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
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, \( p \approx 0.001 \), 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

<table>
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<tr>
<th>Concepts</th>
<th>Definition</th>
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<tr>
<td>Genetic/species diversity</td>
<td>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).</td>
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<tr>
<td>SGDC</td>
<td>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 ( \alpha )-SGDC focuses on correlation between local genetic and species diversities, ( \beta )-SGDC focuses on the correlation between genetic and species dissimilarities among pairs of communities and populations (Kahilainen 2014).</td>
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<tr>
<td>Factor</td>
<td>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).</td>
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<td>Effect</td>
<td>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.</td>
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<td>Ecological similarity</td>
<td>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.</td>
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Figure 1. Distribution (a) and funnel plot (b) of published SGDCs (\( \alpha \)-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 depend 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, $N^*_{s,i}$ 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
The negative effect under scenario 3) occurs when the specie diversity of the community is primarily influenced by its immigration rate, while the genetic diversity of the focal species is primarily influenced by its long-term population size. 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 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 (ΔNiches) and dispersal abilities (ΔDisps). 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.
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.

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 Struwebig 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 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 (Gregoirius et al. 2003). Going one step further, several studies (Papadopoulou et al. 2011, Baselga et al. 2013, Múria 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 (Wéhenkel 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 Blaringleth 1948, Kimura and Weiss 1964, Rousset 1997) and community ecology (Chave and Leigh 2002, Economos and Keitt 2008, Beverolou 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 distant 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.

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**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 multi-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**


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**Statement of authorship** – Thomas Lamy and Fabien Laroche contributed equally to this paper.

**References**


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.