

INVITED REVIEWS AND SYNTHESSES

Drawing ecological inferences from coincident patterns of population- and community-level biodiversity

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Abstract

Biodiversity is comprised of genetic and phenotypic variation among individual organisms, which might belong to the same species or to different species. Spatial patterns of biodiversity are of central interest in ecology and evolution for several reasons: to identify general patterns in nature (e.g. species–area relationships, latitudinal gradients), to inform conservation priorities (e.g. identifying hotspots, prioritizing management efforts) and to draw inferences about processes, historical or otherwise (e.g. adaptation, the centre of origin of particular clades). There are long traditions in ecology and evolutionary biology of examining spatial patterns of biodiversity among species (i.e. in multispecies communities) and within species, respectively, and there has been a recent surge of interest in studying these two types of pattern simultaneously. The idea is that examining both levels of diversity can materially advance the above-stated goals and perhaps lead to entirely novel lines of inquiry. Here, we review two broad categories of approach to merging studies of inter- and intraspecific variation: (i) the study of phenotypic trait variation along environmental gradients and (ii) the study of relationships between patterns of molecular genetic variation within species and patterns of distribution and diversity across species. For the latter, we report a new meta-analysis in which we find that correlations between species diversity and genetic diversity are generally positive and significantly stronger in studies with discrete sampling units (e.g. islands, lakes, forest fragments) than in studies with nondiscrete sampling units (e.g. equal-area study plots). For each topic, we summarize the current state of knowledge and key future directions.

Keywords: community ecology, environmental gradients, functional traits, genetic diversity, population genetics, species diversity

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Introduction

The basic unit of observation in most of ecology and evolution is the individual organism. Organisms can be distinguished from one another based on their traits (e.g. body mass, feeding behaviour, leaf shape) or from their degree of common ancestry, which can be inferred using genetic markers or from taxonomic classifications. The field of biogeography is concerned with describing

patterns in the locations and abundance in space and time of organisms of different kinds, and the processes that create these patterns (Lomolino *et al.* 2010). Striking patterns include some very general tendencies, such as an increase in the number of species in more equatorial regions or various trait–environment associations (e.g. larger-bodied animals in cold regions), and many region-specific patterns, such as abrupt changes in biotic assemblage composition over short distances (e.g. the Wallace line between Asia and Australia) (Lomolino *et al.* 2010). Such patterns are underlain by a combination of deterministic processes such as evolutionary

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adaptation or sorting of species according to various environmental conditions, as well as more historically contingent factors such as dispersal barriers and shifting land masses (Ricklefs & Schluter 1993; Huston 1994; Chase & Leibold 2003; Vellend 2010).

The most commonly used distinguishing feature of an organism is its species identity. Patterns involving distributions and diversity among species fall largely under the purview of the ecological side of biogeography, while patterns involving genetic or phenotypic variation within species generally fall under the purview of the evolutionary and genetic side of biogeography. While ecology and evolution have been sister disciplines for essentially their entire histories as named fields of study, they have often travelled somewhat independent pathways of conceptual advancement (Holt 2005; Vellend 2010). The last 15 years or so has seen a major resurgence of interest in explicit integration of ecological and evolutionary studies (Vellend & Geber 2005; Wiens & Graham 2005; Pelletier *et al.* 2009; Schoener 2011). One manifestation of this has been a focus on the interaction between ecological and evolutionary processes in driving the ongoing dynamics of populations and communities. Studies of such eco-evolutionary dynamics have been subject to many reviews (e.g. Fussmann *et al.* 2007; Pelletier *et al.* 2009; Schoener 2011), and we do not treat this subject in this paper. Here, recognizing the strong parallels that influence diversity patterns within and among species (Vellend 2010), we focus on insights that can be gained from simultaneous consideration of biogeographical patterns at the level of species assemblages and at the level of variation within species.

Simultaneous studies of biogeographical patterns within and among species can yield novel insights in two qualitatively distinct ways. First, starting with a pattern at one level or the other, integrating knowledge of pattern and process at the other level can help distinguish competing hypotheses. For example, distinguishing between explanations for a spatial discontinuity in community composition based on environmental filtering or dispersal barriers can be facilitated by assessing intraspecific genetic diversity and gene flow in some of the component species (e.g. Dexter *et al.* 2012). Second, considering patterns within and among species in concert can lead to the discovery of new biogeographical patterns, such as a positive correlation between species diversity and genetic diversity, which itself leads to the development of process-based explanations (Vellend & Geber 2005). Here, we explore both of these possibilities, and given the potentially vast scope of subject matter, we focus on two areas of particularly active current research: (i) adaptive trait variation within and among species along environmental gradients;

(ii) testing hypotheses and exploring new biogeographical patterns via simultaneous studies of molecular genetic variation within species and species diversity and composition within communities. For each of these, we outline the conceptual issues, review the relevant literature (nonexhaustively), highlight novel recent studies, discuss limitations of different methodological approaches and outline key future directions.

The adaptive significance of trait variation within and among species

Conceptual framework

One of the most striking features of the natural world is a seeming match between the traits of organisms and the environments in which they live. For example, plants with small, thick leaves are typically associated with hot and dry environments (Ehleringer 1985), while animal body size often increases as a function of decreasing temperature (Watt *et al.* 2010). Many such patterns have been observed both among species and among populations of the same species found in different environmental conditions (Reich *et al.* 2003; Gaston *et al.* 2008), although interspecific and intraspecific studies are often conducted in isolation.

Examining both inter- and intraspecific patterns simultaneously, a key hypothesis is as follows: high/low values of trait y confer high fitness at high/low values of environmental variable x , and vice versa. Phrased this way, in the most general terms possible, no distinction is made between whether different values of trait y are possessed by individuals of the same species or of different species. As such, this hypothesis predicts trait–environment relationships in the same direction within and among species (Fig. 1a). When the data do not conform to this prediction (Fig. 1b–d), a more complex or context-dependent set of selection pressures is likely acting upon trait variation over different spatial or temporal scales. However, there is no one-to-one match between general a priori hypotheses and the different outcomes shown in Fig. 1b–d. As such, a major contribution of this line of research is the generation of new hypotheses (often system-specific) and thus potentially deeper insights into trait–environment relationships. Several factors are potentially important in creating different patterns of trait–environment relationships within and among species: strong genetic and/or physiological constraints leading to low intraspecific variation; variation among species in the adaptive significance of a given trait (e.g. for one species, body size is important for thermoregulation, and for another, it is important for mating success); or variation among species in their sensitivity to different

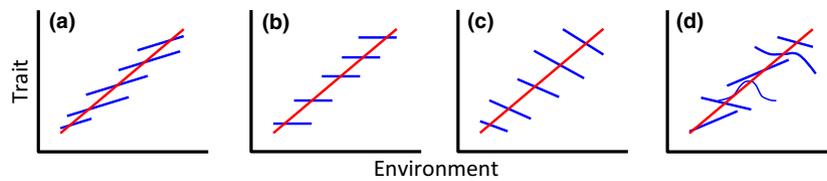


Fig. 1 Hypothetical relationships between a trait and an environmental gradient, with traits measured as an average across species (red line, ‘community level’) or within each species separately (blue lines, one per species, ‘intraspecific’). Adapted from Cornwell & Ackerly (2009). All cases show a significant trait–environment relationship at the community level (red line), with (a) concordance in the direction of relationships within and across species, (b) an absence of intraspecific trait–environment relationships, (c) intraspecific relationships in the opposite direction as the community-level relationship and (d) idiosyncratic intraspecific patterns. For simplicity, we do not show cases in which the trait–environment relationship at the community level is either flat (absent) or nonlinear, both of which are theoretically possible. See Table 1 for specific empirical examples.

components of a complex environmental gradient (e.g. temperature and moisture along a latitudinal gradient). We discuss such explanations in the context of specific examples below.

Interspecific trait variation along gradients is typically studied in one of two ways. First, one can analyse species-level traits directly, asking whether species found in different environments (e.g. low vs. high latitudes) tend to have different mean traits. Alternatively, at each study site, one can first estimate a ‘community-level’ trait value, which is the average across species, typically weighted by the abundance of each species (Shipley 2010), and then ask how these community-level trait values vary along environmental gradients. This is akin to what animal ecologists have called the ‘assemblage-based approach’ (Gaston *et al.* 2008). The species-based approach and the community-level approaches tend to predominate in animal and plant studies, respectively, although they are aimed at the same basic question.

Trait variation in animals

In animals, predictable trait–environment relationships have often been described as ‘ecogeographical rules’ (Ashton 2001; Lomolino *et al.* 2006; Gaston *et al.* 2008), a comprehensive discussion of which is beyond the scope of the present paper. As an illustrative example, we focus here on one of the best-known examples, Bergmann’s rule, which predicts an increase in body size with decreasing temperature and/or increasing latitude (James 1970; Blackburn *et al.* 1999; Watt *et al.* 2010). This relationship has been suggested to result from thermoregulatory adaption, as larger body size reduces the surface-to-volume ratio and thus the energy loss resulting from conduction. Inter- and intraspecific evidence is available for several major groups of animals.

In mammals, as predicted, mean body size across species was shown to increase with latitude and to decrease with temperature in the Nearctic (Rodríguez *et al.* 2008). Studies at the intraspecific level show similar results,

with a majority of species in a broad meta-analysis showing positive body size–latitude or negative body size–temperature correlations (Ashton *et al.* 2000; generic scenario illustrated in Fig. 1a). Similar results have been found for birds, with strong support for Bergmann’s rule both among and within species (Blackburn & Gaston 1996; Ashton 2002b; Meiri & Dayan 2003; Olson *et al.* 2009). Although exceptions can be found, the combination of inter- and intraspecific studies appears to lend strong support to the adaptive role of body size in thermoregulation in endotherms, although one must remain cognizant that correlations do not provide direct evidence of causation (Blackburn *et al.* 1999).

In ectotherms, however, relationships of body size with latitude and temperature are highly variable among studies. Across amphibian species, Bergmann’s rule appears to apply to anurans (frogs and toads), while a reverse Bergmann’s cline was found for urodeles (salamanders and newts) (Olalla-Tárraga & Rodríguez 2007). Within amphibian species, Ashton (2002a) found approximately equal numbers of species showing positive and negative body size relationships with latitude, elevation and temperature (scenario in Fig. 1d), while Adams & Church (2008) found that the vast majority of *Plethodon* salamander species in eastern North America showed no evidence of Bergmann’s rule (Fig. 1b). For reptiles and insects, results are highly variable across studies, both inter- and intraspecific, with positive, negative and a lack of trends found in different cases (Ashton & Feldman 2003; Angilletta *et al.* 2004; Cruz *et al.* 2005; Chown & Gaston 2010; Shelomi 2012).

Several ectotherm studies highlight insights that can emerge when comparing patterns at different levels of organization. First, the lack of general relationships of body size with latitude or temperature across ectotherm species, such as insects, is perhaps not surprising, given that ectotherms are faced with the need not only to prevent heat loss in cold environments (aided by a large body), but also the need to acquire heat energy from the environment (impeded by a large body)

(Ashton & Feldman 2003). Interestingly, small-bodied insect species tend to show intraspecific patterns consistent with Bergmann's rule, perhaps due to energetic processes, while within large-bodied species, there is a tendency for reverse Bergmann clines (Shelomi 2012). This latter result suggests that, for insects, selection on body size across temperature gradients might be mediated by development time, which is more protracted in larger-bodied species: shorter growing seasons in colder environments may select for more rapid development and therefore smaller body size in otherwise large-bodied species (Blanckenhorn & Demont 2004). The contrasting selection pressures within small- vs. large-bodied insects result in no pattern at the interspecific level. In fishes, a study by Wilson (2009) contrasted the closely related *Syngnathus* pipefishes and *Hippocampus* seahorses, both of which show male parental care. A positive body size–latitude correlation was found across *Syngnathus* species, but not across *Hippocampus* species, and an intraspecific study of *S. leptorhynchus* helped reveal a possible mechanistic explanation. The polygynous mating system of *S. leptorhynchus* (and other pipefishes) leads to size-limited reproductive success in males, with increased body size at higher latitudes countering the negative effects of cold temperatures on fitness. In contrast, reproductive success in monogamous male seahorses appears limited by female egg production rather than body size, such that no such selection gradient is observed with latitude (Wilson 2009).

Trait variation in plants

A recent surge of studies with plants has explicitly integrated measurements of trait variation among and within species along environmental gradients (Cornwell & Ackerly 2009; Albert *et al.* 2010; Jung *et al.* 2010; Kembel & Cahill 2011; Hulshof *et al.* 2013; Read *et al.* 2014). Such studies have been especially prevalent in plant ecology, given the very similar resource requirements of virtually all vascular plants, and their many quantitatively comparable leaf, stem and root traits with well-characterized links to physiological functions (Reich *et al.* 2003; Craine 2009). For example, a battery of closely correlated traits, of which specific leaf area (SLA, the surface area/dry mass ratio of a leaf) is the most easily measured, correspond to the 'leaf economics spectrum' across all vascular plants, ranging from short-lived, nitrogen-rich, thin leaves (high SLA) with high photosynthetic rates to long-lived, nitrogen-poor, thick leaves with lower photosynthetic rates (low SLA) (Wright *et al.* 2004). Studies of inter- and intraspecific trait variation speak to the issue of the adaptive significance of traits and also to the relative importance of intraspecific variation (plasticity, genetic variation) and

species turnover (an interspecific phenomenon) in creating community-level trait–environment relationships. The latter is potentially important for predicting ecosystem function, which is underlain by trait–environment interactions (Díaz *et al.* 2007), in a changing environment (e.g. if species are lost or gained to the system).

Several plant studies have found consistent community-level and intraspecific trends of SLA along moisture gradients (Cornwell & Ackerly 2009; Jung *et al.* 2010; Kembel & Cahill 2011) (Table 1), corresponding to the scenario in Fig. 1a. These results bolster the adaptive interpretation that low SLA and correlated traits confer a fitness advantage in water-stressed environments, and vice versa. Stronger trait–environment relationships are sometimes found when using plot-specific trait values for each species (therefore including the intraspecific component of trait variation) rather than their study-wide means when calculating the community-level averages, indicating that intraspecific phenotypic plasticity and/or genetic variation contribute substantially to overall trait–environment relationships. For example, Jung *et al.* (2010) found that 44% of the community-level relationship between SLA and a flooding gradient could be accounted for by intraspecific variation.

Intraspecific trait–environment relationships are not always consistent among species in the same community (Fig. 1d), or between the general intraspecific trend and the community-level trend (Fig. 1c). Rarely have researchers found a *general* tendency for intraspecific trends to be in the opposite direction as the community-level pattern (Fig. 1c), but a general lack of intraspecific trends (Fig. 1b) or idiosyncratic intraspecific trends (Fig. 1d) has been found in several cases (Table 1). For example, Sundqvist *et al.* (2011) found a general decrease in SLA with elevation at the community level, and highly variable intraspecific trends, including unimodal responses (see also Kichenin *et al.* 2013; Read *et al.* 2014). A plausible explanation for such idiosyncratic patterns is that many natural environmental gradients (e.g. elevation, rainfall, soil texture) are multivariate in nature, with multiple abiotic and biotic factors changing in concert (e.g. soil moisture, climate, light, competitors, pathogens); different species may respond to different factors individually or in combination (Albert *et al.* 2010). There may also simply be very little genetic variation or capacity for phenotypic plasticity for a given trait, or gene flow might constrain local adaptation (Garant *et al.* 2007).

Future studies of inter- and intraspecific trait variation

Most interpretations of contrasting or consistent inter- vs. intraspecific trait–environment relationships have been made *post hoc*, and thus are essentially hypotheses,

Table 1 Selected examples of different combinations of community-level and intraspecific trait–environment relationships in plants. See Fig. 1 for a graphical illustration of each scenario a–d.

Scenario	Example	Other examples	Possible interpretations (not a comprehensive list)
(a) Consistent community-level and intraspecific relationships	<ul style="list-style-type: none"> Moisture gradient (wet to dry), California chaparral (Cornwell & Ackerly 2009) Community level: SLA ↑ Intraspecific: SLA ↑ 	<ul style="list-style-type: none"> Kembel & Cahill (2011) – several traits on a moisture gradient Jung <i>et al.</i> (2010) – several traits on a flooding gradient 	<ul style="list-style-type: none"> Selection in the same direction within and among species along a given gradient
(b) No tendency for intraspecific relationships	<ul style="list-style-type: none"> Successional gradient, Chinese forests (Kröber <i>et al.</i> 2012) Community level: SLA ↓, leaf C:N ↑, leaf Ca ↓, leaf K ↑ Intraspecific: no relationships 	<ul style="list-style-type: none"> Andersen <i>et al.</i> (2012) – several traits, nutrient gradient 	<ul style="list-style-type: none"> Minimal intraspecific trait variation, little scope for covariation Local selection opposed by gene flow within species Selection (within species) in opposite directions, possibly via different aspects of environmental gradient
(c) Opposite directions of community-level and intraspecific relationships	<ul style="list-style-type: none"> Elevational gradient, New Zealand (Kichenin <i>et al.</i> 2013) Community level: leaf nutrient content ↑ Intraspecific: leaf nutrient content ↓ 	<ul style="list-style-type: none"> Lepš <i>et al.</i> (2011) – stem dry matter content, mowing gradient; leaf N, fertilization gradient Pérez-Ramos <i>et al.</i> (2012) – leaf N and thickness, soil depth gradient 	<ul style="list-style-type: none"> General intraspecific response to a different aspect of the gradient than the community-level response Environmental influences (which dominate intraspecific variation) and genetic influences (which dominate interspecific differences) oppose each other
(d) Idiosyncratic intraspecific relationships	<ul style="list-style-type: none"> Elevational gradient, Sweden (Sundqvist <i>et al.</i> 2011) Community level: leaf dry matter content ↑ Intraspecific: ↑, ↓, no change, unimodal 	<ul style="list-style-type: none"> Wardle <i>et al.</i> (2009) – leaf litter N:P, soil chronosequences 	<ul style="list-style-type: none"> Different species respond to different aspects of the gradient

all of which are in need of further testing. For example, to what degree does trait variation within different species respond to different factors (e.g. temperature, soil) along the same multivariate gradient (e.g. elevation)? Exposing multiple species in a community to independent variation in environmental factors which covary in nature will allow this question to be addressed (e.g. Shipley & Almeida-Cortez 2003). The studies described above are almost entirely observational, with many opportunities for other kinds of experimental studies to help reveal underlying mechanisms as well. Burns (2004), for example, used a transplant experiment, in combination with an observational study to show that phenotypic plasticity within species was a major contributor to producing a relationship between SLA and a wetland-to-forest gradient.

Explicitly integrated studies of community-level and intraspecific trait variation are still relatively few. Given the effort involved in measuring many traits of many species in many plots, such studies inevitably make trade-offs, such as measuring traits on a small subset of species and/or only measuring a relatively small number of potentially relevant traits. The time seems ripe for a major, multi-investigator research effort to comprehensively characterize community and intraspecific trait variation for a full species assemblage and a large suite of traits across a gradient of broad general interest, such as latitude or elevation, in order to generate more robust answers to the questions discussed above. Several such studies appear to be underway (Baraloto *et al.* 2012; Kröber *et al.* 2012).

Another important avenue for future research is to integrate tried-and-true methods from quantitative

genetics for partitioning the sources of intraspecific variation (genetic variation vs. plasticity) into community-level analysis of trait–environment matching (Collins & Gardner 2009). In using spatial analyses of this type as a guide to predicting temporal change, a large role for phenotypic plasticity would indicate a capacity for rapid, short-term trait–environment matching (e.g. in response to yearly climate fluctuations), potentially buffering fluctuations in community or ecosystem properties such as primary productivity or toxin tolerance (De Laender *et al.* 2014; Walters *et al.* 2013). Adaptive evolution and species turnover should occur much more slowly, but presumably with greater potential for trait changes of large magnitude over the long term (especially for species turnover) (Norberg *et al.* 2012). Finally, while a number of studies have quantified the contribution of intraspecific variation to community-level trait–environment relationships, none have considered the possibility that this contribution itself will vary along the gradient. One might expect, for example, that intraspecific trait variation is of relatively greater importance in less favourable growing conditions (given magnified phenotypic differences among individuals; Hoffmann & Merilä 1999) where fewer species are present. This idea has not been tested.

Combining molecular population genetics and community ecology

Historical biogeography of genes and species

Historical biogeography attempts to explain the changing distributions of species and biotas in terms of processes such as shifting land masses, evolutionary change and barriers to dispersal. Biogeographical data have been used to address a wide range of hypotheses, including those focused on inferring the centre of origin of a particular taxon, inferring pathways of dispersal during range expansion or distinguishing physical barrier formation vs. long-distance dispersal as causes of disjunct distribution patterns (Lomolino *et al.* 2010). For as long as molecular genetic methods have been available, they have been applied to answering such questions and, along with data on spatial and temporal patterns of species distributions and diversity, have greatly advanced our understanding of the underlying processes (Palumbi 1997; Avise 2000; Briggs 2000; Lomolino *et al.* 2010). As such, it is beyond the scope of our paper to comprehensively review this literature. Here, we highlight some relatively recent studies in which novel insights were generated either by revisiting long-standing ecological questions with genetic data or via explicit integration of data at the two levels in the same study.

The recolonization of formerly glaciated terrain by plants has long fascinated ecologists and geographers, in particular the *rate* at which postglacial migration occurs, given the presumed need for migration in response to contemporary climate warming. In eastern North America, widely cited tree migration rates of at least 100 m/year over the past 15–20 thousand years were estimated across many taxa using a spatial network of pollen cores (Davis 1981; Delcourt & Delcourt 1987). Such estimates, which are in many cases surprisingly high in the light of modern-day observations of limited dispersal capacity (Clark *et al.* 1998), mostly assume that tree species' distributions were restricted to the southeastern United States during the last glacial maximum. However, more recent genetic evidence of unique chloroplast DNA haplotypes occurring at the northern range limits of some species is strongly suggestive of the existence of refugial populations much closer to the continental ice sheet during the glacial maximum than was previously assumed (McLachlan *et al.* 2005; Soltis *et al.* 2006). Similar results have been found for some species in Europe (Bhagwat & Willis 2008; Provan & Bennett 2008). Thus, intraspecific genetic patterns suggest that the capacity of species to migrate in response to climate change is not as high as previously thought, and palaeoecologists have been prompted to reconsider the interpretation of pollen found at particular places and time in quantities typically assumed too small to indicate species presence (McLachlan & Clark 2004).

An ongoing debate in community ecology concerns the degree to which patterns of biodiversity are generated via selective processes, such as species-specific environmental tolerance limits, versus nonselective (i.e. neutral) processes such as dispersal and drift (Vellend 2010). This debate echoes the selectionist–neutralist debate in population genetics, except that population geneticists have a key advantage: the existence of non-coding or synonymous regions of the genome, which allows for a neutral (or nearly so) benchmark to be quantified, thereby allowing tests for deviations from such a pattern, which constitute detection of selection (Vitalis *et al.* 2001). Community ecologists have no such benchmark, making the inference of process based on pattern much more difficult if not impossible (Gotelli & McGill 2006). In a recent study, Dexter *et al.* (2012) leveraged the population genetics advantage to test for competing explanations for a narrow zone of marked species turnover in the species composition of trees in the genus *Inga* along a 250-km transect in the Amazon rainforest. Clear genetic breaks within individual *Inga* species suggested population divergence occurring tens or hundreds of thousands of years ago, thereby indicating that the striking community-level pattern

was generated by secondary contact of spatially disjunct biotas rather than species sorting along an environmental gradient. This insight was only possible via the explicit integration of community-level and genetic data. Similar studies using the combination of community and genetic data to infer the processes structuring spatial diversity patterns (see also Bonada *et al.* 2009; Thiel-Egenter *et al.* 2011; Eldon *et al.* 2013) is an important avenue for future research.

Species–genetic diversity correlations

Some of the key links between ecology and genetics were laid out in Janis Antonovics (2003) Ecological Geneticist's Creed, one tenet of which is that 'the forces maintaining species diversity and genetic diversity are similar'. This assertion leads to the following hypothesis: the habitat properties that lead to high species diversity (e.g. large land area, close proximity to areas of similar habitat, environmental heterogeneity) should also lead to high genetic diversity within species, and vice versa. The key prediction of this hypothesis is a positive correlation across space between these two fundamental levels of biodiversity (Vellend 2003; Vellend & Geber 2005). This line of inquiry is of interest both to test the fundamental question of similar processes underlying patterns of biodiversity at different levels, and also potentially practical reasons in so far as it might be possible to use one level of diversity as a surrogate for the other in a conservation context.

Drawing on data sets created for the most part by combining ecological studies of species diversity with independent studies of genetic variation within particular species (using molecular markers) across the same set of sites, a strong tendency for positive species–genetic diversity correlations (SGDCs) has been observed (Vellend 2003; Vellend & Geber 2005). However, there is considerable variation across data sets in the strength of this correlation, and even the direction, with some studies demonstrating strong negative correlations (Karlin *et al.* 1984; Vellend & Geber 2005). Understanding the causes of this variation is one of the key next steps in this line of research.

To date, the vast majority of studies reported SGDCs using one or only a few species for genetic analyses. While this limits the ability of individual empirical studies to establish the generality of any observed SGDC, a sufficient number of data sets have accumulated in the literature to allow general tendencies to be tested (described above). In addition, because we do not necessarily expect genetic diversity in different species to show the same responses to site factors that influence species diversity (e.g. Struebig *et al.* 2011), examining SGDCs with genetic diversity assessed both

for individual species and averaged across species is justified (Taberlet *et al.* 2012).

Over the past 8 years, upwards of 20 new studies have focused explicitly on assessing the relationship between species and genetic diversity, often with genetic data collected for multiple species in the same system (see Appendix S1, Supporting Information). For example, Struebig *et al.* (2011) compared species diversity of bats and genetic diversity (using microsatellites) within three species across fragments of rainforest, finding a strong positive correlation ($r = 0.58$) only for the most dispersal-limited and fragmentation-sensitive species. In a massive study across the Alps and Carpathian mountains, Taberlet *et al.* (2012) sampled plant communities and populations of >20 species (analysed with amplified fragment length polymorphisms, AFLPs) within >650 grid cells of ~500 km² each. In the vast majority of cases, there was no significant correlation between species diversity and genetic diversity (Taberlet *et al.* 2012). Positive SGDCs on ocean islands (Vellend 2003) or habitat fragments (e.g. Struebig *et al.* 2011) and the absence of significant SGDCs observed by Taberlet *et al.* (2012) across contiguous habitat areas, combined with the fact that most molecular markers used in population genetic studies are assumed to be neutral, lead to the hypothesis that SGDCs should be strongest when nonselective factors, such as the size and isolation of sampling units, exert a particularly strong influence on diversity patterns.

Here, we present a new test of this hypothesis. While it is impossible to quantify the importance of selective and nonselective processes underlying each of these diversity patterns without entering into circular logic using the diversity data themselves, we can classify each study a priori as having units of observation that are discrete habitat units (e.g. islands, forest fragments, ponds) vs. arbitrarily delineated areas (e.g. small vegetation plots, or grid cells as in the Taberlet *et al.*'s study). The prediction is that stronger positive SGDCs will be found in discrete habitat units, given the greater potential for strong drift and limited dispersal. We compiled all available data to test this prediction: 115 estimates of SGDC from 40 different studies (see Appendix S1, Supporting Information for details), with a 'study' defined as any set of SGDCs corresponding to the same geographical area (e.g. the Alps) and taxonomic group (e.g. plants). Within a study, each individual SGDC represents either a different species used for genetic analysis, or different subsets of study sites (e.g. disturbed and undisturbed, Wei & Jiang 2012). Twenty-eight studies included only one SGDC, and all but three studies included <10 SGDCs. From the Taberlet *et al.*'s (2012) paper, we considered the data from the Alps (27 SGDCs) and Carpathians (24 SGDCs) as different studies.

We conducted general linear model analyses predicting SGDC as a function of the logarithm of sample size and the categorical variable discrete vs. nondiscrete habitat units. To avoid pseudoreplication, we treated study as the unit of observation in these analyses and calculated the average SGDC and average sample size within studies (similar results were found when treating each SGDC as independent – see Appendix S1, Supporting Information). Note that we could not use study as a random factor in mixed models because there is no variation within studies in the discrete vs. nondiscrete variable. We conducted analyses with or without studies weighted by the number of SGDCs, and again, the same qualitative results were found in both cases (see Appendix S1, Supporting Information). Here, we report the weighted analysis.

Our prediction was clearly supported: studies with discrete habitat units almost always showed positive SGDCs, while the average SGDC in other studies is not different from zero, albeit with some individual studies showing strong positive or negative correlations (Fig. 2). This result is almost certainly not driven by publication

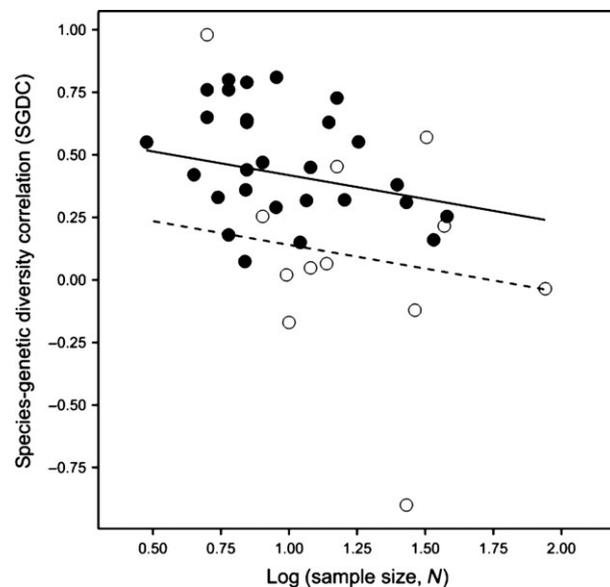


Fig. 2 The correlation between species diversity and genetic diversity (SGDC) in 40 studies classified as either having discrete habitat patches (filled circles, solid line) as units of observation, or not (open circles, dashed line), plotted as a function of the logarithm (base 10) of sample size. A general linear model analysis, with studies weighted by the number of SGDCs reported, showed significant effects of both discrete vs. nondiscrete sampling units and of sample size (SGDC = $0.33 + 0.279 \cdot \text{discrete} - 0.190 \cdot \log(N)$, $F = 11.1$ and $P = 0.002$ for discrete, $F = 4.82$ and $P = 0.034$ for $\log(N)$). The full model has $r^2 = 0.53$, and a model with only discrete has $r^2 = 0.48$. Details of alternative analyses are presented in Appendix S1 (Supporting Information).

bias. First, many of the correlations were calculated from data not collected for this purpose. Second, while the paucity of weak correlations reported at low sample size and the negative SGDC sample size trends (Fig. 2) are indicative of some degree of publication bias (Møller & Jennions 2001), SGDCs remain positive for discrete habitats at larger sample sizes. Finally, the studies of nondiscrete habitat units show that many nonsignificant results have been published.

These results suggest that when comparing discrete units of habitat, similar processes likely underlie spatial variation in species diversity and genetic diversity and that in a conservation context, focusing on either level will tend to benefit the other as well. This contrasts with the more pessimistic conclusions of Taberlet *et al.* (2012), who focused on more arbitrary spatial units, in which case we expect species and genetic diversity to be uncoupled, although there are exceptions (Fig. 2). An important avenue for future research is to achieve a better understanding of what causes so much variation in the SGDC, only some of which we have been able to explain by distinguishing different types of sampling units.

A somewhat different approach to the general question of whether species diversity and genetic diversity show coincident spatial patterns is to test for patterns of genetic diversity along gradients for which there are well-known general patterns at the level of species diversity. For example, most taxa show species diversity declines from equatorial to polar regions: the latitudinal diversity gradient. Declines in genetic diversity with latitude were found in a meta-analysis of 72 vertebrate species (Adams & Hadly 2013) and in an analysis of North American fishes (April *et al.* 2013). Related studies have used molecular genetic methods to show, in some cases, that population divergence and rates of molecular evolution are also highest at low latitudes, although the causal links among these observations remain uncertain (Martin & McKay 2004; Dowle *et al.* 2013). There is clearly great potential for future research to further probe the causes of ecological diversity gradients via molecular analyses of individual species.

Discussion

Our review so far has covered substantial conceptual ground, with topics including complex patterns of selection along multivariate environmental gradients, testing for the processes underlying community-level patterns using intraspecific genetic data and the conditions under which one might expect concordant patterns of species diversity and genetic diversity. The common thread is the argument that new and deeper insights into biogeographical pattern and process can

derive from simultaneous consideration of variation within and across species. In our view, the evidence clearly supports this argument. Throughout the paper, we have also highlighted important future research directions on particular subtopics – we do not reiterate these here. Rather, we focus the discussion on some potentially fruitful research directions that span one or more of the subtopics discussed so far, and we highlight some research questions that we were unable to describe in detail given the need to constrain the range of topics we can cover in one paper.

The sections of this paper focus on the characterization of individual organisms in different ways: traits vs. species/genotypic identity. Traits have the advantage of often having clear functional relevance under different environmental conditions, notwithstanding the frequent presence of variation among species in how trait values correlate with environmental gradients. Data on species diversity and molecular genetic diversity have the advantage of being relatively straightforward to collect – thereby allowing large sample sizes – and the unambiguous isolation of the genetic component of variation among individuals within species. Studies that combine both types of data have the potential to reveal mechanisms underlying some of the relatively ‘simple’ patterns. For example, several hypotheses have been put forward to explain correlations between species diversity and genetic diversity (Vellend & Geber 2005). Some of these hypotheses involve different ways that niche space can be filled by variation within vs. across species, that is, how selection acts simultaneously on trait variation within and among species. For example, high species diversity might lead to strong within-species stabilizing selection on traits related to interspecific competition, and therefore negative SGDCs (Vellend & Geber 2005), which have been observed in some cases (e.g. Karlin *et al.* 1984; Messmer *et al.* 2012). However, the neutral molecular marker data typically collected to characterize genetic diversity in empirical studies have little to say about functional intraspecific trait variation and therefore potential responses to selection (Reed & Frankham 2001). Incorporating analyses of intraspecific trait variation into such studies has the potential to provide stronger tests of such hypotheses. For example, greater species diversity has been shown to cause a decline in intraspecific population size and therefore molecular genetic diversity (Nestmann *et al.* 2011), but whether high species diversity also acts as an agent of selection constraining intraspecific trait variation, or alternatively as an agent of diversifying selection (Vellend & Geber 2005), is unknown.

In a similar vein, a topic we have not addressed directly so far is the use of inter- and intraspecific trait variation to test for the mechanisms underlying

community assembly. A commonly used logical framework is to test for a high degree of trait similarity among co-occurring species (relative to a random draw of species from some predefined ‘species pool’) as evidence of environmental filtering of species, and for an ‘overdispersed’ distribution of trait values among species as evidence that trait-based competition that creates a limit to trait similarity (e.g. Bernard-Verdier *et al.* 2012). In the absence of trait data, many authors have used phylogenetic differences among species to stand in for ecological differences that mediate environmental filtering and competition (Cavender-Bares *et al.* 2009). In some cases, incorporating intraspecific trait variation via the use of plot-level traits for each species rather than just a species mean has strengthened such patterns, leading authors to conclude that intraspecific trait variation has an important influence on community assembly (Jung *et al.* 2010). However, to the extent that intraspecific trait variation is largely due to phenotypic plasticity, intraspecific variation might be as much a *response* to community assembly as a causal factor itself. Genetically based trait variation can play the same role as species-level differences, in that individuals arrive with some genetically determined potential that influences their odds of joining the community. As such, quantifying genetic vs. plastic trait variation in such studies could deepen our understanding of the feedbacks between community assembly and intraspecific trait variation.

As in much of ecology and evolution, some of the earth’s most diverse taxa, for example insects and microbes, are sorely underrepresented in studies of species diversity and genetic diversity. This is beginning to change, particularly with the advent of whole-community sequencing methods or ‘metabarcoding’ (Coissac *et al.* 2012; Baselga *et al.* 2013; Ji *et al.* 2013). In microbial studies, DNA sequences for a barcode gene are generated from a sample of water, air, soil or biological tissue (e.g. a leaf) and subsequently used to identify ‘operational taxonomic units’ based on a predefined genetic similarity cut-off (Pace 1997; Horner-Devine *et al.* 2004). Such data sets present opportunities for simultaneously assessing intra-OTU diversity (the analogue of genetic diversity within species), and therefore SGDCs, although we know of no studies that have done this to date. Whole-community sequencing is beginning to be used for nonmicrobes as well – insects in particular – allowing simultaneous delineation of species (which are often morphologically cryptic) and quantification of diversity patterns within and among many species. Several insect studies have revealed concordant patterns of species diversity and genetic diversity (e.g. Papadopoulou *et al.* 2011; Baselga *et al.* 2013), and such studies promise to allow strong tests of the conditions that influence the strength and direction of SGDCs.

Finally, the population genetic advantage of being able to characterize diversity patterns created purely by neutral processes can provide a benchmark not only for traits or loci under selection in the same focal species studied using molecular markers, but also for patterns in the community in which these species are embedded. Dexter *et al.* (2012) is one of the few studies we know to explicitly bring together genetic and community data to test alternative explanations for a community-level pattern, and there seems to be great potential for applying a similar approach in other systems.

Great progress has been made in recent years in building an eco-evolutionary understanding of biodiversity patterns in space and time, and continued explicit merging of studies within and among species promises to deepen our understanding of the forces structuring biodiversity at all hierarchical levels on earth.

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M.V. planned the review and wrote the first draft of the manuscript. Each author conducted research on one or more sections: plant traits (G.L.), animal traits (A.B. and D.G.), historical biogeography (M.V.) and combining molecular genetics and ecology (C.M., S.K. and M.V.). All authors contributed to manuscript editing.

Data accessibility

The raw data used in our meta-analysis are presented in Appendix S1, Supporting Information.

Supporting information

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

Appendix S1 Meta-analysis of species–genetic diversity correlations (SGDCs).