Received: 9 March 2018 | Revised: 18 June 2018 | Accepted: 22 June 2018

DOI: 10.1111/ddi.12819

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Divergent geographic patterns of genetic diversity among wild bees: Conservation implications

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Funding information
European Commission's Seventh Framework Programme (FP7/2007-2013), Grant/Award Number: #244090; STEP Project, Grant/Award Number: 2.4.613.10.F; Belgian Fonds pour la Recherche Scientifique, Grant/Award Number: 2.4.613.10.F; Fonds Wetenschappelijk Onderzoek (FWO, Belgium); Fonds National de la Recherche Scientifique (FNRS, Belgium), Grant/Award Number: 2.4.613.10.F

Editor: Anna Traveset

Abstract

Aim: Genetic diversity is a key factor to species survival. This diversity is unevenly distributed across the species range, delimiting genetic diversity hotspots (GDH). Focusing conservation efforts on regions where GDH of several species overlap (i.e., multispecies GDH) could rationalize conservation efforts by protecting several taxa in one go. However, recent studies suggest the existence of many species-specific GDH. This would make spatially prioritizing protection even more challenging as it requires the integration of these multiple GDH rather than few hotspots into conservation planning. Here, we characterize GDH of nine co-distributed bee species through an original comparative mapping approach to assess the suitability of a spatial prioritization strategy to protect their genetic diversity.

Location: We studied bee populations from Europe.

Methods: First, we used a sliding window approach to estimate the nucleotide diversity and its geographic distribution to highlight GDH of each species. Second, we assessed the overlap of GDH between species by generating consensus maps based on the species-specific maps of nucleotide diversity. Third, we used the GDH distribution patterns to identify the extent of cost-effective area network that would be needed to protect genetic diversity of all nine species.

Results: Genetic diversity was unevenly distributed across species ranges, but we found no evidence of a large overlap among GDH from all species. Cost-effective area network needed to protect genetic diversity of all species spreads over several large geographic areas including regions under high human development pressures.

Main conclusions: Genetic diversity hotspots' location is species-specific. Therefore, focusing conservation efforts strictly on the few regions harbouring GDH for many bee species is unlikely to be sufficient to ensure long-term persistence of all species. Conservation actions should be implemented simultaneously in different regions according to a complementary-based conservation approach, to optimize the conservation of all bee diversity.

KEYWORDS
conservation genetics, Europe, genetic diversity, geographic distribution, prioritization, wild bees

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1 | INTRODUCTION

Genetic diversity is one of the key factors to species survival (Booy, Hendriks, Smulders, Groenendael, & Vosman, 2000; Frankham, Ballou, & Briscoe, 2010). Indeed, lower genetic diversity limits the ability of species to adapt to a changing environment (Kahilainen, Puurtinen, & Kotiaho, 2014). Therefore, preserving genetic diversity is essential to ensure the long-term survival of species (Frankham et al., 2010). This concern is increasingly addressed by conservation biologists (Frankham et al., 2010; Sgrò, Lowe, & Hoffmann, 2011). However, the development of conservation plans is driven by many contradicting factors (e.g., biological, social, political), including funding limitations and land availability restrictions. For this reason, pragmatic strategies in conservation increasingly take human needs into account to increase the stakeholders' interests. Highlighting ecosystem services provided by a species group of concern is a way to facilitate the development of such a strategy (Chan, Shaw, Cameron, Underwood, & Daily, 2006; Egoh et al., 2007; Goldman, Tallis, Kareiva, & Daily, 2008; Klein et al., 2009). A further step for rationalizing conservation efforts lies in spatial prioritization. This procedure aims to identify cost-effective area networks that would ensure species survival (Chan et al., 2006). This allows focusing funding and land-use regulation on key regions for target species (Margules & Pressey, 2000).

Bees are an example of animals that provide a key ecosystem service: the biotic pollination of wild and cultivated flowering plants (Ollerton, Winfree, & Tarrant, 2011). Many bee populations have been in decline (Nieto et al., 2014; Vanbergen, 2013) probably due to the overuse of pesticides, the spread of diseases, the reduction in habitat availability and/or quality, and the decline in host–plant populations (Goulson, Nicholls, Botías, & Rotheray, 2015). Declining bee populations raise worries that the pollination ecosystem service might be increasingly threatened. To counter this alarming phenomenon, conservation programmes should develop mitigation strategies and ensure long-term survival of bee species including through conservation of their genetic diversity.

Spatial conservation prioritization constitutes a promising approach to improving the conservation of species genetic diversity (Souto et al., 2015; Vandergast, Bohonak, Hathaway, Boys, & Fisher, 2008), as it is unevenly distributed across the range of most species (Avise, 2000; Rauch & Bar-Yam, 2004). For many species, the Quaternary climatic oscillations have played an important role in determining geographic patterns of genetic variability (Hewitt, 2004). During this period, most species went through several climatic cycles, including periods of range reduction during which individuals were restricted to refuge areas, followed by periods of range expansions during which species re-colonized at least portions of their initial range (Hewitt, 2004; Stewart, Lister, Barnes, & Dalén, 2010). This population dynamic has strongly influenced the current patterns of genetic diversity distribution. On the one hand, ancestral genetic diversity was maintained in refuge regions, while secondary re-colonization of non-refuge areas inevitably led to a loss in genetic variation through founder events occurring at the expanding front (Avise, 2000; Hewitt, 2004). On the other hand, the mixing of individuals originating from different refuges in certain newly colonized areas also created regions of high genetic diversity (Avise, 2000; Hewitt, 2004). Refuges and secondary contact areas constitute two examples of regions that tend to host high intraspecific genetic diversity (hereafter referenced as genetic diversity hotspots, GDH). These regions are potentially important targets for conservation prioritization (Souto et al., 2015; Thomassen et al., 2011). Previous comparative phylogeographic studies have established species genetic diversity distributions, allowing the identification of areas where GDH of several co-distributed organisms overlap (e.g., for invertebrates and vertebrates: Hewitt, 2004; Vandergast et al., 2008). These regions host populations with large adaptive potential for multiple species (so-called multispecies GDH). Focusing conservation efforts on these multispecies GDH has been proposed as a rationalization to protect genetic diversity of several species in one go (e.g., Vandergast et al., 2013 for North American vertebrates and invertebrates). While the implementation of such an approach in conservation plans is at its early stages, an increasing number of studies develop multi-taxa analysis of genetic diversity for conservation prioritization (e.g., on plants and vertebrates: Thomassen et al., 2011; Souto et al., 2015). Indeed, focusing on the protection of multispecies GDH should (a) preserve the largest number of intraspecific lineages and (b) increase the resilience of several species to environmental changes (Vandergast et al., 2013). This strategy would be more efficient if a large overlap between GDH of several species could be identified. Although some studies did identify species displaying similar distribution patterns of genetic variation (Hewitt, 2004; Vandergast et al., 2013; Wood et al., 2013), recent analyses underlined unique species-specific phylogeographic histories for several species (e.g., species-specific Ice-Age refuges and recolonization patterns leading to species-specific GDH; Stewart et al., 2010). This could make the congruence of genetic hotspots between bee species unlikely and result in inflating the number of species-specific GDH deserving protection. Therefore, spatial prioritization of conservation efforts could be difficult for bees.

Among bees, it has been shown that phylogeographic patterns can be different between species. However, most studies describing the intraspecific genetic variability of bees have focused on a single species or few species of the same genera (Dellicour, Michez, & Mardulyn, 2015; Dellicour, Michez, Rasplus, & Mardulyn, 2015; Dellicour et al., 2017; Duennes, Lozier, Hines, & Cameron, 2012; Lecocq, Brasero, Martinet, Valterovà, & Rasmont, 2015; Lecocq et al., 2013). In Europe, the recent availability of continental-scale genetic datasets is an opportunity to compare and assess the congruence of GDH through a meta-analysis based on the same statistical approach for each species.

Here, we compare through a meta-analysis the GDH among a group of species providing a pollination ecosystem service. As an example, we focus on nine co-distributed species of bees (Apoidea, Anthophila) across Europe through a comparative mapping approach of genetic diversity. We assess the feasibility of a spatially prioritized conservation plan by identifying GDH for each species (i.e., species-specific GDH) and by comparing them among species to highlight multispecies GDH. We ultimately aim to assess the extent of cost-effective area networks that would be needed to protect genetic diversity of all nine species.

2 | METHODS

2.1 | Studied species, geographic scale and genetic datasets

We focused on nine species of bees displaying a West Palaearctic distribution: *Bombus hortorum*, *Bombus lapidarius*, *Bombus pascuorum*, *Bombus pratorum*, *Bombus terrestris*, *Colletes hederae*, *Melitta leporina*, *Melitta nigricans* and *Melitta tricincta*, from three different families: Apidae, Colletidae and Melittidae, respectively. Each family belongs to one of the three main clades of the bee phylogeny: (a) Melittidae is the sister group to all other bee groups, (b) the Apidae is included in the long-tongued bee lineage and (c) the Colletidae is a part of the short-tongued bee lineage (Danforth, Cardinal, Praz, Almeida, & Michez, 2013). Moreover, the chosen species differ by various species-specific life history traits (which can lead to different dispersal abilities; Bommarco et al., 2010; Nowak, Tarnita, & Wilson, 2010; Warzecha, Diekötter, Wolters, & Jauker, 2016), representative of the diversity found in bees: (a) bumblebees (*Bombus* spp.) are eusocial, while *Colletes* and *Melitta* species are solitary; (b) *Bombus* species are large generalist pollen foragers, while other species are small- to medium-size specialist pollen foragers (Müller & Kuhlmann, 2008; Westrich, 1999). Although this sampling does not include the full range of bee life history traits, it allows considering a substantial part of European bee diversity. Therefore, we consider that the sampling allows providing a first efficient assessment of potential multispecies GDH in European bees and highlighting global trends of pattern of genetic diversity distribution for these bees.

To assess the distribution of species genetic diversity, we considered their entire European range (i.e., mainland and adjacent islands). We used previously published molecular datasets based on specimens sampled across Europe (see Figure 1, Supporting information Table S1; Dellicour et al., 2014; Lecocq, Gérard, Michez, & Dellicour, 2017) for which the sequencing of each sample has been carefully checked: each PCR product had been sequenced in both directions and all sequencing chromatograms had been carefully inspected. *Bombus* sequence data consisted in the mitochondrial gene COI (cytochrome oxidase I; ~1,000 bp) and the two protein-coding

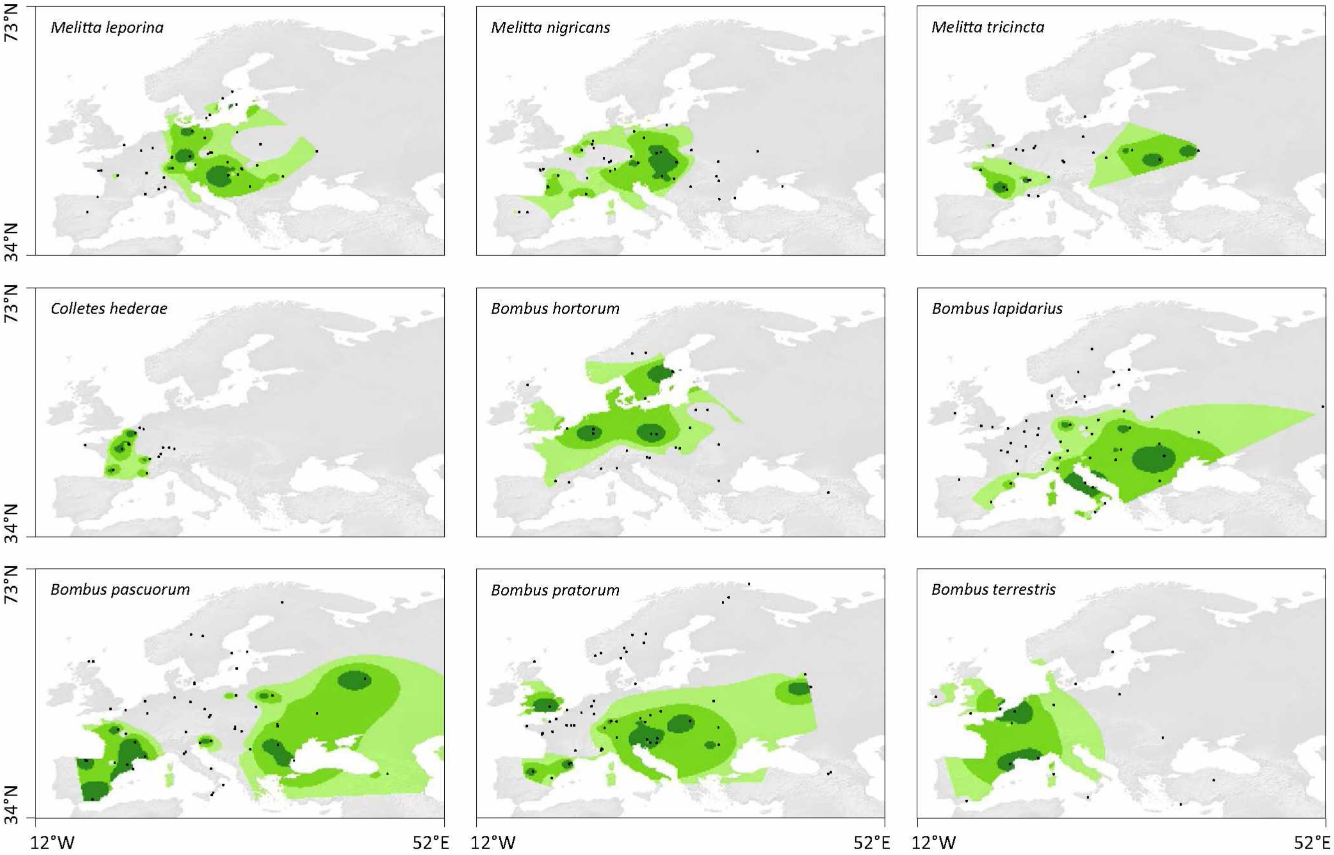

FIGURE 1 For each considered species, areas with nucleotide diversity higher than specific threshold values (0.50, 0.75 and 0.95 quantile values, in shades of increasing darkness). See Material and methods section for a complete description of the method used to generate these surfaces. The black dots are sampled populations with more than two specimens. This figure is based on initial interpolation surfaces based on a sliding window with a radius $r = 50$ km (see Supporting information Figures S1 and S2 for equivalent figures based on sliding window radius $r = 25$ and 100 km, and Supporting information Figure S3 for maps displaying variation of genetic diversity among loci)

nuclear genes EF-1α (elongation factor 1 alpha, F2 copy; ~800 bp) and PEPCK (phosphoenolpyruvate carboxykinase; ~900 bp). The *C. hederae* sequence dataset consisted in three nuclear loci: CAD (conserved ATPase domain; ~1,000 bp), RNAp (RNA polymerase II; ~850 bp) and WgL (wingless; ~750 bp). *Melitta* datasets included the mitochondrial gene COI (~900 bp) and four protein-coding nuclear genes: NaK (sodium–potassium adenosine triphosphatase; ~750 bp), Opsin (long-wavelength rhodopsine; ~850 bp), RNAp (RNA polymerase; ~850 bp) and WgL (Wingless; ~400 bp). While *Bombus* and *Melitta* species had been sampled across nearly their entire West Palaearctic range, *C. hederae* dataset was geographically limited to a few countries (Figure 1). As large occurrence datasets were not available for this species, we cannot assess how our *C. hederae* sampling is representative of the species distribution.

2.2 | Mapping genetic diversity

To compare the spatial distribution of genetic diversity among species sampled at different locations, we generated maps displaying geographic variation in genetic diversity across the range of each species. Because different loci were used for each bee genus, we focused on the distribution of overall genetic diversity (i.e., based on all loci) within the range of each species. This allowed a relative comparison of genetic diversity distribution between species to localize common geographic regions of GDH. The maps were built in four steps. In the first step, for each species, we used a sliding window approach to estimate the nucleotide diversity π (Nei & Li, 1979) averaged over all loci and associated with each cell of a template raster covering the study area (spatial resolution: 12.5 arcmin). In practice, the value assigned to a given grid cell was the nucleotide diversity estimated for the group of sequences sampled within a circle centred on this cell. The sliding window was implemented in R (R Development Core Team, 2017) and based on functions available in the packages "raster" and "fields." Since the outcome depended on the circle surface considered, we tested several values for the radius r (25, 50 and 100 km) used to define this sliding window. Testing different radii allowed assessing and discussing the impact of the sliding window extent on the GDH mapping. In the second step, we performed an inverse distance interpolation on the raster files obtained with the sliding window approach. The interpolations were performed with the inverse distance procedure implemented in the R function "GDivPAL" available with the toolbox SPADS (Dellicour & Mardulyn, 2014) and using a distance weighting parameter $a = 5$. In the third step, a convex hull was drawn around fictive circles of 100 km radius centred on sampling locations for the considered species, for each generated interpolation surface. These convex hulls were used to define the different "study areas" by cropping the surfaces and thus avoiding excessive extrapolation. In the last step, we highlighted GDH of each species by colouring maps according to three threshold values: the 0.50, 0.75 and 0.95 quantile values estimated for each species.

In addition to multi-locus GDH maps described above, we also generated maps displaying, for each species, variation in genetic diversity among loci. For a given raster cell, we computed the standard deviation among locus-specific nucleotide diversities assigned to this cell. As the range of estimated nucleotide diversities varies among loci (as summarized in Supporting information Table S2), nucleotide diversity values assigned to each cell were preliminarily rescaled and standardized across each locus-specific raster before computing standard deviations.

It is important to note that nucleotide diversity (Nei & Li, 1979) is a metric corrected for unequal sequence length but also for unequal sample size, which makes possible their comparison among species for which we have different sample sizes (Dellicour, Michez, Rasplus, et al. 2015). Furthermore, this metric estimated from DNA sequences presents the advantage of providing a genetic diversity measure based on both allelic frequencies and genetic distances between haplotypes, two important/complementary aspects to consider when studying the geographic distribution of genetic variability.

From a methodological point of view, the advantage of a sliding window approach is to avoid the arbitrary delimitation of "populations" within which the nucleotide diversity would be estimated. Indeed, a potential arbitrary delimitation could have been used to consider each sampling location as a distinct population. However, this would lead to the disadvantages of having to discard sampling locations with only one sampled sequence and to estimate nucleotide diversity for globally lower number of sampled sequences. While the circle radius value remains arbitrary in itself, it just corresponds to the size of a given area for which we want to estimate the genetic diversity. The key aspect is to compare maps of genetic diversity obtained with the same radius value.

2.3 | Multispecies GDH

As current actions in conservation genetics aim at protecting genetic diversity (Frankham et al., 2010), we localized the multispecies GDH by generating consensus maps from the species-specific threshold maps of nucleotide diversity: for a given distance weighting parameter a and threshold value, the consensus map displays the number of studied species for which the interpolated value is higher than the considered threshold value. We excluded *C. hederae* from the multispecies GDH analyses because the geographically limited sampling for that species may not reflect its actual spatial distribution of genetic diversity.

2.4 | Spatial prioritization analyses

We identified the best spatial strategy to protect genetic diversity in European bees by using the Zonation software (Moilanen, Kujala, & Leathwick, 2009). We here focused on the genetic diversity reported on the interpolation surfaces instead of on species distributions. This allowed evaluating the importance of particular grid cells for the conservation of genetic diversity. We applied the Core Area Zonation function (Moilanen, 2007) to genetic datasets of all species, minimizing the loss of conservation value computed as the highest remaining proportion of a feature (in this case, genetic diversity of a species) remaining in a cell. This complementarity-based priority ranking of geographic areas ensured that diversity hotspots of every species were at least partly represented in the top priority areas even if they did not overlap with genetic hotspots of other species. The analysis produced a priority ranking for each cell, with the least important grid cell receiving a value of 0.0 and the most important cell receiving a value of 1.0. This analysis was replicated with the different radii of the sliding window. As for the building of multispecies GDH consensus maps, we excluded *C. hederae* from Zonation analyses.

3 | RESULTS

3.1 | Species-specific GDH

Interpolation surfaces based on a sliding window defined by circles of different radii *r* highlighted similar portions of the distributions where genetic diversity was higher than defined threshold values (0.50, 0.75 and 0.95 quantiles; see Figure 1, Supporting information Figures S1-S2). Genetic diversity was unevenly distributed across species ranges for all thresholds (Figure 1). Comparing the distributions of species-specific GDH among species showed that regions associated with high genetic diversity differed among species for all threshold values (Figure 1). For each species, we also detected small differences among loci in their genetic diversity distribution (Supporting information Figure S3), which further underlines the necessity to base genetic diversity measures on multiple loci to account for stochastic variability among loci.

3.2 | Multispecies GDH and spatial prioritization analyses

The multispecies GDH hosting more than four species were restricted to some areas (e.g., inside the south-western quarter of France and Central Europe; Figure 2, Supporting information Figure S4) and included a small amount of species-specific GDH (Table 1). This trend increased with higher threshold values (Figure 2, Supporting information Figure S4).

The top 5% priority areas identified by the Zonation analyses mainly included areas of overlap among GDH for several species (Supporting information Figure S5). However, some regions of GDH for only one or two species were also identified as priority areas (Supporting information Figure S5). Compared to the consensus maps, the Zonation analyses thus provided additional information by identifying areas of high irreplaceability. The results based on the three sliding window radii did not differ notably, except that the largest radius led to the identification of fewer, larger priority areas.

4 | DISCUSSION

4.1 | Potential limitations

While a small sampling size at each sampling location can bias the conclusions on GDH patterns, the sliding window approach allows to a certain extent to minimize this deleterious effect. Indeed, the approach estimates the genetic diversity for particular point of the map from several individuals sampled within a given radius around this location. This means that a large number of specimens are considered to estimate the genetic diversity in a particular location, even when only few specimens have been collected at each sampling place. However, the sliding window approach can be limited in areas where sampling places are scattered and distant from each other (i.e., more distant than the sliding window radius, e.g., *B. terrestris*). Therefore, GDH patterns in such areas should be carefully considered and further supported by future genetic assessments.

The present GDH analysis is based on mitochondrial and nuclear sequences. This choice was primarily motivated by the availability of these markers for the studied species. Other markers such as single nucleotide polymorphisms (SNPs) or simple sequence repeats

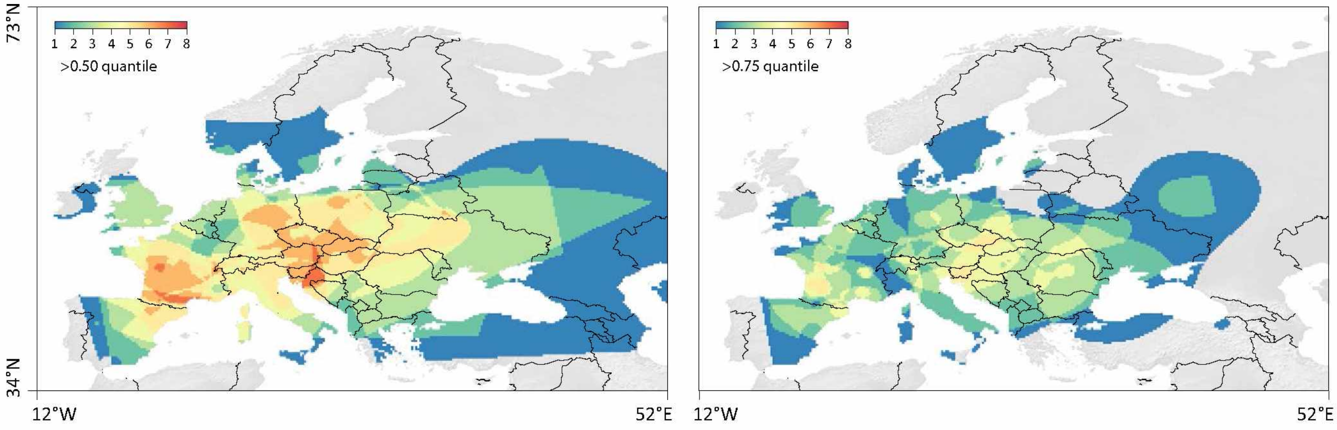

FIGURE 2 Consensus maps based on the specific threshold maps built from interpolation surfaces based on sliding windows with a radius $r = 50$ km. The colour scale reports the number of species for which the nucleotide diversity is higher than the threshold value of 0.50 and 0.75 quantiles. Black lines indicate the position of national borders. See Supporting information Figure S4 for consensus maps based on alternative sliding window radius

TABLE 1 Percentage of areas of consensus maps with a given number of species associated with a nucleotide diversity higher than a specific threshold value

Threshold value	Sliding window radius (*r*)	Number of species with a nucleotide diversity higher than the threshold value: 1	2	3	4	5	6	7	8
0.50 quantile	25 km	100%	65.8%	50.9%	32.4%	20.7%	7.1%	1.7%	0.2%
	50 km	100%	64.3%	50.7%	30.2%	20.0%	7.5%	0.9%	0.0%
	100 km	100%	60.9%	49.5%	31.1%	22.0%	6.1%	0.3%	0.0%
0.75 quantile	25 km	100%	64.9%	32.1%	10.0%	2.2%	0.0%	0.0%	0.0%
	50 km	100%	62.1%	34.8%	11.8%	1.7%	0.0%	0.0%	0.0%
	100 km	100%	56.3%	31.7%	11.5%	1.1%	0.0%	0.0%	0.0%
0.95 quantile	25 km	100%	19.5%	4.2%	0.1%	0.0%	0.0%	0.0%	0.0%
	50 km	100%	23.0%	3.7%	0.1%	0.0%	0.0%	0.0%	0.0%
	100 km	100%	20.4%	1.7%	0.0%	0.0%	0.0%	0.0%	0.0%

("microsatellites") are currently not available at the continental scale for European bees. Because in general a larger number of loci can be genotyped with this type of markers, they would give us access to genetic variation from a much larger portion of the genome, and future GDH studies should seriously consider to include them. Nonetheless, the mitochondrial and nuclear sequences analysed for the present study offer a sufficient number of alleles per species to provide important information regarding recent population history.

4.2 | Few and small multispecies GDH

Comparison of sampling efforts of analysed genetic datasets shows discrepancies between species (Figure 1). As observed in many European invertebrate and vertebrate taxa (Avise, 2000; Hewitt, 2004), genetic diversity of *Bombus* and *Melitta* species is unevenly distributed and scattered in several hotspots across their distribution range (Figure 1). The hotspot locations could correspond to Ice-Age refugia or hybrid zones between previously isolated gene pools (Avise, 2000). The restricted dispersal ability of many bees (Lecocq et al., 2017; Murray, Kuhlmann, & Potts, 2009) may explain the maintenance of such geographic structure through time. In contrast, *C. hederae* displays a more even distribution of its genetic diversity, which may be associated with the very recent (since the 1990s) range expansion with relatively high migration rates of this species (Dellicour et al., 2014). However, our geographically limited sampling for this species should be expanded to assess this hypothesis.

Some areas clearly exhibit higher genetic diversity levels for a majority of the examined species (Figure 1). However, our analyses did not highlight a large common pattern of genetic diversity distribution shared by most studied species (i.e., multispecies GDH are small and scattered; Figure 2). This could be explained by differences in ecological niches among species (i.e., spatial distribution patterns of genetic hotspots can differ among taxa according to their specific ecological requirements, as observed in South American trees; Souto et al., 2015) and/or by specific demographic histories (Hewitt, 2004; Stewart et al., 2010). First, current patterns of genetic variation for specialist pollen forager bees (e.g., *Melitta*) have likely been impacted by past and current abundance of host plant species (Dellicour, Michez, & Mardulyn, 2015; Dellicour, Michez, Rasplus, et al. 2015), while those for generalist bees (e.g., *Bombus* spp. that can shift to alternative pollen resources; Roger et al., 2017) were likely and mostly influenced by climate only (Dellicour et al., 2017; Kerr et al., 2015). This can explain the GDH species specificity in specialist bees. However, even between wide-ranging generalist and closely related species (i.e., the five bumblebee species), substantial differences in the spatial distributions of GDH can still be observed (Figure 1) most likely due to species-specific ecological requirements (i.e., studied bumblebee taxa have different climatic niches; Rasmont et al., 2015). Second, European bee species have (a) experienced different range shrinking during the last Ice Age (Dellicour, Michez, Rasplus, et al. 2015; Dellicour et al., 2017), (b) followed different re-colonization routes leading to species-specific gene pool mixing zones (e.g., Dellicour, Michez, & Mardulyn, 2015; Dellicour, Michez, Rasplus, et al. 2015; Lecocq et al., 2013) and (c) different times of range expansion (e.g., *C. hederae*, Dellicour et al., 2014) that further increase the probability of GDH pattern divergence. Similar species specificity in demographic histories has been observed in other organisms, even when comparing closely related taxa (e.g., in insects: Ikeda, Kubota, Cho, Liang, & Sota, 2009; birds: Álvarez-Varas, González-Acuña, & Vianna, 2015; plants: Wu et al., 2006; echinoderms: Taboada & Pérez-Portela, 2016) making similar conclusion likely for other species groups.

Overall, while one may expect to find overlapping genetic diversity hotspots when comparing sympatric wide-ranging and closely related taxa with similar ecological tolerances (e.g., Souto et al., 2015), our results show the analysed European bees display different GDH most likely due to their specific ecological requirements and/or their specific demographic histories. This GDH species specificity suggests that the hotspots locations of one European bee species cannot be predicted using data from other closely related species. Therefore, identifying all GDH of European bees requires a relatively extensive and detailed genetic assessment of all species of interest. This could make the GDH definition unpractical from a financial (i.e., costs of genetic analysis) or sampling (e.g., ethical and legal issues to sample rare and declining species) point of view. However, this issue could be overcome in the future assuming analytic advances (i.e., non-invasive genetic sampling) and decrease in genetic analysis costs.

4.3 | Conservation of genetic diversity

Current conservation strategies aim at protecting bees by minimizing habitat loss and making agricultural habitat bee-friendly across most of the species distribution ranges (Brown & Paxton, 2009; Potts et al., 2011). However, such ambitious plans are still facing the issues raised by agricultural practices, funding limitations and anthropogenic pressures (Brown & Paxton, 2009; Potts et al., 2011). Therefore, there is a risk that if large geographic-scale conservation management fails, it would not be possible to preserve large population sizes to ensure the long-term persistence of bee genetic diversity. In this context, the spatial prioritization approach could provide a complementary solution to protect genetic diversity of several bee species by intensifying conservation efforts on multispecies GDH. These multispecies hotspots could be managed as bee natural reserves (i.e., strict natural reserves or national park sensu IUCN protected area categories), while urban and semi-natural areas should be "pollinator-friendly" to act at least as corridors (Holzschuh, Steffan-Dewenter, & Tscharntke, 2009) assuring flow of genes, individuals and pollination service towards other regions and between GDH.

In practice, however, our results suggest that the usefulness of spatial prioritization for bee conservation biology is limited. On the one hand, selecting the only few areas displaying high genetic diversity for a majority of species would considerably reduce the portion of genetic diversity protected for each species (i.e., multispecies GDH including at least half of the nine studied species include less than 25% of the area of each species-specific GDH, Table 1), which would then be insufficient for species long-term viability. On the other hand, the existence of multiple hotspots, unique to one or a few species, prevents from identifying a reasonable number of target geographic areas to be protected. This is acknowledged by Zonation analyses that emphasize the conservation value (including irreplaceability, Pressey, Johnson, & Wilson, 1994) of many large geographic areas (Supporting information Figure S5) including regions under high human development pressures (Kukkala & Moilanen, 2013). While bee conservation in natural reserves already existing in multispecies GDH areas should be maintained, a strict land protection cannot be established over such large regions. Therefore, there is no alternative to current conservation strategies which aim at maintaining bee populations overall species distributions by embedding bee biodiversity maintenance within agricultural development (Brown & Paxton, 2009) or developing urban "pollinator-friendly" green infrastructure in cities (Dicks et al., 2016). As European bee species are distributed across several countries, ensuring bee survival requires the development of bee conservation plans at both national and international levels, as underlined by the concept of national responsibility (Schmeller et al., 2008).

The present study shows that GDH is species-specific for several European bee taxa. Therefore, focusing conservation efforts strictly on the few regions harbouring GDH for many species is unlikely to be sufficient to ensure genetic diversity of all closely related species. As species-specific demographic history has been observed in other organisms and in other parts of the world, similar results could be expected for other declining species groups. Subsequently, the suitability of a spatial prioritization strategy to protect genetic diversity should be carefully considered in all species groups across the world.

ACKNOWLEDGMENTS

We are grateful to two anonymous reviewers for their helpful comments. We acknowledge funding from the European Commission's Seventh Framework Programme (FP7/2007-2013); grant agreement #244090), STEP Project (www.step-project.net) and the Belgian Fonds pour la Recherche Scientifique (FRFC project 2.4.613.10.F). SD was supported by the Wiener–Anspach Foundation and is currently funded by the Fonds Wetenschappelijk Onderzoek (FWO, Belgium) and the Fonds National de la Recherche Scientifique (FNRS, Belgium). Computational resources have been provided by the Consortium des Équipements de Calcul Intensif (CÉCI) funded by the Belgian F.R.S.-FNRS.

DATA ACCESSIBILITY

GenBank accession number for each DNA sequences is given in Dellicour, Michez, & Mardulyn, 2015; Dellicour, Michez, Rasplus, et al. 2015 and Lecocq, Brasero, et al. 2015; Lecocq, Dellicour, et al. (2015, 2016). The R function developed to perform the sliding window operation has been added to the toolbox SPADS (Dellicour & Mardulyn, 2014) along with a tutorial.

COMPETING INTERESTS

We have no competing interests.

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BIOSKETCH

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Authors' contributions: TL and SD designed the study, and TL, JD and SD analysed the data. All authors interpreted the data and the analyses. TL and SD wrote the manuscript. All authors revised the manuscript critically and approved the final version.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Lecocq T, Michez D, Gérard M, et al. Divergent geographic patterns of genetic diversity among wild bees: Conservation implications. *Divers Distrib*. 2018;00:1–9. https://doi.org/10.1111/ddi.12819

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