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**Title:** Conservation implications of species–genetic diversity correlations

**Year:** 2014

**Version:** Published version

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**Please cite the original version:**

Kahilainen, A., Puurtinen, M., & Kotiaho, J. S. (2014). Conservation implications of species–genetic diversity correlations. *Global Ecology and Conservation*, 2(December), 315-323.  
<https://doi.org/10.1016/j.gecco.2014.10.013>



## Review paper

## Conservation implications of species–genetic diversity correlations

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## ARTICLE INFO

## Article history:

Received 20 July 2014

Received in revised form 28 October 2014

Accepted 28 October 2014

Available online 30 October 2014

## Keywords:

Opinion

Review

SGDC

Conservation planning

Conservation prioritization

## 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.  $\alpha$ -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  $\alpha$ -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  $\alpha$ -SGDCs can also drive correlations between differentiation of community and genetic compositions (i.e.  $\beta$ -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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## 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).

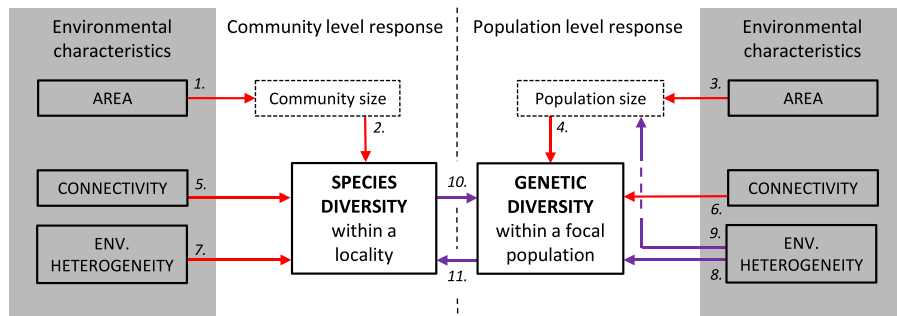
The neglect of intrapopulation genetic diversity in conservation planning is perhaps understandable, given the challenges of practical conservation work. With considerable gaps even in species diversity data (Walpole et al., 2009), mapping intrapopulation genetic diversity could be considered secondary 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.  $\alpha$  diversity),  $\alpha$ -SGDC describes the relationship between species diversity in a local community and intrapopulation genetic diversity within the species, and both positive and negative  $\alpha$ -SGDCs have been observed in natural systems (Karlin et al., 1984; Wehenkel et al., 2006; Marshall and Camp, 2006; Papadopolou et al., 2011; Vellend et al., 2014). The sign of the  $\alpha$ -SGDC directly indicates whether there is a conflict between the conservation of the two levels of biodiversity: Positive  $\alpha$ -SGDCs suggest that conservation actions focusing on local species diversities also conserves intrapopulation genetic diversity, whereas negative  $\alpha$ -SGDCs suggest that conservation of one level of diversity may compromise diversity on the other level. Furthermore, the mechanisms behind the  $\alpha$ -SGDCs (stochastic processes, dispersal, and selection) also influence differentiation between localities (i.e.  $\beta$  diversity). Therefore they can drive correlations between differentiation of community compositions and genetic differentiation of populations (i.e.  $\beta$ -SGDCs). Thus, focusing on the mechanistic explanations behind  $\alpha$ - and  $\beta$ -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  $\alpha$ - and  $\beta$ -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.  $\alpha$ -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  $\alpha$ -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  $\beta$ -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  $\alpha$ -SGDCs. Like area, also connectivity is expected to influence the degree of community and genetic differentiation in parallel and result in a positive  $\beta$ -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  $\alpha$ -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  $\alpha$ -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

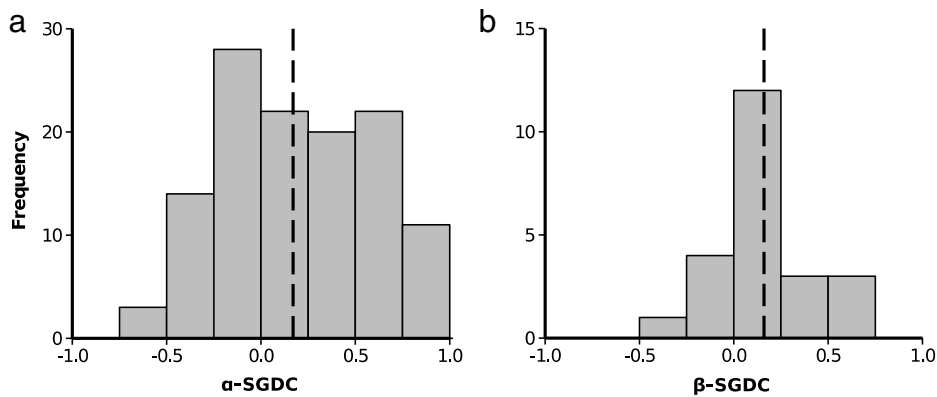
In addition to locality characteristics creating SGDCs, species diversity and genetic diversity can also influence each other directly via selection (e.g. due to competitive and facilitating interactions between con- and heterospecific individuals). Adaptive genetic diversity, rather than neutral genetic 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  $\alpha$ -SGDCs of natural populations are positive (Vellend, 2003; Vellend and Geber, 2005; Vellend et al., 2014). The median  $\alpha$ -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)  $\alpha$ -SGDCs and (b)  $\beta$ -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  $\alpha$ -SGDCs measured from discrete island-like habitat patches and continuous habitats, with  $\alpha$ -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  $\alpha$ -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  $\alpha$ -SGDCs, since significant negative  $\alpha$ -SGDCs are also observed (Fig. 2(a)), and connectivity and area are not expected to drive negative  $\alpha$ -SGDCs. However, the drivers of negative  $\alpha$ -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  $\alpha$ -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  $\alpha$ -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  $\alpha$ -SGDCs.

The distribution of  $\beta$ -SGDCs is very similar to the ones observed for  $\alpha$ -SGDCs (Fig. 2(b); median  $\beta$ -SGDC = 0.16; S.D. = 0.26; Supplementary material A, Table A3). However, there are slight differences to the  $\alpha$ -SGDCs in the sense that a larger proportion of the reported  $\beta$ -SGDCs fall close to zero and all statistically significant  $\beta$ -SGDCs seem to be positive (Fig. 2(b); Supplementary material A, Table A3). The  $\beta$ -SGDCs seem to emphasize connectivity since four of the seven studies reporting statistically significant  $\beta$ -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  $\beta$ -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 $\alpha$ -SGDC for conserving diversity within localities

An obvious application of the  $\alpha$ -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 $\beta$ -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  $\beta$ -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  $\beta$ -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

We thank two anonymous reviewers, K. Kuitunen, K. E. Knott, M. Mönkkönen, A. Moilanen, and the members of Journal Club and Moday Coffee Club (JYU) for valuable comments during the preparation of this manuscript. This study was funded by the Academy of Finland (via Centre of Excellence in Evolutionary Research, Centre of Excellence in Biological interactions, Biological Interactions Graduate School, and project funding of MP [grant number 258385]), and Kone foundation (personal grant of AK).

## 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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