Aapo Kahilainen

Interactions and Patterns between Species Diversity and Genetic Diversity

JYVÄSKYLÄN YLIOPISTO

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UNIVERSITY OF JYVÄSKYLÄ

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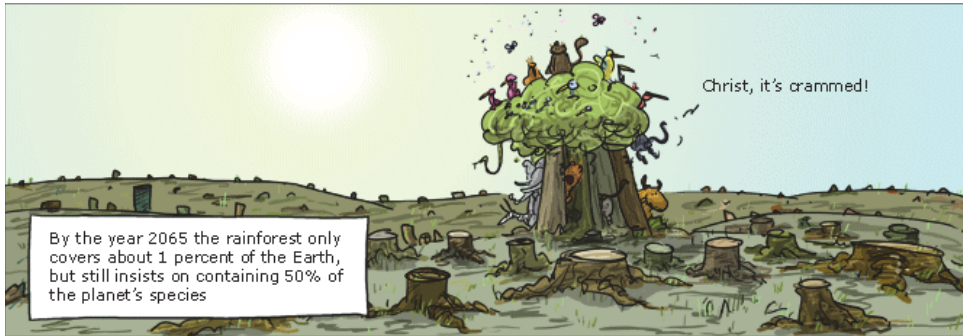
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ABSTRACT

The similarities in the theories of community ecology and population genetics suggest that species diversity within and between communities and genetic diversity within and between populations are driven by the same four general mechanisms: (1) drift, (2) dispersal, (3) selection, and (4) the formation of new variants (i.e. speciation and mutation). Since, for both species diversity and genetic diversity, the relative significances of each of the first three mechanisms are very much influenced by characteristics of the environment, correlations between species diversity and genetic diversity, i.e. species-genetic diversity correlations (SGDCs), are expected. Considering that practical conservation most often focuses on species diversity (or surrogates thereof), SGDCs could provide information on how conservation and management decisions influence genetic diversities of populations, and thus also their viabilities. Furthermore, teasing apart the drivers of the SGDCs can offer mechanistic explanations for diversity and therefore suggest a process-based approach to conservation. I studied the generalizability of SGDC and the role of environmental characteristics by means of a literary review and empirical studies on natural dragonfly and damselfly communities. I then conducted individual-based simulations to assess how inbreeding depression due to loss of genetic diversity can influence extinction rates in neutral multispecies metacommunities. My results suggest that SGDCs are highly variable in natural systems and that interactions between ecologically similar species can influence their genetic structures. Therefore, the results question the utility of using species diversity or genetic structures of ecologically similar species as surrogates for genetic diversity of species of conservation concern. Furthermore, my results suggest that if intraspecific genetic diversity is not explicitly considered, the extinction rates in multispecies metacommunities might be underestimated.

Keywords: Community ecology; population genetics; conservation biology; interspecific interactions; Calopteryx; Odonata; simulation modelling

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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III Kahilainen, A., Elo, M., Keränen, I., Knott, K. E., Kuitunen, K., Marjeta, M., Mönkkönen, M. & Kotiaho, J. S. Species-genetic diversity correlation in *Calopteryx* damselflies. Submitted manuscript.

IV   Kahilainen, A, Kotiaho, J. & Puurtinen, M. The effects of fragmentation, connectivity and inbreeding depression on the persistence of species in neutral metacommunities. Submitted manuscript.

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AK = Aapo Kahilainen, IK = Inka Keränen, JSK = Janne S. Kotiaho, KEK = K. Emily Knott, KK = Katja Kuitunen, ME = Merja Elo, MMa = Maria Marjeta, MMö = Mikko Mönkkönen, MP = Mikael Puurtinen

1 INTRODUCTION

1.1 The conceptual unification of community ecology and population genetics

1.1.1 The similarities between community ecology and population genetics

Biological diversity is commonly considered to consist of genetic diversity, species diversity, and diversity of ecosystems (Anon. 1987, 1993). Documenting and explaining patterns of biodiversity lies at the very heart of ecological, taxonomical, evolutionary, and conservation related research (Magurran 2005). Furthermore, all levels of biodiversity are often considered to be positively associated with ecosystem functioning and ecosystem services, and are therefore also essential for the well-being of mankind (Balvanera *et al.* 2006, Maestre *et al.* 2012, Cardinale *et al.* 2012, Harrison *et al.* 2014, Whitlock 2014). However, biodiversity has been declining dramatically due to human actions and the rate of decline shows no signs of slowing down (Anon. 2005, Butchart *et al.* 2010). Therefore, arguably, research focusing on biodiversity and conservation has never been as topical as it is today.

Among the primary goals of biodiversity research at the species and genetic levels is to explain the richness, relative abundances, and spatial distributions of biological variants (Hartl and Clark 1997, Magurran and McGill 2011). Due to similar aims, the theoretical foundations of research at the two levels have a lot of analogies, despite more or less independent histories in their development (Watterson 1974, Antonovics 1976, 1992, Amarasekare 2000, Hubbell 2001, Chave 2004, Vellend and Geber 2005, Leigh 2007, Vellend and Orrock 2009). For example, the theory of island biogeography (MacArthur and Wilson 1967) is conceptually very similar to the earlier island model of population genetics (Wright 1940, 1943), and the relative abundance distributions of species resemble those of alleles (Ewens 1972, Watterson 1974, Hubbell 2001).

Although the similarities between community ecology and population genetics were first acknowledged several decades ago (Watterson 1974,

Antonovics 1976, Caswell 1976), only recently have they started to gain increased attention and a conceptual unification of community ecology and population genetics has been proposed (Amarasekare 2000, Vellend and Orrock 2009, Vellend 2010). The main idea of the conceptual unification is that – following population genetics theory and the modern synthesis of evolutionary biology – the processes shaping biodiversity can be grouped under four major mechanisms: (1) drift, (2) dispersal, (3) selection, and (4) formation of new variants (i.e. speciation and mutation) (Vellend 2010). Below I will briefly summarize the mechanisms and their influence on both species and genetic diversity.

1.1.2 Drift

Within a limited pool of units the relative abundances of variants (i.e. species or alleles) are subject to stochastic variability in time (i.e. drift), which leads to random loss of variants and ultimately results in fixation of a single variant, if not counteracted by other forces (Wright 1955, Kimura and Crow 1964, Caswell 1976, Hubbell 2001). The strength of drift is related to the size of the pool, with fluctuations in relative abundances being greater in smaller pools, which therefore also experience faster loss of variants (Kimura and Crow 1964, Hubbell 2001). At the species level, this means that smaller communities experience greater extinction rates due to ecological drift, which can be considered a synonym for demographic stochasticity (Hubbell 2001). At the genetic level, smaller populations experience faster loss of alleles due to increased genetic drift (Kimura and Crow 1964, Frankham 1996). Stochastic drift also increases compositional differences between communities and genetic differences between populations (Wright 1943, Hubbell 2001).

Traditionally, the importance of drift has been emphasized by neutral theories, which make the assumption that the relative abundances of variables are not influenced by selection (Kimura 1968, Caswell 1976, Hubbell 2001). The assumption is controversial, and therefore both ecological and genetic neutral models have been met with abundant criticism (Ohta and Gillespie 1996, Leigh 2007). However, whereas genetic drift has been successfully incorporated into population genetics theory and has thus resulted in an abundance of theoretical and methodological advances, the debate around ecological drift still remains heated (Leigh 2007, Clark 2009, Rosindell *et al.* 2011). This is probably partly due to practical difficulties in deciphering the relative importance of drift in shaping the diversity and structure of communities (Vellend *et al.* 2014b).

1.1.3 Dispersal

Dispersal counteracts the effects of drift by bringing in new variants (i.e. immigration at the species level and gene flow at the genetic level) and by connecting abundance dynamics between communities or populations (Wright 1940, Hubbell 2001, Leibold and Miller 2004, Cadotte 2006). Therefore dispersal increases diversity within, and decreases differentiation between populations or communities (Slatkin 1985, Bohonak 1999, Cadotte 2006). In neutral models

dispersal is assumed to be stochastic, with no differences in dispersal propensity or dispersal distance between individuals representing different genotypes (Wright 1940, 1943) or species (Caswell 1976, Hubbell 2001). However, although dispersal can influence diversity independent of selection, it should be noted that dispersal abilities differ between and within species and are often considered to trade-off with other life-history characteristics such as competitive ability (e.g. Tilman 1994, Rees 1995, Calcagno *et al.* 2006) or fecundity (Yu *et al.* 2001, Yu and Wilson 2001).

1.1.4 Selection

The literature on empirical and theoretical aspects of selection is extensive and most likely not all aspects apply similarly to the species and genetic levels (Bell 2008). However, for the purpose of the conceptual unification, it suffices to determine selection as a deterministic mechanism that shapes variation in systems of self-replicating variants by favouring variants with the highest replication rate (Bell 2008, p. 19). If resources available for replication are limited, faster replicating lineages will increase in frequency at the expense of the slower replicating ones, resulting in changes in their relative frequencies. Depending on the case, selection can either decrease variation by constantly favouring a variant (i.e. directional or stabilizing selection), or maintain variation by either favouring variants at low numbers (i.e. negative frequency-/density-dependent selection) or favouring different variants at different times or places (i.e. temporally or spatially variable selection) (Bell 2008).

In an evolutionary and population genetic context selection shapes the population-specific frequencies of alleles that influence phenotypic traits related to the fitness of individuals (Hartl and Clark 1997, Bell 2008). Although the term selection is not usually used in community ecology, the same basic principle is implicit in niche-based theories of community ecology (Vellend 2010). In classic niche-based theories individuals of different species differ in their abilities to survive and reproduce in a set of abiotic and biotic conditions, which is reflected as different growth rates for populations of different species (e.g. Hutchinson 1957, Hardin 1960, Connell 1961). During the last decade there has been an increase in studies focusing on how selection within species is linked with selection among species resulting in a so-called eco-evolutionary feedback (e.g. Lankau and Strauss 2007, Hughes *et al.* 2008).

1.1.5 Formation of new variants

Drift, dispersal and selection shape existing variation. Ultimately, however, variation has to emerge one way or the other before the above-mentioned mechanisms can shape it. At the species level, new variants arise via speciation and at the genetic level via mutation. Although details behind speciation and mutation are not exactly analogous (Long *et al.* 2003, Butlin *et al.* 2012), these two processes are nevertheless conceptually similar in that they create new variants. Furthermore, there is a direct link between speciation and mutation, since mutations create hybrid incompatibilities, which lead to speciation

(Presgraves 2010a, b). Indeed, increasing mutation rates have been associated with increasing speciation rates in birds, reptiles and plants (Barraclough and Savolainen 2001, Lanfear *et al.* 2010, Eo and DeWoody 2010; but see Goldie *et al.* 2011).

1.1.6 Why is a conceptual unification of community ecology and population genetics needed?

The benefits of a conceptual unification are twofold. First, a mechanistic grouping of the existing theories could clarify the differences and similarities between the myriad of theories and models explaining diversity and coexistence patterns of species (Vellend 2010). Second, a unified framework for community ecology and population genetics could speed up development of both fields by enabling the usage of a shared toolbox. Indeed, some examples of such benefits can already be seen. For example, adopting the idea of neutrality and random drift from population genetics has given rise to highly influential ecological neutral theories (Caswell 1976, Hubbell 2001, Leigh 2007), and statistical advancements in assessing species diversity have yielded tools for more accurate description of genetic diversity [e.g. rarefaction methodology (Hurlbert 1971, Petit *et al.* 1998) and differentiation metrics (Jost 2007, 2008)].

1.2   Species–genetic diversity correlation

Among the interesting manifestations of the conceptual unification of community ecology and population genetics is the idea that in communities of trophically similar species, genetic diversity and species diversity are often correlated (Vellend 2003, Vellend and Geber 2005). Since both levels of diversity are driven by the same mechanisms, correlations between species diversity and genetic diversity (i.e. species-genetic diversity correlations; SGDCs) can arise if a mechanism simultaneously influences both levels (Vellend 2005). In particular, characteristics of the environment (e.g. area, habitat quality, connectivity, environmental heterogeneity and biogeographic history of the region) have been proposed to influence species diversity and genetic diversity in parallel, and are therefore potential drivers of positive SGDCs (Vellend 2003, 2004, Cleary *et al.* 2006, Odat *et al.* 2010, Robinson *et al.* 2010, Papadopoulou *et al.* 2011, Blum *et al.* 2012).

For example, area (or any other characteristic that increases community size) and connectivity of localities can be expected to similarly influence drift and dispersal at both levels (Vellend 2005). With increasing community size population sizes may be expected to increase and therefore both ecological and genetic drift may decrease (Kimura and Crow 1964, Hubbell 2001, Vellend 2005). Similarly, increasing connectivity allows greater rates of dispersal, with an expected increase in the flow of species between communities (MacArthur and Wilson 1967, Hubbell 2001, Cadotte 2006), and genes between populations (Wright 1940, 1943, Slatkin 1985, Bohonak 1999). Therefore, community size and

connectivity are expected to drive positive correlations between species diversity within localities and genetic diversity within populations (i.e. α-SGDCs) (Vellend 2003, Odat *et al.* 2010, Robinson *et al.* 2010, Papadopoulou *et al.* 2011, Blum *et al.* 2012, Lamy *et al.* 2013). Furthermore, since drift and dispersal influence also differentiation, community size and connectivity are expected to drive correlations between the differentiations at the two levels (i.e. β-SGDCs) (Sei *et al.* 2009, Odat *et al.* 2010, Papadopoulou *et al.* 2011, Blum *et al.* 2012). In addition to the contemporary or recent effects of community size and connectivity, SGDCs can result from historic events, such as habitat disturbance, post-glacial re-colonization and range expansions, that have influenced drift and dispersal on both levels in the past, and are still reflected in biodiversity patterns today (Gaston 2000, Hewitt 2000, Hillebrand 2004, Vellend 2004, Cleary *et al.* 2006, Eckert *et al.* 2008, Palma-Silva *et al.* 2009, Messmer *et al.* 2012).

Although SGDCs due to community size and connectivity point towards neutral drivers of both species diversity and genetic diversity (Papadopoulou *et al.* 2011, Baselga *et al.* 2013), also selection can be expected to create SGDCs (Vellend and Geber 2005). Environmental heterogeneity, in particular, has been suggested to be a potential selection-based driver of SGDCs (Vellend 2005). The rationale is that increasing heterogeneity selects for increasing number of species within communities and increasing non-neutral genetic variability within populations (Via and Lande 1985, Vellend 2005, Stein *et al.* 2014). However, environmental heterogeneity can also select for generalist species and/or genotypes (Via and Lande 1985, Kassen 2002, Allouche *et al.* 2012, Ketola *et al.* 2013), leading to an expected decrease in variation at both levels. The predictions are mixed also for neutral genetic variation. If environmental heterogeneity generally increases the number of species within localities, as suggested by a recent review (Stein *et al.* 2014), it might also decrease population sizes (Kadmon and Allouche 2007, Allouche *et al.* 2012), leading to loss of genetic variability and a negative α-SGDC, when considering neutral genetic diversity. On the other hand, for some species, increasing environmental heterogeneity might increase the amount of available habitat, thus increasing population sizes and reducing the effect of genetic drift (Vellend 2005). Therefore, it is difficult to predict whether environmental heterogeneity creates positive or negative α-SGDCs for any particular system. Furthermore, since the influence of environmental heterogeneity on selection and drift at the species and genetic levels can be considered ambiguous, it is also difficult to make predictions regarding the role of environmental heterogeneity in driving β-SGDCs.

Selection due to direct interactions between species diversity and genetic diversity can also drive SGDCs and the predictions are similar and equally ambiguous to the effects environmental heterogeneity (Vellend and Geber 2005, Lankau and Strauss 2007, Costa *et al.* 2008, Hughes *et al.* 2008). This is hardly surprising, since interactions between the two levels can be considered biotic environmental heterogeneity. Like in the case of environmental heterogeneity, the focus should generally be on non-neutral genetic variation since the interest is in selection. However, the influence of direct interactions can also be seen in

neutral genetic diversity via their effects on population sizes and genetic drift (explained below). In short, species diversity within a locality can maintain non-neutral genetic variation within populations via disruptive selection (Vellend and Geber 2005, Adams and Vellend 2011), reduce non-neutral genetic variation by selecting for a genotype specialized in interspecific competition (Lankau and Strauss 2007), reduce non-neutral genetic variation by narrowing down the ecological niche of a population (Costa *et al.* 2008, Silvertown *et al.* 2009) and reduce neutral genetic variation by reducing population sizes (Ranta *et al.* 2009, Östman 2011, Nestmann *et al.* 2011). Similarly, genetic diversity within a population of a dominant species can enable coexistence of other species in the community (Vellend 2006, Fridley and Grime 2010) or fill up niche space, which can lead to reduced population sizes, or even competitive exclusion of other ecologically similar species (Crutsinger *et al.* 2008).

Another noteworthy point here is that genetic diversity can influence species diversity simply by influencing the persistence of the species itself. If genetic diversity is reduced it can eventually be reflected at the species level, since loss of genetic diversity most often leads to reduced viability (i.e. inbreeding depression) and increased extinction risk (Saccheri *et al.* 1998, Crnokrak and Roff 1999, Reed and Frankham 2003, Spielman *et al.* 2004, Frankham 2005b, O'Grady *et al.* 2006).

Even though genetic diversity is recognized as vital for the long-term persistence of populations (e.g. Saccheri *et al.* 1998, Crnokrak and Roff 1999, Frankham 2005, O'Grady *et al.* 2006), it is seldom taken into consideration in the planning and implementation of national and international conservation strategies for ecosystems and species (Laikre 2010, Laikre *et al.* 2010). This neglect of genetic diversity is understandable when considering the realities of practical conservation, since the simultaneous explicit consideration of genetic diversities of several species is simply neither feasible nor realistic in most cases (but see Diniz-Filho and Telles 2006, Vandergast *et al.* 2008, Thomassen *et al.* 2011, Taberlet *et al.* 2012). Therefore, surrogates for genetic diversity would be in high demand.

SGDCs could be a promising tool to facilitate conservation of genetic diversity if they prove common and predictable. For example, if the focus of conservation is on local diversity, α-SGDCs can help predict the circumstances when species diversity and genetic diversity can be conserved simultaneously and when the two levels are in conflict. On the other hand, modern spatial conservation prioritization aims at conserving biodiversity at landscape scales, and is therefore more concerned with compositional differences between localities (Margules and Pressey 2000, Moilanen *et al.* 2009). Therefore, from the perspective of spatial conservation prioritization, β-SGDCs might prove more useful as they suggest parallels in compositional variation at both levels.

1.3   Aims of the thesis

Since the publication of two seminal reviews c.a. decade ago (Vellend 2003, Vellend and Geber 2005), over twenty studies on the SGDC have been published (I, Supplementary material A). Studies have reported positive (He *et al.* 2008, He and Lamont 2010, Odat *et al.* 2010, Papadopoulou *et al.* 2011, Baselga 2013, Lamy *et al.* 2013), negative (Wehenkel *et al.* 2006, Marshall and Camp 2006, Puşcaş *et al.* 2008, Taberlet *et al.* 2012), and non-significant SGDCs (Odat *et al.* 2004, Derry *et al.* 2009, Helm *et al.* 2009, Taberlet *et al.* 2012). Although some generalizations have been suggested (Vellend and Geber 2005, Vellend *et al.* 2014a), there obviously are still uncertainties in the relationship, and the number of studies explicitly focusing on the SGDC is still relatively small. Furthermore, SGDC is rarely discussed explicitly in the context of conservation (but see Taberlet *et al.* 2012, Fuller *et al.* 2013).

With these limitations in the existing theory in mind, the general aims of my thesis are (1) to discuss the utility and importance of SGDCs to conservation of biodiversity (I, IV), and (2) to contribute to the empirical literature on the SGDC by determining the importance of environmental characteristics and interspecific interactions in shaping species diversity and genetic diversity in a natural odonate system (II, III).

1.4   Study questions

1. Can α- and β-SGDCs benefit the conservation of biodiversity (I)?

Existing reviews on the SGDC have supported the view that, although variable in strength, α-SGDC are generally positive (Vellend 2003, Vellend and Geber 2005, Vellend *et al.* 2014a). This suggests potential for simultaneous conservation of species diversity and genetic diversity, particularly when aiming to conserve diversity within localities. On the other hand, for conserving diversity at scales beyond the locality, β-SGDCs might be more useful (see above). Although some studies have reported positive β-SGDCs (e.g. Sei *et al.* 2009, Odat *et al.* 2010, Papadopoulou *et al.* 2011, Baselga 2013) less is known about how common positive β-SGDCs are.

2. Are the patterns of genetic diversity and differentiation of ecologically similar *Calopteryx splendens* and *C. virgo* concordant with each other and are any such patterns related to similar environmental characteristics (II)?

Since ecology of the species and characteristics of the environment strongly influence the distribution of genetic diversity within and between populations, sympatric and ecologically similar species can be expected to exhibit similar genetic patterns (Whiteley *et al.* 2006, Fortuna *et al.* 2009, Dawson 2012, Hughes *et al.* 2013). On the other hand, increasing ecological similarity of species can be

expected to increase interactions between them, and can therefore create differences between their genetic structures (Ranta *et al.* 2009, Nestmann *et al.* 2011). Which brings me to the next question.

3. Can interactions between ecologically very similar *C. splendens* and *C. virgo* influence their genetic structures (II)?

Indeed, the two *Calopteryx* species are known to interact with each other in several ways, such as interspecific aggression due to competition for breeding territories (Tynkkynen *et al.* 2004, 2006). Interspecific aggression may influence the evolution of the two species by driving character displacement in their sexual signals (Tynkkynen *et al.* 2005, Honkavaara *et al.* 2011, Kuitunen *et al.* 2011) therefore, interspecific aggression may impact the genetic structures of these congeners.

4. Are there α- and/or β-SGDCs between communities of river inhabiting Odonata and *Calopteryx* populations (III)?

SGDCs have previously been described from freshwater systems including gastropods in ponds (Evanno *et al.* 2009, Lamy *et al.* 2013), amphipods in desert springs (Sei *et al.* 2009) and stream fish assemblages (Blum *et al.* 2012). Hence, it is possible, that SGDCs exist also in odonates. However, previous studies on freshwater systems have been conducted with strictly aquatic organisms, which can translate to greater dispersal limitation and stronger SGDCs compared with semi-aquatic organisms, such as odonates.

5. Do environmental characteristics influence species diversity of odonate communities and genetic diversity of *Calopteryx* populations in parallel (III)?

This question is closely linked with the previous one, since SGDCs are often considered to be caused by a parallel influence of some environmental characteristic (Vellend and Geber 2005). However, detecting the environmental drivers of SGDC and disentangling their relative contributions is challenging in practice (but see Lamy *et al.* 2013). Furthermore, although some environmental characteristic may influence species diversity and genetic diversity in parallel, others might counteract the effect leading to negligible net SGDCs even in the presence of parallel effects.

6. How does inbreeding depression due to impoverished genetic diversity influence species diversity in multispecies metacommunities (IV)?

Genetic impoverishment is frequently considered to lead to inbreeding depression and increased extinction risk of populations (Crnokrak and Roff 1999, Frankham 2005b). This is particularly the case for populations in fragmented landscapes (Saccheri *et al.* 1998, Reed 2004, Lehmann and Perrin 2006, Robert 2011a, b). However, to my knowledge, no study has assessed how inbreeding depression due to lowered genetic diversity is manifested within communities of multiple species.

2 METHODS

2.1 Literature review on species–genetic diversity correlations and associated environmental characteristics (I)

In order to assess the generalizability of the SGDC, a literature review was conducted. After summarizing the mechanisms and related environmental characteristics potentially driving SGDCs, a review of α- and β-SGDCs obtained from natural systems was conducted. SGDCs were first derived from previous reviews that had been published prior starting the preparation of manuscript I (Vellend 2003, Vellend and Geber 2005) and from studies citing either one of them [search conducted using online search engines Thomson Reuters Web of Science (http://www.webofknowledge.com) and Google Scholar (http://scholar.google.com)]. For calculation of median α- and β-SGDCs, only studies on natural systems were considered.

During the preparation of the manuscript an update of the previous reviews was published (Vellend *et al.* 2014a). That review contained one additional study not discovered in search (but lacked two others), which was subsequently included in the review. In addition, unpublished data on the α- and β-SGDCs between odonate communities and *Calopteryx* populations (III) was included.

The suggested drivers of statistically significant SGDCs were obtained based on the conclusions of the original manuscripts. Finally, the utility of α- and β-SGDC for conservation of biodiversity at both local and landscape scales was explored with an emphasis on spatial conservation prioritization (Moilanen *et al.* 2009).

2.2 *Calopteryx* populations and odonate communities (II and III)

2.2.1 *Calopteryx* populations and odonate communities as a study system

In Finland there are breeding populations of 55 species of Odonata (i.e. dragonflies and damselflies), of which about 30 are frequently observed in rivers and streams (Karjalainen 2010). Odonates are semi-aquatic, meaning that they have aquatic egg and larval stages that can live for several years, after which the larvae climb above water, and emerge as flying adults (Corbet 1999, Stoks and Córdoba-Aguilar 2012).

Among the common odonates inhabiting rivers and streams in Finland are *Calopteryx splendens* and *C. virgo*, which are sympatric across most of their ranges in Europe (Askew 2004, Dijkstra and Lewington 2006, Karjalainen 2010, Karjalainen and Hämäläinen 2013). These two species are considerably similar in their appearance, behaviour, life-history and habitat choice (Askew 2004, Wellenreuther *et al.* 2012, Karjalainen and Hämäläinen 2013; but see Sternberg and Buchwald 1999) and therefore make for an appropriate system for comparing spatial genetic structures between ecologically similarity species.

2.2.2 The genetic structures of *Calopteryx splendens* and *C. virgo* (II)

In order to compare the genetic structures of the two *Calopteryx* species, adult *Calopteryx* individuals were collected from a total of 40 localities (Fig. 1) and genotyped at microsatellite loci (12 and 9 loci for *C. splendens* and *C. virgo*, respectively). All of the localities contained a *C. virgo* population, whereas *C. splendens* was present in 19 of the localities. However, one of the *C. splendens* populations was excluded from the analysis since only two individuals were collected, leaving a sample size of 18 populations.

Environmental characteristics considered to be related to colonization history (latitude and longitude), genetic drift (density of conspecific males) and dispersal (potential connectivity, measured as the total length of river habitat within a 5-km-radius zone from each sampling locality) were recorded for each population. Also, to estimate the frequency of interspecific interactions the density of heterospecific *Calopteryx* males at each population was recorded. The environmental characteristics were tested for spatial autocorrelation prior incorporation into analyses.

After collecting data, the distribution of genetic diversity within (rarefied allelic richness and heterozygosity) and differentiation between populations (isolation-by-distance, population specific F_{ST}s, pairwise F_{ST}s and D_{est}s, and number of genetic clusters) were determined for both species. To study how environmental characteristics and density of heterospecific males are related to genetic diversity and differentiation, a series of generalized linear models were constructed. Furthermore, since the datasets for the two species differed in both numbers of loci and numbers of samples, a set of subset analyses was run to confirm the results obtained from the whole dataset.
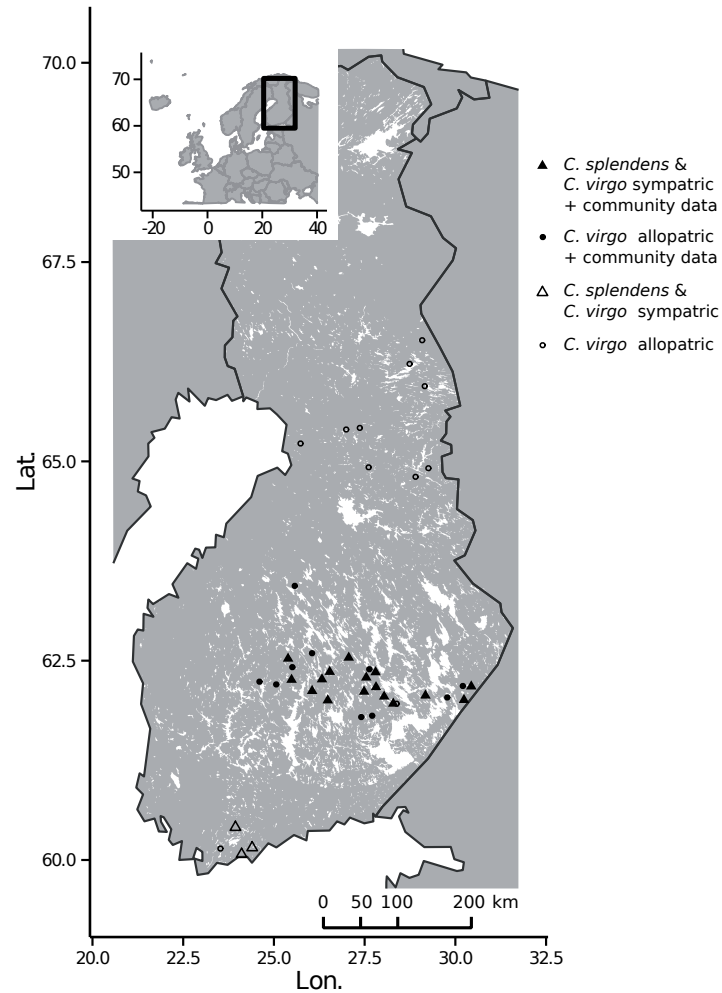
FIGURE 1   Sampling localities within Finland. Triangles correspond to sympatric *C. splendens* and *C. virgo* populations and circles to allopatric *C. virgo* populations. Closed symbols correspond to localities from which both the odonate community and *Calopteryx* sub-populations were sampled and open symbols correspond to localities from which only *Calopteryx* sub-populations were sampled.

2.2.3 SGDCs between odonate communities and *Calopteryx* populations (III)

To examine if there are α- or β-SGDCs between the odonate (i.e. dragonflies and damselflies) communities and the genetic structures of *C. splendens* and *C. virgo* populations, odonate species diversities were estimated for 26 river localities within Central and Eastern Finland (Fig. 1), representing a subset of the localities that were sampled for study II. Of the 26 localities, all contained a *C. virgo* population, whereas *C. splendens* was present in 16 of the localities.

Odonate species diversities were estimated using standardized sampling of larvae and exuviae and each locality was sampled twice, in June and July 2009. For each locality, environmental characteristics considered to be associated with drift (community size; measured as the number of larvae and exuviae collected at the site), dispersal (potential connectivity; as in II), and selection (environmental heterogeneity; a principal component describing structural environmental heterogeneity of the stream) were recorded.

To determine the α-SGDCs, odonate species diversity (measured as species richness) was correlated against genetic diversities (measured as rarefied allelic richness) of both *Calopteryx* species with Pearson's product moment correlation coefficient. For determining β-SGDCs, pairwise Bray-Curtis dissimilarity indices between sampled communities and pairwise F_{ST}s between subpopulations were calculated. Then, two different approaches to test for β-SGDCs were used. In the first approach, the correlation between the pairwise distance matrices was tested using a Mantel test (Mantel 1967). In the second approach, community and population specific differentiation metrics were derived from the pairwise differentiations (distance to the centroid) and correlation between them was tested using Pearson's product moment correlation coefficient. In the latter approach, the community and population specific differentiation metrics correspond to differentiation from an expected average community or population.

A covariance decomposition method suggested by Lamy *et al.* (2013) was used to assess the contributions of environmental characteristics to the α-SGDCs and to the β-SGDCs between community and population specific differentiation. In this method, the effects of the environmental characteristics on species diversity and genetic diversity are first assessed using multiple linear regressions. Standardized regression coefficients from these analyses are then used to partition the SGDC with respect to the contributions of the environmental characteristics. To assess the contributions of the environmental characteristics to the β-SGDCs between pairwise community dissimilarities and F_{ST} matrices, distance-based redundancy analyses (dbRDA; Legendre and Anderson 1999) were conducted separately for both the pairwise Bray-Curtis dissimilarities and F_{ST}s. Note that although the dbRDAs do not explicitly partition the β-SGDC between pairwise differences, a parallel effect can be detected if both levels are influenced by the same environmental characteristics.

2.3 Individual-based simulation (IV)

In order to explore how loss of intraspecific genetic diversity can be reflected in species diversity through inbreeding depression, individual-based simulations of neutral metacommunities were conducted. The simulations started from an initial community of 10 000 individuals belonging to 70 species. The initial relative abundances of the species were simulated using a community size of 10 000 individuals and a biodiversity number (θ) of ten in a protocol described by Hubbell (2001, p. 291). The individuals of the initial community were then

assigned a diploid neutral genotype of 20 biallelic loci and were then placed in zero-sum metacommunities subject to one of three different levels of inbreeding depression (i.e. relationship between heterozygosity and reproductive fitness), habitat fragmentation (i.e. division into different numbers of local communities), and dispersal limitation between local communities (i.e. relationship between dispersal probability and distance). All possible combinations of the three factors were considered, with the obvious exception that when the community was left unfragmented (i.e. a single large community), different levels of dispersal limitation between local communities do not exist. All combinations were repeated five times.

Each metacommunity was simulated for 2000 cycles (corresponding to c.a. 40 generations) of sequential mortality, reproduction, dispersal, and establishment. Species richness within the metacommunity and local communities was tracked through every time step of the simulation and the effects of fragmentation, dispersal limitation and inbreeding depression on species richness were analysed by comparing their respective effect sizes.

3 RESULTS AND DISCUSSION

3.1 Conservation implications of the species–genetic diversity correlations (I)

In total, the review encompassed 130 taxa derived from 27 studies. Of these, α-SGDCs could be derived for 110 taxa and β-SGDCs for 23 taxa. In the reviewed literature the median α-SGDC was 0.17. Although the median suggests the α-SGDC to be slightly positive, the variation is high (S.D.=0.40). Indeed, α-SGDCs have been found to be highly variable for different species in the same study system (Wehenkel *et al.* 2006, Marshall and Camp 2006, Taberlet *et al.* 2012), and for the same species in different study systems (Wei and Jiang 2012). Since significant negative α-SGDCs have been discovered, it is possible that in some cases conservation of species diversity conflicts with that of genetic diversity when focusing on locality scale diversity. However, it needs to be noted, that α-SGDCs seem to be more commonly positive when studied in island-like systems (Vellend and Geber 2005, Vellend *et al.* 2014a).

The median β-SGDC was 0.16, which is nearly identical to that of the α-SGDC and the variation was somewhat lower (S.D.=0.26). A positive β-SGDC could benefit conservation at scales larger than the locality, since it suggests that complementary site selection conducted at the species level would translate into complementarity also at the genetic level, or vice versa (Fuller *et al.* 2013). But there is a caveat to this idea: β-SGDCs can exist only if the species, for which genetic diversity and structure is determined, is present in all of the studied communities. Therefore, there is a limit to how different the species compositions of communities can be in order for β-SGDCs to arise. In other words, if community compositions of localities are different enough, they have no species in common and therefore there can be no genetic differentiation and β-SGDCs. This suggests that differentiation at the species level can match that at the genetic level only when it is manifested as differences in relative abundances of species. Therefore, complementarity at the species level might not match that at the genetic level after all.

The usefulness of SGDCs for conservation also depends on the characteristics driving them. Most studies that reported a significant positive SGDC suggested that the underlying driver was related to community size (I, Supplementary material A). The fact that positive SGDCs seem to be related to community size can be problematic for conservation as increasing community size often means increasing area, which can then translate into larger costs. Indeed, one of the primary questions that spatial conservation prioritization tries to address is how to conserve as much biodiversity features (most often species or surrogates thereof) as possible with a limited amount of resources (i.e. maximum coverage problem; Cabeza and Moilanen 2001). Therefore, the observation that we would need to focus on conserving large communities in order to simultaneously conserve species and their genetic diversities certainly does not contribute to minimizing the costs of conservation.

3.2 Spatial genetic structures of *C. splendens* and *C. virgo* (II)

Despite their similar ecologies, the two *Calopteryx* species exhibited substantial differences in genetic patterns. The genetic characteristics differed with respect to isolation-by-distance (II, Fig 2), the number of genetic clusters detected (Fig. 2; II, Fig. 3), and the environmental characteristics that were related to genetic differentiation and diversity (II, Tables 1 and 2). The results therefore do not support the hypothesis that ecologically similar species would exhibit similar genetic patterns (Whiteley *et al.* 2006, Dawson 2012).

The genetic patterns of *C. splendens* seemed to be very much influenced by genetic drift. There was no clear isolation-by-distance pattern, since pairwise genetic differentiation was in many cases clear already between neighbouring populations (II, Appendix S4, Tables S7 and S8). Furthermore, spatial genetic clustering produced six clusters, many of which corresponded to single populations (Fig. 2; II, Fig. 3). The role of drift is further supported by the positive relationship between genetic diversity (measured as heterozygosity) and the density of conspecific males, which was considered to reflect population size (II, Table 1). However, there were also some signs of gene flow, since the genetic diversities of *C. splendens* populations increased with increasing potential connectivity whereas the population specific differentiation (population specific F_{ST}) decreased.

Interestingly, the genetic diversity of *C. splendens* was also negatively related to the density of *C. virgo* males, supporting the idea that interspecific interactions with *C. virgo* may, in fact, influence the genetic architecture of *C. splendens*. Unfortunately, with the data at hand, it is not possible to single out any particular type of interaction as the definitive cause of the relationship. Nevertheless, a likely explanation is interspecific aggression inflicted by *C. virgo*, since it is known to decrease the proportion of territorial *C. splendens* males (Tynkkynen *et al.* 2004, 2006). Since males with a territorial mating strategy have much better mating success than non-territorial ones (Plaistow and Siva-Jothy 1996), *C. virgo* can decrease the effective population size by

increasing the reproductive skew of *C. splendens*. An alternative explanation for the pattern could be that there is habitat partitioning between the species and that because of this the population sizes of *C. splendens* would be smaller when *C. virgo* is abundant. Indeed, water temperature preferences of the two species have been reported to differ in Central Europe (Sternberg and Buchwald 1999, Schütte and Schrimpf 2002). However, our data on the water temperature preferences of the two species does not support this view, but rather suggests that, in Finland, the range of water temperatures preferred by *C. splendens* and *C. virgo* are largely overlapping. Furthermore, a separate study on these two species in Finland reported similar results and the authors also suggested similar reasoning for the observed pattern (Viitaniemi 2009).

The genetic patterns of *C. virgo* were very different from those of *C. splendens*, with all aspects of the genetic patterns corresponding to latitudinal variation (isolation-by-distance, genetic diversity, clustering and population specific F_{ST}). The genetic characteristics of *C. virgo* seem to point towards high gene flow between populations and signs of post-glacial colonization. The reason why the genetic patterns of *C. virgo* do not seem to show any signs of interspecific interactions with *C. splendens* could be due to the fact that, in Finland, *C. virgo* is competitively dominant and acquires the best breeding habitats (Tynkkynen *et al.* 2004, 2005, 2006).

The different genetic patterns of the *Calopteryx* species caution indirect inferences of genetic characteristics based on ecologically similar surrogate species. Furthermore, in the context of the SGDC, the differing genetic patterns indirectly imply that the two species likely exhibit different SGDCs, which was explored in depth in the next study (III).
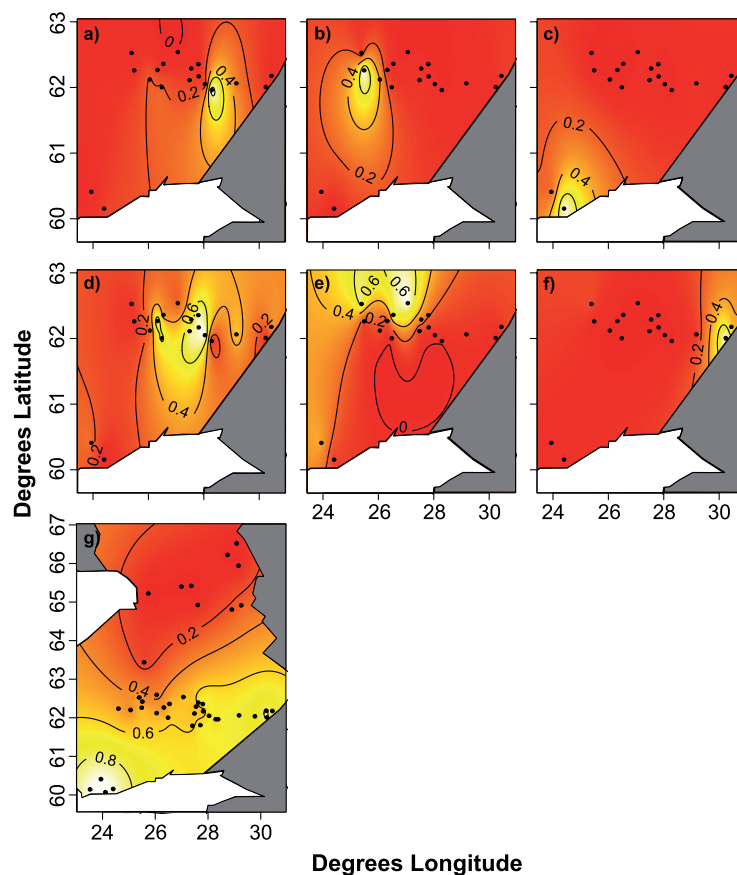
FIGURE 2. Spatial positioning of genetic clusters of *C. splendens* (a-f) and *C. virgo* (g). The curves represent admixture coefficients for the particular cluster. For *C. virgo*, a single plot is displayed since the two clusters are indentical but inverse. Note the different scales in the y-axis of the *C. splendens* panels (a-f) and the *C. virgo* panel (g).

3.3 The species–genetic diversity correlation between odonate communities and *Calopteryx* populations (III)

C. splendens did not exhibit an α-SGDC and neither species exhibited β-SGDCs. However, a statistically significant α-SGDC was observed between the rarefied allelic richness of *C. virgo* and odonate species richness (III, Fig. 2a, b). Although there were no α- or β-SGDCs between *C. splendens* genetic characteristics and the odonate community, the covariance decomposition suggested that there is a slight parallel effect of community size, which is counteracted by an opposite effect of connectivity. This pattern was observed for both α-SGDC and β-SGDC between community specific and population specific differentiation (III, Fig. 3a, c). For *C. virgo*, a slight parallel effect of longitude was observed to contribute to the positive α-SGDC. However, the contribution of longitude was minor, and

majority of the positive α-SGDC was left unexplained (III, Fig. 3b). Although the studied environmental characteristics do not seem to contribute to the positive α-SGDC observed for *C. virgo* (or to the lack of other SGDCs due to opposite effects), they were nevertheless related to diversity and differentiation patterns of both the odonate communities (species richness, pairwise dissimilarities, and community specific dissimilarities) and *Calopteryx* populations (allelic richness, pairwise differentiation, and population specific differentiation), which suggests that the choice of the studied environmental characteristics was reasonable (III, Tables 2 and 3).

Three characteristics of the Finnish Odonata-*Calopteryx* study system likely contribute to the lack of a generalizable SGDC. First, SGDCs are more prevalent if measured from island-like habitat patches and are often weak or non-existent if measured from arbitrary localities from a continuous landscape (Vellend and Geber 2005, Vellend *et al.* 2014a). Although odonate larvae are restricted to water habitats, several species are strong flyers as adults, and from their perspective the sampling design can resemble that of sampling arbitrary localities from a continuous landscape. Second, it is possible that the Finnish odonate communities and the studied *Calopteryx* populations still reflect signs of post-glacial colonization and have not yet reached equilibrium conditions. Third, interspecific interactions with *C. virgo* likely influence the genetic structures of the competitively subordinate *C. splendens* (II), which could explain why SGDCs are not observed for *C. splendens* although a positive α-SGDC observed for *C. virgo*.

Other studies that have looked at SGDCs in multiple species simultaneously have discovered similar variability between species (Wehenkel *et al.* 2006, Marshall and Camp 2006, Robinson *et al.* 2010, Taberlet *et al.* 2012; but see Messmer *et al.* 2012). Therefore, the contrasting SGDCs observed for the two *Calopteryx* species are no exception. Furthermore, differences between the SGDCs of the two species were expected, since their genetic structures differed (II).

3.4 Inbreeding depression and persistence of species in neutral metacommunities (IV)

Inbreeding depression clearly increased extinction rates at the metacommunity scale (IV, Fig. 1, Table 1). Both weak and strong inbreeding depression [as determined by Crnokrak and Roff (1999)] increased extinction rates, but the clearest effects were observed for strong inbreeding depression (IV, Fig. 1). However, the level of fragmentation or dispersal limitation did not seem to have noticeable impacts on extinction rates at the metacommunity scale, and they did not seem to interact with inbreeding depression (IV, Table 1), which runs counter to results of single species studies (Saccheri *et al.* 1998, Reed 2004, Lehmann and Perrin 2006, Robert 2011a, b). This is probably due to similar dispersal abilities of different species in the model and inbreeding depression being modelled as a reduction in reproductive fitness relative to other species.

With similar dispersal abilities the differences between species in the loss of heterozygosity (and in reproductive output) likely remain similar irrespective of fragmentation and dispersal limitation. Although increasing fragmentation and dispersal limitation increases the absolute rate of loss of heterozygosity, it does so for all (or at least most) of the species and therefore the differences between them stay similar and no clear effects are observed for fragmentation and dispersal limitation.

However, fragmentation and dispersal limitation did influence diversity within local communities, as could be expected (Hubbell 2001, Economo and Keitt 2008). The obvious effect of fragmentation was that with less fragmentation the local communities were larger and therefore initially sampled more species (IV, Table 2). When only the fragmented metacommunities were included in the analyses, the effect of dispersal limitation increased considerably (IV, Table 2), with the rate of local extinctions being much higher in local communities with no dispersal than in limited or unlimited dispersal (IV, Fig. 2).

Interestingly, the species that seemed to be influenced by inbreeding depression the most were those of intermediate rank-abundances (IV, Fig. 3), whereas the extinction rates of very rare species were in practice unaffected (IV, Fig. 3). This is probably due to rare species going extinct before inbreeding depression has time to influence their fitness. This suggests that if inbreeding depression is overlooked, the extinction risks of demographically viable species might be underestimated.

4 CONCLUSIONS AND FUTURE DIRECTIONS

4.1 Conclusions

According to published literature and empirical examinations of odonate communities and *Calopteryx* populations, SGDCs in natural systems seem to be highly variable in both strength and direction (I, III). The variability in the sign and strength of α- and β-SGDCs question the use of one level of diversity as a surrogate for the other (I). Furthermore, negative α-SGDCs have also been observed, suggesting that conservation of species diversity might conflict conservation of genetic diversity at local scales. The situation is not much more promising when aiming to conserve diversity at scales beyond the locality. β-SGDCs are generally close to zero and they can exist only when species level differentiation is relatively minor (I). Therefore, complementary site selection conducted at the species level might not result in conserving genetically complementary populations (but see Fuller *et a*l. 2014).

Nevertheless, studies reporting strong positive α- and/or β-SGDCs suggest that given the right conditions SGDCs can prove useful for conservation (Papadopoulou *et al.* 2011, Blum *et al.* 2012, Baselga *et al.* 2013, Lamy *et al.* 2013). Indeed, a statistically significant positive α-SGDC was observed also in this thesis (III). However, with few exceptions, not much is know about the conditions under which environmental characteristics are likely to drive positive SGDCs. According to recent work, SGDCs seem to be more commonly positive in island-like habitats (Vellend *et al.* 2014a). This is probably due to drift and dispersal playing a large role in habitats that are isolated and limited in size. Also, positive SGDCs have been suggested to be increasingly likely with increasing ecological similarity between the species of interest (i.e. the species from which genetic diversity is measured) and the species group of comparison (i.e. the group of species from which species diversity is measured; He and Lamont 2010). The rationale here is that species diversity and genetic diversity of a focal species are more likely to be influenced similarly by the environment if the focal species is ecologically similar to the species group of comparison.

However, the results of this thesis are to some extent in conflict with the latter prediction, since it was observed that interactions between ecologically similar species might influence their genetic diversities (II). This may also contribute to the variability in SGDCs observed in natural systems (III). It has been suggested that since interactions between species diversity and genetic diversity mostly correspond to selection, studies addressing that aspect of the SGDC should primarily focus on non-neutral genetic diversity (Vellend and Geber 2005). However, interactions between species can influence effective population sizes and therefore become reflected in neutral genetic diversity (Ranta *et al.* 2009, Nestmann *et al.* 2011). Although the comparison between the genetic structures and interactions between the two *Calopteryx* species (II) does not exactly qualify as an SGDC study, it does point towards an interaction between community composition and genetic diversity and therefore indirectly suggests that the two levels of diversity can influence each other (Vellend and Geber 2005).

Furthermore, the results of this thesis also point out that the interaction between species diversity and genetic diversity can work the other way round as well: intraspecific neutral genetic diversity can be reflected at the species diversity level, if it is related to inbreeding depression (IV), which generally seems to be the case in the wild (Crnokrak and Roff 1999, Reed and Frankham 2003, Spielman *et al.* 2004, Frankham 2005a; but see e.g. Slate *et al.* 2004). Incorporating inbreeding depression into the simulations of neutral multispecies metacommunities increased the extinction rates of species, suggesting that decreasing genetic diversity can eventually lead to decreasing species diversities (IV). In essence, such a relationship between genetic diversity and population viability represents the simplest possible case of an interaction between species diversity and genetic diversity. From the perspective of conservation planning the results highlight the importance of explicit consideration of genetic diversity, since extinction rates may be underestimated if genetic characteristics are neglected.

4.2 Future directions

In the current literature on the SGDC, the majority of studies do not quantitatively address the relative roles of different environmental characteristics and conditions under which SGDCs are prevalent. SGDC studies usually focus on a single distinguishable characteristic or phenomenon, often a disturbance of some kind (e.g. Vellend 2004, Cleary *et al.* 2006, Evanno *et al.* 2009, Struebig *et al.* 2011, Wei and Jiang 2012, Blum *et al.* 2012). While I think it is important to highlight the effects of habitat disturbances, especially with respect to human land use, a more inclusive approach assessing the relative contributions of different environmental characteristics could help in achieving better generalizations (e.g. Lamy *et al.* 2013). This, of course, is easier said than done, since in order to accurately disentangle the relative contributions of different environmental characteristics and the associated mechanisms, large

numbers of populations and individuals within populations need to be sampled (Nazareno and Jump 2012). Noticeably missing are the studies that would explicitly address the role of environmental heterogeneity on the SGDC (but see Marshall and Camp 2006), even though environmental heterogeneity was considered to be among the primary drivers of SGDCs in the studies that laid the theoretical foundations for the field (Vellend and Geber 2005, Vellend 2005).

Although increasing ecological similarity of the species group of comparison has been suggested to increase the likelihood of positive SGDCs (He and Lamont 2010), the level of ecological similarity required for an SGDC to be observed is still unresolved. In fact, if interspecific interactions increase with increasing ecological similarity and if these interactions can alter genetic structures of populations (II), there might be some optimal level of similarity in which SGDCs are most likely. However, the level of ecological similarity required for SGDCs to be observed can depend on the study system. Indeed, Eldon *et al.* (2013) suggested that the generalizability of SGDCs and parallel processes is best studied by broadening the species group of comparison to cover ecologically very different and taxonomically distant species. If SGDCs are observed even when species group of comparison consists of species that are ecologically different from the species from which genetic characteristics are measured, it suggests that some mechanism is particularly strong in the system.

The idea proposed by Eldon *et al.* (2013) points towards a very interesting and general future direction for SGDC research. SGDCs could be used to distinguish the characteristics that limit diversity within each system and apply that information to conservation. An SGDC driven by community size and connectivity would suggest that both levels are influenced by drift and dispersal, and that by increasing community size and connectivity more diversity could be maintained. Alternatively, a lack of an SGDC could point towards more complicated (possibly selection related) processes. By focusing on the mechanisms driving diversity across levels, we could target conservation or management actions that are based on process rather than pattern. Such an approach has been called for by ecologists, conservationists and evolutionary biologists alike (Frankel 1974, Smith *et al.* 1993, Bowen 1999, Mace and Purvis 2008, Laikre 2010, Diniz-Filho and Bini 2011).

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Vuorovaikutukset ja yhteydet lajistollisen ja geneettisen monimuotoisuuden välillä

Lajiensisäistä geneettistä monimuotoisuutta ja lajistollista monimuotoisuutta käsittelevät tutkimusalat, populaatiogenetiikka ja yhteisöekologia, ovat hyvin samankaltaisia siinä mielessä, että molempien tavoitteena on pyrkiä selittämään biologisten muotojen (geenien tai lajien) runsautta, runsaussuhteita ja tilallista jakautumista. Koska perimmäiset kysymykset yhteisöekologiassa ja populaatiogenetiikassa ovat hyvin samankaltaisia, niiden teorioiden välillä voidaan havaita selkeitä yhteneväisyyksiä. Näiden yhteneväisyyksien tunnistaminen on nostanut esille ajatuksen populaatiogenetiikan ja yhteisöekologian käsitteistöjen yhtenäistämisestä. Tämän näkemyksen mukaan monimuotoisuutta ja sen tilallista jakautumista sekä lajistollisella että geneettisellä tasolla ohjailevat samat neljä päämekanismia: (1) satunnaisajautuminen, (2) levittäytymien, (3) valinta ja (4) uusien muotojen syntyminen.

Ympäristötekijät, kuten alueen koko (tai jokin muu tekijä, joka vaikuttaa alueen yksilöiden lukumäärä), kytkeytyneisyys toisiin samankaltaisiin alueisiin ja elinympäristöjen monimuotoisuus, vaikuttavat olennaisesti kolmen ensimmäisen mekanismin suhteellisiin voimakkuuksiin sekä lajistollisella että geneettisellä tasolla. Esimerkiksi suurissa yhteisöissä lajistollinen satunnaisajautuminen on hidasta ja lajien sukupuutot sen vuoksi harvinaisia, ja koska suurissa yhteisöissä populaatiokoot ovat usein suuria, on myös geneettisestä satunnaisajautumisesta johtuva geneettisen monimuotoisuuden häviäminen hyvin hidasta. Vastaavasti korkea kytkeytyneisyys toisiin samankaltaisiin alueisiin mahdollistaa sen, että alueelle voi muuttaa uusia lajeja toisilta alueilta, ja samalla geenivirta eri alueilla olevien populaatioiden välillä lisääntyy. Tästä johtuen voidaan ennustaa, että yhteisön lajistollinen monimuotoisuus on positiivisesti yhteydessä yhteisön populaatioiden sisäisiin geneettisiin monimuotoisuuksiin. Toisaalta taas esimerkiksi elinympäristöjen monimuotoisuus saattaa vaikuttaa lajistolliseen ja geneettiseen monimuotoisuuteen päinvastaisesti. Jos yhteisössä olevien habitaattien määrä kasvaa, mutta yhteisökoko ei muutu, voi lajistollinen monimuotoisuus kasvaa valinnan seurauksena, mutta lajien populaatiokoot voivat samalla pienentyä. Tämä voi johtaa geneettisen satunnaisajautumisen voimistumiseen ja geneettisen monimuotoisuuden vähenemiseen. Tällöin lajistollisen ja geneettisen monimuotoisuuden välinen yhteys on negatiivinen.

Mikäli positiiviset yhteydet lajistollisen ja geneettisen monimuotoisuuden välillä ovat luonnossa yleisiä ja helposti ennustettavissa, voivat ne hyödyttää luonnonsuojelua. Populaatioiden geneettisten monimuotoisuuksien on osoitettu olevan yhteydessä populaatioiden elinkelpoisuuksiin, mutta geneettisten ominaisuuksien määrittäminen useille lajeille voi olla käytännössä hankalaa ja kallista. Yhteys lajistollisen ja geneettisen monimuotoisuuden välillä voisi mahdollistaa geneettisten monimuotoisuuksien ennustamisen lajistollisten monimuotoisuuksien avulla. Positiiviset yhteydet lajistollisen ja geneettisen moni-

muotoisuuden välillä saattaisivat myös mahdollistaa molempien tasojen samanaikaisen suojelun.

Väitöskirjani ensimmäisessä osassa tarkastelen kirjallisuuskatsauksen avulla, kuinka yleistettäviä yhteydet lajistollisen ja geneettisen monimuotoisuuden välillä ovat ja mitkä ympäristötekijät näihin yhteyksiin liittyvät. Kirjallisuuskatsaukseni perusteella nämä yhteydet ovat hyvin vaihtelevia, sillä sekä tilastollisesti merkitseviä positiivisia että negatiivisia yhteyksiä on havaittu. Niissä tutkimuksissa, jotka raportoivat tilastollisesti merkitseviä positiivisia yhteyksiä, päätellään yhteyden useimmiten johtuvan joko yhteisön koosta tai kytkeytyneisyydestä toisiin samankaltaisiin alueisiin. Negatiivisille yhteyksille ei ole juurikaan esitetty selityksiä.

Väitöskirjani toinen kokonaisuus koostuu kahdesta osasta, joista ensimmäisessä vertailin immen- (*Calopteryx splendens*) ja neidonkorentopopulaatioiden (*Calopteryx virgo*) geneettisiä monimuotoisuuksia ja populaatiorakenteita, ja toisessa osassa tutkin näiden geneettisten ominaisuuksien yhteyksiä sudenkorentoyhteisöjen lajistolliseen monimuotoisuuteen. Tämän lisäksi pyrin erottelemaan eri ympäristötekijöiden vaikutuksia näihin yhteyksiin. Immen- ja neidonkorentopopulaatioiden geneettisten rakenteiden tarkastelu osoitti, että näiden lajien geneettiset populaatiorakenteet olivat hyvin toisistaan poikkeavat, ja että vuorovaikutukset neidonkorennon kanssa mahdollisesti vähentävät immenkorennon geneettistä monimuotoisuutta. Vertailu sudenkorentoyhteisöjen lajistollisten monimuotoisuuksien ja immen- ja neidonkorentopopulaatioiden geneettisten monimuotoisuuksien välillä paljasti, että lajirunsaus ei ollut yhteydessä immenkorentopopulaatioiden geneettiseen monimuotoisuuteen. Sen sijaan neidonkorentopopulaatioissa positiivinen yhteys oli havaittavissa, mutta yksikään mitatuista ympäristömuuttujista ei yksiselitteisesti kyennyt selittämään tätä yhteyttä.

Väitöskirjani viimeisessä osassa tarkastelin sekä geneettisen monimuotoisuuden vähenemisestä johtuvan sisäsiitosheikkouden että elinympäristöjen pirstoutumisen ja kytkeytyneisyyden vaikutuksia lajistolliseen monimuotoisuuteen. Tähän käytin yksilöpohjaisia simulaatioita useista paikallisyhteisöistä koostuvista metayhteisöistä. Simulaatioissa sisäsiitosheikkous selkeästi kiihdytti metayhteisöjen sukupuuttonopeuksia, mutta elinympäristöjen pirstoutuminen tai kytkeytyneisyyden väheneminen eivät. Sisäsiitosheikkoudella ei myöskään ollut yhdysvaikutuksia pirstoutumisen tai kytkeytyneisyyden kanssa. Paikallisyhteisöissä taas pirstoutumisen ja kytkeytyneisyyden vaikutukset olivat suuremmat kuin sisäsiitosheikkouden. Sisäsiitosheikkous lisäsi eniten keskimääräisesti runsaiden lajien sukupuuttonopeuksia.

Yhteenvetona voin todeta, että lajistollisen ja geneettisen monimuotoisuuden väliset yhteydet ovat luonnossa hyvin vaihtelevia, ja että ympäristötekijöiden lisäksi myös lajienväliset vuorovaikutukset saattavat vaikuttaa näihin yhteyksiin. Lajistollisen ja geneettisen monimuotoisuuden välisen yhteyden vaihtelevuudesta johtuen geneettisen monimuotoisuuden ennustaminen lajistollisen monimuotoisuuden perusteella on epäluotettavaa. Tämän vuoksi voi olla luonnonsuojelun kannalta välttämätöntä, että luonnonpopulaatioiden geneettisiä

monimuotoisuuksia ja rakenteita mitataan, sillä mikäli geneettistä monimuotoi-
suutta ei huomioida, saatetaan aliarvioida sukupuuttonopeuksia.

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44

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ORIGINAL PAPERS

I

CONSERVATION IMPLICATIONS OF SPECIES–GENETIC DIVERSITY CORRELATIONS

by

Aapo Kahilainen, Mikael Puurtinen & Janne Kotiaho 2014

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Review paper

Conservation implications of species–genetic diversity correlations

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ABSTRACT

Despite its importance for the long-term viability of populations and functioning of ecosystems, the genetic diversity of populations is seldom given explicit consideration in conservation prioritization. Research on the species–genetic diversity correlation (SGDC) suggests that species diversity within a community and intrapopulation genetic diversity are positively correlated, due to the parallel influences of environmental characteristics (area, connectivity, and environmental heterogeneity) on both levels of diversity. A positive locality scale SGDC (i.e. α-SGDC) thus provides potential for simultaneous conservation of both species diversity within a locality and intrapopulation genetic diversity. However, caution is needed, since in some situations environmental characteristics can influence species diversity and genetic diversity differently, resulting in a negative α-SGDC. In such cases there can be a conflict between conservation of species diversity within localities and genetic diversity within populations. SGDCs provide useful information also for conservation planning, which considers compositional differences between localities, since the mechanisms behind α-SGDCs can also drive correlations between differentiation of community and genetic compositions (i.e. β-SGDCs). We suggest that emphasizing locality area and connectivity between similar localities in conservation planning best conserves both species and intrapopulation genetic diversity, and that focusing on highly complementary species richness may compromise conservation of genetic diversity.

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Contents

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1. Introduction

Intrapopulation genetic diversity is important for the long-term persistence of populations for two primary reasons: (1) genetically determined phenotypic variation is equated with adaptive potential of populations (e.g. Blows and Hoffmann, 2005; Bell and Collins, 2008; Hoffmann and Sgrò, 2011), and (2) neutral genetic variation of natural populations reflects inbreeding and genetic drift, which reduce the viability of populations (Reed and Frankham, 2003; Puurtinen et al., 2004; Spielman et al., 2004; Frankham, 2005a; O'Grady et al., 2006). However, even though neutral genetic diversity cannot be expected to be directly equated with variation in any particular phenotypic characteristic (Reed and Frankham, 2001), it can be expected to reflect evolvability and adaptive potential in the long-term due to its link with effective population size (Robertson, 1960; Frankham, 2005b; Willi et al., 2006; Lanfear et al., 2014). Consequently, reduced intrapopulation genetic diversity, be it neutral or adaptive, is related to increased extinction risk in natural populations.

Since the ultimate goal of conservation actions is to ensure the long-term persistence of species, the conservation of intrapopulation genetic diversity should be of high priority. However, despite increasing calls for explicit consideration of genetic and evolutionary mechanisms in conservation planning (Frankel, 1974; Smith et al., 1993; Bowen, 1999; Laikre, 2010; Vasconcelos et al., 2012; Ponce-Reyes et al., 2014), intrapopulation genetic diversity has been considered only in certain species-specific conservation programs (Mace and Purvis, 2008; Walpole et al., 2009; GEO BON, 2011).

The neglect of intrapopulation genetic diversity in conservation planning is perhaps understandable, given the challenges of practical conservation work. With considerable gaps even in species diversity data (Walpole et al., 2009), mapping intrapopulation genetic diversity could be considered secondary in importance. Furthermore, even if information on intrapopulation genetic diversities is available, the objectives for the conservation of intrapopulation genetic diversity might conflict with conservation objectives at higher levels of the biological hierarchy such as species diversity (Bowen, 1999; Arponen, 2012). Although spatial conservation prioritization methodology in systematic conservation planning can aid the simultaneous achievement of multiple objectives (Moffett and Sarkar, 2006; Moilanen et al., 2009) and alleviate conflicts between them, incorporating numerous targets in conservation planning can reduce performance of target based conservation planning (Di Minin and Moilanen, 2012). Incorporating explicit targets for conservation of intrapopulation genetic diversity of multiple species could thus lead to sub-optimal outcomes with respect to other targets (but see Diniz-Filho and Telles, 2006; Vandergast et al., 2008; Thomassen et al., 2011).

Research on the species–genetic diversity correlation (SGDC) can provide valuable information on whether the conservation of intrapopulation genetic diversity can conflict with the conservation of species diversity or *vice versa*. Within localities (i.e. α diversity), α-SGDC describes the relationship between species diversity in a local community and intrapopulation genetic diversity within the species, and both positive and negative α-SGDCs have been observed in natural systems (Karlin et al., 1984; Wehenkel et al., 2006; Marshall and Camp, 2006; Papadopoulou et al., 2011; Vellend et al., 2014). The sign of the α-SGDC directly indicates whether there is a conflict between the conservation of the two levels of biodiversity: Positive α-SGDCs suggest that conservation actions focusing on local species diversities also conserves intrapopulation genetic diversity, whereas negative α-SGDCs suggest that conservation of one level of diversity may compromise diversity on the other level. Furthermore, the mechanisms behind the α-SGDCs (stochastic processes, dispersal, and selection) also influence differentiation between localities (i.e. β diversity). Therefore they can drive correlations between differentiation of community compositions and genetic differentiation of populations (i.e. β-SGDCs). Thus, focusing on the mechanistic explanations behind α- and β-SGDC provides an interesting avenue for predicting diversity patterns also among localities, which is of interest in practical conservation, when designing conservation area networks consisting of localities complementary to each other (Moilanen et al., 2009).

Here, we briefly outline α- and β-SGDCs and summarize how they can arise in groups of ecologically similar species. We explore how environmental characteristics integral to conservation biology (area, connectivity, and environmental heterogeneity) are related to stochastic processes (i.e. demographic stochasticity and genetic drift), dispersal, and selection, all of which affect species diversity and intrapopulation genetic diversity on ecological timescales (ignoring mutation and formation of new species). Our main emphasis is on assessing the utility of SGDCs in conservation biology, and on providing guidelines for practical conservation in order to avoid conflicts between the conservation of species diversity and intrapopulation genetic diversity.

2. Environmental characteristics and SGDCs

Ecological theory stresses the importance of the area of suitable habitat (from here on referred to simply as area), connectivity to other localities with similar qualities, and environmental heterogeneity on local species diversity (MacArthur and Wilson, 1967; Connor and McCoy, 1979; Hubbell, 2001; Evans et al., 2005; Stein et al., 2014). Similarly, genetic diversity within populations (e.g. haplotype diversity, allelic richness, heterozygosity, or quantitative genetic variation) is influenced
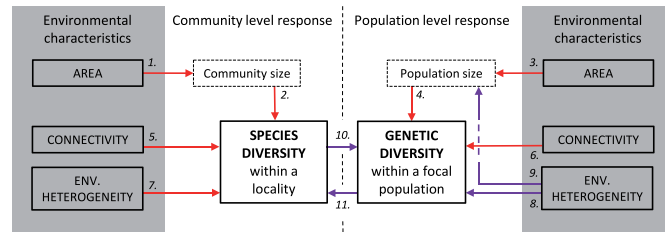
Fig. 1. The drivers of local scale species–genetic diversity correlations (i.e. α-SGDCs). Analogous effects of environmental characteristics (gray) influence both community and population level responses. Positive connections are indicated with a red arrow and connections that are ambiguous are indicated with a purple arrow. Numbered arrows are described in detail in the text. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

by population size, gene flow, and selection, all of which can be driven by the very same environmental characteristics that influence species diversity (Vellend, 2005; Manel and Holderegger, 2013).

Area, connectivity and environmental heterogeneity are often correlated and, in practice, their relative contributions to diversity patterns can be difficult to disentangle (MacArthur and Wilson, 1967; Connor and McCoy, 1979; Ricklefs and Lovette, 1999). However, the characteristics influence diversity via different mechanisms, and therefore, we discuss them independent of each other, i.e. assuming that all other environmental characteristics are held constant.

2.1. Area

When there is a positive relationship between community size (i.e. the number of individuals) and area (Fig. 1, arrow 1), area can drive positive α-SGDCs via sampling effect and stochastic processes (Vellend, 2003). Since increasing area supports increasing community sizes, the number of observed species increases with increasing area (Fig. 1, arrow 2) as more species are sampled from the regional species pool (MacArthur and Wilson, 1967; Connor and McCoy, 1979; Evans et al., 2005). Furthermore, also extinction rate is reduced due to reduced demographic stochasticity (MacArthur and Wilson, 1967; Hubbell, 2001). Area has an analogous effect on intrapopulation genetic diversity. The average population size increases with increasing area (Fig. 1, arrow 3), resulting in more genetic diversity sampled from the regional gene pool, and reduced intensity of genetic drift. In general, larger populations tend to be more genetically diverse (Fig. 1, arrow 4) (Kimura and Crow, 1964; Frankham, 2005a; Hoeck et al., 2010).

In addition to influencing diversity within localities, area can also influence the degree of differentiation in species compositions between communities and genetic differentiation between populations. Since demographic stochasticity increases with decreasing number of individuals, smaller communities differentiate more easily than larger communities (Hubbell, 2001). Similarly, the genetic composition of smaller populations in smaller communities can drift to different allele frequencies faster than it does in large populations in larger communities (Kimura and Crow, 1964). Therefore, area is expected to drive positive β-SGDCs. Besides area, any factor influencing the community size of a locality can drive species and genetic diversity in the same direction. Ultimately, the community size is determined by a limiting resource of some sort, be it e.g. space, nutrients, or water (Evans et al., 2005; Honkanen et al., 2010).

2.2. Connectivity

Connectivity influences the dispersal of individuals between localities, and well-connected localities receive immigrants from more species than less well-connected localities (Fig. 1, arrow 5) (MacArthur and Wilson, 1967). Analogously, well-connected populations receive more alleles with immigrants than less well-connected populations (Fig. 1, arrow 6) (Vellend, 2005), and therefore connectivity can be expected to drive positive α-SGDCs. Like area, also connectivity is expected to influence the degree of community and genetic differentiation in parallel and result in a positive β-SGDC: In a well-connected landscape, dispersal can prevent stochastic processes and selection from creating differences between the species compositions of communities and genetic compositions of populations in different localities (Hartl and Clark, 1997; Bohonak, 1999; Hubbell, 2001; Cadotte, 2006).

2.3. Environmental heterogeneity

Environmental heterogeneity can be spatial, temporal or spatio-temporal (i.e. spatially structured temporal environmental variability) (Chesson, 2000; Kassen, 2002; White et al., 2010; Stein et al., 2014). Majority of ecological literature (including literature on the SGDC) and spatial conservation planning has focused on spatial heterogeneity, however, predictions for the influence of temporal and spatio-temporal environmental heterogeneity are very similar to spatial heterogeneity

(Kassen, 2002; White et al., 2010). Environmental heterogeneity influences species diversity primarily through selection, and intrapopulation genetic diversity through both selection and genetic drift. Increasing environmental heterogeneity can mean that more species can find suitable conditions and persist in a locality (i.e. competitive exclusion less likely), and thus, heterogeneous localities can maintain more species than homogeneous localities (Fig. 1, arrow 7) (Stein et al., 2014). From the point-of-view of non-neutral genetic variation, environmental heterogeneity can also create disruptive selection, and therefore support different genotypes within populations (Fig. 1, arrow 8) (Via and Lande, 1985). On the other hand, environmental variation can select for generalist species or a generalist genotype capable of exploiting a wide variety of habitats, reducing the number of species and genetic variation (Via and Lande, 1985; Kassen, 2002; Ketola et al., 2013). Thus, selection due to environmental heterogeneity can cause both positive and negative α-SGDCs when considering neutral and non-neutral genetic diversity.

Environmental heterogeneity also influences the intensity of genetic drift by affecting population size (Fig. 1, arrow 9). Environmental heterogeneity can increase or decrease population size, depending on the requirements of the species. If increasing environmental heterogeneity leads to an increase in the amount of rare habitat, the population sizes of species requiring this kind of habitat are likely to increase (Vellend, 2005). However, with increasing amount of more rare or extreme habitats the average amount of area suitable for each species is reduced, resulting in smaller populations on average (Vellend, 2005; Allouche et al., 2012). By increasing the number of species while simultaneously decreasing population sizes, environmental heterogeneity can drive a negative α-SGDC when considering neutral genetic diversity.

All else being equal, increasing environmental heterogeneity within localities likely decreases the differences in the community compositions between localities. If increasing environmental heterogeneity within localities leads to the localities representing a larger fraction of the environmental conditions available within a region, each locality harbors an increasing proportion of species from the landscape scale species pool, and their community compositions become increasingly similar. Differentiation between local communities decreases also in the case that increasing heterogeneity within localities selects for few generalist species in all of them. On the other hand, since increasing environmental heterogeneity can lead to decreasing average population sizes, environmental heterogeneity can increase the genetic differentiation between populations at different localities due to increased genetic drift, particularly at neutral loci. Thus the differentiation at the community level might not match that at the genetic level.

3. Direct interactions between levels of diversity

In addition to locality characteristics creating SGDCs, species diversity and genetic diversity can also influence each other directly via selection (e.g. due to competitive and facilitating interactions between con- and heterospecific individuals). Adaptive genetic diversity, rather than neutral genetic diversity, is more likely to reveal the influence of direct interactions (Fig. 1, arrows 10 and 11) (Vellend and Geber, 2005; Vellend, 2006; Lankau and Strauss, 2007; Costa et al., 2008; Hughes et al., 2008). However, the influence of direct interactions can also be seen in neutral genetic diversity via their effects on population sizes and genetic drift (explained below).

The direct effects of species diversity can be expected to be largely similar to those of environmental heterogeneity. Like environmental heterogeneity, species diversity within a locality can maintain genetic diversity within populations of a focal species by disruptive selection, as different species select for different genetically determined phenotypes of the focal species (Vellend and Geber, 2005; Adams and Vellend, 2011). However, the surrounding community of species can also select for a single genotype specialized in interspecific competition (Lankau and Strauss, 2007), narrow down the ecological niche of a population (Van Valen, 1965; Vellend, 2006; Costa et al., 2008; Silvertown et al., 2009) and reduce population sizes (Fig. 1, arrow 10) (Ranta et al., 2009; Nimmo et al., 2011; Östman, 2011; Nestmann et al., 2011; Kahilainen et al., 2014). Thus, whether the species diversity in a community drives positive or negative SGDCs seems to depend on context and community composition.

Just as increasing species diversity within a locality can increase or decrease genetic diversity within a population, so can increasing genetic diversity of a particular population either increase or decrease the species diversity within localities (Fig. 1, arrow 11) (Vellend and Geber, 2005). Genetic variation within a population of competitively dominant species can enable coexistence of other species and even determine the species composition in the community (Vellend, 2006; Lankau and Strauss, 2007; Fridley and Grime, 2010). However, genetic variation within a dominant species can also allow for a wider niche for that particular species, filling up the available niche space which leads to reduced population sizes, or even competitive exclusion of other ecologically similar species (Crutsinger et al., 2008).

4. The generalizability of SGDCs

Four reviews on the SGDC exist (Vellend, 2003; Vellend and Geber, 2005; Vellend et al., 2014; Whitlock, 2014), with three of them suggesting that the majority of α-SGDCs of natural populations are positive (Vellend, 2003; Vellend and Geber, 2005; Vellend et al., 2014). The median α-SGDC derived from the results of studies on natural populations included in previous reviews, two additional studies missing from previous reviews (Robinson et al., 2010; Lamy et al., 2013) and our own unpublished data on *Calopteryx* damselfly populations and odonate stream communities (*Calopteryx splendens* and *C. virgo* damselfly populations) is 0.17 (Fig. 2(a); Supplementary material A). However, the variation in the sign and
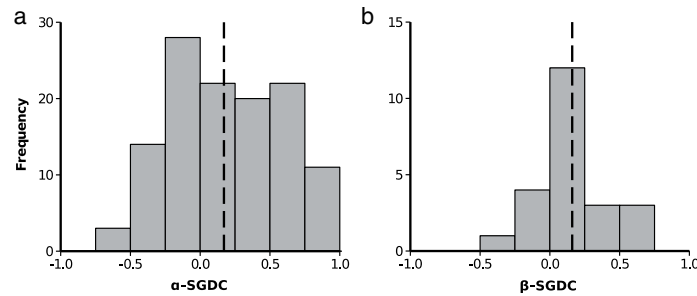
Fig. 2. The frequencies of (a) α-SGDCs and (b) β-SGDCs reported from natural populations. The dash line represents the median. See supplementary material (Tables A1, A2 and A3) for details.

magnitude of the correlation is high (S.D. $= 0.40$). A proportion of the variation can be attributed to differences between α-SGDCs measured from discrete island-like habitat patches and continuous habitats, with α-SGDCs on island-like habitats being stronger and more often positive (Vellend and Geber, 2005; Vellend et al., 2014). The rationale here is that species diversities and intraspecific genetic diversities on island-like habitats are more likely to be driven in parallel by dispersal and stochastic processes, the consequences of which are more predictable than those of different highly context dependent selection scenarios. That stochastic processes and dispersal indeed are the most likely contributors to positive SGDCs is supported by a closer inspection of the individual studies: Of the 16 studies that reported statistically significant positive α-SGDCs, six considered the relationship to be driven by area or some other factor related to community size (e.g. habitat quality or productivity), two by connectivity, and four by some combination of the two (Supplementary material A, Tables A1 and A2).

The difference between island-like and mainland-like habitats is not able to explain all the variation observed in α-SGDCs, since significant negative α-SGDCs are also observed (Fig. 2(a)), and connectivity and area are not expected to drive negative α-SGDCs. However, the drivers of negative α-SGDCs are rarely discussed in the empirical literature, and when they are, the mechanistic explanations are speculative at best. Thus, the role of environmental heterogeneity and direct interactions in creating α-SGDCs largely remains unresolved with two exceptions. Marshall and Camp (2006) suggested environmental heterogeneity to be positively related to both the richness of lungless salamander species (Plethodontidae) and their respective allelic richnesses. On the other hand, Taberlet et al. (2012) suggested that environmental heterogeneity in glacial refugia could be responsible for the negative and zero α-SGDCs in the flora of European Alpine regions. Environmental heterogeneity (in this case topographic variation) in glacial refugia could have enabled the coexistence of a large variety of species, but each species would have been represented by only a small number of individuals, making the populations prone to genetic drift in the absence of gene flow. Furthermore, a study on breeding bird distributions in Catalonia concluded that increasing environmental heterogeneity leads to decreased population sizes. Allouche et al. (2012), which indirectly suggests that environmental heterogeneity can increase the magnitude of genetic drift, leading to negative α-SGDCs.

The distribution of β-SGDCs is very similar to the ones observed for α-SGDCs (Fig. 2(b); median β-SGDC $= 0.16$; S.D. $= 0.26$; Supplementary material A, Table A3). However, there are slight differences to the α-SGDCs in the sense that a larger proportion of the reported β-SGDCs fall close to zero and all statistically significant β-SGDCs seem to be positive (Fig. 2(b); Supplementary material A, Table A3). The β-SGDCs seem to emphasize connectivity since four of the seven studies reporting statistically significant β-SGDCs considered connectivity to be related to parallel patterns of community and population differentiation (Sei et al., 2009; Odat et al., 2010; Papadopoulou et al., 2011; Blum et al., 2012). In addition, three studies suggested selection due to some ecological characteristic of the communities to drive the positive β-SGDCs at least to some extent (Odat et al., 2004; Yu et al., 2009; Odat et al., 2010).

In order to study how species diversity and genetic diversity within populations can directly influence each other, experimental manipulations of species diversity and non-neutral genetic diversity are needed. The experimental studies available illustrate that direct interactions between species diversity and genetic diversity can create both positive and negative SGDCs. Genotypes can differ in their competitive abilities against different heterospecific competitors (Powell and Wistrand, 1978; Lankau and Strauss, 2007; Fridley and Grime, 2010), and, on the other hand, experimentally increasing species diversities of communities can reduce intrapopulation genetic diversity by reducing population sizes and niche availability (Silvertown et al., 2009; Östman, 2011; Nestmann et al., 2011). Nevertheless, a recent meta-analysis suggests that non-neutral genetic diversity in plant populations is positively related to species diversity within communities (Whitlock, 2014). However, it needs to be noted that studies included in that analysis often considered species diversity across different trophic levels and functional groups, and therefore may largely reflect processes related to trophic cascades (e.g. Wimp et al., 2004, Crawford and Rudgers, 2013).

5. SGDC and conservation

From a practical conservation perspective, it seems encouraging that the majority of the SGDCs are positive. Furthermore, the locality characteristics related to stochastic processes and increased dispersal – area and connectivity – drive positive SGDCs allowing for predicting diversity at one level based on the other. However, the variation in SGDCs is high, and the role of selection is very context and community dependent, suggesting that making conservation decisions based on characteristics influencing the selective regime (i.e. environmental heterogeneity) should be done cautiously.

5.1. The usefulness of the α-SGDC for conserving diversity within localities

An obvious application of the α-SGDC is to use the biodiversity at one level as a surrogate of that at the other level. Since landscape level spatial genetic information for multiple species are still mostly lacking (Marshall and Camp, 2006; Fortuna et al., 2009; Robinson et al., 2010; Papadopoulou et al., 2011; Messmer et al., 2012; Taberlet et al., 2012), an intuitive approach for using SGDCs would be to predict patterns of intrapopulation genetic diversity based on information on species diversity. Such an approach could be useful for example in evaluating how different anthropogenic disturbance regimes influencing the species diversity of a community can simultaneously influence genetic diversities and thus also the viabilities of the remaining constituent populations (Vellend, 2004; Cleary et al., 2006; Evanno et al., 2009; Struebig et al., 2011). Conversely, it might be possible to use genetic diversities of common species to predict localities of high species diversity in cases where species diversity is difficult to sample. However, to our knowledge this has not yet been attempted. It should be noted, however, that to utilize either level of diversity as a surrogate for the other, the mechanism underlying the diversity at the observed level needs to be known. For example, if species diversities of localities in a landscape are mostly driven by community size or connectivity, the genetic diversities of the constituent populations are likely to be concordant with the species diversities. On the other hand, if species diversity patterns are driven by environmental heterogeneity, predicting the patterns of genetic diversity can be less reliable.

5.2. The usefulness of β-SGDCs for conserving diversity between localities

In addition to diversity within localities, differences between localities need to be taken into account to adequately cover diversity across localities. In spatial conservation prioritization the conservation of diversity at the landscape scale is achieved by selecting localities that best complement each other with respect to the desired biodiversity features (Margules and Pressey, 2000; Arponen et al., 2008; Moilanen et al., 2009). At first, it may appear that complementary site selection conducted at the species level also leads to complementarity at the genetic level or vice versa. For example, in seven studies, pairwise genetic differentiation between populations sampled from different localities (i.e. genetic population structure) positively correlated with the pairwise community differentiation (i.e. community structure) of the localities (Vellend, 2004; Odat et al., 2004; Yu et al., 2009; Sei et al., 2009; Odat et al., 2010; Papadopoulou et al., 2011; Blum et al., 2012) and two additional studies gave support for a positive β-SGDC although it was not explicitly tested (Evanno et al., 2009; Baselga et al., 2013). Indeed, Fuller et al. (2013) suggested that genetic differentiation of common species could be used as surrogate for species diversity in systematic conservation planning, since genetic complementarity seems to reflect species complementarity. However, it is important to note that β-SGDCs can only arise when the set of species, for which genetic diversities are measured, are present in all of the communities. This condition can conflict complementarity of species composition. To put it another way, if a conservation area network is designed based on complementarity of species composition, each species might be represented only few times in the network (in an extreme case only once), and complementarity at the genetic level cannot be expected. Such a scenario of strict complementarity could reduce intrapopulation genetic diversity by reducing connectivity between populations and increasing genetic drift, leading to increased extinction risk of populations.

An additional level of complication arises when the economic limitations are taken into account. The link between costs and area set aside for conservation is self-evident: an attempt to minimize the costs while covering a set of biodiversity features leads to searching for solutions where minimum total area is set aside for conservation (but see Kareksela et al., 2013). Thus, the localities that cover many features and those that are complementary to each other are likely to be incorporated into the conservation area network (i.e. maximization of complementary richness; Arponen et al., 2008). Under this scenario it is likely that environmentally heterogeneous areas are favored since larger fractions of the regional species diversity can be covered within smaller areas (Bonn and Gaston, 2005; Kati et al., 2010). This may pose a threat because while increasing environmental heterogeneity can select for increasing number of species, it can simultaneously lead to smaller populations, which then lose genetic diversity due to drift and are thus more prone to extinction (see above).

Thus, in a hypothetical worst-case scenario, putting a high emphasis on cost-efficiency and complementarity at the species level can lead to a conservation area network consisting of highly diverse but small local communities that are strictly complementary to each other. Although a large initial number of species can be covered with low costs using such a design, populations are likely to be small and receive no gene flow because of the strict complementarity at the species level. If gene flow is very low, genetic diversity at the small populations will erode due to genetic drift and inbreeding, making the populations prone to extinction. Eventually this initially appealing scenario is likely to lead to reduced diversity

at the species level as well. In practice, however, the conflict is unlikely to be as severe as suggested by the above worst-case scenario, since the number of species is rarely the only biodiversity feature given priority in the spatial conservation prioritization (Moffett and Sarkar, 2006; Moilanen et al., 2009).

Although prioritizing large areas (or large community sizes) and high connectivity between the local communities likely contradict cost-efficiency and complementarity, these environmental characteristics can serve as safe simple aggregate targets to conserve diversity at both levels of biodiversity. Indeed, increasing locality size and connectivity between localities are associated with increased persistence of species diversity in meta-communities (Cabeza and Moilanen, 2003, Rybicki and Hanski, 2013, see also Ponce-Reyes et al., 2014). An interesting direction in the future will be to devise ways to implement conservation area networks that allow persistence of large meta-community sizes via enhanced connectivity that would be likely to succeed in conserving simultaneously both species diversity and intrapopulation genetic diversity. An interesting opening to this direction, coined as the third-of-third approach, suggests that one third of the landscape should be managed as a conservation landscape and within that landscape one third of land area would be set aside for conservation (Hanski, 2011).

Although with the use of simple environmental targets, such as larger area or increased connectivity, some relevant biological complexity is inevitably missed simplicity in prioritization is likely to increase the chances that the prioritization will be applied in practice (Arponen, 2012). Furthermore, since the area and connectivity are fundamentally related to stochastic processes and dispersal, focusing on these environmental characteristics is linked to the process based conservation prioritization many evolutionary biologists and conservation geneticists have been calling for. Finally, studying SGDCs can provide information about the mechanisms driving diversity within each landscape and can therefore give insight on which features to focus on when making conservation decisions.

Acknowledgments

Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.10.013.

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CONSERVATION IMPLICATIONS OF SPECIES-GENETIC DIVERSITY CORRELATIONS

Supplementary material A

Description of literature search for Figure 2 of main text and supplementary tables A1, A2 and A3:

We derived species-genetic diversity correlations (SGDCs) of natural populations (no experimental studies with manipulations were included) from previous reviews we were aware of during the preparation of the manuscript (i.e. Vellend 2003, Vellend & Geber 2005, Vellend et al. 2014). We continued by searching for articles explicitly focusing on SGDCs of natural populations using online search engines (Thomson Reuters Web of Science, http://www.webofknowledge.com; Google Scholar, http://scholar.google.com) to track studies citing either Vellend (2003) or Vellend & Geber (2005). We did not include SGDCs in which genetic diversity was measured from a species belonging to a different trophic level than the species group of comparison (e.g. Wimp et al 2004; Eldon et al. 2013).

We found 26 studies encompassing a total of 128 taxa. Of the 128 taxa, we could derive α-SGDCs for 108 and β-SGDCs for 21 taxa either directly from the studies or by calculating them ourselves, if SGDCs were not reported but information on species diversity and genetic diversity was provided. Additionally, we included two unpublished datasets on α- and β-SGDCs of two damselfly species (*Calopteryx splendens* and *C. virgo*). For the statistically significant SGDCs in supplementary tables A1, A2 and A3 we derived the suggested cause for the relationship based on discussion in the original manuscripts. When it was possible, the suggested causes were grouped under the environmental characteristics of "locality area or quality", "connectivity" or "environmental heterogeneity". For Figure 2a, we prioritized α-SGDCs between species richness and allelic richness if multiple different α-SGDCs for the same taxa from the same area were reported. For Figure 2b, we prioritized β-SGDCs between pairwise differentiation metrics that were based on abundance data rather than presence-absence data. Furthermore, for both and α- and β-SGDCs we prioritized SGDCs in which species diversity was derived from ecologically similar species.

Table A1. Observed α-SGDCs in natural communities of vascular plants. Most of the studies correlated genetic diversity within populations of species to species diversity in the community. One of the studies [10], however, took a trans-specific approach to genetic diversity by correlating species richness either to genetic diversity across different genera and in this study effective number of variants (v_2, Gregorius 1978) in both species richness and genetic diversity within species was used. The strength and direction of the correlation is indicated with a correlation coefficient (r) and statistical significance of the correlation is indicated with asterisk (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$). Studies that give tentative evidence for an SGDC but report no test, or have insufficient reporting to allow for testing the SGDC, are indicated with a cross (†). In cases where the direction of the correlation cannot be read from the correlation coefficient the suggested direction is indicated with a plus (+) or minus (-) sign in parentheses.

Study	Species	Marker	Relationship	Region	Correlation	Driver of SGDC
[1]	*Androsace obtusifolia*	AFLP	SR-AFLP	EU: Alps	r=0.26	
[2]	*Anthyllis vulneraria*	AFLP	SR-H	EU: Belgium	**r=0.55***	Not specified
[1]	*Arabis alpina*	AFLP	SR-AFLP	EU: Alps	r=-0.04	
[3]	*Ardisia crenata*	Micros.	SR-AR	AS: China, Gutianshan national nature reserve	r=-0.08[a]	
[4]	*Banksia attenuata*	Micros.	SR-AR	OC: S-W Australia	**r=0.62***[a]	
			SR-H		**r=0.50**[a]	Locality area or quality
			SD-AR		**r=0.46*[a]	& direct interactions
			SD-H		r=0.30[a]	
[5]	*Briza media*	Az	SR-AR	EU: Estonia,	r=-0.02	
			SR-H	Saaremaa & Muhu	r=0.16	
[1]	*Campanula alpina*	AFLP	SR-AFLP	EU: Carpathians	r=-0.11	
[1]	*Campanula barbata*	AFLP	SR-AFLP	EU: Alps	**r=-0.24***	Not specified[6]
[1]	*Campanula serrata*	AFLP	SR-AFLP	EU: Carpathians	r=0.43	
[6]	*Carex curvula*	AFLP	SR-AFLP	EU: Alpine system	(-)†	
			SR-AFLP$_{w.ind.}$		**r=-0.52***	Different responses of
			SR-AFLP$_{btw.ind.}$		(0)†	species diversity and
			SD-AFLP		(-)†	genetic diversity to
			SD-AFLP$_{w.ind.}$		(0)†	glacial cycles and
			SD-AFLP$_{btw.ind.}$		(0)†	recolonization
[1]	*Carex firma*	AFLP	SR-AFLP	EU: Alps	r=-0.18	
[1]	*Carex sempervirens*	AFLP	SR-AFLP	EU: Alps	r=-0.01	
			SR-AFLP	EU: Carpathians	**r=0.65***	Not specified[6]
[2,7]	*Carex rariflora*	Az	SR-H	NA: Subarctic Quebec	**r=0.81***	Not specified
[1]	*Cerastium uniflorum*	AFLP	SR-AFLP	EU: Alps	**r=0.33***	Not specified[6]
[1]	*Cirsium spinosissimum*	AFLP	SR-AFLP	EU: Alps	r=0.18	
[8]	*Daviedsia triflora*	Microsat.	SR$_{similar}$-AR	OC: SW Australia	**r=0.44*[a]	Locality area or quality & direct interactions
[1]	*Dryas octopetala*	AFLP	SR-AFLP	EU: Alps	**r=-0.22***	Not specified[6]
[9]	*Euptelea pleiospermum*	Microsat.	SR-AR	AS: China, Nan river	r=-0.44[a]	
			SD-H	AS: China, Nan river	r=0.38[a]	
			SR-AR	AS: China, Yandu river	r=0.57[a]	Locality area or quality
			SD-H	AS: China, Yandu river	**r=0.73[a]	
[10]	*Fagus sylvatica*	Az	$v_{2,sp.}$ -$v_{2,gen.}$	EU: Central Germany	**r=-0.48***	Not specified
[1]	*Festuca carpathica*	AFLP	SR-AFLP	EU: Carpathians	r=0.16	
[1]	*Festuca supina*	AFLP	SR-AFLP	EU: Carpathians	r=-0.31	
[1]	*Festuca versicolor*	AFLP	SR-AFLP	EU: Carpathians	r=0.02	
[10]	Forest tree species	Az	$v_{2,sp.}$ -$v_{2,trans\,sp.\,gen.}$	EU: Central Germany	**r=0.71*** †	Species rich communities consist of pioneer species which are also more genetically diverse than climax species.
[1]	*Gentiana nivalis*	AFLP	SR-AFLP	EU: Alps	r=-0.03	
			SR-AFLP	EU: Carpathians	r=0.59	
[1]	*Geum montanum*	AFLP	SR-AFLP	EU: Alps	r=0.02	
			SR-AFLP	EU: Carpathians	r=-0.05	
[1]	*Geum reptans*	AFLP	SR-AFLP	EU: Alps	**r=-0.30***	Not specified[6]

Table A1 continued.

Study	Species	Marker	Relationship	Region	Correlation	Driver of SGDC
[11]	*Gossypium darwinii*	Az	SR-H	SA: Galápagos	**r=0.76***	Locality area or quality
[1]	*Gypsophila repens*	AFLP	SR-AFLP	EU: Alps	r=0.17	
[2,12]	*Gypsophila fastigiata*	Az	SD-H	EU: Öland, Sweden	r=0.28	
[1]	*Hedysarum hedysaroides*	AFLP	SR-AFLP	EU: Alps	**r=-0.40*****	Not specified[b]
			SR-AFLP	EU: Carpathians	r=-0.45	
[1]	*Hornungia alpina*	AFLP	SR-AFLP	EU: Alps	**r=-0.24***	Not specified[b]
[1]	*Hypochaeris uniflora*	AFLP	SR-AFLP	EU: Alps	r=-0.03	
			SR-AFLP	EU: Carpathians	r=-0.12	
[1]	*Juncus trifidus*	AFLP	SR-AFLP	EU: Alps	r=0.14	
			SR-AFLP	EU: Carpathians	r=-0.04	
[1]	*Ligusticum mutellionoides*	AFLP	SR-AFLP	EU: Alps	r=0.11	
[11]	*Lobularia canariensis*	Az	SR-H	AF: Canary Islands	**r=0.80***	Locality area or quality & connectivity
[1]	*Loiseleuria procumbens*	AFLP	SR-AFLP	EU: Alps	r=-0.17	
			SR-AFLP	EU: Carpathians	r=-0.04	
[1]	*Luzula alpinopilosa*	AFLP	SR-AFLP	EU: Alps	r=-0.19	
[1]	*Maianthemum bifolium*	AFLP	SR-H	EU: Belgium	r=0.45	
[1]	*Peucedanum ostruthium*	AFLP	SR-AFLP	EU: Alps	r=0.01	
[1]	*Phyteuma betonicifolium*	AFLP	SR-AFLP	EU: Alps	r=0.11	
[1]	*Phyteuma confusum*	AFLP	SR-AFLP	EU: Carpathians	r=-0.69	
[1]	*Phyteuma hemisphaericum*	AFLP	SR-AFLP	EU: Alps	r=0.20	
[2]	*Picea abies*	Az	SD-H	EU: Central Germany	r=-0.05	
[13]	*Plantago lanceolata*	AFLP	SR-H	EU: Central Germany	**r=0.52***	
			SD-H		r=0.49	Locality area or quality
[2]	*Primula elatior*	AFLP	SR-H	EU: Belgium	r=0.32	
[1]	*Primula minima*	AFLP	SR-AFLP	EU: Carpathians	r=-0.01	
[14]	*Ranunculus acris*	AFLP	SR-H	EU: Central Germany	r=-0.17	
[1]	*Ranunculus alpestris*	AFLP	SR-AFLP	EU: Alps	**r=-0.38****	Not specified[b]
[1]	*Rhododendron ferrugineum*	AFLP	SR-AFLP	EU: Alps	**r=0.21***	Not specified[b]
[1]	*Rhododendron myrthifolium*	AFLP	SR-AFLP	EU: Carpathians	r=0.22	
[1]	*Saxifraga stellaris*	AFLP	SR-AFLP	EU: Alps	r=-0.17	
			SR-AFLP	EU: Carpathians	r=0.14	
[1]	*Saxifraga wahlenbergii*	AFLP	SR-AFLP	EU: Carpathians	r=0.51	
[1]	*Sempervivum montanum*	AFLP	SR-AFLP	EU: Carpathians	r=0.25	
[1]	*Sesleria caerulea*	AFLP	SR-AFLP	EU: Alps	r=-0.01	
[1]	*Soldanella pusilla*	AFLP	SR-AFLP	EU: Carpathians	r=-0.31	
[1]	*Trifolium alpinum*	AFLP	SR-AFLP	EU: Alps	r=-0.08	
[15]	*Trillium grandiflorum*	Az, Micros., cpDNA-RFLP	SR-AR	NA: NE USA	r=0.35	
			SR-H		r=0.31	Locality area or quality & disturbance history
			SD-AR		r=0.31	
			SD-H		**r=0.51***	
[1]	*Veronica baumgartenii*	AFLP	SR-AFLP	EU: Carpathians	r=0.48	

Markers: AFLP = Amplified Fragment Polymorphisms; Micros. = Microsatellite loci; Az = Allozyme loci; cpDNA-RFLP = chloroplast DNA Restriction Fragment Length Polymorphisms.

Species diversity indices used in the relationships: SR = Species richness (also with logarithmic transformation); SRsimilar = Species richness of ecologically similar species; SD = Species diversity index (several).

Genetic diversity indices used in the relationships: AFLP = AFLP band diversity within a population; AFLPw.ind. = AFLP band diversity within individuals; AFLPbtw.ind. = AFLP band diversity between individuals; AR = Allelic richness; ARwithin ind. = Allelic richness within individuals; H = Heterozygosity.

Regions: EU=Europe; AS=Asia; OC=Oceania; NA=North-America; SA=South-America; AF=Africa.

a) Correlation not reported by the original authors but calculated based on the diversity values reported

b) Taberlet et al (2012) conclude that species diversity and genetic diversity are not congruent in Alpine landscapes when simultaneously focusing on multiple species. Thus, they do not discuss the statistically significant SGDCs observed for single species. The lack of a generalizable SGDC is suggested to be due to glacial cycles differently influencing species diversity and genetic diversity.

Table A2. Observed α-SGDCs on natural populations of animals. Most of the studies correlated genetic diversity within populations of species to species diversity in the community. Three of the studies ([16], [19] & [21]), however, took a trans-specific approach to genetic diversity by correlating species richness to genetic diversity within a genus. The strength and direction of the correlation is indicated with a correlation coefficient (r) and statistical significance of the correlation is indicated with asterisk (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$). In one study [27] only the coefficient of determination (R^2) was reported. Studies that give tentative evidence for an SGDC but report no test, or have insufficient reporting to allow for testing the SGDC, are indicated with a cross (†). In cases where the direction of the correlation cannot be read from the correlation coefficient the suggested direction is indicated with a plus (+) or minus (-) sign in parentheses.

Study	Species	Marker	SD-GD	Region	Correlation	Driver of SGDC
Invertebrates						
[16]	*Ammobius*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.42	
		NC	SR-π		r=-0.08	
[17]	*Aplexa marmorata*	Micros.	SR-GR	NA: Lesser Antilles	**r=0.48***	Connectivity
Unpub.	*Calopteryx splendens*	Micros	SR-AR	EU: Finland	r=-0.08	
Unpub.	*Calopteryx virgo*	Micros	SR-AR	EU: Finland	**r=0.434***	Unexplained
[18]	*Crassostrea virginica*	mtDNA	SR- π	NA: Georgia, SE USA	r=0.16	
[16]	*Dailognatha*	mtDNA	SR-Hd	EU: Aegean islands	r=0.52	
		NC	SR-π		r=-0.04	
[16]	*Dendarus*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.35	Locality area or quality &
		NC	SR-π		**r=1.00***	connectivity
[16]	*Dichomma*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.18	
		NC	SR-π		r=0.26	
[17]	*Drepanotrema depressissimum*	Microsat	SR-AR	NA: Lesser Antilles	**r=0.54***	Connectivity
[11]	48 *Drosophila sp.*	Az	SR-AR raref.	OC: Hawaii	(ns.)	
[19]			SR-AR		(-)*†	
[20]	*Drupadia theda*	Micros.	SR-AR	AS: E Borneo	**r=0.98***	Connectivity, disturbance history
[16]	*Erodius*	mtDNA	SR-Hd	EU: Aegean Islands	**r=0.68***	Locality area or quality &
		NC	SR-π		r=-0.03	connectivity
[16]	*Eutagenia* (Sand dwelling)	mtDNA	SR-Hd	EU: Aegean Islands	r=0.42	
		NC	SR-π		r=0.59	
[16]	*Eutagenia* (Soil dwelling)	mtDNA	SR-Hd	EU: Aegean Islands	**r=0.75***	Locality area or quality &
		NC	SR-π		**r=0.92***	connectivity
[21]	*Gammarus spp.*	Az	SR-AR	NA: N Chihuahua desert	(0)†	
[18]	*Geukensia demissa*	mtDNA	SR-π	NA: Coastal Georgia	**r=0.77***	Connectivity
[16]	*Graecopachys*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.28	
		NC	SR-π		r=0.02	
[16]	*Idastrandiella*	mtDNA	SR-Hd	EU: Aegean Islands	r=1.00	
[18]	*Ilyanassa obsoleta*	mtDNA	SR-π	NA: Coastal Georgia	r=0.17	
[22]	*Leptodiaptomus minutus*	mtDNA	SR-Hd	NA: Ontario	r=0.17	
			SD-H		r=0.26	
[18]	*Littoraria irrorata*	mtDNA	SR-π	NA: Georgia, SE USA	r=0.62	
[18]	*Melampus bidentatus*	mtDNA	SR-π	NA: Georgia, SE USA	r=0.79	
[16]	*Micrositus*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.04	
		NC	SR-π		r=-0.27	
[16]	*Opatrum*	mtDNA	SR-Hd	EU: Aegean Islands	r=0.47	
[16]	*Pachyscelis*	mtDNA	SR-Hd	EU: Aegean Islands	r=0.26	
[16]	*Pedinus*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.36	
		NC	SR-π		r=-0.89	
[18]	*Petrolisthes armatus*	mtDNA	SR-π	NA: Georgia, SE USA	r=0.11	
[16]	*Pimelia*	mtDNA	SR-Hd	EU: Aegean Islands	**r=1.00***	Locality area or quality & connectivity
[23]	*Radix balthica*	AFLP	SD-H	EU: SE France	(+)†	
[16]	*Raiboscelis*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.30	
[16]	*Stenosis*	mtDNA	SR-Hd	EU: Aegean Islands	r=0.98	
[16]	*Tentyria*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.08	
		NC	SR-π		r=-0.98	
[18]	*Uca minax*	mtDNA	SR-π	NA: Georgia, SE USA	r=0.37	
[18]	*Uca pugnax*	mtDNA	SR-π	NA: Georgia, SE USA	r=0.52	
[16]	*Zophosis*	mtDNA	SR-Hd	EU: Aegean Islands	r=-0.26	
		NC	SR-π		r=0.50	

Table A2 continued.

Study	Species	Marker	SD-GD	Region	Correlation	Driver of SGDC
Vertebrates						
[2]	*Aribeus jamaicaensis*	mtDNA	SR-H	NA: Lesser Antilles	r=0.15	
[11]	*Anolis cristatellus*	Az	SR-H	NA: Carribean	r=0.64	
[2]	*Brachyphylla cavernarum*	mtDNA	SR-H	NA: Lesser Antilles	r=0.51	
[24]	*Campostoma anomalum*	Micros.	SR-AR	NA: Ohio, Midwestern USA	**r=0.53****	Locality area or quality & connectivity
[2]	*Centronella prosoblepon*	mtDNA	SR-H	CA: Costa Rica	r=0.65	
[25]	*Chaetodon citrinellus*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[25]	*Chaetodon lunulatus*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[25]	*Chaetodon trifascialis*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[25]	*Chaetodon vagabundus*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[25]	*Chromis atripectoralis*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[25]	*Chromis viridis*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[11]	*Coereba flaveola*	mtDNA	SR-Hd	NA: West Indies	**r=0.79***	Locality area or quality & connectivity
[26]	*Desmognathus fuscus*	Az	SR-H	NA: E USA	**r=−0.74***	Direct interactions (competition between congeners reduces the niche width of *D. fuscus*)
[27]		Az	SR-AR	NA: E USA	**R²=0.41*(+)**	Locality area or quality & environmental heterogeneity
[27]	*Desmognathus ochropaeus*	Az	SR-AR	NA: E USA	**R²=0.39*(+)**	Locality area or quality & environmental heterogeneity
[27]	*Ensatina eschscholtzii*	Az	SR-AR	NA: W USA	R²=0.14(+)	
[27]	*Eurycea bislineata*	Az	SR-AR	NA: E USA	R²=0.00(-)	
[2]	*Falco tinnunculus*	Micros.	SR-H	AF: Cape Verde	r=0.44	
[11]	*Fringilla coelebs*	Az	SR-H	AF: Canary Islands	r=0.18	
[21]	*Gambusia nobilis*	Az	SR-AR	NA: N Chihuahua desert	(0)†	Not discussed.
[11]	*Geospiza fortis*	Az	SR-H	SA: Galápagos	r=0.39	
[11]	*Geospiza fuliginosa*	Az	SR-H	SA: Galápagos	r=0.19	
[25]	*Gobion quinquestrigatus*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(0)† / (+)†	
[28]	*Kerivoula papillosa*	Micros.	SR-AR / SRsimilar-AR	AS: Peninsular Malaysia	r=0.58 / r=0.49	
[11]	*Mus musculus*	Az	SR-H	EU: British Isles	r=0.15	
[25]	*Paracirrhites arcatus*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(0)† / (-)†	
[25]	*Paracirrhites fosteri*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(0)† / (0)†	
[11]	*Peromyscus*	Az	SR-H	NA: Baja California	r=0.47	
[11]	*Peromyscus maniculatus*	Az	SR-H / SR-H	NA: California Channel / NA: Gulf of Maine	r=-0.01 / r=0.76	
[27]	*Plethodon glutinosus*	Az	SR-AR	NA: E USA	R²=0.00	
[27]	*Plethodon jordani*	Az	SR-AR	NA: E USA	**R²=0.12*(-)**	Not specified
[28]	*Rhinolophus lepidus*	Micros.	SR-AR / SRsimilar-AR	AS: Peninsular Malaysia	r=-0.02 / r=0.02	
[28]	*Rhinolophus trifoliatus*	Micros.	SR-AR / SRsimilar-AR	AS: Peninsular Malaysia	r=0.40 / r=-0.20	
[11]	*Urocyon littoralis*	Minis.	SR-H	NA: California Channel	**r=0.73***	Locality area or quality & connectivity
[11]	*Uta stansburiana*	Az	SR-H	NA: Gulf of California	**r=0.63***	Locality area or quality & connectivity
[25]	*Zebrasoma scopas*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (-)†	
[25]	*Zebrasoma veliferum*	mtDNA	SR-Hd / SR-π	OC: Great Barrier Reef	(+)† / (+)†	
[11]	*Zosterops lateralis*	Minis.	SR-ARw.ind.	OC: Great Barrier Reef	r=0.63	

Markers: mtDNA = Mitochondrial DNA; NC = Nuclear coding gene; Micros. = Microsatellite loci; Az = Allozyme loci; AFLP = Amplified Fragment Polymorphisms; Minis. = Minisatellite loci.

Species diversity indices used in the relationships: SR = Species richness (also with logarithmic transformation); SRsimilar = Species richness of ecologically similar species; SD = Species diversity index (several).

Genetic diversity indices used in the relationships: Hd = Haplotype diversity; π = nucleotide diversity; GR = Genotypic richness; AR = Allelic richness (also with logarithmic transformations); ARraref. = Rarefied allelic richness; ARw.ind. = Allelic richness within individuals; H = Heterozygosity.

Regions: EU=Europe; NA=North-America; OC=Oceania; AS=Asia; CA=Central America; SA=South-America; AF=Africa.

Table A3. Observed β-SGDCs on natural populations of vascular plants, invertebrates and vertebrates. and the pairwise genetic differentiation as Three of the studies ([16], [21] & [30]), took a trans-specific approach and used genetic distances based on haplotypes across a wide variety of species. The strength and direction of the correlation is indicated with a correlation coefficient (*r*) and statistical significance of the correlation is indicated with asterisk (*: P<0.05; **: P<0.01; ***: P<0.001). Studies that give tentative evidence for an SGDC but report no test, or have insufficient reporting to allow for testing the SGDC, are indicated with a cross (†). In cases where the direction of the correlation cannot be read from the correlation coefficient the suggested direction is indicated with a plus (+) or minus (-) sign in parentheses.

Study	Species	Marker	Relationship	Region	Correlation	Driver of β-SGDC
Plants						
[29]	*Carex sempervirens*	RAPD	BC-F_{ST}	EU: Swiss Alps	r=0.23**	Selection due to gazing
[9]	*Euptelea pleiospermum*	Microsat.	F_{STC}-F_{ST}	AS: China, Yandu river	r=-0.02[a]	
			F_{STC}-F_{ST}	AS China, Nan river	r=0.11[a]	
[13]	*Plantago lanceolata*	AFLP	BC-F_{ST}	EU: Central Germany	r=0.64***	Connectivity & ecological differences between localities
[14]	*Ranunculus acris*	AFLP	ΔE-Nei	EU: Central Germany	r=0.62*	Ecological differences between localities
			ΔSR-Nei	EU: Central Germany	r=-0.17	
[15]	*Trillium grandiflorum*	Az, Micros., cpDNA-RFLP	F_{STC}-F_{ST}	NA: NE USA	r=0.48*	Locality area or quality & disturbance history
			RC-Fst	NA: NE USA	r=-0.45*	
Invertebrates						
[30]	Aquatic beetles (274 GMYC entities)	mtDNA	[1-$\beta_{sim(sp)}$]-[1-$\beta_{sim(hap.)}$]	Europe	(+)†	
unpub.	*Calopteryx splendens*	Micros.	BC-F_{ST}	EU: Finland	r<0.01	
unpub.	*Calopteryx virgo*	Micros.	BC-F_{ST}	EU: Finland	r=-0.02	
[18]	*Crassostrea virginica*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=0.45	
[21]	*Gammarus* spp.	Az.	QS-Nei	NA: N Chihuahua desert	r=0.68**	Connectivity
[18]	*Geukensia demissa*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=-0.33	
[18]	*Ilyanassa obsoleta*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=-0.11	
[22]	*Leptodiaptomus minutus*	mtDNA	F_{STC}-F_{ST}	NA: Ontario	(0)†	
[18]	*Littoraria irrorata*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=0.05	
[18]	*Melampus bidentatus*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=0.08	
[18]	*Petrolisthes armatus*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=-0.23	
[23]	*Radix balthica*	AFLP	F_{STC}-F_{ST}	EU: SE France	(+)†	
[16]	Tenebrionid beetles	mtDNA	QS-Nei	EU: Aegean islands	r=0.32*	Connectivity
		NC	QS-Nei	EU: Aegean islands	r=0.50*	
[18]	*Uca pugnax*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=0.22	
[18]	*Uca minax*	mtDNA	QS-F_{ST}	NA: Georgia, SE USA	r=0.09	
Vertebrates						
[24]	*Campostoma anomalum*	Micros.	BC-F_{ST}	NA: Ohio, Midwestern USA	r=0.20***	Connectivity
[21]	*Gambusia nobilis*	Az.	QS-Nei	NA: N Chihuahua desert	r=0.16	
[28]	*Kerivoula papillosa*	Micros.	C_H-D_{est}	AS: Peninsular Malaysia	r<0.01	
			$C_{H(similar)}$-D_{est}	AS: Peninsular Malaysia	r=0.02	
[28]	*Rhinolophus lepidus*	Micros.	C_H-D_{est}	AS: Peninsular Malaysia	r=0.11	
			$C_{H(similar)}$-D_{est}	AS: Peninsular Malaysia	r=0.18	
[28]	*Rhinolophus trifoliatus*	Micros.	C_H-D_{est}	AS: Peninsular Malaysia	r=0.03	
			$C_{H(similar)}$-D_{est}	AS: Peninsular Malaysia	r=0.19	

Markers: RAPD = Random Amplified Polymorphic DNA; Micros. = Microsatellite loci; AFLP = Amplified Fragment Polymorphisms; Az = Allozyme loci; cpDNA-RFLP = chloroplast DNA Restriction Fragment Length Polymorphisms; mtDNA = Mitochondrial DNA; NC = Nuclear coding gene.

Pairwise community dissimilarity indices used in the relationships: BC = Bray-Curtis dissimilarity; FSTC = community-FST; RC = Raup-Crick index; ΔE = Difference in evenness; ΔSR = difference in species richness; 1-βsim(sp) = Simpson's index of community similarity; QS = Sørensen index, J = Jaccard index, CH = Morisita-Horn index; CH(similar) = Morisita-Horn index based on ecologically similar species.

Pairwise genetic differentiation indices used in the relationships: FST = pairwise genetic FST; Nei = Nei's distance; 1-βsim(hap.) = Simpson's index of haplotype similarity, Dest = Jost D.

Regions: AS=Asia; EU=Europe; NA=North-America; OC=Oceania

a) Correlation not reported by the original authors but calculated based on the values reported in the supplement. Statistical significance was estimated using 1000 permutations.

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II

INTERSPECIFIC INTERACTIONS INFLUENCE CONTRASTING SPATIAL GENETIC STRUCTURES IN TWO CLOSELY RELATED DAMSELFLY SPECIES

by

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III

SPECIES–GENETIC DIVERSITY CORRELATION IN CALOPTERYX DAMSELFLIES

by

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IV

THE EFFECTS OF FRAGMENTATION, CONNECTIVITY AND INBREEDING DEPRESSION ON THE PERSISTENCE OF SPECIES IN NEUTRAL METACOMMUNITIES

by

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