

LETTER

Genetic diversity in widespread species is not congruent with species richness in alpine plant communities

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Abstract

The Convention on Biological Diversity (CBD) aims at the conservation of all three levels of biodiversity, that is, ecosystems, species and genes. Genetic diversity represents evolutionary potential and is important for ecosystem functioning. Unfortunately, genetic diversity in natural populations is hardly considered in conservation strategies because it is difficult to measure and has been hypothesised to co-vary with species richness. This means that species richness is taken as a surrogate of genetic diversity in conservation planning, though their relationship has not been properly evaluated. We tested whether the genetic and species levels of biodiversity co-vary, using a large-scale and multi-species approach. We chose the high-mountain flora of the Alps and the Carpathians as study systems and demonstrate that species richness and genetic diversity are not correlated. Species richness thus cannot act as a surrogate for genetic diversity. Our results have important consequences for implementing the CBD when designing conservation strategies.

Keywords

alpine vascular plants, Alps, biodiversity conservation, Carpathians, genetic diversity, species richness.

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INTRODUCTION

Loss of biodiversity is currently occurring at rates unequalled in geological times and is induced, among other causes, by human land use change. This loss is of major ecological, economical and societal concern (Frankham & Ralls 1998). Implementation of efficient conservation measures that limit the extinction of species and preserve the evolutionary processes that sustain biodiversity is thus an imperative challenge.

The concept of biodiversity as described by the Convention on Biological Diversity (CBD; www.cbd.int/convention/text/) encompasses three fundamental levels: ecosystems, species and genes. The gene level corresponds to the genetic diversity within species and is an integral part of biodiversity according to the CBD. Genetic diversity defines the evolutionary potential of species and is consequently of prime importance to allow populations to adapt to new environmental conditions as well as for the long-term preservation of biodiversity under global change.

The gene level of biodiversity is important not only for preserving the evolutionary potential of species but also for ecosystem functioning. Genetic diversity has, however, received much less attention in biodiversity assessments than the diversity of ecosystems and species (Laikre *et al.* 2009), despite recent studies that clearly demonstrate the importance of genetic diversity for the fitness and persistence of populations (Frankham & Ralls 1998; Saccheri *et al.* 1998). For instance, genetic diversity within dominant plant species enhances ecosystem resistance to disturbance (Hughes & Stachowicz 2004) and ecosystem recovery after climatic extremes (Reusch *et al.* 2005). Finally, genetic diversity promotes primary productivity as well as the diversity of herbivorous and predatory arthropod communities (Crutsinger *et al.* 2006), and the intraspecific genetic diversity of crops has been shown to limit disease susceptibility and to contribute to sustainable crop production in monoculture fields (Zhu *et al.* 2000). Genetic diversity should therefore be considered when designing strategies for the preservation of biodiversity.

Intraspecific genetic diversity is difficult to measure at large scales (i.e. over large areas and for many species), because of the need for rigorous field sampling, the demand for specialised technical skills, and the still high costs of genetic analysis. A common solution to overcome these difficulties is to find a reliable surrogate for genetic diversity that can be easily and efficiently assessed. Current practice suggests that species richness is a suitable surrogate for genetic diversity, and the relationship between species diversity and genetic diversity has recently gained renewed interest. Species richness and genetic diversity have been hypothesised to co-vary (Vellend 2005; Vellend & Geber 2005), as both should theoretically respond to the same local processes, or because one level might directly influence the other level of biodiversity (Vellend & Geber 2005). The influence of local characteristics such as area, isolation and spatial/temporal heterogeneity seems to induce parallel effects on species and genes via migration, drift and selection (Vellend & Geber 2005). For example, a higher level of immigration that is connected with lower isolation of a locality will promote both species diversity and gene diversity. In the same way, the level of drift that is linked to area will influence both species (community drift) and allele (genetic drift) diversity. For instance, a high level of drift will lead to more extinctions of species and genes. In consequence, substantial co-variation between the two levels of biodiversity is theoretically expected.

The co-variation between species diversity and genetic diversity tends to be supported by modelling (Vellend 2005; Adams & Vellend 2011) and empirical studies (Cleary *et al.* 2006; He *et al.* 2008; Sei *et al.* 2009; He & Lamont 2010; Odat *et al.* 2010; Struebig *et al.* 2011; Blum *et al.* 2012). However, the empirical data available are still contradictory and do not allow to confirm or reject the hypothesis of a significant correlation between species richness and genetic diversity. For instance, three recent studies did not confirm a positive relationship between species richness of plant communities and the genetic diversity of locally dominant species at the plot level (Odat *et al.* 2004; Puscas *et al.* 2008; Silvertown *et al.* 2009). Similarly, a meta-analysis in the Mediterranean basin showed that the genetic diversity of trees does not co-vary with vascular plant species richness (Fady & Conord 2010). In contrast, positive correlations were found in island-like systems for many organisms such as butterflies (Cleary *et al.* 2006), woody shrubs (He *et al.* 2008) or legumes (He & Lamont 2010), bats (Struebig *et al.* 2011) and stream fishes (Blum *et al.* 2012). The relationship between species richness and genetic diversity at the plot level probably comprise scale-dependent effects, which could result in inconsistent outcomes. Hence, the issue of a possible correlation between genetic diversity and species richness remains controversial and lacks large-scale empirical tests. The absence of a correlation between these two levels of biodiversity would have consequences for conservation strategies, because the design of reserves only based on species diversity might not properly preserve genetic diversity.

In this study, our primary goal was to test at a large scale whether the species and gene levels of biodiversity co-vary and whether species diversity is an appropriate surrogate for genetic diversity. We relied on a full assessment of plant species richness and a multi-species approach for estimating plant genetic diversity. We chose the high-mountain vascular flora of the Alps and the Carpathians as study systems because well-established floristic data in clearly delimited biomes are available for both mountain ranges. Mountain ecosystems also exhibit high species richness, making them relevant for global biodiversity conservation (Körner 2002). Within continental Europe, the alpine ecosystem (i.e. the area above timberline) is the least disturbed by human activities. The Alps and Carpathians represent ecologically and geographically well-defined areas with known, but different Quaternary histories. The two mountain ranges have experienced different magnitudes of ice cover during Quaternary climatic oscillations with respective effects on their regional flora. While the Alps have been largely covered by ice during cold periods, but nevertheless harboured potential glacial refugia for plants (Schönswetter *et al.* 2005), the Carpathians have been less affected by glaciation (Ronikier 2011).

We specifically addressed the following main question. Are there consistent correlations between indices of species and genetic diversities in the Alps and the Carpathians? Given the theoretical foundations of Vellend & Geber (2005), we hypothesised that species richness and genetic diversity may show spatial coincidence as a result of distinct historical processes acting on species and genomes in a parallel way. For practical conservation issues, we were further interested in locating those areas that comprise relevant components of species and genetic diversity to assess whether current hotspots of biodiversity are considered in the network of protected areas in the Alps.

MATERIAL AND METHODS

Study system

We separately assessed both levels of biodiversity (i.e. species and genes), putting a particular emphasis on data consistency (Gugerli *et al.* 2008). We adopted a regular grid system implemented for the mapping of the flora of the Alps and the Carpathians (Gugerli *et al.* 2008). Cells comprised 20' longitude and 12' latitude (ca. 25 × 22 km), with longitudinal cell size varying according to latitude (Fig. S1). To estimate genetic diversity, we included only cells comprising area higher than 1500 m above sea level. Additionally, we only considered every second cell in the Alps (Fig. S2) to comply with restrictions given by the workload of genetic analyses: this led to a total of 149 cells considered for genetic analyses in the Alps. In the Carpathians, genetic sampling encompassed all 30 cells containing larger alpine areas (Fig. S2). All cells in the Alps and the Carpathians were considered for species richness.

Species and genetic diversity

We estimated three common diversity indices for both the species and gene levels of biodiversity: diversity, rarity and endemism. The three indices of biodiversity used here are similar to total, threatened and endemic species richness as described in Orme *et al.* (2005), or to species richness, threatened species and restricted-range species referred to in Ceballos & Ehrlich (2006). The rarity indices took into account the number of occurrences of species or genetic markers, with high values indicating the presence of a species or marker in only a limited number of cells. The endemism indices were estimated such that species or genetic markers showing low average geographical distance among occurrences obtained high values. Note that our sampling comprised all species within each grid cell, while we only sampled three individuals in one location per species (widespread high-mountain species) per grid cell for genetic diversity.

Species richness corresponded to the total number of species recorded per cell. Based on a list of high-mountain taxa of the vascular plants of the Alps and the Carpathians, species occurrences were mapped across the grid laid over both mountain ranges (Gugerli *et al.* 2008; Fig. S1). We integrated data from mapping initiatives at national levels, with additional herbarium, literature and field surveys for filling gaps. Only cells with > 50 species were included in the analysis (Fig. S3). Among the grid cells excluded from the floristic data set, there was only one grid cell matching the genetic sampling, which was thus excluded from the subsequent analyses. All infraspecific taxonomic levels were aggregated to the species level. Rarity and endemism per cell were estimated separately for the Alps and the Carpathians. The estimation of per cell floristic rarity was calculated as the inverse of the number of cells in which each species occurs, averaged for each target cell (Crisp *et al.* 2001). As rare species cover only a few cells, they contribute heavily to rarity. Endemism of a species was expressed as the inverse of the mean geographical distance among all cells where a species occurs. The estimation of the per cell endemism was calculated as the mean endemism among all species occurring in the target cell.

To estimate genetic diversity, amplified fragment length polymorphisms (AFLPs) were produced for 27 and 29 widespread high-mountain species in 149 and 30 cells of the Alps and the

Carpathians, respectively (Table 1; Fig. S2). The large majority of AFLP markers can be considered to be selectively neutral (Bonin *et al.* 2006; Manel *et al.* 2012). We carefully selected the species in the assessment of genetic diversity based on a series of criteria detailed in Gugerli *et al.* (2008). We took into account biogeographical distribution types (European alpine species, arctic-alpine species), life forms (forbs, graminoids, dwarf shrubs), life history traits (breeding system, pollination and dispersal mode, altitudinal range; Tribsch 2004), unambiguous field identification, wide distribution in one or both of the two mountain ranges, frequent occurrence and consistency of ploidy level.

Several precautions were taken in the genotyping procedure to ensure data quality. (1) We performed extensive preliminary trials to select taxa and primer/enzyme combinations that produced reliable AFLP profiles (Vos *et al.* 1995). (2) All samples per species were run in one laboratory, using constant protocols (Gugerli *et al.* 2008). (3) Standard samples, within-plate replicates, blind duplicates and negative samples were included in all steps from DNA isolation to AFLP profiling (Bonin *et al.* 2004; Pompanon *et al.* 2005) for marker evaluation and to calculate mismatch error rates. Details on the laboratory protocols are given in Gugerli *et al.* (2008).

Within each species, we selected those AFLP markers which had > 1 or < $n - 1$ occurrences in the samples from the Alps and the Carpathians to calculate the mean number of genetic differences between individuals per location (gene diversity; Nei 1973). We standardised the data (mean = 0, standard deviation = 1) to account for differences among species in their overall level of polymorphism (Thiel-Egenter *et al.* 2011). Subsequently, species-specific genetic diversity was averaged over all species genotyped for a particular grid cell to avoid bias owing to different numbers of species sampled per cell. Only cells with ≥ 10 species sampled for genetic analyses were used in the analysis.

Genetic rarity and genetic endemism were calculated in a similar way as species rarity and endemism, except that alleles replaced species (Schönswetter & Tribsch 2005). Genetic rarity represents the mean of the per species average of the inverse of the number of cells occupied by each allele that occurred in a target cell. Likewise, genetic endemism was calculated as the mean of the inverse of the per species average geographical distances among cells occupied by each allele found in a target cell.

Correlations between species diversity and genetic diversity

Pearson's pairwise correlation coefficients, with Bonferroni correction for significance levels (Holm 1979), were computed to test correlations among species richness and genetic diversity, endemism and rarity variables. These correlations included only those cells for which genetic data were available (Fig. S2). In addition to the main analysis, we carried out two tests in the Alps to evaluate whether genetic diversity was affected by (1) low sample numbers per grid cell and (2) inconsistent numbers and combinations of species genotyped per grid cell. First, we collapsed grid cells into larger cells by merging 2 × 2 and 3 × 3 cells (Figs. S4 and S5) and re-calculated genetic diversity on six and 12 or 15 individuals respectively (Gugerli *et al.* 2008). We also performed an analysis based on only ten species sampled for the genetic data (*Arabis alpina*, *Carex sempervirens*, *Cirsium spinosissimum*, *Dryas octopetala*, *Geum montanum*, *Gypsophila repens*, *Peucedanum ostruthium*, *Rhododendron ferrugineum*, *Saxifraga stellaris*

Table 1 Plant taxa used for assessing genetic diversity, including the number of localities and samples in the Alps and the Carpathians, and the number of polymorphic amplified fragment length polymorphism (AFLP) markers

Taxon	Family	Code	Localities/samples (Alps)	Localities/samples (Carpathians)	AFLP markers (Alps/Carpathians)
<i>Androsace obtusifolia</i> All.	Primulaceae	Aob	45/131	–	134/–
<i>Arabis alpina</i> L.	Brassicaceae	Aal	129/385	19/57	150/97
<i>Campanula alpina</i> Jacq.	Campanulaceae	Cal	–	19/57	–/108
<i>Campanula barbata</i> L.	Campanulaceae	Cba	104/307	–	113/–
<i>Campanula serrata</i> (Kit.) Hendrych	Campanulaceae	Csr	–	22/65	–/187
<i>Carex firma</i> Mygind	Cyperaceae	Cfi	76/214	3/9	58/35
<i>Carex sempervirens</i> Vill.	Cyperaceae	Cse	137/408	22/66	121/72
<i>Cerastium uniflorum</i> Clairv.	Caryophyllaceae	Cun	44/130	–	89/–
<i>Cirsium spinosissimum</i> (L.) Scop.	Asteraceae	Csp	110/325	–	95/–
<i>Dryas octopetala</i> L.	Rosaceae	Doc	124/370	15/45	101/58
<i>Festuca carpathica</i> F. Diétr.	Poaceae	Fca	–	9/27	–/103
<i>Festuca supina</i> (= <i>F. airoides</i>) Schur	Poaceae	Fai	–	28/84	–/174
<i>Festuca versicolor</i> Tausch s.l.	Poaceae	Fve	–	17/50	–/170
<i>Gentiana nivalis</i> L.	Gentianaceae	Gni	74/218	6/17	154/95
<i>Geum montanum</i> L.	Rosaceae	Gmo	122/363	19/57	93/56
<i>Geum reptans</i> L.	Rosaceae	Gre	51/153	8/24	61/24
<i>Gypsophila repens</i> L.	Caryophyllaceae	Gyr	107/319	–	94/–
<i>Hedysarum hedysaroides</i> Schinz & Thell. s.l.	Fabaceae	Hhe	76/220	11/31	122/85
<i>Hornungia alpina</i> (L.) Appel s.l.	Brassicaceae	Hal	97/284	3/9	225/44
<i>Hypochaeris uniflora</i> Vill.	Asteraceae	Hun	59/177	27/80	94/84
<i>Juncus trifidus</i> L.	Juncaceae	Jtr	91/269	23/69	88/66
<i>Ligusticum mutellinoides</i> (Cr.) Vill.	Apiaceae	Lmu	56/159	4/11	95/50
<i>Loiseleuria procumbens</i> (L.) Desv.	Ericaceae	Lpr	90/270	13/39	121/101
<i>Luzula alpinopilosa</i> (Chaix) Breist.	Juncaceae	Lal	82/245	19/57	218/119
<i>Peucedanum ostruthium</i> (L.) W.D. Koch	Apiaceae	Pos	117/350	–	113/–
<i>Phyteuma betonicifolium</i> Vill. s.l.	Campanulaceae	Pbt	104/305	–	158/–
<i>Phyteuma confusum</i> A. Kern.	Campanulaceae	Pco	–	7/20	–/97
<i>Phyteuma hemisphaericum</i> L.	Campanulaceae	Phm	76/225	–	234/–
<i>Primula minima</i> L.	Primulaceae	Pmi	–	19/57	–/100
<i>Ranunculus alpestris</i> L. s.l.	Ranunculaceae	Ral	79/235	7/20	434/111
<i>Rhododendron ferrugineum</i> L.	Ericaceae	Rfe	126/377	–	111/–
<i>Rhododendron myrtilifolium</i> Schott & Kotschy	Ericaceae	Rmy	–	18/54	–/111
<i>Saxifraga stellaris</i> L.	Saxifragaceae	Sst	101/286	12/33	190/89
<i>Saxifraga wahlenbergii</i> Ball	Saxifragaceae	Swa	–	4/12	–/127
<i>Sempervivum montanum</i> L. s.l.	Crassulaceae	Smo	–	10/30	–/107
<i>Sesleria caerulea</i> (L.) Ard.	Poaceae	Sco	137/389	7/18	70/56
<i>Soldanella pusilla</i> Baum.	Primulaceae	Spu	–	8/24	–/34
<i>Trifolium alpinum</i> L.	Fabaceae	Tal	64/187	–	95/–
<i>Veronica baumgartenii</i> Roem. & Schult.	Plantaginaceae	Vba	–	13/39	–/93

and *Sesleria caerulea*). These ten species were selected so as to maximise the number of cells with a set of species occurring in all those cells. This selection reduced the number of cells for analysis to 58, mostly located in the central areas of the Alps (Fig. S6). For this analysis, AFLP markers were retained even if they became monomorphic as a consequence of sample reduction.

Correlations between species diversity and genetic diversity within single species

Pearson's pairwise correlation coefficients, with Bonferroni correction for significance levels (Holm 1979), were computed to test correlations between total species richness and genetic diversity (standardised data) within each of the 27 species from the Alps and each of the 24 species from the Carpathians separately, ignoring species genotyped in less than six grid cells. Only cells containing genetic data for the respective species were taken into account.

Correlations between species diversity and genetic diversity within functional groups

Two subsets of the data set from the Alps corresponding to two functional groups were considered: graminoids and legumes. Five graminoid species were comprised in the genetic data set (*Carex firma*, *C. sempervirens*, *Juncus trifidus*, *Luzula alpinopilosa* and *S. caerulea*), and 217 taxa within 23 genera and three families (Poaceae, Cyperaceae and Juncaceae) were included in the species data set. For the legumes, genetic data were available for two species (*Hedysarum hedysaroides* and *Trifolium alpinum*), and 67 taxa (including subspecies and aggregates) within 12 genera of Fabaceae were included in the species data set. Pearson's pairwise correlation coefficients, with Bonferroni correction for significance levels (Holm 1979), were computed to test correlations between species richness and genetic diversity (standardised data) within each of the two functional groups.

Zonation

Zonation is a framework and software for spatial conservation planning (Moilanen *et al.* 2005). It identifies areas important for species' long-term persistence by focusing on maximising habitat amount, quality and connectivity simultaneously for many conservation features, such as species, genes, habitat types or ecosystem services. Zonation produces a hierarchical prioritisation of the landscape by iteratively removing the least valuable remaining cell, accounting for complementarity, remaining range sizes, species priority weights and connectivity in the process (Moilanen *et al.* 2005, 2009; Moilanen 2007; Moilanen & Kujala 2008).

We here considered the complete species and AFLP data sets to evaluate the importance of particular grid cells for biodiversity preservation. The additive benefit function (ABF) variant of Zonation (Moilanen 2007) was applied to both species and genetic data sets, thus assuming additive contributions of species or genes to aggregate conservation priority. For genetic diversity, we considered AFLP markers instead of species, and Zonation was run on the genetic data of each species independently, using alleles as the unit of conservation instead of species. The genetic analysis produced a

priority ranking for each species, with the least important grid cells receiving priority rank 0.0 and the most important cells receiving a priority rank 1.0. These values were then standardised (mean = 0; standard deviation = 1). Finally, the mean value per cell was calculated across all species of the genetic data set and mapped. When calculating this mean, we accounted for different numbers of species genotyped per cell. Thus, our strategy did not implicitly give higher priority to cells with more species analysed for genetic diversity, and consequently was independent of the number of species genotyped and total species richness per grid cell. The parameter of the ABF analysis was set to $\alpha = 0.25$, corresponding to modelling of extinction risk via the species area curve (Moilanen 2007). As the grid cells in our analysis were geographically large, neighbourhood effects (connectivity) between grid cells were not modelled.

RESULTS

Altogether, 109 305 records were collected in the floristic database for 1057 high-mountain vascular plant species within the 671 cells studied (Alps: 893 species in 386 cells; Carpathians: 518 species in 285 cells; Figs S1 and S3). Species richness per single grid cell ran-

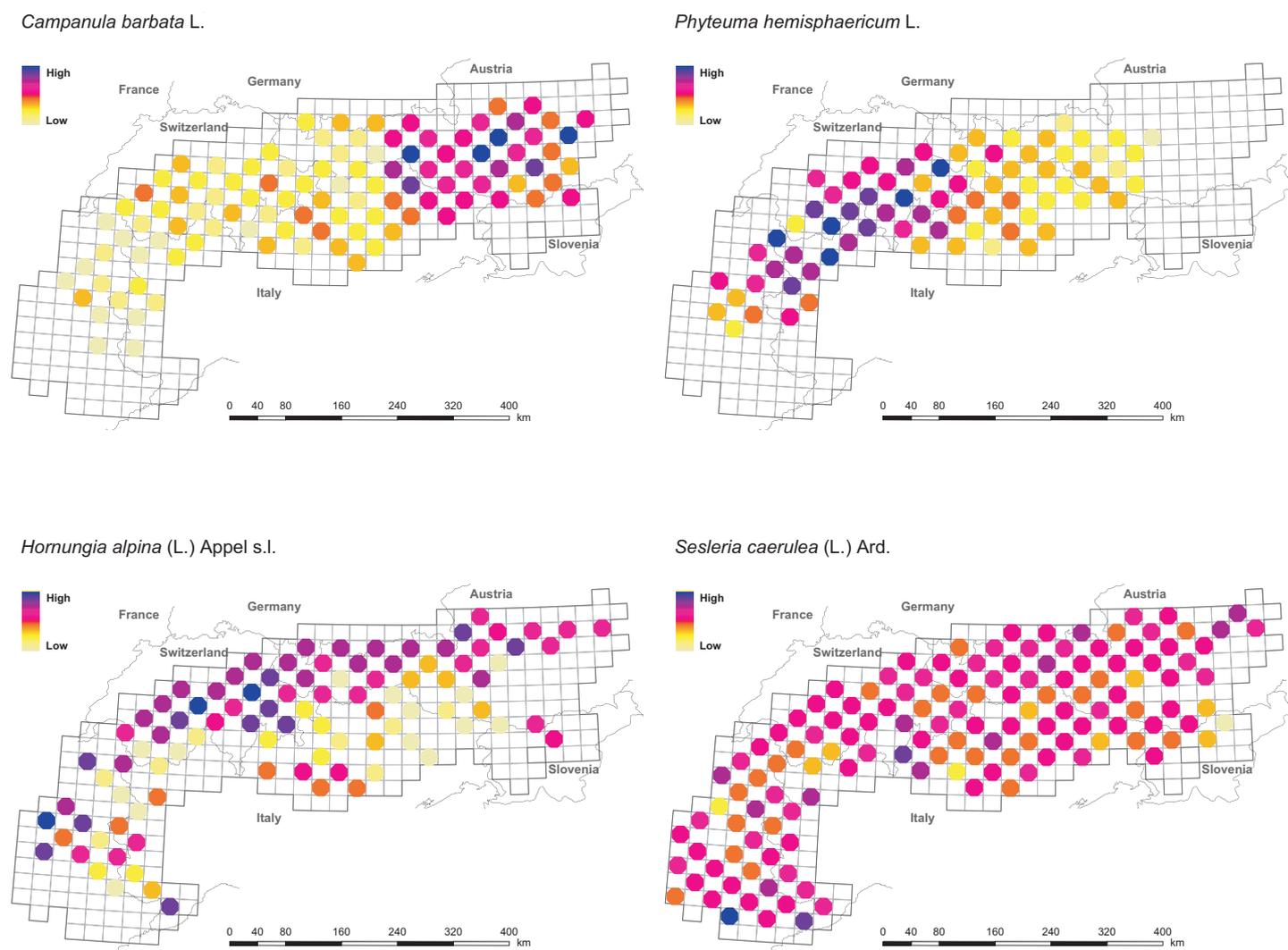


Figure 1 Examples of maps obtained for four species showing the main types of spatial distribution of genetic diversity in the Alps.

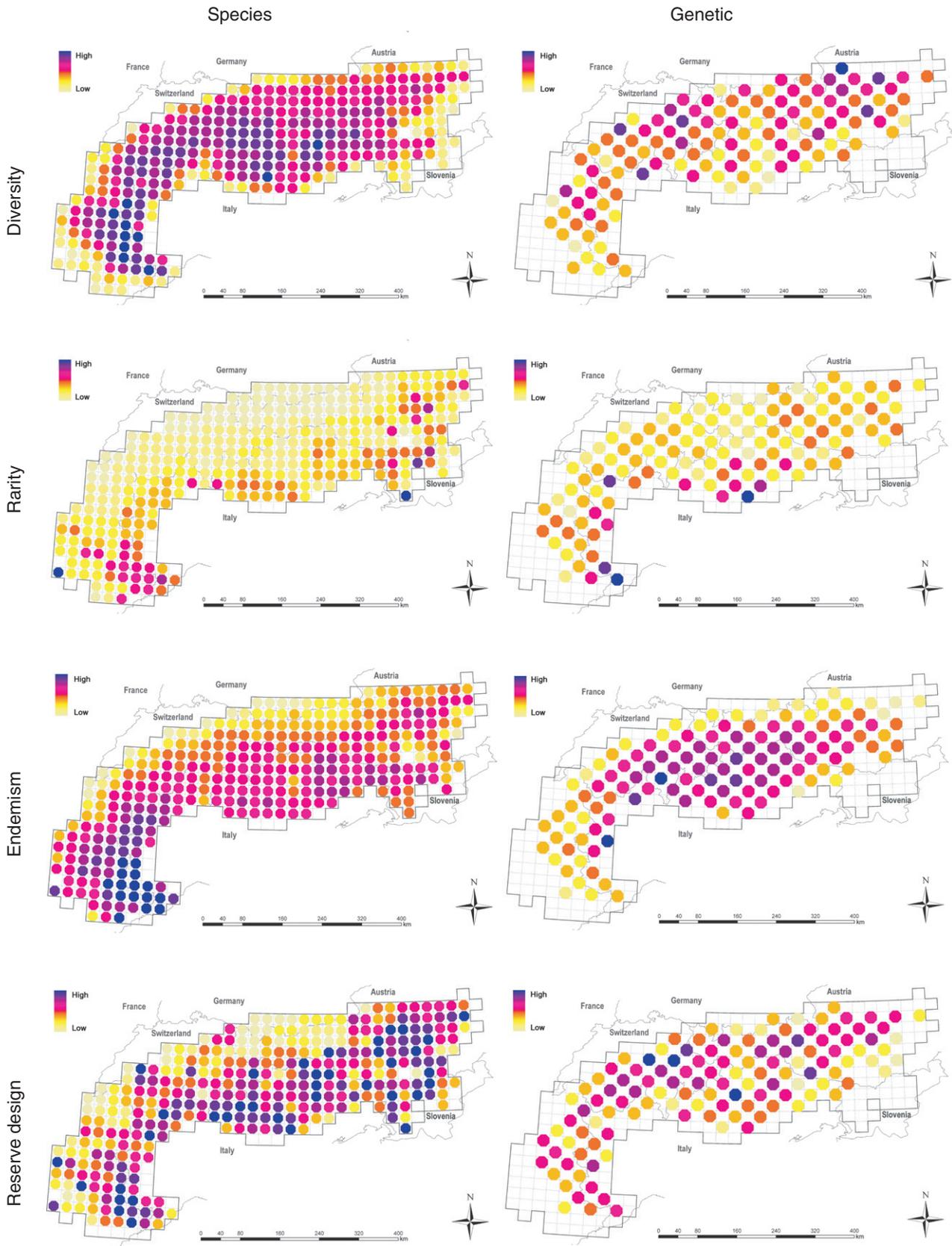


Figure 2 Comparison between species and genetic diversity in alpine vascular plants of the Alps. The results for three diversity indices (richness/diversity, rarity and endemism) and the results of an algorithm for reserve design (Zonation, additive benefit function; Moilanen 2007) are shown.

Table 2 Correlations between species and genetic diversity indices in alpine vascular plants from the Alps and the Carpathians (averaged across species)

	Species richness	Species rarity	Species endemism
Alps			
Genetic diversity	$r = -0.134$ $P = 0.140$	$r = -0.291$ $P = 0.001^*$	$r = -0.377$ $P < 0.001^{***}$
Genetic rarity	$r = 0.055$ $P = 0.546$	$r = 0.436$ $P < 0.001^{***}$	$r = -0.431$ $P < 0.001^{***}$
Genetic endemism	$r = -0.244$ $P = 0.006$	$r = -0.129$ $P = 0.154$	$r = 0.082$ $P = 0.370$
Carpathians			
Genetic diversity	$r = -0.051$ $P = 0.831$	$r = 0.290$ $P = 0.214$	$r = -0.286$ $P = 0.221$
Genetic rarity	$r = -0.251$ $P = 0.286$	$r = -0.022$ $P = 0.927$	$r = -0.173$ $P = 0.466$
Genetic endemism	$r = 0.170$ $P = 0.472$	$r = -0.148$ $P = 0.533$	$r = 0.835$ $P < 0.001^{***}$

Bonferroni-corrected significance of correlations: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

ged from 11 to 503 in the Alps, and from two to 335 in the Carpathians. More than 1 100 000 AFLP data points (0/1) were produced for over 14 000 plant samples, excluding replicates used to check and ensure data quality. The genetic analysis revealed patterns of intraspecific diversity in the studied species (Fig. 1), demonstrating that the sampling protocol implemented (three individuals per species per grid cell) combined with the analysis of a large number of AFLP markers were appropriate for recording the spatial distribution of intraspecific biodiversity. We observed three main types of patterns. These patterns are exemplified by *Campanula barbata* and *Phyteuma hemisphaericum* showing higher genetic diversity in the eastern and the western part of their distributions, respectively, *Hornungia alpina* being more diverse in the external part of the Alps, and *S. caerulea* showing a relatively homogeneous pattern across the Alps (Fig. 1).

Figure 2 summarises the results of all diversity indices for the Alps. Considering the species level, areas along the periphery of the Alpine arc had lower species richness because of lower altitudinal ranges and less area above the chosen altitudinal threshold (i.e. 1500 m above sea level). The southwestern part of the Alps, along the border between France and Italy, exhibited highest species richness, number of rare species and degree of endemism. Samples from the peripheral and northern parts of the Alps almost exclusively comprised species with wide distributions; the corresponding cells therefore contained few rare species. In contrast, greatest genetic diversity was not located in the southwestern region, but in the central and eastern parts of the Alps, in Switzerland and Austria. We observed areas of high genetic rarity in the southwestern Alps and in the vicinity of the Monte Baldo region of northeastern Italy, which is well known for its many endemic species (Tribusch 2004). These two regions correspond to Quaternary refugia from which species did not greatly expand after glaciation. The easternmost part of the Alps, showing high genetic diversity and many genetic markers with wide distributions, likely corresponds to an extensive refugial area for many plant species, which greatly contributed to the post-glacial re-colonisation of large areas of the Alps, in particular its northern regions.

Table 2 shows the correlations between species and genetic diversity indices for the Alps and the Carpathians. In both ranges,

Table 3 Pearson correlations between species richness and genetic diversity within two plant functional groups in the Alps

Functional group	Correlation	P-value
Graminoids	0.020	0.825
Legumes	-0.263	0.007**

Bonferroni-corrected significance of correlations: $**P < 0.01$.

patterns of species richness and genetic diversity were not congruent and did not co-vary. When collapsing neighbouring cells to analyse more individuals from the same species within each compound cell and when only taking into account cells containing a consistent set of ten species that were genetically studied, all correlation tests virtually remained the same (Figs S4–S6 illustrate species richness and genetic diversity for the three additional analyses). The discordance between species richness and genetic diversity also clearly appeared when running Zonation (Fig. 2). The species data set emphasised the conservation value of the southern fringe of the Alps, with a few additional cells in the East, whereas the genetic data set highlighted the central part of the Alps, mainly in eastern Switzerland.

The few significant correlations we observed in the overall diversity correlations were in the rarity and endemism indices. In the Alps, genetic rarity was correlated with species rarity and species endemism, and genetic diversity was negatively correlated with species rarity and species endemism (Table 2). In turn, we found only one significant positive correlation between species and genetic endemism in the Carpathians. Within the floristic data sets of the Alps and the Carpathians, species richness did not correlate with species rarity or areas of endemism.

Figure 3 summarises the results of the correlations between single-species genetic diversity and total species richness. Both in the Alps and in the Carpathians, the different species analysed showed a wide range of positive and negative correlations centred around zero without any obvious trends. Table 3 shows the results of the correlations between species richness and genetic diversity in the two functional groups analysed. For graminoids, no significant correlation was found, while we recorded a significant negative correlation for legumes. This negative correlation corresponds to the highly significant negative single-species correlation of genetic diversity with total species richness found for *H. bedysaroides* (Fig. 3).

DISCUSSION

Our large-scale multi-species analysis of species richness and genetic diversity clearly shows that these two levels of biodiversity do not co-vary in high-mountain vascular plants across two major European mountain ranges (Tables 2 and 3, Figs 2 and 3). Whereas it is well known and empirically proven that species richness is related to habitat diversity (Shmida & Wilson 1985), our results show that genetic diversity is rather associated with the glacial and post-glacial history of species, which is tightly linked to environmental and ecological characteristics of glacial refugia, range shifts and associated demographic processes. Small refugia can harbour many species if habitat diversity is high. However, effective population sizes may be small under refugial conditions, leading to genetic drift and random loss of alleles. In other words, the effects of demographic history would tend to override the potential co-variation of species richness

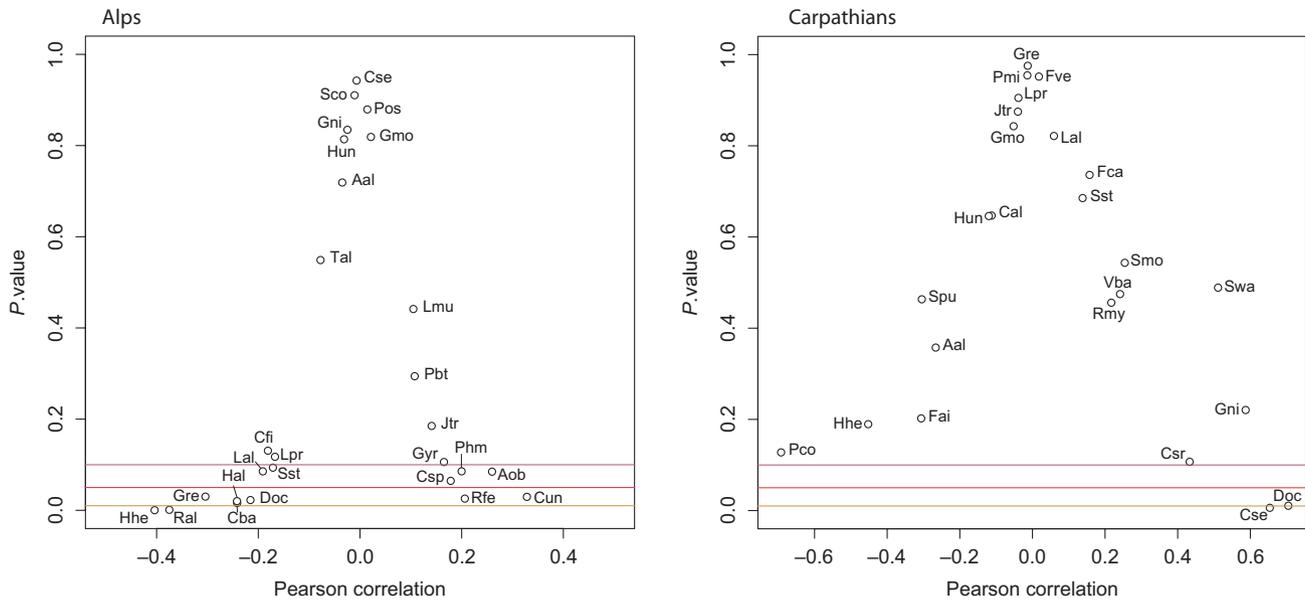


Figure 3 Correlation coefficients and P -values of correlations between single-species genetic diversity and total species richness for the Alps and the Carpathians. The coloured lines refer to the 0.1, 0.05 and 0.01 P -values without correction for multiple testing. The codes corresponding to each species are given in Table 1.

and genetic diversity. It should be noted, however, that we assessed neutral genetic diversity, and the observed relationships in this study might change if genetic diversity was measured at adaptively relevant genetic loci. Even though genetic diversity of a few species in our data set revealed significant positive correlations with total species richness, namely *C. sempervirens* and *D. octopetala* out of 24 species in the Carpathians, and *R. ferrugineum* and *Cerastium uniflorum* among 27 species in the Alps, there were also six species showing significant negative correlations in the Alps (*C. barbata*, *D. octopetala*, *Geum reptans*, *H. hedyсарoides*, *H. alpina* and *Ranunculus alpestris*; Fig. 3). Such an outcome questions the generality of the assumption that the two levels of biodiversity co-vary (Vellend 2005; Vellend & Geber 2005). Even more so, it becomes clear from our consistently sampled data that any type of correlation may be found when testing single species, supporting our multi-species approach. Nevertheless, parallel processes acting at the level of species and genetic diversity may have led to the positive correlation found between species rarity and genetic rarity, which conforms to the theoretical framework of Vellend (2005) and Vellend & Geber (2005). The few cases reported in the literature, where species richness and neutral genetic diversity were found to co-vary, correspond to island situations, that is, oceanic islands (MacArthur & Wilson 1967), forest patches (Vellend 2004; Cleary *et al.* 2006; Struebig *et al.* 2011), isolated spring or stream ecosystems (Sei *et al.* 2009; Blum *et al.* 2012) and patchily distributed sand dunes (He *et al.* 2008; He & Lamont 2010). The number of species able to colonise small islands is smaller than for large islands (MacArthur & Wilson 1967). Accordingly, both the number of colonisers per species and population sizes will be smaller, with a correspondingly reduced genetic diversity. At small geographical scales, such as in island situations, equilibrium is quickly reached and may result in co-variation of species richness and genetic diversity. This is not necessarily the case for continuous continental populations in temperate regions. The incessant Quaternary climatic fluctuations induced several range shifts with great changes in population sizes, larger effective population sizes retaining more genetic diversity (Hewitt 2004). In such a context, equilib-

rium may not have been attained yet. Thus, genetic diversity has predominantly been shaped by recent population history. Nevertheless, Thiel-Egenter *et al.* (2011) found astonishingly high congruence in the locations of contact zones at species and gene levels across the European Alps, suggesting that similar historical processes affected the migration patterns of genes and species during post-glacial re-colonisation.

In the Alps, genetic rarity is correlated with both species rarity (i.e. rare markers tend to be located in the same cells as rare species) and species endemism (i.e. rare markers in widespread species tend to be located in the same cells as endemic species). Rare markers may become fixed in long-term isolated refugial populations, which may therefore harbour high genetic rarity (Paun *et al.* 2008). This effect may explain why species and genetic rarity correlate in the Alps, where distinct glacial refugia occurred (Schönswetter *et al.* 2005), whereas in the Carpathians, alpine plants found suitable habitat over extended areas during the last glacial maximum (Ronikier 2011). In the latter case, the vast foothills of the Carpathians provided ample room for alpine plants to endure cold periods. In addition, the smaller size of this mountain range and its generally lower elevations than in the Alps allowed for comparatively rapid reimmigration and population establishment (Ronikier 2011). Furthermore, genetic diversity is negatively correlated with species rarity and species endemism in the Alps (i.e. greater genetic diversity coincides with the occurrence of many common species). These results were not confirmed by the Carpathian data set, where only a single significant positive correlation between areas of endemism for species and alleles was detected. In our analyses, as well as in other large-scale studies (Orme *et al.* 2005; Ceballos & Ehrlich 2006), species richness did not correlate with species rarity or with areas of endemism.

Our results have important consequences for designing conservation strategies. Clearly, spatial patterns of species richness in plants cannot generally be used as a surrogate for their intraspecific diversity. This becomes especially evident from the single-species patterns shown in Fig. 3. The importance of intraspecific diversity for ecosystem functioning and for preserving the evolutionary potential of spe-

cies demands that genetic diversity should not be neglected when designing conservation strategies and networks of protected areas (Lankau & Strauss 2007). According to our results obtained for both the Alps and the Carpathians, the protection of both levels of biodiversity within the same protected area might be difficult. One possible strategy would be to dedicate some protected areas towards the conservation of species richness, and others to genetic diversity. In the Alps, fortunately, many national parks have already been established in those regions exhibiting high species richness (from the border between Italy and France to Austria), while the Swiss national park in the central Alps is located in an area of high genetic diversity of alpine vascular plants. The current revolution in DNA sequencing technology will soon permit large-scale evaluation of genetic diversity, including adaptive loci of ecological relevance, and consequently will allow a better implementation of the CBD by integrating intraspecific genetic biodiversity into conservation programmes.

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AUTHOR CONTRIBUTIONS

PT, AT, HN and FG conceived this study. All authors were involved in collecting floristic and/or genetic data with the assistance of those mentioned in the Acknowledgements. PT, NEZ, TE, AT, RH, NA, AM, KS, CT-E and FG carried out the data analyses. PT, NEZ, RH and FG were the main contributors to the writing of the manuscript, and all authors contributed to and approved the final manuscript.

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DATA ACCESSIBILITY

Species distribution data and genetic data deposited in the Dryad Repository: <http://dx.doi.org/10.5061/dryad/s4q6s>

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