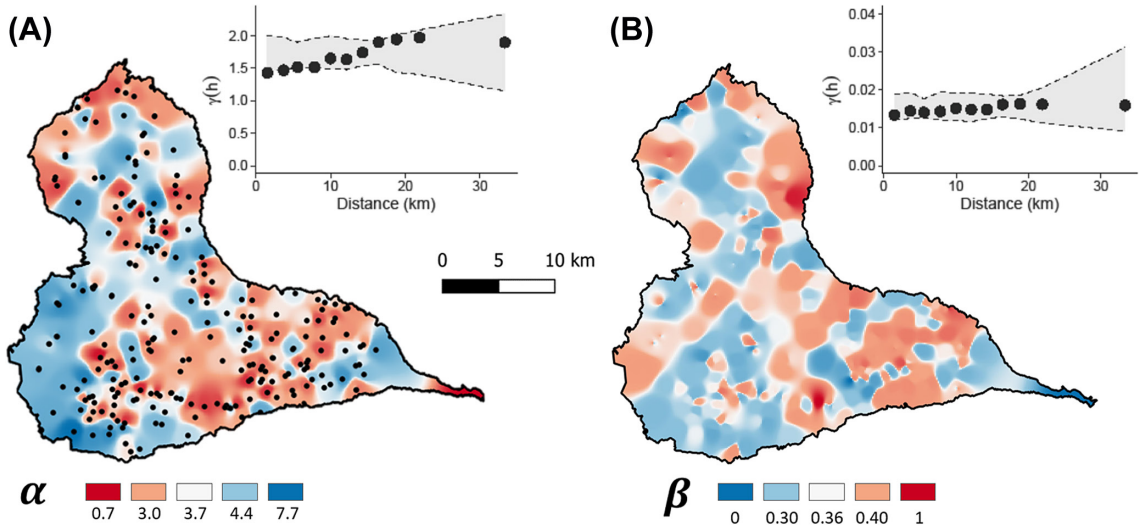

Figure 1. Patterns of species richness (α-richness) and temporal lag-1 dissimilarity in freshwater mollusk communities in Grande-Terre. (A) Spatial distribution of mean richness (averaged over years within sites) with red to blue color indicating increasing richness. Black dots on the map represent sampled sites. (B) Spatial distribution of temporal lag-1 dissimilarity (β_{sor}) between two samples from the same site, with blue to red color indicating sites with increasing temporal dissimilarity. Sub-panels represent spatial autocorrelation with the semi-variance $\gamma(h)$ (a measure of dissimilarity) as a function of geographic (Euclidean) distance between site pairs, envelops were computed by permutation.

We represented dissimilarities between community samples as a function of time and geographical distance (Fig. 2A) or time and environmental distance (Fig. 2B). Within each site, local communities drifted away from their initial state, as shown by increasing dissimilarity with time at distance zero (lower line, light red). However, after 17 years, this dissimilarity remained lower than that between two different sites taken at the same time, even within the shortest geographical distance (brown curve in Fig. 2A; note that larger geographical distances further increased dissimilarity). Confirming previous analysis, dissimilarity among sites depends more on environmental than on geographic distances (larger spread of the color gradient in Fig. 2B versus A). As a result, the dissimilarity between communities taken in the same site at different times (light red curve) becomes comparable to that between contemporaneous communities in different sites with similar environments (first two environmental distance classes, brown) after approximately 10 years (Fig. 2B).

Alpha richness

Alpha richness (species richness per site and visit) varied from 0 to 12, with a mean of 3.69 ± 2.05 species in wet sites, dropping to 3.46 ± 2.17 species when counting dry sites as zeroes (5.8% of data points). Species richness was highest

Table 2. Effects of spatial environmental variables on α-richness and temporal lag-1 β-diversity between temporal samples within sites. The effects and their standard errors were derived from a LMM with spatial autocorrelation. For the habitat factor, *M* and *R* holds for backmangrove and river respectively, and pond served as reference type (intercept). The significance of effects (p) was tested using likelihood-ratio tests and significant effects at $\alpha = 0.05$ are highlighted in bold. The 'Matérn$(1|x+y)$' row gives the two correlation parameters (smoothness ν and scale ρ, Rousset and Ferdy 2014) of spatially autocorrelated residuals. The fixed effects explained 43.9% and 8.6% of the total variance for α-richness and temporal lag-1 β-diversity respectively.

	α-Richness			lag-1 β-diversity		
Variable	Estimate	Cond. SE	p	Estimate	Cond. SE	p
Intercept	3.434	0.146		0.367	0.010	
Size	0.302	0.106	**0.006**	0.003	0.014	0.839
Vegetation	0.236	0.071	$\mathbf{8 \times 10^{-4}}$	–0.025	0.009	**0.006**
Connectivity	0.572	0.105	$\mathbf{< 10^{-6}}$	0.003	0.013	0.784
Litter	–0.184	0.075	**0.018**	–0.008	0.010	0.375
Depth	0.240	0.128	0.060	–0.006	0.017	0.728
Water quality	0.191	0.080	**0.022**	–0.013	0.010	0.196
Stability	–0.122	0.097	0.234	–0.012	0.012	0.297
Habitat	$M = 1.038$	$M = 0.400$	**0.003**	$M = 0.007$	$M = 0.043$	0.855
	$R = 0.742$	$R = 0.323$		$R = 0.005$	$R = 0.038$	
Matérn$(1\|x+y)$	$\nu = 1.896$		**< 0.001**	$\nu = 16.04$		0.587
	$\rho = 9.3 \times 10^{-4}$			$\rho = 5.0 \times 10^{-6}$		

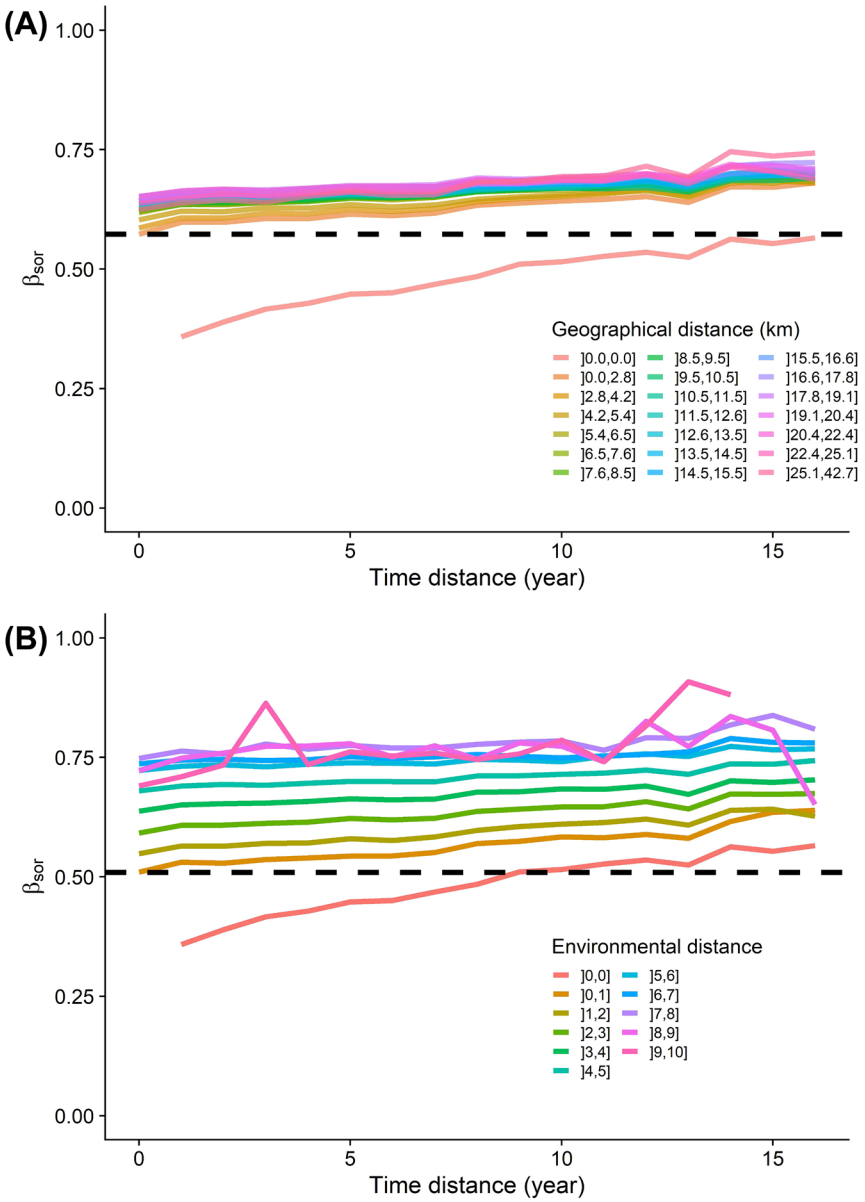

Figure 2. Relationship between dissimilarities (β_{sor}) and temporal (A and B), geographical (A) or environmental (B) distance between pairs of communities. The geographical distance classes were defined from quantiles (0.05 range steps, i.e. 20 classes). The environmental distances were divided into ten even classes (unit). The lower curves report temporal dissimilarities between communities within the same site in both panels (i.e. geographical distance = 0 in A, environmental distance = 0 in B). The dissimilarity between a site an itself at null time distance (light red dot on the lower, left part of each graph) is β_{sor} (= 0.23) between replicate samples of a site made during the same field campaign, which is due to observation error. Horizontal dashed lines report the level of dissimilarity expected between two contemporaneous communities in different sites within the smallest distance class (left end of the brown curve) for ease of reading.

in the south–west of Grande-Terre and decreased towards the (drier) eastern and northern parts (Fig. 1A). A moderate spatial autocorrelation was detected, with differences in diversity plateauing at a 10–15 km distance (Fig. 1A). Site-specific variables explained 44% of the variance in species richness, all variables, but depth and stability, having significant effects (Table 1). Ponds harbored approximately one species less than other habitats. Connectivity, size, vegetation cover and water quality positively influenced richness, while increasing amounts of litter had the reverse effect. Spatial autocorrelation of residuals was significant and Matérn parameters (Table 2) implied that within the spatially autocorrelated fraction of variance (18% of total) correlations were divided by 2 at distances higher than 2 km and by 100 at 8 km. The mean species richness over all sites also varied from year to year, between 3 and 5, but without temporal trend or autocorrelation (Supporting information). In addition, we detected no influence of year-specific rainfall (LRS and RS) on species richness (Supporting information).

Hierarchical modelling of species communities

The HMSC explained nearly as much variance in the validation dataset as in the training dataset (Supporting information), suggesting no overfitting and good predictive power. The model explained 25% of total variance in species presence. Of these 25%, 51% reflected the effect of environmental covariates, the remaining being associated with previous-year species occupancies (29%), and site (14%) or year (6%) random effects.

No influence of environmental variables was detected in 69% of the environment–species combinations (credible intervals included zero), and some variables, such as depth and size, had practically no detectable influence on any species (Supporting information). However, other variables (connectivity, vegetation, stability) affected many species with sometimes strong effects. Some variables affected most species in the same direction, though with different intensities (connectivity and water quality: positive effects; rainfall variables: negative effects). Other ones, including stability, litter and vegetation, elicited opposite responses in different groups of species. These results were summarized using PCA (Fig. 3). The first axis (46.4% inertia) mainly opposed species very sensitive (positively) to connectivity to species indifferent to connectivity. The second axis (27.9%) opposed on one side species that preferred vegetated, unstable sites, and were sensitive to LRS, and on the other side species preferring stable sites without vegetation, and sensitive to RS. Most pulmonates were on the upper-left corner of the factorial plane, i.e. less dependent on connectivity, and with more preference

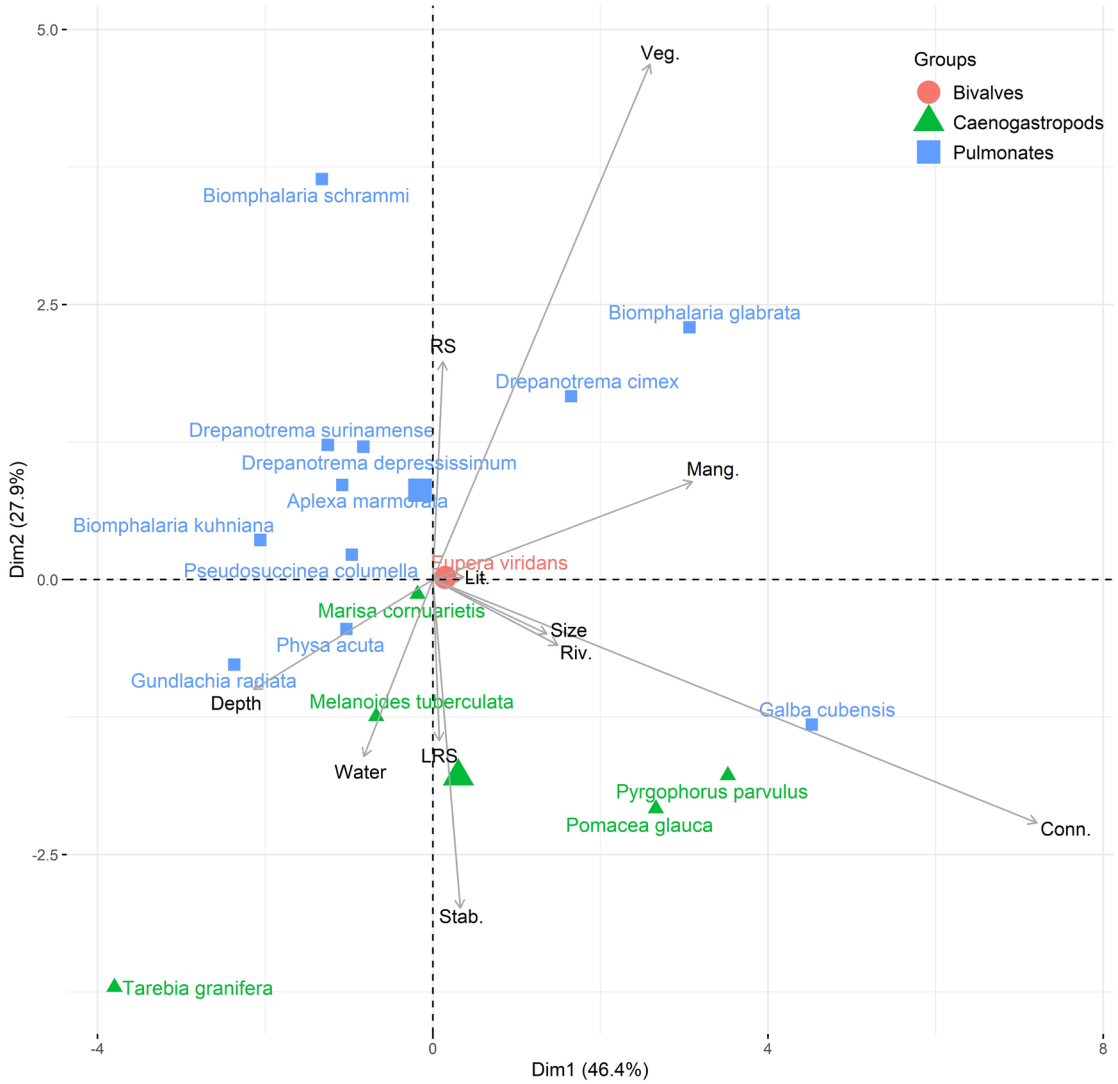

Figure 3. Principal component analysis on relative environmental effects on the species studied. The first two axes accounted for 74.3% of the total variance. The analysis was run on transformed effects of environmental variables estimated using the HMSC model (see text for details, Supporting information for intercepts and for full effects). The main molluscan clades (Supporting information) are distinguished by different colors/shapes, and the largest symbols represent clade centroids.

for unstable, vegetated sites, than caenogastropods. Note that five species on the right side of the factorial plane (*B. glabrata*, *D. cimex*, *G. cubensis*, *P. parvulus* and *P. glauca*) are often found in back-mangroves or small rivers and are associated with characteristics of such habitats (high connectivity and large size).

The diagonal of the matrix representing effects of previous-year species occupancy was entirely positive (Fig. 4), meaning that the presence of a species at year t is well predicted by its presence at year $t-1$. In addition, both positive and negative interspecific effects were detected. Some were reciprocal, such as the negative effects in the *M. cornuarietis–B. glabrata* and *P. acuta–A. marmorata* pairs, but others were not (e.g. *P. acuta–Gundlachia radiata*).

Fourteen percent of the explained variance of the HMSC was due to spatial (site-specific) random effects, while 6% was temporal (year-specific). These random effects resulted in residual covariances in species presences reported in the Supporting information. Interestingly, all covariances with credibility intervals excluding zero were positive. A large block including most pulmonates and the bivalve *Eupera viridans* showed positive spatial covariances (Supporting information), meaning they tended to co-occur in the same sites, on top of what was already predicted by the site variables. Year effects (i.e. temporal variation not explained by RS and LRS) also generated positive covariance among all species, except *T. granifera* (Supporting information).

Discussion

A freshwater metacommunity with a strong but very dynamical spatial heterogeneity

Communities of freshwater molluscs have long been studied using spatial surveys, mostly in temperate or cold environments

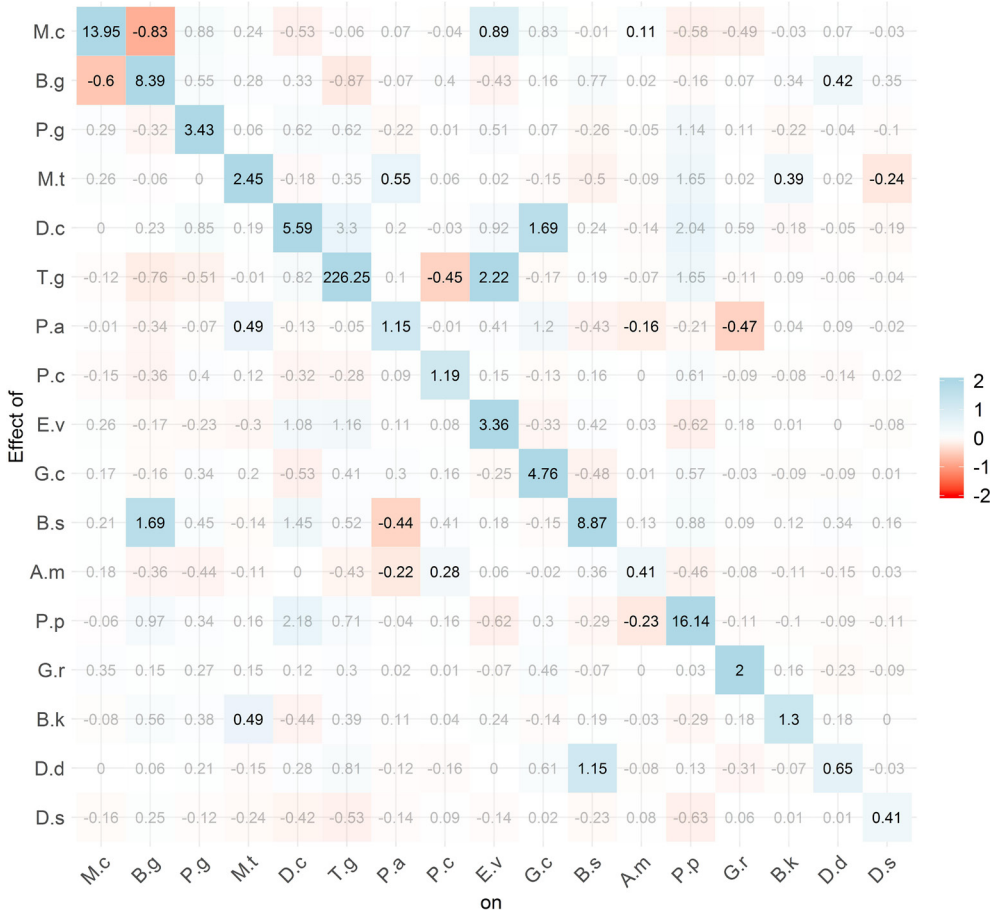

Figure 4. Effects of previous-year occupancy of other species. This effect was computed as $[\Phi(\mu_i+\beta_{ij}) - \Phi(\mu_i)]/\Phi(\mu_i)$, with μ_i the intercept for species i, β_{ij} the estimated effect of species j on species i in probit scale and $\Phi()$ the CDF of the standard normal distribution. Negative effects are depicted by red color, positive effects by blue color and color intensity reflects the strength of the effect. Cells are half-transparent and numbers are in grey when the 90% confidence interval was overlapping with 0 (on probit scale). Species acronyms: M.c : *Marisa cornuarietis*, B.g : *Biomphalaria glabrata*, P.g : *Pomacea glauca*, M.t : *Melanoides tuberculata*, D.c : *Drepanotrema cimex*, T.g : *Tarebia granifera*, P.a : *Physa acuta*, P.c : *Pseudosuccinea columella*, E.v : *Eupera viridans*, G.c : *Galba cubensis*, B.s : *Biomphalaria schrammi*, A.m : *Aplexa marmorata*, P.p : *Pyrgophorus parvulus*, G.r : *Gundlachia radiata*, B.k : *Biomphalaria kuhniana*, D.d : *Drepanotrema depressissimum*, D.s : *Drepanotrema surinamense*.

(reviewed by Dillon 2000, Supporting information for examples). Common features of the Guadeloupe metacommunity with these studies include a quite small regional species pool (24 taxa), and a within-site richness (3.69 on average) much smaller than the regional pool, and very variable among sites (Supporting information). Correlatively, β-diversity among sites is large (0.63). However, spatial differences are not necessarily stable, as β-diversity estimates vary due to both imperfect species detection and natural turnover (extinction and colonization). Strikingly, our replicate samples suggest that imperfect species detection alone explains approximately one third of the apparent β-diversity. This source of bias should therefore be routinely (but is rarely) estimated in communities (Guillera-Arroita 2017). In addition, extinction–colonization dynamics generate temporal β-diversity, already detectable from one year to the next, and stabilizing at around two-thirds of the spatial estimate after 15 years. Thus, only a relatively small fraction of the spatial structure of this metacommunity is stable. However, this stable component does exist, as local communities resemble more their past state, even after 17 years, than contemporaneous communities in other sites.

Strikingly, neighboring communities from Guadeloupe resemble each other only slightly more than distant ones, and this resemblance vanishes after a few years (Fig. 2). Weak distance-decay suggests that species recruitment is more limited by local characteristics than by distance, as in previous studies of freshwater molluscs (Heino and Muotka 2006, Turner and Montgomery 2009, Hoverman et al. 2011). Although local communities are recruitment-limited (i.e. lacking some species at time *t* and 'waiting' for recolonization to recruit them), colonization is probably unaffected by the range of distances of our study (up to tens of km). Birds can indeed disperse molluscs over large distances (Kappes and Haase 2012, Van Leeuwen et al. 2012, Incagnone et al. 2015). In contrast, temporal distance matters more to community dissimilarity than spatial distance (Fig. 2), likely reflecting the enrichment of the species pool by invasive species (*P. acuta*, *M. cornuarietis*) during the 20 years of survey.

The most important determinant of β-diversity is the environmental distance, showing that local characteristics are the main determinants of the long-term identity of local communities. This raises three issues: 1) which characteristics underlie species richness gradients: structural features (area, connectivity, stability) as in neutral models, or local habitat descriptors (vegetation, litter, water quality) as expected from niche-filtering? 2) Does each characteristic elicit homogeneous or heterogeneous responses in different species? 3) To what extent are species distributions affected by interspecific interactions?

Gradients of species richness are determined by both structural and habitat quality variables.

Freshwater mollusc communities are classical illustrations of island biogeography theory, as their species richness is well predicted by size and accessibility of water bodies (Aho 1978a, b, Brönmark 1985, Lewis and Magnuson 2000, Carlsson 2001, Heino and Muotka 2006). However, local variables related to ecological niches also frequently affect molluscan diversity: water chemistry (hardness and pH) (Boycott 1936, Aho 1978b, Friday 1987, Lodge et al. 1987, Pip 1987, Savage and Gazey 1987, Dillon 2000, Carlsson 2001, Hoverman et al. 2011) and macrophyte abundance (Brönmark 1985, Friday 1987, Pip 1987, Carlsson 2001) have positive effects, while abundant litter (responsible for acidification, Boycott 1936, Jurkiewicz-Karnkowska 2008, Hoverman et al. 2011) has negative effects. In our study too, both structural variables (size, connectivity) and variables reflecting the quality of local habitat (positive effect of macrophytes and water quality, negative effect of litter), as well as variables reflecting a mix of both (back-mangrove type, combining high connectivity and peculiar chemistry with brackish influences) significantly affect species richness. Importantly, as in previous studies, all 'habitat quality' variables can be considered as indirect indicators of ecosystem productivity and, more generally, shared requirements of most molluscs (Boycott 1936, Lassen 1975, Lodge et al. 1987). This illustrates the limits of inferences based on α-richness. While effects of area and connectivity are predicted by neutral community models and have been used to validate them, habitat variables, usually considered as components of ecological niches, might act the same way. In both cases, α-richness gradients emerge because many species perceive the same range of sites as accessible for colonization and/or favorable for persistence. This condition does not mean neutrality, and could at best be considered a very attenuated form of species equivalence. To investigate the impact of differences among species, we must consider how each taxon responds to these variables.

Species–environment relationships and niche filtering in the molluscan metacommunity

Previous studies identified the ability to withstand desiccation and reach small isolated ponds, rather than diet, as the main source of niche differentiation among freshwater snails. Some species deemed 'fugitive' or 'r-selected', usually small pulmonates (Boycott 1936, Calow 1978, Lodge et al. 1987, Taylor 1988, Dillon 2000), are often found in all sites, including small temporary ponds, while bigger species (including most caenogastropods) seem more restricted to large, permanent or riverine habitats – where competition (and sometimes predation) is often assumed to reduce the occurrence of pulmonates (Lodge et al. 1987, Turner and Montgomery 2009, Hoverman et al. 2011). Effects of isolation and temporariness are difficult to separate as these characteristics are usually positively correlated.

In Guadeloupe, the HMSC analysis revealed species–habitat relationships partly in line with these previous studies. We here discuss the main patterns, keeping a more detailed account for the Supporting information. PCA on HMSC effects classified species along two main axes, the first associated with connectivity, the second with vegetation and stability. Connectivity here reflects the frequency of hydrological

connection to neighboring water bodies: a connective site will therefore, on average, collect propagules from a larger 'effective' area. The effect of connectivity (when present) was positive, but species were unequally affected (Supporting information): pulmonates were relatively indifferent, especially the smallest species, while caenogastropods were very dependent on high connectivity. This agrees with the 'colonist' trait syndrome associated with pulmonates (Dillon 2000). The second PCA axis reflects responses to hydrological stability and vegetation cover, contrasting groups of species with opposite preferences (rather strong versus weak preference, as for axis 1): some species, mostly caenogastropods, respond positively to stability and negatively to vegetation, while others, mostly drought-resistant pulmonates with a capacity of aestivation in dry ponds, show the reverse pattern.

Although both connectivity and the stability/vegetation gradient filter communities of freshwater mollusks, they do not play similar roles. Connectivity underlies a richness gradient, as unconnected ponds are accessible to a nonrandom subsample of the regional pool (i.e. species with high colonization capacity). In contrast, the stability/vegetation gradient acts as 'niche segregator', different sets of species being favored at each end of the gradient. This suggests two things. First, gradients of richness associated with connectivity, although predicted by an essentially neutral theory (island biogeography), may not reflect neutral processes as connectivity may filter species based on colonization-related traits (Lowe and McPeek 2014, Resetarits et al. 2019, for a similar conclusion on patch area). Second, although perturbations are represented in many models as 'random resets' generating empty space in metacommunities (Hastings 1980, Tilman 1994, Calcagno et al. 2006), they can in fact positively select some species. Unstable sites are not only 'younger' on average, therefore missing slow recolonizers, they are also enriched in species equipped to tolerate perturbation (here, desiccation). This echoes freshwater mesocosm experiments (Chase et al. 2001) showing an exploration–exploitation tradeoff in snails, leading to inverted dominance patterns depending on resource patchiness. Species associated with unstable sites may not like drought in itself (they merely survive through aestivation) but they may be better at exploring ephemeral patches of vegetation when a site is drying or refilling, whereas species associated to stable, vegetation-poor sites are better at exploiting low, evenly distributed resource.

Our model explains only 25% variance in species presence. This is partly expected from the probabilistic nature of species extinction and colonization. However, it also suggests that species filtering was not fully captured by linear effects of our environmental variables. Indeed, the positive spatial and, especially, temporal residual covariances suggest that species show parallel responses to unmeasured environmental effects exhibiting spatial or temporal variations (might be driven by e.g. site use by waterbirds, amount of nutriments and/or parasite communities). For example, positive temporal covariances among nearly all species suggest there were bad and good years, beyond what could be predicted based on rainfall variables. Residual variance is also probably inflated by uncontrolled seasonal effects – the stage at which we visit ponds in the seasonal cycle cannot be exactly the same every year. Unfortunately, the number of variables (and nonlinear effects) that can be included in a model is limited and the number of parameters estimated in our models is already quite high.

Species interactions only weakly affect local communities

Species interactions can alter species (co-)occurrence patterns driven by environmental variables. Competition may reinforce niche segregation, as species tend to be excluded from their non-preferred habitats by competitors (Vellend 2016, Leibold and Chase 2017). In addition, if competition is hierarchical, and if poor competitors tend to be better colonists (Hastings 1980, Tilman 1994) or more tolerant to perturbation (Muller-Landau 2010), a segregation can arise between communities dominated by high-rank competitors (in accessible and/or stable sites) versus low-rank competitors (in isolated and/or perturbed sites). Previous attempts at measuring competition in freshwater snails have come to mixed conclusions. Species co-occurrences turned out very hard to interpret in terms of competitive displacement, due to high stochasticity in local communities (Dillon 2000). Yet, cage and laboratory experiments have demonstrated the potential for strong interspecific competition (Osenberg 1989, Byers 2000, Chase et al. 2001), and accidental or controlled introductions have often had large impacts on resident species (Byers 2000, Pointier and David 2004, Chapuis et al. 2017), suggesting that temporal changes may bear more reliable information on competition than spatial patterns. A merit of HMSC is its potential to capture this information through year-to-year changes. The model indirectly estimates competition by considering how the presence of one species is affected by that of another species in the previous year, thus capturing how the latter reduces the colonization and/or persistence of the former. Some caution is needed, as negative coefficients may reflect indirect effects such as temporal changes in conditions with opposite effects on two species, instead of competition. Reassuringly, however, we do recover significant negative coefficients for two known competitor pairs from Guadeloupe, in both cases one introduced and one local species: *P. acuta–A. marmorata* (competition inferred by two-species metapopulation models; Chapuis et al. 2017, Dubart et al. 2019) and *M. cornuarietis–B. glabrata* (based on an introduction experiment; Pointier and David 2004). The HMSC suggests that competitive effects were reciprocal (in agreement with previous studies for the first pair, the only one where reciprocity was evaluable). Other negative effects detected in our study represent more dubious cases of competition, especially when involving rare species (e.g. *B. schrammi*, *P. parvulus*). Similarly, the few positive effects may reflect parallel effects on two species rather than facilitation. Overall, our results suggest a weak impact of competition, and it does not seem hierarchically organized, as in competition–colonization or competition–tolerance tradeoff

models (Hastings 1980, Tilman 1994). It therefore seems unlikely that competition has profoundly altered species–habitat relationships determined by stability, vegetation and connectivity.

Conclusion and perspectives

Our study provides several insights on a freshwater metacommunity. Our long temporal series reveals that the spatial distribution of communities is subject to important stochastic variation in time due to colonization–extinction dynamics. Despite stochasticity, community composition revolves around attractors associated with site characteristics maintained over time, as expected from niche filtering. A first filter is based on connectivity, resulting in nested sets of species able to reach all versus only the most connective sites. A second filter is based on hydroperiod and vegetation, opposing species adapted to temporary and vegetated sites, to species adapted to permanent and unvegetated sites. While competition results in occasional species displacement, there is little evidence for a widespread effect such as exclusion of good colonists or drought-tolerant species from connective and permanent sites.

Our study illustrates three principles of general interest to metacommunity ecology, already identified in the literature, though in our opinion, far from systematically applied. The first is the benefit of temporal series, allowing to disentangle ephemeral from permanent community structure, and to estimate competitive interactions, both inaccessible to snapshot studies (Damgaard and Weiner 2017, Zurell et al. 2018, Gomes-Mello et al. 2021). Second, connectivity and/or perturbation frequency, classical predictors of species richness in neutral models, may in fact selectively filter species based on their traits – they may either produce richness gradients or separate subgroups of species with opposite responses. Connectivity and perturbation can thus be considered as dimensions of a species' ecological niche at the metacommunity level, in addition to local habitat characteristics. Finally, observation errors produce important biases in α-richness and β-diversity, and should be more routinely estimated in metacommunity studies (Guillera-Arroita 2017).

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Author contributions

Philippe Jarne and **Patrice David** contributed equally to this publication. **Maxime Dubart**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jean Pierre Pointier**: Funding acquisition (equal); Investigation (equal); Supervision (equal); Writing – review and editing (supporting). **Philippe Jarne**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Patrice David**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pk0p2ngr0> (Dubart et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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