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The contribution of species–genetic diversity correlations to the understanding of community assembly rules

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Community genetics aims at understanding how within-species variation, species diversity and environmental factors interact to shape community assembly. An approach that emerged a few years ago has been to quantify the correlation between the neutral genetic diversity of a focal species and species diversity of the surrounding community (species–genetic diversity correlations, or SGDCs). We here review this approach and discuss its interpretative framework in a community ecology context. First, we show that the case for mostly positive SGDCs is probably overstated due to publication bias – only 11% are significantly positive, a fraction comparable to the significantly negative ones. This suggests that variation in area and connectivity among habitat patches, theoretically leading to positive SGDCs, is not the only factor affecting SGDCs. Second, building upon previous contributions, we propose a general framework to identify the multiple factors underpinning SGDCs, and argue that it will help deepen our understanding of community assembly, especially with regard to the ecological factors playing at metacommunity scale. Our framework distinguishes between site and community factors which can affect SGDCs either positively or negatively, depending on whether the focal species and the rest of the community are similar or dissimilar, in terms of realized niches and dispersal abilities. Empirical studies should thus go beyond simply computing SGDCs, and we provide statistical methods (e.g. structural equation modelling) to decompose SGDCs into the multiple contributions of site and community factors. As an example, we use a published dataset (freshwater snail metacommunity), and show how the role of focal population size on SGDCs had hitherto not been detected. We further discuss how considering several focal species and various delimitations of the community may help one to identify clusters of ecologically similar species. We eventually highlight the benefit that SGDC studies would get from integrating β-diversities.

Biodiversity harbours several levels of organization, from genes to ecosystems. Although each of them corresponds to a separate research field (e.g. population genetics, community ecology), connections and feedbacks between levels have been repeatedly highlighted (Birch 1960, Antonovics 1976, 2003, Urban and Skelly 2006, Vellend 2006, 2010, Lankau and Strauss 2007, Crutsinger et al. 2008, Urban et al. 2008). In particular, community genetics (Antonovics 1976, 2003) aims at integrating intra-specific and inter-specific variation into a unified framework. Most studies in this research field have focused on the influence of non-neutral genetic diversity in a focal species, frequently a dominant species, on species diversity as a result of genotype-specific interactions (reviewed by Hughes et al. 2008, Violle et al. 2012, Ehlers et al. 2016). By contrast, the neutral genetic diversity in focal species has received less attention. This is probably because neutral genetic diversity, generally measured at microsatellite, SNP (single-nucleotide polymorphism) or mitochondrial DNA (mtDNA) loci, is usually not correlated to phenotypes and fitness in outcrossing, sexual species (i.e. no linkage disequilibrium with selected loci). Due to this absence of correlation neutral variation will not predict any direct impact of genetic diversity on community composition. However, even if neutral loci are not associated to any particular niche (Craft et al. 2010, Baselga et al. 2015), their polymorphism depends on processes affecting the population size and immigration rate of the focal species. The abundance and recruitment of other species can be affected by the same processes in parallel and/or by direct interactions with the focal species (e.g. through competition). By providing information on colonization, migration and ecological drift, neutral genetic diversity can therefore be a valuable asset to understand the processes shaping community assembly.

How can this neutral genetic information be used in community studies? If ecological processes determine the joint distribution of neutral genetic diversity (see Table 1 for definitions) and community (species) composition, then simultaneously analysing species and gene diversity in the

Table 1. Glossary of key SGDC concepts.

Concepts	Definition
Genetic/species diversity	Any genetic/species diversity index controlling for sample size, for example Nei's gene diversity or rarefied allelic richness (Petit et al. 1998) at the genetic level, and rarefied species richness or Simpson concentration index at the species level (Magurran 2004).
SGDC	Species genetic diversity correlation, used here for correlations between neutral genetic diversity and species diversity. SGDC has been used in a broader context, sometimes including adaptive genetic variation (Vellend et al. 2014, Kahilainen et al. 2014). As any correlation, a SGDC lies between –1 and 1. While α-SGDC focuses on correlation between local genetic and species diversities, β-SGDC focuses on the correlation between genetic and species dissimilarities among pairs of communities and populations (Kahilainen 2014).
Factor	Any variable describing sites or communities. We distinguish factors that describe the environmental conditions and geographical features of sites (site factors; e.g. area, connectivity or environmental gradients) from those describing interspecific interactions (community factors; e.g. population size of the focal species).
Effect	The causal effect of a particular factor on both genetic diversity and species diversity that explains part of the SGDC. Effects can be positive or negative. A SGDC can be explained by multiple effects.
Ecological similarity	Species are ecologically similar for a given site factor if, other site factors being held constant, their population sizes (on average) or immigration rates vary in the same direction with increased values of that site factor.

light of the appropriate factors may constitute a fruitful approach. Vellend (2003) made a first step in this direction by suggesting that, in fragmented landscapes (e.g. archipelagos), the neutral genetic diversity of a focal species can be positively correlated to species richness in the surrounding community. The basic argument is that variation in area and connectivity among habitat patches should affect positively both genetic diversity within populations (as shown in neutral mainland–island models of population genetics; Wright 1931) and species diversity within communities (as contended by the theory of island biogeography; MacArthur and Wilson 1967). This idea was later extended to include any environmental or historical factor having a positive effect on both levels of diversity, and thus predicting positive SGDCs on the basis of "parallel effects" (Vellend and Geber 2005). These initial studies suggested that positive SGDCs (Table 1) should be widespread in nature.

Following the seminal work of Vellend (2003), several empirical studies have reported positive SGDCs in a wide variety of ecological systems (Supplementary material Appendix 1). Two meta-analyses suggested that a large fraction of SGDCs are indeed positive (Kahilainen et al. 2014, Vellend et al. 2014). However, another one concluded that there was no positive trend across published SGDCs in plant communities (Whitlock 2014). Although this is not our main goal here, we add to this synthesis effort and provide in the Supplementary material Appendix 1 an updated dataset including 161 SGDCs. This allows an even more documented view of potential trends in published SGDCs. While we found that 80% of SGDCs are indeed positive (one sample t-test, $p < 0.001$, mean SGDC = 0.298), only 11% of them are significantly positive. Moreover, significantly negative SGDCs have about the same frequency as significantly positive ones (6%, Fig. 1a). We also found that the value of published

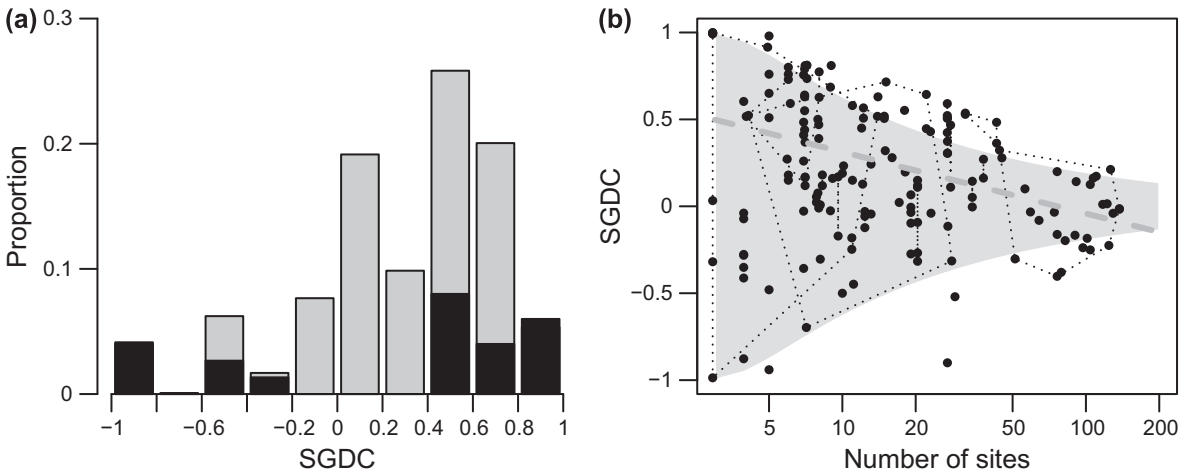

Figure 1. Distribution (a) and funnel plot (b) of published SGDCs (α-SGDCs) based on genetic and species diversity within sites. Fifty independent datasets and 161 SGDCs are considered, and each dataset is given the same weight. When *n* SGDCs are calculated from the same dataset, each SGDC is given a weight of $1/n$ (see details in Supplementary material Appendix 1). (a) Statistically significant SGDCs are indicated in black. (b) SGDC as a function of the number of sampled sites (each point represents a SGDC value). SGDCs computed from the same dataset are connected with a dotted line. The significance area (i.e. funnel plot; based on a symmetrical Pearson test) is indicated by the grey overlay. The grey dashed line corresponds to the negative effect of the number of sampled sites (log transformed; $p = 0.025$) on SGDC values.

SGDCs decreases with the number of sampled sites (Fig. 1b; in line with Vellend et al. 2014). This suggests a publication bias towards positive and extreme values, as often detected by "funnel" representations of sample size–effect size relationships (Palmer 2000). Moreover, the effect of the number of sampled sites remained significant when including other, potentially confounding, features (Supplementary material Appendix 1) such as the number of sampled individuals per site and the geographical extent of studies, which is consistent with the meta-analysis of Whitlock (2014). These additional features did not exhibit any significant effect on the observed SGDCs. Our analysis strengthens the idea of a publication bias, and we can conclude that SGDCs are probably not systematically positive, based on the currently available datasets.

In this forum, we consider an explanation for this result: many factors can affect SGDCs and, contrary to common belief, these factors may act in both positive and negative ways, generating large variation in the sign and intensity of SGDCs among studies (Fig. 1a). Therefore, considering the sign or value of SGDCs without further analysis will always yield ambiguous conclusions about the underlying ecological factors. We propose that research on SGDCs should now focus on disentangling the antagonistic effects of underlying factors. Our first main contribution is to provide a framework rooted in the theories of population genetics and community ecology which allows both defining several categories of factors affecting SGDC and describing their effects on SGDCs. Importantly, this framework is tied with the concept of ecological similarity among species, i.e. the similarity of their realized niches and dispersal abilities, which is a key to interpret the contribution of any factor (e.g. variation in connectivity among communities) to SGDCs. Our second main contribution is to show how the relative importance of these factors can be quantified in empirical datasets using structural equation modelling. We then clarify how SGDCs critically depends on the choice of one or several focal species and the delimitation of the community. Ultimately, we enlarge the present framework by 1) showing how the analysis of β-SGDCs, i.e. correlations between β-diversities at species and genetic levels, could further contribute to our understanding of community assembly, provided an appropriate theoretical framework is developed, and 2) relating SGDC decomposition to the other approaches that make use of molecular data for the study of community assembly processes.

Site and community factors underpinning SGDCs

Previous attempts at synthesizing the factors underpinning SGDCs (Vellend and Geber 2005, Kahilainen et al. 2014) focused on genetic diversity sensu lato and lacked a conceptual framework rooted in the neutral theory of biodiversity. The latter has since then been developed by Laroche et al. (2015). In this section, we build upon these previous contributions to provide such a framework for interpreting SGDCs when genetic diversity is derived from neutral genetic markers. In such a situation, two types of factors affect SGDCs (Fig. 2): 1) spatial variation in some key characteristics among sites, such as their environmental condition, area or connectivity in the landscape, which we call 'site factors' and 2) species interactions within communities, which we call 'community factors' and are responsible for non-independent fluctuations of population sizes of different species in a given site with fixed characteristics. We examine the influence of these two types of factors in turn to illustrate how they can have both positive and negative effects on SGDCs.

Site factors

Site factors can influence SGDCs by simultaneously affecting the species diversity of local communities and the genetic diversity of the focal species. Whether a site factor has a positive or a negative effect on SGDCs critically depends on its relationship with the 'ecological similarity' (Table 1) between the focal species and the other species from the community. A set of species are ecologically similar with respect to a given site factor if, other site factors being held constant, the population sizes and/or immigration rates of all species correlate with this factor in the same way. A typical example of a site factor for which species are expected to be ecologically similar is site area – a factor which is often mentioned in SGDC studies (Vellend 2003). Indeed, all species are expected to harbour larger population sizes in larger sites (as contended by the theory of island biogeography; MacArthur and Wilson 1967). Similarly, when all species disperse in a similar way (e.g. freshwater snails passively disperse during flood events in a pond network; Lamy et al. 2013a), these species are ecologically similar with respect to some aspects of connectivity: all species have higher immigration rates in highly connected sites (e.g. ponds being more often flooded during the rainy season). A last example of ecological similarity is the effect of disturbance (e.g. logging of forest patches, drying ponds) on species from a similar successional stage. All these species have low or zero population sizes right after a perturbation and then follow similar recolonization processes. The time since the last disturbance is then a site factor with respect to which all species belonging to the same successional stage are ecologically similar. By contrast, it is not the case for species belonging to distinct successional stages. Ecological similarity can affect SGDCs as detailed below.

Case 1. A site factor with respect to which the focal species and the other species are ecologically similar affects SGDCs positively

Our first case occurs when species are ecologically similar for a given site factor (Fig. 2). Such a site factor is expected to create positive covariances between the average long-term population sizes and/or the immigration rates of all species among sites, which should affect SGDCs positively. This has been clearly supported by theoretical contributions based on the neutral theory of community assembly (Vellend 2005, Laroche et al. 2015). Indeed, in the neutral model of Hubbell (2001), community assembly within a site depends only on two site factors: its carrying capacity N^* (the number of individuals at equilibrium) and the proportion of immigrant individuals received at each generation m^*. In particular, both the average population size of the focal species, N^*_P, and the average size of the rest of the community, N^*_C, are positively related to N^*. Species diversity of a local community (excluding the focal species) depends positively on the

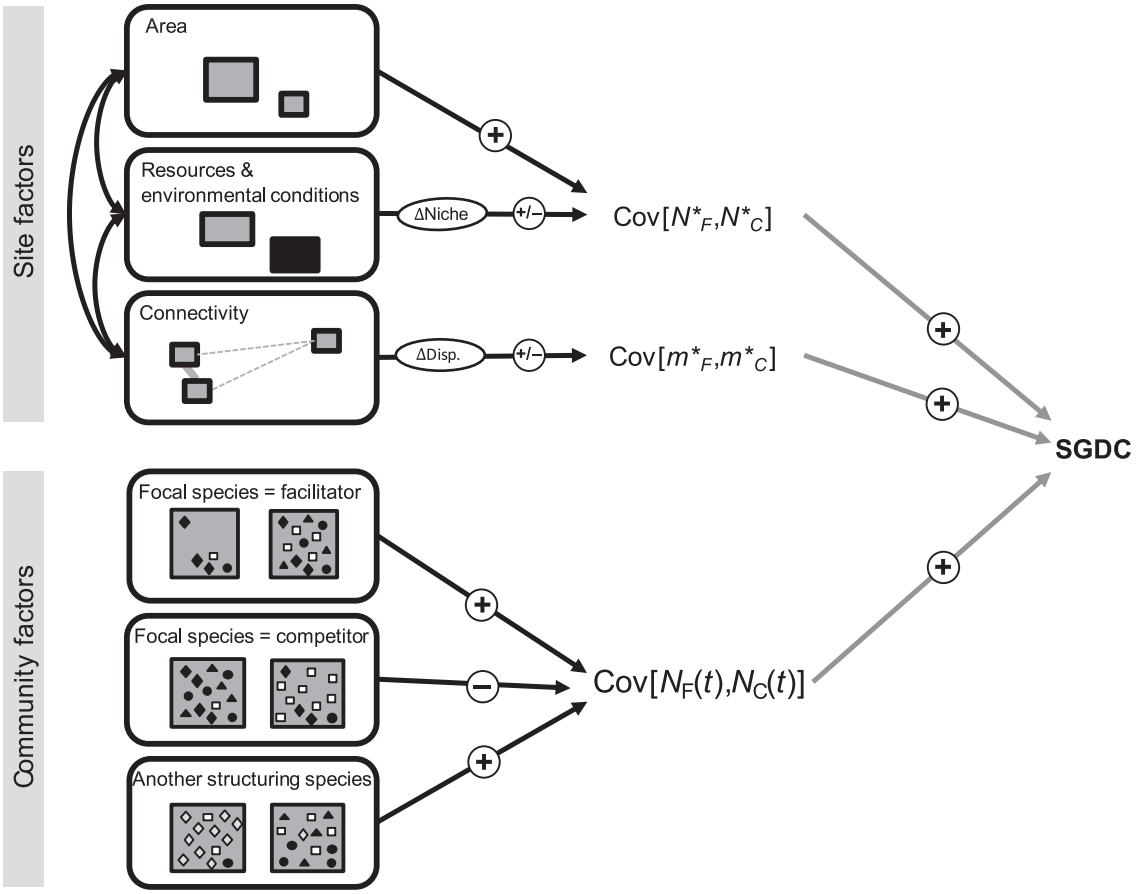

Figure 2. Roadmap to the site and community factors underpinning SGDCs. Site factors (upper panel) result from the spatial variation in site characteristics such as area, resources, environmental conditions and connectivity. These variations cause spatial covariance between the average population size of the focal species (N^*_F) and that of all other species considered together (N^*_C), or between the immigration rate of the focal species (m^*_F) and that of the other species (m^*_C). The effects of these factors on covariances (and therefore on the SGDC) is indicated by black arrows. '–' indicates a negative effect and '+'a positive effect. '+/–' indicates that the factor can have any kind of effect depending on the degree of ecological similarity among species. Notably, the sign and magnitude of this effect will be mediated by the degree of ecological similarity between the focal species and the other species with respect to their realized niches ('ΔNiche') and dispersal abilities ('ΔDisp.'). Black arrows on the left side of the boxes represent spatial covariance between site factors. Community factors (lower panel) stem from the covariance between the population size of the focal species ($N_F(t)$) and the population size of other species (considered together: $N_C(t)$) among sites with similar characteristics, due to species interactions. Effects on SGDC emerge when the focal species (white squares) has a strong impact (facilitation or competition) on the rest of the community (other black shapes) or when another species (grey diamonds) has a strong impact (facilitation or competition, note that only competition is represented) on the community. Positive spatial covariances between the average population sizes among sites with different characteristics, the average immigration rates among sites with different characteristics, and population sizes among sites with similar characteristics all affect SGDCs positively, which is illustrated using grey thick arrows.

number of immigrants per generation ($\approx N^*_C\, m^*$; Etienne and Olff 2004), while the genetic diversity of the focal species depends on two parameters (Laroche et al. 2015): the number of focal immigrants per site and generation ($\approx N^*_F\, m^*$) and the number of focal mutants per generation ($\approx N^*_F\, \nu$, where ν is the mutation rate of the neutral genetic marker under consideration).

It is then possible to distinguish between three types of effects through which a site factor can influence SGDCs based on the neutral theory of SGDCs: 1) if a site factor affects either N^* or m^* (but not both of them), then it has a positive effect on SGDCs; 2) if a site factor affects both N^* and m^* in the same direction, then it has a positive effect on SGDCs; 3) if a site factor affects N^* and m^* in opposite directions, then it may have either a positive or a negative effect on SGDCs (Laroche et al. 2015). The negative effect under scenario 3) occurs when the species diversity of the community is primarily influenced by its immigration rate, m^*_C, while the genetic diversity of the focal species is primarily influenced by its long-term population size N^*_F – a likely situation when the mutation rate ν is high compared to the immigration rate m^*. The latter condition can be fulfilled when using genetic markers with high mutation rates (e.g. microsatellites; Jarne and Lagoda 1996, Ellegren 2002). However, the whole set of conditions leading to negative SGDC under scenario 3 has hitherto not been reported in the studies we reviewed for our synthesis (Supplementary material Appendix 1).

Excluding scenario 3), situations of ecological neutrality lead by definition to ecological similarity in our framework,

and site factors should have a positive effect on SGDCs. However, even if strict ecological neutrality is not realistic in natural communities, species can still be ecologically similar with respect to some site factors. Such factors will hence affect SGDCs positively. For instance, in a simulation study including species that differed with respect to their sensitivity to micro-environmental conditions, but were ecologically similar with respect to their perception of area and connectivity, Vellend (2005) detected a positive effect of site area and connectivity on SGDCs. However, more theoretical studies on the effect of site factors on SGDCs when species are not fully ecologically similar are necessary to assess the robustness of our first case. For instance, even if several empirical studies have suggested that the time since the last disturbance should be a site factor affecting SGDCs positively for species belonging to the same successional stage (Cleary et al. 2006, Evanno et al. 2009, Wei and Jiang 2012), no theoretical study has, to our knowledge, validated this idea.

Case 2. A site factor for which the focal species and the other species are not ecologically similar has no or negative effects on SGDCs

Our second case occurs when the focal species and the other species in the community are not ecologically similar for a given site factor (i.e. the focal species reaches high population sizes or high immigration rates at different values of the site characteristic than other species); this factor will have no or negative effects on SGDCs (Fig. 2). To illustrate this point, we consider the special case in which all, but the focal, species are ecologically equivalent. Assume that the focal species and the rest of the community compete for two resources A and B (see Supplementary material Appendix 2 for further modelling details; this example is inspired from Chase and Leibold 2003, p. 46). If the focal species is more specialized on A than other species, an increase in the availability of A (S_A) both increases N^*_F and decreases N^*_C due to competition. Variance in S_A among sites generates a negative covariance between N^*_F and N^*_C (Fig. 3), and hence negatively affects the SGDC. The study of Silvertown et al. (2009) on the effects of fertilizers on grass communities illustrates this outcome. Plots in which the amount of nutrients (N, P, K, Mg) was artificially increased were characterised by 1) an increase in the biomass and the genetic diversity of the focal species, *Anthoxanthum odoratum* and 2) a decrease in grass species diversity. This resulted in a negative SGDC due to asymmetrical resource competition: *A. odoratum* may be more specialized for exploiting mineral nutrients than most of its competitors so that the addition of mineral nutrients through fertilization is a site-specific factor negatively affecting the SGDC. More generally, any environmental variable that is spatially variable and responsible for niche partitioning among species should cause a negative covariance between N^*_F and N^*_C and thus be a site factor negatively affecting SGDC. This is the case of nutrients in the example above, but other variables, which differentially affect species within the community, such as temperature or acidity (Derry et al. 2009), may also constitute negative site factors. Note, however, that other site characteristics such as area may underlie a positive covariance between S_A and S_B, as larger sites are likely to harbour more resources of all types, which in turn could have a positive effect on the SGDC (Fig. 3). Even if species are specialized on distinct resources, variables such as area may constitute a site factor for which all the species are ecologically similar.

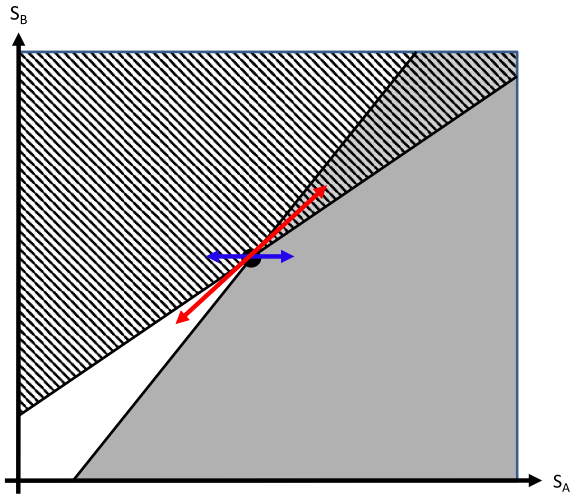

Figure 3. Variation of long-term population size of the focal species (N^*_F) and of the rest of the community (N^*_C) as a function of the amount of two substitutable resources (S_A, S_B). The focal species is specialized on A. The dot is an arbitrary reference position (e.g. the average amount of resources across the metacommunity). The grey area presents amounts of resources at which the focal species is more abundant than at the reference position. The stripped area presents amounts of resources at which the abundance of the rest of the community is higher than at the reference position. Variation of only one resource among sites (blue arrow) generates a negative covariance between abundance of the focal species and the rest of the community. Positive covariance between the two resources among sites (red arrow) can generate a positive covariance between the abundance of the focal species and that of the rest of the community.

Importantly, when the non-focal species are not ecologically similar with respect to a given site factor, their species diversity may not be significantly related to this factor. The site factor may then have no significant effect on SGDC instead of the negative effect mentioned above. Resource availability may be such a factor, as in the previous example. Site factors related to habitat connectivity provide another example when, for instance, the non-focal species differ in their dispersal abilities such that they differentially perceive landscape permeability (e.g. barriers, corridors; Van de Meutter et al. 2007, Flinn et al. 2010). As a result, heterogeneity in dispersal among species is likely to dampen the positive effect of variation in connectivity predicted by the neutral framework, but will not contribute negatively to SGDCs, as illustrated by the study of Struebig et al. (2006; discussed below). The only case in which landscape attributes might negatively affect SGDCs is when the sites that are easily accessible to the focal species tend to be poorly accessible to the other species, causing m^*_F and m^*_C to be negatively correlated among sites. However, we know of no empirical study in which this effect has been evidenced.

Community factors

Site factors are related to variation in average population sizes and are mediated by site characteristics. However, even

among sites exhibiting similar characteristics, variation in population sizes around their average values might be correlated because of species interactions. For instance, let us consider two species A and B interacting through competition within site 1 displaying a set of characteristics F. If species A is more abundant in site 1 than in other sites displaying the same characteristics F, we expect species B to be less abundant in site 1 than in other sites displaying characteristics F. If interactions lead to a negative (resp. positive) correlation between the population size of the focal species and that of many other species in the community, they will represent a community factor with a negative (resp. positive) effect on SGDCs. This may occur in the two particular cases detailed below.

Case 3. Strong competitive interactions from the focal species on the other species is a community factor affecting the SGDC negatively

If the focal species is a dominant competitor in the community, then all the other species may harbour low population sizes in sites where the focal one is abundant. As noticed in previous conceptual works (Vellend and Geber 2005), such competition is a community factor that should negatively affect SGDCs. By contrast, a strong positive effect of the focal species on the rest of the community represents a community factors having a positive effect on SGDCs. For example, it has been shown that the presence of thyme in Mediterranean herbaceous communities (Ehlers et al. 2014) or cushion plants in arid ecosystems (Cavieres and Badano 2009) increases plant species richness at very fine scale (ca 1 m). Thyme and cushion plants can therefore be considered as facilitator species, and species diversity may be higher in sites where facilitators are abundant. This can be illustrated using the data on cushion plant communities from Cavieres and Badano (2009). In this system, cushion cover has a positive effect on species richness even when controlling for elevation, the main environmental gradient of the study. If the focal species is the facilitator species itself, we might thus expect facilitation to be a positive community factor.

Case 4. Strong competitive or facilitative interactions from a non-focal species on the other species and the focal species is a community factor affecting SGDC positively

If the presence or abundance of a non-focal species A in the community has a positive (facilitation) or negative (competition) effect on the average population size of all the other species (including the focal species), then the presence or abundance of species A represents a community factor. Because we here assume that all species are ecologically similar with respect to the effect of species A, we expect this community factor to have a positive effect on SGDC (Fig. 2). Note that this community factor also acts in the same way as a site factor, as the SGDC is driven by the spatial variation of species A among sites.

To conclude, our framework indicates that different factors with contrasted effects drive SGDCs. In particular, SGDCs may be either positive or negative, explaining that our compilation of published correlations covers all range of possible values and does not exhibit any general trend toward high positive values (Fig. 1, Supplementary material Appendix 1). More importantly, similar SGDC values may stem from very different underlying processes. We thus advocate that empirical studies should systematically go beyond the simple computation of a SGDC and try to decompose this correlation into the contribution of site and community factors. We provide efficient tools for this purpose in the following section.

Decomposing SGDCs into the effects of underpinning factors

To decompose SGDCs it is necessary to measure explanatory variables that describe the underpinning factors presented in the previous section. Site factors can be described based on environmental variables while community factors can be described based on temporal surveys of population sizes. We show below how this can be implemented in practical cases, using a published dataset from a freshwater snail metacommunity (Lamy et al. 2013a). Genetic diversity was analysed in *Drepanotrema depressissimum* (focal species) based on ten microsatellite loci, and species diversity was that of the freshwater snail community. These data were complemented with an environmental and geographic characterization of the 32 ponds studied, including their connectivity with surrounding freshwater habitats, temporal stability of water availability, vegetation cover and pond area.

Different methods can be used to decompose SGDCs into the effects of the abovementioned factors, or of their proxies, including partial correlations, multiple regressions, covariance decomposition and structural equation modelling (SEM; Grace et al. 2010, Legendre and Legendre 2012, Gotelli and Ellison 2013). Partial correlations only deal with one variable at a time and do not account for correlation among variables which prevents exploring the effects of covariance among factors. Because most community ecology studies consider more than a single environmental variable at a time, we here focus on multiple regressions and covariance decomposition. The output of multiple regressions can be pictured in a causal diagram (Fig. 4a), as it represents a particular form of SEM (Shipley 2002). Two multiple regressions can be carried out to evaluate the effect of the explanatory variables on species diversity (SD) and on genetic diversity (GD), and then combined to assess the effects of the variance of each variable and of the covariances between variable pairs on the SGDC (Fig. 4b). This allows a direct assessment of the effect of each variable on a given SGDC while accounting for correlation among variables. For instance, covariance decomposition in the case of the freshwater snail metacommunity indicated that the variation in connectivity among sites is a site factor having a strong positive effect on the SGDC (Lamy et al. 2013a). It also allowed quantifying this positive effect, which is responsible for 71% of the SGDC. In addition, the positive effect of connectivity is reduced by 7% due to its negative correlation with pond area. This analysis also shows that pond stability acts as a site factor having a negative effect on the SGDC, reducing the latter by 7%. We provide a R script (<www.r-project.org>) to perform this decomposition as an electronic enhancement in the online version of this article (Supplementary material Appendix 3).

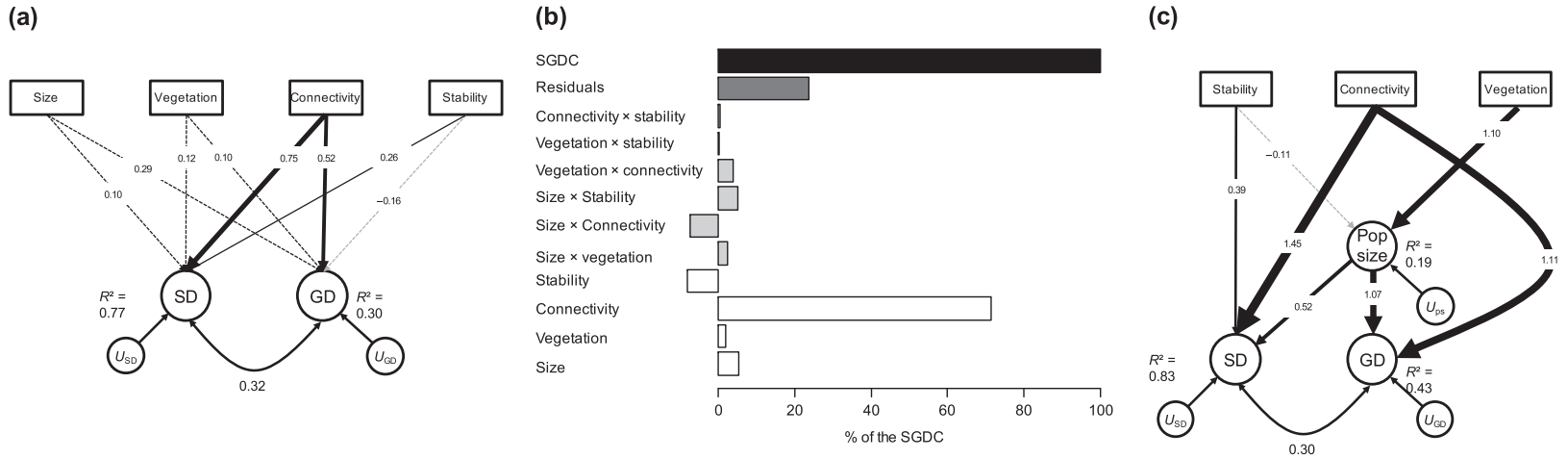

Figure 4. Illustration of three methods (multiple regression, SGDC decomposition and structural equation modelling) that can be used to uncover the factors underpinning SGDCs. Methods are illustrated using data from a freshwater snail metacommunity from Guadeloupe, Lesser Antilles (Lamy et al. 2013a). The focal species is *Drepanotrema depressissimum*, the genetic diversity (GD) of which was assessed in 32 populations using rarefied allelic richness at ten microsatellite markers. The occurrence of other snail species from the metacommunity was used to compute species diversity (SD; species number). Four environmental variables were measured at each site, namely pond area, vegetation cover, connectivity with surrounding sites and temporal stability in water availability. (a) Results of multiple regressions of the four environmental variables on SD and GD (taken separately) pictured as a causal diagram. Arrows represent putative causal effects through standardized path coefficients (positive values: black arrows; negative: grey; significant values: solid arrows; non-significant: dotted; arrow width proportional to coefficient value). U_{SD} and U_{GD} represent unspecified factors influencing SD and GD respectively. The double arrow between SD and GD corresponds to the residual correlation. (b) SGDC decomposition. Each bar represents the effect of either an environmental variable (white), or the covariation between variable pairs (light grey), on the SGDC (black). Residuals correspond to the effect of unmeasured variables. (c) Causal diagram of the best structural equation model (SEM) explaining SGDC in *D. depressissimum*. Non-significant links were removed after model selection with AICc. All model fit indices suggest that the present model adequately explain SGDC (root mean square error of approximation, RMSEA < 0.01; standardized f SGDC root mean square residual < 0.08; and $\chi^2 = 0.285$, DF $= 4$, p $= 0.99$). Note that site area was not retained during model selection.

Although covariance decomposition can deal with multiple variables, it cannot deal with hierarchical relationships among them, e.g. variable X influencing variable Y and both of them influencing the response variable, which typically occur when both site and community factors contribute to the explanation of a SGDC. One way to deal with such relationships when decomposing a SGDC is to include a new proxy representing the population size of the focal species. However, because population sizes can be partially determined by site variables, covariance decomposition becomes inappropriate. In this case, SEM (Grace et al. 2010) offers a valuable alternative (He et al. 2008), although it requires large datasets, which contrast with the relatively small number of sites that most SGDC studies have considered (Fig. 1b). To illustrate the use of SEM in our case study, we added the population size of the focal species to the causal diagram (Fig. 4a) and tested for both direct effect of environmental characteristics on the SGDC and for indirect effect of environmental characteristics mediated by the population size. The selected model (Fig. 4c) suggests that the positive effect of connectivity on both levels of diversity is not mediated by the population size of the focal species. However, including the population size of *D. depressissimum* as an extra variable reveals new properties. The model suggests that a larger population size of *D. depressissimum* may favour species diversity. This effect is probably due to either an important unmeasured site factor for which *D. depressissimum* and the other non-focal species are ecologically similar (following case 1 from our framework), or an unmeasured community factor induced by another non-focal species (following case 4 from our framework). Any of these two unmeasured factors can result in a large residual relationship between species diversity and *D. depressissimum* population size.

In the freshwater snail metacommunity, habitat connectivity is the site factor having by far the largest positive effect on the SGDC. This suggests that most snail species from this community are ecologically similar with respect to habitat connectivity, presumably because they display very similar dispersal abilities. Indeed, snail dispersal mainly occurs during the rainy season when floods ensure hydrographic connection among ponds (Lamy et al. 2013a). Most individuals can be transported passively, irrespective of species identity. Covariance decomposition and SEM further outline that another site factor, habitat stability, has a small negative effect on the SGDC. An explanation is that *D. depressissimum* performs much better in unstable sites than most other snail species of the Guadeloupe metacommunity. Indeed, unlike the other species, *D. depressissimum* can aestivate in dry ponds (Pointier and Combes 1976, Lamy et al. 2013b), and the lack of ecological similarity between the focal and other species with respect to this life-history trait probably underpins the negative effect of stability on the SGDC. Finally, the positive effect of *D. depressissimum* population size on SD suggests the existence of an undetected positive site and/or community factor. This example illustrates the use of SEM to decipher complex hierarchical and indirect effects underlying a SGDC. Of course, such an approach requires an appropriate characterization of variables used for describing both the focal and non-focal species and site characteristics, and an appropriate number of sites.

SGDCs in a multi-species context: choosing the community boundary and the focal species

Quantifying the relative effect of site and community factors on SGDCs (Fig. 4) helps understand how the ecological similarity between the focal species and the other species of the community in terms of their ecological niche and dispersal abilities. However, these conclusions critically depend on 1) the delimitation of communities (i.e. which species are included) and 2) the choice of the focal species. Here we discuss how varying community boundaries and selecting one or several focal species can improve our understanding of community assembly.

Delimitation of the community

Quantifying the effects of different site factors on SGDCs provides a new tool to analyse the degree of ecological similarity among species. It can be used in an exploratory way to find a set of species which maximizes the positive effects of different site factors. This can also allow validating some a priori biological knowledge about species environmental preferences. He and Lamont (2010) explored this idea using ant-dispersed species of the Australian flora. When considering nitrogen-fixing species only, they found a positive SGDC. However, the SGDC was not significant anymore when adding species from other functional groups. It is possible to hypothesize that the SGDC based on nitrogen-fixing species only stemmed from the positive effect of a site factor for which these species are ecologically similar (case 1). The lack of ecological similarity between nitrogen-fixing species and species from other functional groups drove down the SGDC value (case 2). In this case, decomposing the SGDC into the contribution of site and community factors would help shed light on their respective influence, sign and magnitude.

Considering several focal species simultaneously

With the increased availability of molecular data, it is now possible to consider the genetic diversity of several species simultaneously (Taberlet et al. 2012, Gugerli et al. 2013). We suggest that, rather than selecting a given focal species for the genetic analysis, SGDC studies should adopt a multi-species approach to provide a broader view on community assembly processes. Few SGDC studies have considered genetic diversity in multiple species (Supplementary material Appendix 1). Moreover, multi-species genetic data have been analysed in different ways, thus affecting the factors that multi-species SGDCs ultimately capture.

A first group of studies have combined information from all genotyped species to compute a single multispecies SGDC per community, averaging either genetic diversity (Wehenkel et al. 2006, Papadopoulou et al. 2011), or SGDCs (Robinson et al. 2010), among species. However, averaging genetic variability over different species is not appropriate when genetic markers display heterogeneous levels of variation across species, as more variable markers will have a disproportionate impact on the average diversity or SGDC. Other studies ignored species boundaries

when using DNA sequences with clear homologues in all species from the community and computed a trans-specific genetic diversity based on all individuals irrespective of species identity (Gregorius et al. 2003). Going one step further, several studies (Papadopoulou et al. 2011, Baselga et al. 2013, Múrria et al. 2015) suggested to analyse mitochondrial DNA (mtDNA) in a "multi-hierarchical macro-ecology approach" (Baselga et al. 2015). It consists, on one hand, in directly investigating the diversity of mtDNA haplotypes (which constitutes the genetic level) in communities and, on the other hand, in tracing haplotype genealogies back in time to define operational taxonomic units (OTUs; which constitutes the species level) and investigating the diversity of OTUs across communities.

These approaches summarize in different ways the genetic diversity across all genotyped species and lead to a single 'pooled' SGDC. We expect site factors linked to case 1 to affect this pooled SGDC positively. By contrast we expect site factors linked to case 2 to be averaged out by considering the genetic diversity of all the species simultaneously. Consequently, we might expect 'pooled' SGDCs to be more often positive than those centred on a single focal species. The empirical studies that pooled genetic data indeed found positive and significant multispecies SGDCs (Wehenkel et al. 2006, Robinson et al. 2010, Papadopoulou et al. 2011, Bergmann et al. 2013) while invariably detecting non-significant single-species SGDCs. Decomposing these SGDCs should further reveal the environmental factors and/or the landscape features (e.g. area and geographic connectivity) acting as positive site factors.

Another way of dealing with several genotyped species is to compute one SGDC per genotyped species (as done in a few studies; Struebig et al. 2011, Taberlet et al. 2012, Lamy et al. 2013a). This should bring different insights, mostly contributing to a better understanding of ecological similarity among species. Indeed, comparing SGDCs among species may contribute to single out species that markedly differ from other species in the community with respect to particular environmental characteristics. For instance, a study investigating the effect of habitat fragmentation on bat communities in the Malaysian rainforest (Struebig et al. 2011) showed that the papillose woolly bat *Kerivoula papillosa* harbours a positive and nearly significant SGDC while the Blyth horseshoe bat *Rhinolophus lepidus* has a non-significant SGDC. Using partial correlations further showed that the area of forest patches affected the SGDC positively in *K. papillosa.* Differences in dispersal abilities between the two species can explain these contrasted results. *R. lepidus* is indeed able to move over longer distances than *K. papillosa*, and is therefore less sensitive to the area of forest patches. In addition, our framework suggests that most of the other species in the community are probably dispersal-limited like *K. papillosa* (as suggested by the corresponding positive SGDC; Fig. 3b in Struebig et al. 2011), while *R. lepidus* is an outlier species with respect to its dispersal ability. However, the strong variability of SGDCs among species in Struebig et al. (2011) may be partially due to statistical artefacts, because genetic diversity was evaluated in a very small number of individuals in some sites (Nazareno and Jump 2012).

Some perspectives for SGDC studies

From α- to β-SGDCs?

Our framework tackles diversity at species and genetic levels within sites as a function of environmental conditions and species interactions. However, an additional aspect of SGDC studies should also be accounted for: spatially close sites should be more similar than distant ones in terms of both their species composition (the "distance-decay" pattern; Soininen et al. 2007) and their genetic structure (the "isolation by distance" pattern; Rousset 1997). Part of the distance-decay pattern is often due to underpinning environmental gradients ("induced spatial structure"; Legendre and Legendre 2012): spatially close sites share similar environmental conditions leading to similar communities. In addition, adjacent sites from dispersal-limited communities should display more similar species and genetic composition because they exchange more migrants compared to distant sites, i.e. some form of isolation by distance. Unmeasured environmental gradients and migrant exchanges among close sites can generate a spatial structure ("spatial auto-correlation"; Legendre and Legendre 2012) in α diversity of genes and species that our framework does not take into account, and potentially leads to inflated false positive discovery rates when testing factors underpinning SGDCs in the decomposition methods presented above (Lennon 2000).

It is possible to control for these biases by taking into account spatial autocorrelation as a statistical nuisance reducing the effective sample size (Lennon 2000, Cerioli 2002). However, the spatial autocorrelation of diversity contains additional information about the factors that we identified (Fig. 2) and is not merely a statistical nuisance. For instance, when species exhibit similar dispersal abilities, both genetic and community dissimilarities can increase with the geographic distance among sites. This provides a complementary view on the site factors related to habitat connectivity (Fig. 2) and a better understanding of variation in dispersal ability among species, as discussed above in the context of α-SGDC. Incorporating spatial structure as a biologically meaningful signal calls for analysing not only the diversity within sites, but also the dissimilarity in composition among sites, at both genetic and species diversity levels.

Few empirical studies have compared species dissimilarity between communities and neutral genetic dissimilarity between populations of a focal species (Supplementary material Appendix 1), a pattern called "β-SGDC" (Kahilainen et al. 2014). Here again, the bulk of empirical studies have been dominated by the intuitive assumption that distance among sites should similarly affect dissimilarity at both levels (Baselga et al. 2013), implying that dispersal limitation affects all species in the same way (Fig. 2). We report all published values in Supplementary material Appendix 1 and Fig. A1, extending the dataset of Kahilainen et al. (2014). Most β-SGDCs seem to be positive. Although the average value (0.221) is lower for β-SGDCs than for α-SGDCs, a larger fraction of values is significantly different from 0.

However, we believe that compiling β-SGDCs across empirical studies will not bring more insights upon community assembly processes than compiling α-SGDCs did over the last 15 years for the very same reasons: the positive effect of isolation on β-SGDCs, which has been strongly

emphasized in empirical studies, is only one of several factors potentially affecting β-SGDCs, positively or negatively. For instance, if dissimilarity among communities is primarily driven by an environmental gradient, while genetic structure is explained by isolation by distance, negative β-SGDCs could emerge when the environmental variation among sites displays a strongly negative spatial autocorrelation (Fig. 5, Derry et al. 2009). Empirical studies thus need to decompose β-SGDCs into different factors. The framework proposed above for α-SGDCs might serve as a first basis, and we call for theoretical approaches, for example following Laroche et al. (2015).

We further suggest simultaneously analyzing α- and β-SGDCs. From a theoretical perspective, a necessary starting point would be to extend the neutral theory of SGDCs to a spatially explicit context, using the literature on spatially explicit neutral models in both population genetics (Malécot and Blaringhem 1948, Kimura and Weiss 1964, Rousset 1997) and community ecology (Chave and Leigh 2002, Economo and Keitt 2008, Beeravolu et al. 2009). From an empirical perspective, it is possible to test for the influence of different dispersal schemes on β-SGDCs, for instance by considering both geographic distances among sites and functional distances that take into account how dispersal proceeds in complex landscapes (e.g. barriers to dispersal, dispersal corridors or directional dispersal: Dray et al. 2006, Blanchet et al. 2008). One can then assess the effect of these landscape features, summarized as distance matrices, on β-SGDCs. This should be interpreted as was done for the positive and negative site factors when considering α-SGDCs and would clarify whether species from a metacommunity are ecologically similar with respect to their dispersal ability and their response to some environmental conditions.

Drawing connections with other molecular approaches of communities

SGDC based on neutral markers is one of the approaches that make use of molecular data for inferring community assembly processes. Other approaches include community adaptive genetics (i.e. based on adaptive genotypes) and community phylogenetics which have both been extensively developed over the last years. We briefly consider below how they can be related to the SGDC approach. As mentioned above, community genetics has primarily focused on the adaptive genetic variation of a focal species (Whitham et al. 2003, Wimp et al. 2005, Johnson and Stinchcombe 2007, Lankau and Strauss 2007, Crutsinger et al. 2008, Hughes et al. 2008, Whitlock 2014). All the factors included in our framework should also play a role when considering adaptive genotypes. In addition, the genetic composition of the focal species populations should affect its own population size as well as the population size of other species through selective effects (Johnson and Stinchcombe 2007). However, our framework does not consider these effects. They should notably depend on how variation in adaptive genotypes affects coexistence within and among species. Characterizing interactions among genotypes requires a tremendous amount of empirical investigations and, to date, this aspect is understood in only a few systems (see Ehlers et al. 2016 for a review in plant communities). Even if our approach, which focuses on neutral genetic diversity, only addresses the importance of species interactions, it can serve as a basis for deriving general rules on the relationship between genetic and species diversities. These rules could be applied to understand the nature of the site and community factors underpinning SGDCs. We suggest that adaptive community genetics can follow the SGDC approach in ecosystems and communities in which adaptive genotypes are expected to play an important role in species coexistence.

Community phylogenetics is another approach that has been recently developed to make inferences on the processes shaping ecological communities (Webb et al. 2002, Cavender-Bares et al. 2009, Mouquet et al. 2012). Like our approach, it focuses on interactions at species level. However, while we seek to provide additional insights about community dynamics from the neutral polymorphism within species, community phylogenetics rather uses the phylogenetic relationships among species derived from genetic markers. The core assumption of this approach is that closely related species are phenotypically and ecologically more similar than distantly related ones. Thus, high phylogenetic proximity among co-occurring species indicates that community assembly is shaped by environmental filtering while phylogenetic overdispersion indicates that competitive exclusion

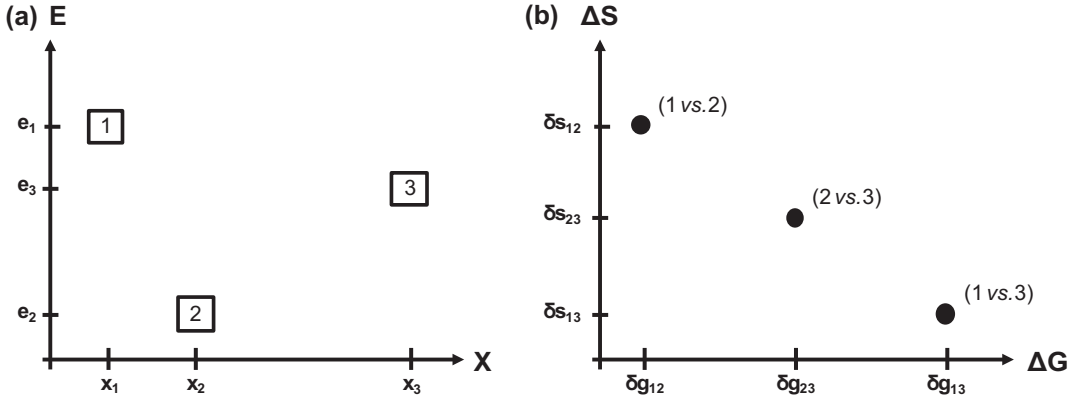

Figure 5. Geographic distance, environmental conditions and β-SGDCs. (a) Three sites (squares) with different geographic positions (X-axis) and experiencing different environmental conditions (E-axis). (b) β-SGDC pictured as the dissimilarity in species composition among sites (ΔS-axis) against the genetic dissimilarity between populations of the focal species (ΔG-axis). A negative β-SGDC emerges when ΔS mainly depends on environmental conditions and ΔG is driven by distance.

of ecologically similar species predominates (Cavender-Bares et al. 2009). In principle, community phylogenetics and SGDC decomposition can be performed in parallel to yield complementary insights into community assembly processes. First, our SGDC approach is particularly adapted to pinpointing the effects of immigration and local demographic stochasticity, two key features of metacommunity dynamics poorly addressed by community phylogenetics. Second, community phylogenetics can provide additional elements to depict species interactions within communities and to characterize community effects. However, there are several caveats when using community phylogenetics (Gerhold et al. 2015). Among others, phylogenetic similarity should reliably indicate trait similarity. In addition, traits should act as niche attributes (i.e. determining the most limiting environmental factors for species persistence) so that competitive exclusion is frequent among similar species; if, on the contrary, traits determine a competitive hierarchy, then the likelihood of competitive exclusion increases between dissimilar species (Mayfield and Levine 2010). These limits suggest that phylogenetic information should (when possible) be replaced by explicit functional traits of species, which can more precisely be related to ecological interactions (e.g. relating plant growth speed to hierarchical competition for light) when analysing proximity among species within and among communities.

A more balanced way of using phylogenetic relationships among individuals is the mutli-hierarchical macro-ecology approach which we discussed above already. This approach fits in the SGDC framework, but it has been suggested that it may even go beyond: variation in haplotype composition within assemblages could constitute a reference of ecological neutrality against which to compare the variation of assemblages at the species level (Baselga et al. 2013, 2015). However this interpretation is highly debatable to date. Indeed, the neutral genetic diversity within species is influenced by non-neutral interactions of species among themselves and with their environment. Consequently, the patterns of genetic diversity obtained from mtDNA might not constitute a neutral reference.

Conclusion

By offering a way of using neutral genetic information to study community assembly processes, SGDCs constitute a new pattern of interest for community ecologists. However, estimating SGDCs only makes sense when correlations are decomposed into the effects of factors acting on population sizes and immigration rates of species. This decomposition brings new insights on species interactions, by quantifying the influence of community factors, and on niche and dispersal similarities among species through site factors. These results cannot be easily obtained through population genetics, even when considering several species in a single study, or through community ecology on their own. The SGDC approach is complementary to other approaches across biodiversity levels, such as community phylogenetics, with the merit of being rooted in a well understood theoretical framework and potentially usable at various geographic and temporal scales over a large number of sites.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.52ch2> (Lamy et al. 2016).

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Supplementary material (available online as Appendix oik-03997 at <www.oikosjournal.org/appendix/oik-03997>). Appendix 1. Correlations between species diversity and genetic diversity (SGDCs) in empirical studies: a critical appraisal. Appendix 2. How does varying the amount of resources affects the density of two competing species? Appendix 3. R function to compute a decomposition of species–genetic diversity correlations (SGDCs) into the effect of different variables.

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Appendix 1. Correlations between species diversity and genetic diversity (SGDCs) in empirical studies: a critical appraisal

Appendix 2. How does varying the amount of resources affect the density of two competing species?

Appendix 3 (supplied in a separate file: Appendix3:R). R-codes

Appendix 1

Correlations between species diversity and genetic diversity (SGDCs) in empirical studies: a critical appraisal

Collection of SGDCs from the literature

We conducted a literature survey to search for studies that computed at least one SGDC. We extensively searched for references by keywords (e.g. SGDC) and by looking at studies referring to the seminal papers on the topic (Vellend 2003, Vellend and Geber 2005). We finally selected studies that reported correlations between the genetic diversity of at least one (focal) species and the species diversity of the surrounding community. Two studies were discarded because they either did not compute the SGDC (Evanno et al. 2009), or because the SGDC was computed based on three sites only (Messmer et al. 2012). We distinguished between studies that computed SGDCs based on local species and genetic diversity (α-SGDC; Table A1) from those that computed SGDCs based on community dissimilarity and genetic differentiation (β-SGDC; Table A2, Fig, A1).

Correlations between genetic diversity and species diversity (α-SGDC). Studies that computed α-SGDCs differed in three aspects. First, based on the same dataset, some studies computed only a single α-SGDC while other studies computed several α-SGDCs using various combinations of species and genetic diversity indices. For instance, some studies crossed species richness or Simpson index with either allelic richness or gene diversity to compute several α-SGDCs on the same dataset. In such cases, we included all computed α-SGDCs, since there is no reason to favour one combination of indices over another and it is also important to account for the heterogeneity in the way SGDCs were computed within studies. In our statistical analyses, each dataset was given the same weight. Accordingly, if a given study computed n α-SGDCs on the same dataset, each α-SGDC was given a weight of $1 / n$ in order to account for pseudo-replication. Second, some studies genotyped several species per community (several focal species). In such a case, one to several (i.e. several combinations of indices) α-SGDCs were available per species, all of which were collected for our analysis. The number of populations used per species was here variable, since the focal species cannot necessarily be collected from the same sites. Third, some studies that focused on several focal species averaged α-SGDCs across species (Papadopoulou et al. 2011, Taberlet et al. 2012). These studies also provided α-SGDC per focal species and we only collected the latter values for the reasons exposed in the main text. Finally, we also divided some studies into independent datasets when they explored SGDC in geographically distinct areas (e.g. Alps versus Carpathians in Taberlet et al. 2012; Yandu versus Nan River in Wei and Jiang 2012). In total we obtained 161 α-SGDCs that were computed based on 50 independent datasets (Table A1).

These datasets included the 14 ones that were used in the seminal paper of Vellend (2003),

as well as the 14 extra studies analysed by Vellend and Geber (2005); we did not include their study no. 13 because no genetic information was used. Vellend et al. (2014) compiled a slightly smaller dataset than ours including 115 α-SGDCs computed from 40 studies. We here included 24 additional α-SGDCs retrieved from seven studies not considered by Vellend et al. (2014), i.e. Silvertown et al. (2009), Yu et al. (2009), Robinson et al. (2010), Finn and Poff (2011), Lamy et al. (2013a), Csergő et al. (2014), Han et al. (2014).

We analysed the effect of three sampling-based factors on the published α-SGDCs using a multiple regression. The three factors correspond to the number of sampled sites, the mean number of individuals sampled per site and the spatial scale of the study. We retrieve the first two factors from the original studies. For the spatial scale, we used the maximum pairwise distance among sites. It was computed based on either 1) available maps from the original publication, 2) plots of pairwise distances available in the original study (e.g. distance decay of genetic or species similarity) or 3) looking at the study system on Google Earth. We then classified each study into a twelve-class variable that captured the spatial scale of the study, from very small scales (1 km) to the largest (1000's of km).

Correlations between genetic differentiation and species dissimilarity (β-SGDC). Similarly, we looked for studies that computed β-SGDCs and used the same criteria when several combinations of dissimilarity indices were used per dataset and when several focal species were under investigation. In total we found 43 β-SGDCs computed from 13 independent datasets (Table A2, Fig. A1). Only the study of Kahilainen et al. (2014) has previously dealt with the distribution of β-SGDCs, and included 108 β-SGDCs.

Results. α-SGDCs have been estimated in a fairly large number of studies, covering a variety of ecosystems and taxa. The whole range of possible values has been detected (Fig. 1a), from strongly positive (Cleary et al. 2006) to strongly negative (Sei et al. 2009), although a majority are positive (80% of the weighted distribution; one sample weighted t-test, $p < 0.001$; weighted mean α-SGDC = 0.298), as already highlighted in previous reviews (Vellend et al. 2014, Kahilainen et al. 2014). Two-sided Pearson tests with 5% error rate reveal that only 10.8% of these positive α-SGDCs are significantly different from zero (Fig. 1a), which is significantly more than the expected 5% under the null assumption. However, no trend in α-SGDCs sign remains when considering significant correlations only (one sample weighted t-test, $p = 0.58$, weighted mean SGDC = 0.15). A "funnel graph" (Palmer 2000) of collected α-SGDCs confirms that most of the positive correlations are statistically not significant (Fig. 1b). It also reveals that the magnitude of α-SGDCs reported in empirical studies decreases as the number of sampled sites increase, which indicates a publication bias towards positive values (Palmer 2000). In particular, α-SGDCs are no more significantly different from zero when the number of sites increases. It could also be that sampling a

larger number of sites increases spatial sampling beyond the dispersal capacities of the focal species. However, we did not find any significant relationship between the spatial scale of the studies and the number of sampled sites ($F_{1,149} = 0.090$, $p = 0.764$). Many small-scale studies (He et al. 2008, He and Lamont 2010) sampled more sites separated by less than 10's of km than large-scale studies in which distances among sites exceed 100's of km (Vellend 2003). It is also possible that sampling more sites comes at the cost of sampling less individuals, increasing measurement errors and hence lowering the final SGDC. However, such a tradeoff in sampling effort would produce the reverse relationship to the one documented in Fig. 1a, and we did not find any support for such a tradeoff based on the published studies. When analysed together, only the number of sites significantly explained α-SGDCs ($F_{1,149} = 14.403$, $p < 0.001$), not spatial scale ($F_{1,149} = 0.090$, $p = 0.764$), nor the number of sampled individuals per site ($F_{1,149} = 1.330$, $p = 0.251$).

We highlight that too few studies have included a large number of sampled sites, precluding definitive conclusions. Indeed, α-SGDCs measured on more than 50 sites all correspond to the same dataset (Taberlet et al. 2012). As the large number of sites was associated with limited sampling per site (three individuals per site in more than 140 sites; Taberlet et al. 2012), a note of caution is required here, since for example large measurement errors arise when genetic diversity is estimated on small sample sizes. Measurement errors of genetic and species diversity decrease the expected absolute value of α-SGDCs by a factor $\sqrt{R_G R_S}$, where R_G and R_S stand for the repeatability of genetic diversity and species diversity respectively (Lamy et al. 2013). Repeatability can easily be computed when diversity has been estimated on several occasions at the same site, as the proportion of variance explained by the 'site' random effect. When samples are not replicated, repeatabilities can be estimated using re-sampling analyses at least for genetic data (for species richness data, it can also be done if species lists come from standardized counts, but usually not if they come from long-term published data on species distributions). For example, (Lamy et al. 2013) estimated R_G to be 68% and R_S to be 87% in their study of a freshwater snail community which sets the expected sample correlation coefficient, r, to 0.766 times the true correlation. More generally, increasing the number of sites at the expense of lowering the number of individuals per site may decrease the repeatability of diversity measures and result in a possibly large downward bias, which would explain the absence of any clear trend in α-SGDCs measured by Taberlet et al. (2012).

β-SGDCs have been estimated in a far lower number of studies (43 values from 13 independent datasets; Fig. A1). Again, the majority of values are positive (80% of the weighted distribution). The weighted β-SGDC across datasets is 0.221 (one sample weighted t-test: $t = 2.550$, $DF = 12$, $p = 0.013$). A large fraction of β-SGDCs are significant (Fig. A1). However, it is important to stress that the significance of all β-SGDCs is based on the Mantel test, which has been shown to provide erroneous results and inflated type I error, especially in the presence of strong

spatial autocorrelation (Guillot and Rousset 2013, Legendre et al. 2015). This issue can be addressed with Moran's Eigenvector Maps (MEM) to first assess the spatial structure in both the genetic and community compositions (Dray et al. 2006).

Practical implications for future studies

More studies with more extensive sampling of both sites and individuals per site are critically required to draw firm conclusions about a general trend in SGDC sign. A note of caution is also needed for future meta-analyses: exploring a large number of potential environmental or spatial factors without any clear theoretical motivation is likely to generate some misleading false positives just because of random noise in the collection of datasets. We recommend focusing instead on individual analyses of single SGDCs in order to identify their underlying factors. It might then turn out that some factors are systematically highlighted in such studies.

Table A1. List of correlations between genetic diversity and species diversity (α-SGDC) reported in the literature based on 50 independent datasets ordered per publication year. For each SGDC, we indicate the dataset from which it was computed, the number of sites sampled (n), its significance (p), the bibliographic reference, the type of genetic marker used to compute genetic diversity, and the index of genetic (GD) and species (SD) diversity. Some studies (reference column) were split to account for distinct geographic area in which information has been collected. Others used different indices of genetic and species diversities. Note that we included data from previous meta-analyses (Vellend [2003]). Marker code: Az = allozymes, Minisat = minisatellites, mtDNA = mitochondrial DNA, cpDNA = chloroplastic DNA, ncDNA = nuclear DNA, Microsat = microsatellites, AFLP = amplified fragment length polymorphism, RAPD = random amplified polymorphic DNA. More details in Appendix 1.

Dataset	n	SGDC	p	Reference	Marker	GD	SD
1	6	0.8	<0.05	Vellend 2003	Az	genetic diversity	species richness
2	6	0.76	<0.05	Vellend 2003	Az	genetic diversity	species richness
3	14	0.63	<0.05	Vellend 2003	Az	observed heterozygosity	species richness
4	7	0.64	<0.1	Vellend 2003	Az	genetic diversity	species richness
5	8	0.47	>0.1	Vellend 2003	Az	observed heterozygosity	species richness
6	11	0.15	>0.1	Vellend 2003	Az	genetic diversity	species richness
7	8	–0.01	>0.1	Vellend 2003	Az	genetic diversity	species richness
8	6	0.73	<0.05	Vellend 2003	Minisat	band diversity	species richness
9	5	0.76	<0.1	Vellend 2003	Az	genetic diversity	species richness
10	6	0.18	>0.1	Vellend 2003	Az	genetic diversity	species richness
11	10	0.19	>0.1	Vellend 2003	Az	observed heterozygosity	species richness
12	8	0.39	>0.1	Vellend 2003	Az	observed heterozygosity	species richness
13	7	0.63	<0.1	Vellend 2003	Minisat	band diversity	species richness
14	7	0.79	<0.05	Vellend 2003	mtDNA	nucleotide diversity	species richness
15	27	0.35	0.07	Vellend 2004	Az/AFLP/ pDNA	allelic richness	species richness
15	27	0.31	0.11	Vellend 2004	Az/AFLP/ pDNA	genetic diversity	species richness
15	27	0.31	0.13	Vellend 2004	Az/AFLP/ pDNA	allelic richness	Simpson
15	27	0.51	0.01	Vellend 2004	Az/AFLP/ pDNA	genetic diversity	Simpson

16	10	–0.17	0.64	Odat et al. 2004	AFLP	genetic diversity	species richness
16	10	0.15	0.68	Odat et al. 2004	AFLP	genetic diversity	evenness
17	7	0.44	0.32	Vellend and Geber 2005	MS	genetic diversity	species richness
18	6	0.15	0.78	Vellend and Geber 2005	mtDNA	genetic diversity	species richness
19	5	0.51	0.38	Vellend and Geber 2005	mtDNA	genetic diversity	species richness
20	9	0.81	0.01	Vellend and Geber 2005	Az	genetic diversity	species richness
21	16	0.28	0.29	Vellend and Geber 2005	Az	genetic diversity	Shannon
22	12	0.45	0.14	Vellend and Geber 2005	AFLP	genetic diversity	species richness
23	18	0.552	0.02	Vellend and Geber 2005	AFLP	genetic diversity	species richness
24	15	0.32	0.24	Vellend and Geber 2005	AFLP	genetic diversity	species richness
25	5	0.65	0.12	Vellend and Geber 2005	mtDNA	genetic diversity	species richness
26	27	–0.9	<0.00 1	Vellend and Geber 2005	Az	observed heterozygosity	species richness
27	5	–0.48	0.05	Wehenkel et al. 2006	Az	equivalent number of variants	species richness
28	5	0.98	0.002	Cleary et al. 2006	Microsat	allelic richness	species richness
29	27	0.6	<0.05	He et al. 2008	Microsat	allelic richness	species richness
29	27	0.51	<0.05	He et al. 2008	Microsat	genetic diversity	species richness
29	27	0.51	<0.05	He et al. 2008	Microsat	allelic richness	Simpson
29	27	0.41	<0.05	He et al. 2008	Microsat	genetic diversity	Simpson
30	29	–0.52	0.004	Puscas et al. 2008	AFLP	band diversity	species richness
31	20	–0.096	NA	Yu et al. 2009	RAPD	polymorphism	species richness
31	20	–0.266	NA	Yu et al. 2009	RAPD	polymorphism	Shannon
31	20	–0.313	NA	Yu et al. 2009	RAPD	polymorphism	evenness
31	20	0.123	NA	Yu et al. 2009	RAPD	genetic diversity	species richness
31	20	0.141	NA	Yu et al. 2009	RAPD	genetic diversity	Shannon

31	20	0.112	NA	Yu et al. 2009	RAPD	genetic diversity	evenness
32	38	0.17	0.3	Derry et al. 2009	mtDNA	allelic richness	species richness
32	38	0.26	0.11	Derry et al. 2009	mtDNA	evenness	evenness
33	5	–0.94	0.015	Sei et al. 2009	Az	allelic richness	species richness
34	10	0.87	0.351	Silvertown et al. 2009	AFLP	genetic diversity	species richness
35	34	0.05	0.763	Helm et al. 2009	Az	polymorphism	species richness
35	34	–0.02	0.902	Helm et al. 2009	Az	allelic richness	species richness
35	34	0.16	0.366	Helm et al. 2009	Az	genetic diversity	species richness
36	23	0.43	0.043	He and Lamont 2010	MS	allelic richness	species richness
37	15	0.52	0.049	Odat et al. 2010	AFLP	genetic diversity	species richness
37	15	0.49	0.066	Odat et al. 2010	AFLP	genetic diversity	evenness
38	7	0.16	0.76	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	8	0.77	0.04	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	7	0.17	0.75	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	8	0.62	0.14	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	7	0.79	0.06	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	7	0.11	0.83	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	4	0.52	0.29	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
38	7	0.37	0.76	Robinson et al. 2010	mtDNA	nucleotide diversity	species richness
39	4	–0.418	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	14	0.515	<0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	4	–0.347	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	11	–0.175	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	9	0.679	<0.05	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	7	0.42	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	7	0.75	<0.05	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness

39	4	–0.276	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	3	0.995	<0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	7	–0.036	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	7	0.473	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	7	0.262	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	7	–0.362	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	3	1	<0.05	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	3	–0.304	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	3	0.982	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	4	–0.081	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	11	–0.26	>0.1	Papadopoulou et al. 2011	mtDNA	nucleotide diversity	species richness
39	8	0.078	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	4	–0.037	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	3	1	<0.00 1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	6	0.261	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	9	–0.029	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	4	0.589	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness

39	5	0.916	<0.05	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	3	0.024	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	4	–0.274	>0.1	Papadopoulou et al. 2011	ncDNA	Nucleotide diversity	Species richness
39	4	–0.889	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	3	–0.978	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
39	8	0.495	>0.1	Papadopoulou et al. 2011	ncDNA	nucleotide diversity	species richness
40	11	0.58	0.08	Struebig et al. 2011	Microsat	allelic richness	species richness
41	7	0.55	0.1	Finn and Poff 2011	mtDNA	allelic richness	species richness
42	12	0.51	0.01	Wei and Jiang 2012	Microsat	allelic richness	species richness
42	12	0.56	0.005	Wei and Jiang 2012	Microsat	genetic diversity	Simpson
43	8	0.05	0.58	Wei and Jiang 2012	Microsat	allelic richness	species richness
43	8	0.02	0.31	Wei and Jiang 2012	Microsat	genetic diversity	Simpson
44	28	0.46	0.01	Blum et al. 2012	Microsat	allelic richness	species richness
44	28	0.09	0.65	Blum et al. 2012	Microsat	Shannon	Shannon
45	45	0.26	0.085	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	12 9	–0.035	0.719	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	10 4	–0.242	0.016	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	76	–0.181	0.131	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	13 7	–0.007	0.942	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	44	0.328	0.03	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	11 0	0.178	0.065	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	12 4	–0.215	0.023	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	74	–0.025	0.835	Taberlet et al. 2012	AFLP	genetic diversity	species richness

	12			Taberlet et al. 2012			
45	2	0.021	0.819		AFLP	genetic diversity	species richness
45	51	–0.304	0.03	Taberlet et al. 2012	AFLP	genetic diversity	species richness
	10			Taberlet et al. 2012			
45	7	0.165	0.106		AFLP	genetic diversity	species richness
			<0.00	Taberlet et al. 2012			
45	76	–0.404	1		AFLP	genetic diversity	species richness
45	97	–0.242	0.02	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	59	–0.031	0.814	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	91	0.141	0.185	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	56	0.105	0.442	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	90	–0.167	0.117	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	82	–0.191	0.085	Taberlet et al. 2012	AFLP	genetic diversity	species richness
	11			Taberlet et al. 2012			
45	7	0.014	0.879		AFLP	genetic diversity	species richness
	10			Taberlet et al. 2012			
45	4	0.108	0.294		AFLP	genetic diversity	species richness
45	76	0.2	0.086	Taberlet et al. 2012	AFLP	genetic diversity	species richness
45	79	–0.375	0.001	Taberlet et al. 2012	AFLP	genetic diversity	species richness
	12			Taberlet et al. 2012			
45	6	0.206	0.026		AFLP	genetic diversity	species richness
	10			Taberlet et al. 2012			
45	1	–0.171	0.094		AFLP	genetic diversity	species richness
	13			Taberlet et al. 2012			
45	7	–0.011	0.91		AFLP	genetic diversity	species richness
45	64	–0.078	0.549	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	19	-0.266	0.357	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	19	-0.112	0.647	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	22	0.433	0.107	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	22	0.654	0.006	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	15	0.705	0.011	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	9	0.157	0.736	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	28	–0.306	0.202	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	17	0.018	0.952	Taberlet et al. 2012	AFLP	genetic diversity	species richness

46	6	0.587	0.221	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	19	–0.052	0.843	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	8	–0.013	0.975	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	11	–0.452	0.189	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	27	–0.12	0.646	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	23	–0.04	0.875	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	13	–0.039	0.905	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	19	0.059	0.822	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	7	–0.692	0.128	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	19	–0.014	0.954	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	18	0.217	0.456	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	12	0.138	0.685	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	4	0.511	0.489	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	10	0.254	0.543	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	8	–0.305	0.463	Taberlet et al. 2012	AFLP	genetic diversity	species richness
46	13	0.241	0.475	Taberlet et al. 2012	AFLP	genetic diversity	species richness
47	32	0.54	<0.00 1	Lamy et al. 2013	Microsat	allelic richness	species richness
47	32	0.537	<0.00 1	Lamy et al. 2013	Microsat	genetic diversity	species richness
47	43	0.484	<0.00 1	Lamy et al. 2013	Microsat	allelic richness	species richness
47	43	0.354	<0.01	Lamy et al. 2013	Microsat	genetic diversity	species richness
48	12	–0.114	0.6	Avolio and Smith 2013	AFLP	nucleotide diversity	species richness
48	12	–0.017	0.94	Avolio and Smith 2013	AFLP	nucleotide diversity	evenness
48	12	–0.058	0.79	Avolio and Smith 2013	AFLP	nucleotide diversity	shannon
49	7	0.818	<0.05	Csergő et al. 2014	RAPD	genetic diversity	species richness
49	7	0.746	0.054	Csergő et al. 2014	RAPD	band diversity	species richness
50	8	0.128	0.762	Han et al. 2014	AFLP	genetic diversity	species richness
50	8	0.178	0.674	Han et al. 2014	AFLP	genetic diversity	evenness

Table A2. List of correlations between genetic differentiation and species dissimilarity (β-SGDC) reported in the literature based on 13 independent datasets. For each value (a line in the table) we indicate the dataset from which it was computed, the number of sites sampled (n), its significance (*P*), the bibliographic reference, the type of genetic marker used to compute genetic diversity, and the index used to compute genetic differentiation and community dissimilarity. Marker code is the same as in Table A1.

Dataset	n	SGDC	p	Reference	Marker	Genetic differentiation	Community dissimilarity
1	27	–0.450	0.02	Vellend 2004	Az/AFLP/cpDNA	F_{ST} (Nei 1977)	Raup and Crick
1	25	0.480	0.01	Vellend 2004	Az/AFLP/cpDNA	F_{ST} (Nei 1977)	community F_{ST}
2	10	0.076	0.01	Adams et al. 2011	AFLP	Euclidean distance	Bray–Curtis
2	10	0.095	0.09	Adams et al. 2011	AFLP	Euclidean distance	Bray–Curtis
2	10	0.064	0.30	Adams et al. 2011	AFLP	Euclidean distance	Bray–Curtis
2	10	–0.012	0.52	Adams et al. 2011	AFLP	Euclidean distance	Bray–Curtis
3	28	0.200	<0.001	Blum et al. 2012	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Bray–Curtis
4	10	0.620	0.02	Odat et al. 2004	AFLP	F_{ST} (Nei 1978)	Euclidean distance
4	10	–0.170	0.22	Odat et al. 2004	AFLP	F_{ST} (Nei 1978)	Euclidean distance
5	15	0.433	0.00	Odat et al. 2004	AFLP	Φ_{ST} from AMOVA	Bray–Curtis
6	15	0.323	<0.05	Papadopoulou et al. 2011	mtDNA	F_{ST} (Nei 1987)	Bray–Curtis
6	15	0.482	<0.001	Papadopoulou et al. 2011	mtDNA	F_{ST} (Nei 1987)	Bray–Curtis
6	15	0.500	<0.05	Papadopoulou et al. 2011	ncDNA	F_{ST} (Nei 1987)	Bray–Curtis
6	15	0.438	NS	Papadopoulou et al. 2011	ncDNA	F_{ST} (Nei 1987)	Bray–Curtis
7	12	0.001	0.49	Struebig et al. 2011	Microsat	Jost'*D*	Morita–Horn

7	10	0.026	0.09	Struebig et al. 2011	Microsat	Jost'*D*	Morita–Horn
7	13	0.115	0.09	Struebig et al. 2011	Microsat	Jost'*D*	Morita–Horn
7	12	0.002	0.33	Struebig et al. 2011	Microsat	Jost'*D*	Morita–Horn
7	10	0.191	0.06	Struebig et al. 2011	Microsat	Jost'*D*	Morita–Horn
7	13	0.177	0.10	Struebig et al. 2011	Microsat	Jost'*D*	Morita–Horn
7	12	0.034	0.15	Struebig et al. 2011	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Morita–Horn
7	10	0.084	0.14	Struebig et al. 2011	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Morita–Horn
7	13	0.087	0.10	Struebig et al. 2011	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Morita–Horn
7	12	0.003	0.42	Struebig et al. 2011	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Morita–Horn
7	10	0.190	0.07	Struebig et al. 2011	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Morita–Horn
7	13	0.106	0.19	Struebig et al. 2011	Microsat	linearized F_{ST} [F_{ST} / (1–F_{ST})]	Morita–Horn
8	5	0.390	0.13	Sei et al. 2009	Az	F_{ST} (Nei 1978)	Sørensen
8	5	0.160	0.41	Sei et al. 2009	Az	F_{ST} (Nei 1978)	Sørensen
8	<9	0.680	0.00	Sei et al. 2009	Az	F_{ST} (Nei 1978)	Sørensen
8	<9	0.450	0.04	Sei et al. 2009	Az	F_{ST} (Nei 1978)	Sørensen
9	7	0.450	0.09	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
9	8	–0.330	0.15	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
9	7	–0.110	0.70	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
9	8	0.050	0.84	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen

9	7	0.080	0.79	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
9	7	–0.230	0.41	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
9	4	0.090	0.94	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
9	7	0.220	0.43	Robinson et al. 2010	mtDNA	F_{ST} (Nei 1987)	Sørensen
10	20	0.227	0.00	Yu et al. 2009	RAPD	F_{ST} (Nei 1978)	Euclidean distance
11	7	0.526	<0.01	Csergő et al. 2014	RAPD	F_{ST} (Nei 1978)	Euclidean distance
12	7	–0.180	0.54	Finn and Poff 2011	mtDNA	linearized FST [FST / (1–FST)]	community F_{ST}
13	8	0.798	<0.05	Han et al. 2014	AFLP	F_{ST} (Nei 1978)	Euclidean distance
13	8	0.010	0.41	Han et al. 2014	AFLP	F_{ST} (Nei 1978)	Euclidean distance

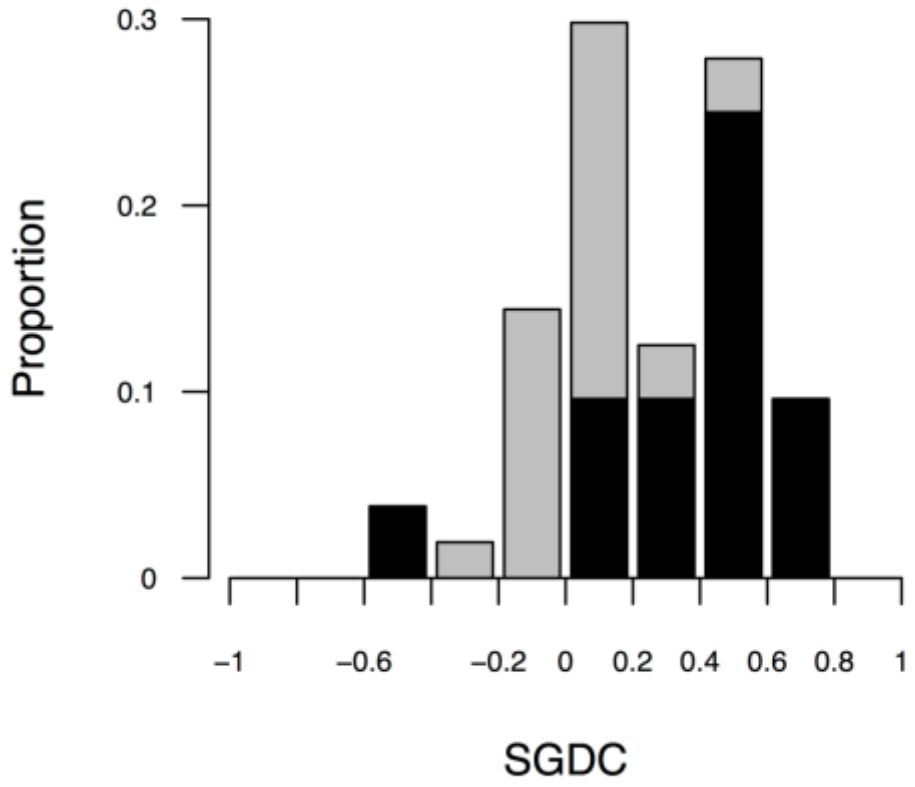

Figure A1. Histogram of 43 β-SGDCs computed based on 13 independent datasets. Each dataset is given the same weight. Weighted β-SGDC across datasets is 0.221 (one sample weighted t-test: t = 2.550, DF = 12, p = 0.0127).

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Appendix 2

How does varying the amount of resources affect the density of two competing species?

We consider the competition dynamics between a focal species of the community (label F) versus the rest of the community which we assume behaves as a single second species (label C). F and C compete for two distinct substitutable resources A and B. In line with Chase and Leibold (2003; p. 46), we assume the following dynamics of the system:

$$\frac{dN_F}{dt} = (\lambda_F^A R_A + \lambda_F^B R_B - \mu_F)N_F \quad (1a)$$

$$\frac{dN_C}{dt} = (\lambda_C^A R_A + \lambda_C^B R_B - \mu_C)N_C \quad (1b)$$

$$\frac{dR_A}{dt} = \pi_A(S_A - R_A) - \chi_F^A R_A N_F - \chi_C^A R_A N_C \quad (1c)$$

$$\frac{dR_B}{dt} = \pi_B(S_B - R_B) - \chi_F^B R_B N_F - \chi_C^B R_B N_C \quad (1d)$$

where:

- N_F, N_C are the densities of the focal species and the rest of the community;
- λ_X^Y is the per-capita per-unit of resource Y reproduction rate of species X;
- R_A, R_B are the densities of resource A and B;
- μ_F, μ_C are the death rates of the focal species the rest of the community;
- π_A, π_B describe the speed of renewal of resources A and B;
- S_A, S_B are the maximal amounts of resources A and B in the absence of consumer (just called "amount" below and in the main text);
- χ_X^Y is the per-capita per-unit of resource Y consumption rate of resource Y by species X.

An equilibrium at which the two species coexist must verify:

$$\lambda_F^A R_A^* + \lambda_F^B R_B^* - \mu_F = 0 \quad (2a)$$

$$\lambda_C^A R_A^* + \lambda_C^B R_B^* - \mu_C = 0 \quad (2b)$$

$$\pi_A(S_A - R_A^*) - \chi_F^A R_A^* N_F^* - \chi_C^A R_A^* N_C^* = 0 \quad (2c)$$

$$\pi_B(S_B - R_B^*) - \chi_F^B R_B^* N_F^* - \chi_C^B R_B^* N_C^* = 0 \quad (2d)$$

This system admits the unique solution:

$$R_A^* = \frac{\tilde{\lambda}_C^B - \tilde{\lambda}_F^B}{\tilde{\lambda}_F^A \tilde{\lambda}_C^B - \tilde{\lambda}_C^A \tilde{\lambda}_F^B} \quad (3a)$$

$$R_B^* = \frac{\tilde{\lambda}_F^A - \tilde{\lambda}_C^A}{\tilde{\lambda}_F^A \tilde{\lambda}_C^B - \tilde{\lambda}_C^A \tilde{\lambda}_F^B} \quad (3b)$$

$$N_F^* = \frac{\left(\frac{S_A}{R_A^*} - 1\right)\tilde{\chi}_C^B - \left(\frac{S_B}{R_B^*} - 1\right)\tilde{\chi}_C^A}{\tilde{\chi}_F^A \tilde{\chi}_C^B - \tilde{\chi}_F^B \tilde{\chi}_C^A} \quad (3c)$$

$$N_C^* = \frac{\left(\frac{S_B}{R_B^*}-1\right)\tilde{\chi}_F^A - \left(\frac{S_A}{R_A^*}-1\right)\tilde{\chi}_F^B}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A} \quad (3d)$$

We assume that the equilibrium described by Eq. 3a–d is admissible and stable (the interested reader can refer to Chase and Leibold (2003) and references inside for the corresponding analytical conditions). We just retain the following necessary condition for the equilibrium resource density to be positive [deduced from Eq. 3a–b]:

$$\frac{\tilde{\lambda}_F^A - \tilde{\lambda}_C^A}{\tilde{\lambda}_C^B - \tilde{\lambda}_F^B} > 0 \quad (4)$$

We consider the sensitivity of the density of each species to variation in the amount of resource A:

$$\frac{\partial N_F^*}{\partial S_A} = \left[\frac{1}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A}\right]\frac{\tilde{\chi}_C^B}{R_A^*} \quad (5a)$$

$$\frac{\partial N_C^*}{\partial S_A} = -\left[\frac{1}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A}\right]\frac{\tilde{\chi}_F^B}{R_A^*} \quad (5b)$$

Equation 5a–b imply that if $\frac{\tilde{\chi}_F^A}{\tilde{\chi}_F^B} > \frac{\tilde{\chi}_C^A}{\tilde{\chi}_C^B}$ then the focal species density increases with the amount of resource A while the density of the rest of the community decreases. Similarly, for resource B, one obtains:

$$\frac{\partial N_F^*}{\partial S_B} = -\left[\frac{1}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A}\right]\frac{\tilde{\chi}_C^A}{R_B^*} \quad (6a)$$

$$\frac{\partial N_C^*}{\partial S_B} = \left[\frac{1}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A}\right]\frac{\tilde{\chi}_F^A}{R_B^*} \quad (6b)$$

Equation 6a–b imply that if $\frac{\tilde{\chi}_F^A}{\tilde{\chi}_F^B} > \frac{\tilde{\chi}_C^A}{\tilde{\chi}_C^B}$ then the focal species density decreases with the amount of resource B while the density of the rest of the community increases.

$\frac{\tilde{\chi}_F^A}{\tilde{\chi}_F^B} > \frac{\tilde{\chi}_C^A}{\tilde{\chi}_C^B}$ means that species A allocates a higher proportion of its resource intake to resource A than the rest of the community. This is niche specialization on resource A. By contrast the rest of the community shows niche specialization on resource B.

Ultimately, we consider the effect on densities of simultaneous variations of the amount of both resources. Let us assume that the amount of both resources is modified by δS_A and δS_B, then an approximation to order 1 yields the corresponding changes in densities δN_F^* and δN_C^*:

$$\delta N_F^* = \frac{\frac{\delta S_A}{R_A^*}\tilde{\chi}_C^B - \frac{\delta S_B}{R_B^*}\tilde{\chi}_C^A}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A} \quad (7a)$$

$$\delta N_C^* = \frac{\frac{\delta S_B}{R_B^*}\tilde{\chi}_F^A - \frac{\delta S_A}{R_A^*}\tilde{\chi}_F^B}{\tilde{\chi}_F^A\tilde{\chi}_C^B - \tilde{\chi}_F^B\tilde{\chi}_C^A} \quad (7b)$$

If $\frac{\tilde{\chi}_F^A}{\tilde{\chi}_F^B} > \frac{\tilde{\chi}_C^A}{\tilde{\chi}_C^B}$,

$$\delta N_F^* > 0 \Leftrightarrow \frac{\delta S_B}{\delta S_A} < \left(\frac{\tilde{\lambda}_F^A - \tilde{\lambda}_C^A}{\tilde{\lambda}_C^B - \tilde{\lambda}_F^B}\right)\frac{\tilde{\chi}_C^B}{\tilde{\chi}_C^A} \quad (8a)$$

$$\delta N_C^* > 0 \Leftrightarrow \left(\frac{\tilde{\lambda}_F^A - \tilde{\lambda}_C^A}{\tilde{\lambda}_C^B - \tilde{\lambda}_F^B}\right)\frac{\tilde{\chi}_F^B}{\tilde{\chi}_F^A} < \frac{\delta S_B}{\delta S_A} \quad (8b)$$

And $\frac{\tilde{\chi}_F^A}{\tilde{\chi}_F^B} > \frac{\tilde{\chi}_C^A}{\tilde{\chi}_C^B}$ combined with Eq. 4 also implies:

$$0 < \left(\frac{\tilde{\lambda}_F^A - \tilde{\lambda}_C^A}{\tilde{\lambda}_C^B - \tilde{\lambda}_F^B}\right)\frac{\tilde{\chi}_F^B}{\tilde{\chi}_F^A} < \left(\frac{\tilde{\lambda}_F^A - \tilde{\lambda}_C^A}{\tilde{\lambda}_C^B - \tilde{\lambda}_F^B}\right)\frac{\tilde{\chi}_C^B}{\tilde{\chi}_C^A} \quad (9)$$

Equation 8a–b and 9 mean that there exists an intermediary range of values of $\frac{\delta S_B}{\delta S_A}$ such that both the focal species and the rest of the community increase in density. This range of value is positive (i.e. the amount of both resources increase). Figure 3 presents this result in a more graphical way.

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