



Distant but related: genetic structure in the circum-boreal bumblebee *Bombus jonellus* (Kirby, 1802)

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Abstract

Whilst the Arctic and boreal bumblebee fauna is increasingly studied worldwide, information is missing about the genetic connections between circum-boreal populations of some widespread species, especially those living in remote regions like North-East Siberia and Alaska. Here, we study one of the most common boreal bumblebee species, *Bombus* (*Pyrobombus*) *jonellus* (Kirby, 1802), as a model to investigate current circum-boreal genetic connections and relations with relictual populations in its post-glacial refugia in Southern Europe. Our haplotype network analysis based on a fragment of the cytochrome oxidase 1 gene reveals two main conspecific lineages, one in Europe including the Southern relictual populations from the Pyrenees and the second comprising Eastern Palearctic and Nearctic populations. However, West-Siberian populations of *Bombus jonellus* share haplotypes with the two distinct lineages. These results could indicate a postglacial, multidirectional and circum-boreal recolonization both in Europe and East-Palearctic from refugia in Siberia, in addition to other recolonization ways from Southern European refugia and Beringia. These findings highlight that a priori distant and isolated conspecific populations of *B. jonellus* could presently remain connected or have only presented a recent break in gene flow.

Keywords Polar species · Relictual populations · Bumblebees · Genetic connections · Post-glacial recolonization · Ice ages

Introduction

Bumblebees (Hymenoptera: Apidae) constitute a genus of mostly cold-adapted pollinators living in some of the highest latitude and altitude ecosystems of the world. High species diversity is reached in the Arctic, boreal and mountain regions (Williams 1998; Williams et al. 2014). They are relevant models for biogeographic reconstructions as (i) their presence in each area relies on the concomitant distribution of flowering plants, (ii) they are not able to disperse

across large water barriers and (iii) have undergone serious redistribution patterns following the last ice ages (Reinig 1937; Bolotov et al. 2013; Potapov et al. 2018; Martinet et al. 2018).

The origin of the genus *Bombus* is estimated at the late Eocene to mid-Oligocene (25–40 Ma) in Asian mountains (Hines 2008; Dehon et al. 2019), nowadays still hosting their highest species richness (Williams 1991; Williams et al. 2010; Streinzer et al. 2019; Ghisbain et al. 2020). Throughout the later diversification of the genus following the oscillations of climate, movements between West- and East-Palearctic regions were frequently involving long distances (Hines 2008). Connections between the Old and the New World took place across the Bering Strait (Williams 1985) along with a large diversification in Nearctic regions between 20 and 10 Ma. At this period, the taiga biome, extending further south than present, was a key facilitator for the dispersion of bumblebees. The separation between Palearctic and Nearctic regions by the Bering Strait (ca. 3.5 Ma ago) later resulted in repeated processes of vicariant speciation in many organisms (Sanmartin et al. 2001), including bumblebees (Williams et al. 2019). These

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two territories were later reconnected (ca. 1–1.5 Ma ago) allowing new migration events between the Palearctic and Nearctic regions. Currently, most Arctic bumblebee taxa are still distributed on both sides of the Bering Strait (Ito and Kunarishi 2000). As a result, several bumblebee species now present a circum-Arctic distribution (Williams et al. 2014, 2019) such as *Bombus (Alpinobombus) polaris* (Curtis, 1835), *Bombus (Pyrobombus) lapponicus* (Fabricius, 1793) and *Bombus (Pyrobombus) jonellus* (Kirby, 1802) (Martinet et al. 2019) with potential speciation processes involved (Williams et al. 2019).

Amongst bumblebees, *Pyrobombus* Dalla Torre, 1880 constitutes a diversified subgenus including around 50 species worldwide (Williams 1998; Hines 2008). *Pyrobombus* are most diversified in the Nearctic, but also comprise numerous Palearctic species. Several of them present a widespread distribution and occur both in the Nearctic and Palearctic regions. The heath bumblebee, *Bombus (Pyrobombus) jonellus* (Fig. 1) is just such a case. It is a circum-boreal bumblebee species, distributed from Iceland and the British Islands, through Northern Europe with southern populations (e.g. in Pyrenees), West- and East-Palearctic Russia, to Alaska and Western Canada (Løken 1973; Pekkarinen 1981; Proshchalykin and Kupianskaya 2005; Williams et al. 2014; Levchenko and Tomkovich 2014; Rasmont et al. 2015; Kratochwil 2016) (Fig. 2). Compared to other insect taxa (Sikes et al. 2016; Combe et al. 2021), the apparent conspecificity of both the Nearctic and Palearctic lineages of *B. jonellus* (Williams et al. 2014) is quite remarkable given that the distribution of this species spans across North America (limited to the far Northwest Nearctic, Koch et al. 2015), Europe (where it includes several isolated relictual populations) and Russia. Overall, the global distribution of *B. jonellus* gives it an almost unrivalled large distribution



Fig. 1 Photo of *Bombus jonellus*. A male of the heath bumblebee (*Bombus jonellus*) visiting a fireweed (*Epilobium latifolium*) in Toolik field Station, N-Alaska. Photo by P. Rasmont

amongst bumblebees. In most parts of its distribution, *B. jonellus* is associated with heathlands, mountain meadows and tundra partly characterized by a large abundance of plants of the family Ericaceae (Alford 1975; Falk and Lewington 2017; Parkkinen et al. 2018) (Fig. 3). Whilst the species seems especially associated with open habitats, it also occurs in forests in Eastern Europe (Poland) (Dylewska 1996) and boreal taiga forest in the central part of European Russia (Panfilov 1982). In the taiga and tundra regions, *B. jonellus* is one of the main pollinators of berries (e.g. *Vaccinium* spp.), an important food resource for the subsistence human populations. In Europe, the distribution of *B. jonellus* is well known (Rasmont et al. 2015), although we do not have sufficient data to establish its worldwide conservation status (Data deficient in Hatfield et al. 2016; but see Nieto et al. 2014 for Europe). However, this species seems to be sensitive to environmental stress such as climate change (Martinet et al. 2021a,b) and habitat fragmentation especially for relictual and isolated populations. Particularly, in central and eastern regions of Russia, there is an unfortunately large lack of data for this species (Rasmont and Iserby 2014; Potapov et al. 2018; Potapov and Kolosova 2020), understanding us of knowing the genetic connections with the other parts of its distribution. In this study, we provide new genetic data including Siberian and European isolated populations for a better understanding of population genetic connections in *B. jonellus*.

In a context of climate change, populations of *B. jonellus* are expected to suffer from a significant reduction in suitable climatic areas in Europe (Rasmont et al. 2015) and North America (Sirois-Delisle and Kerr 2018). From a conservation point of view, it is critical to understand the genetic structures between these circum-boreal populations to get a more comprehensive overview of the connections of these boreo-alpine pollinators with a disjunct distribution, especially in a context of global changes. Genetic tools, such as barcoding at large geographical scale provide crucial data to explore genetic connections between populations across species' ranges (e.g. Martinet et al. 2019; Williams et al. 2020; Lhomme et al. 2021). In this paper, we explore the genetic connections of *B. jonellus* populations across the distribution range of the species in the Holarctic region. As for many other bumblebee taxa distributed across the Holarctic (e.g. Martinet et al. 2018; Potapov et al. 2019; Williams et al. 2019), we expect a clear genetic structure between the Nearctic and Palearctic populations of *B. jonellus*. Because polytypic bumblebee taxa can show signs of population structuring in the *COI* barcode fragment (Williams et al. 2020; Brasero et al. 2021; but see Lecocq et al. 2015), some degree of genetic differentiation in the phenotypically divergent subspecies *B. jonellus hebridensis* is expected (Potapov et al. 2018). Finally, the isolated Pyrenean population of

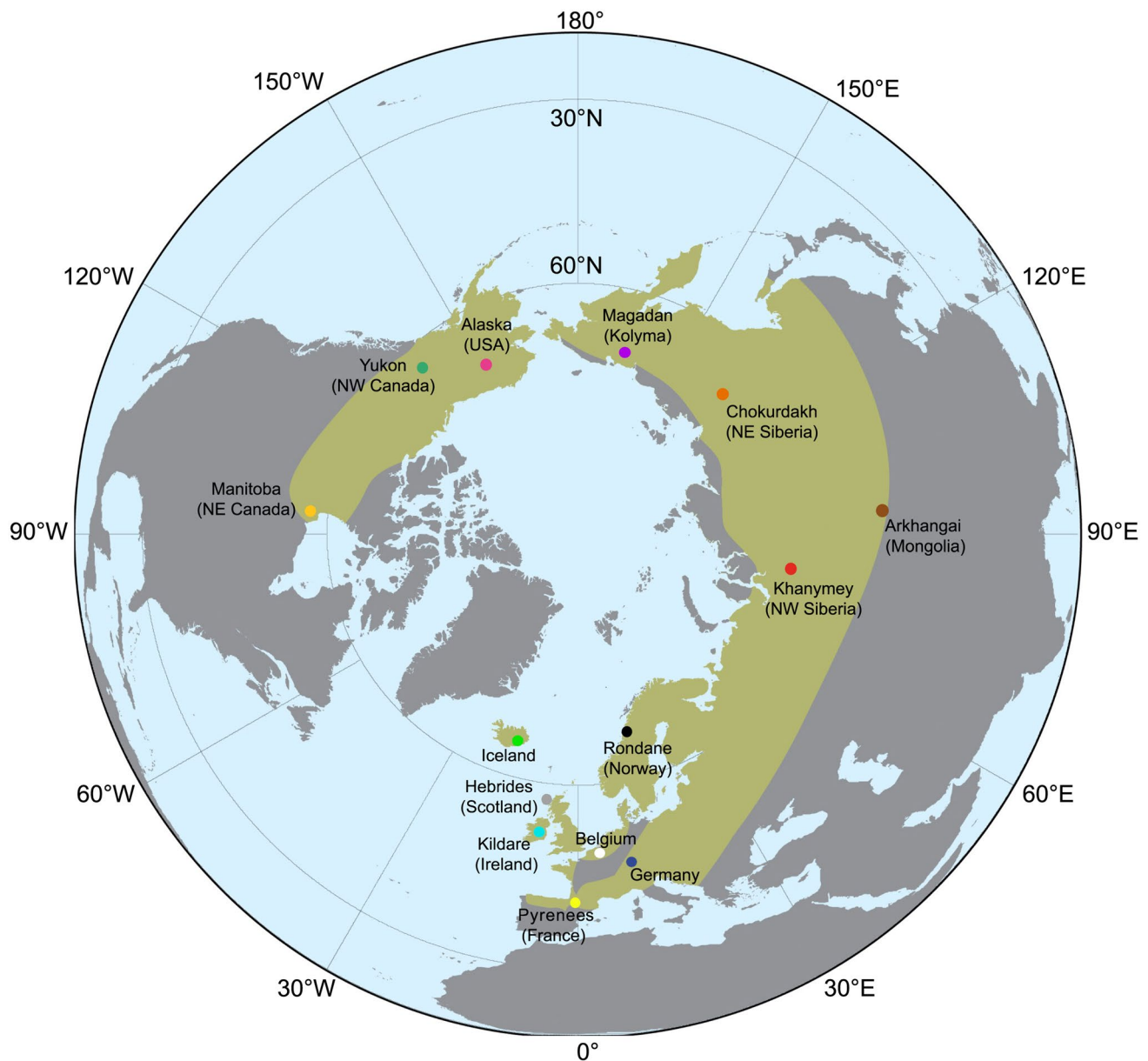


Fig. 2 Distribution map and collecting sites. Global distribution (green area) and sampling localities (coloured points) of *Bombus jonellus* adapted from Løken (1973), Panfilov (1957), Davydova (2003), Proshchalykin (2004), Proshchalykin et al. (2004), Proshchalykin and Kupianskaya (2005), Kupianskaya et al. (2011), Williams et al. (2014), Rasmont et al. (2015), Paukkunen and Kozlov (2015,

2020), Madsen et al. (2016), Byvaltsev et al. (2016) and Potapov and Kolosova (2020). Colored points displayed on this map correspond to the colors used in haplotype network analysis (Fig. 4). Distributional ranges are approximated based on literature records and thus are not meant to be accurate at a fine scale

B. jonellus is also expected to appear as a distinct genetic cluster, as observed in other bumblebee whose distributions encompass isolated high-altitude habitats in the southern part of their range (Martinet et al. 2018; Brasero et al. 2021).

Materials and methods

Data sampling

We collected specimens of *B. jonellus* from W-Pyrenees ($n=6$), Belgium ($n=3$), Outer Hebrides ($n=10$), N-Alaska ($n=5$), W-Siberia (Yamalo-Nenets region, Khanymey) ($n=5$), E-Siberia (Chokurdakh) ($n=9$) and Mongolia ($n=3$), completing the genetic data with 19 available on



Fig. 3 Foraging habitats. Typical foraging habitats of *Bombus jonellus* in the north-Alaskan tundra with *Epilobium angustifolium* and *Epilobium latifolium* (Toolik field station, N-Alaska). Photo by P. Rasmont

NCBI GenBank and the Barcode of Life Database (Online Resource 1). Overall, 60 samples could be gathered to constitute the dataset from 14 regions across three continents (Fig. 1; Table 1). Newly sequenced specimens are deposited in the collection of the University of Mons (Mons, Belgium). Bumblebees were identified in the field and confirmed in the lab following Løken (1973) and Williams et al. (2014). Several subspecies with little differentiated colour pattern, are currently recognized (Rasmont et al. 2021): (i) *hebridensis* from Hebrides; (ii) *martes* from Alps, Belgium, Ills of Central Europe; (iii) *monapiae* from Island of Man; (iv)

subborealis from Fennoscandia, Iceland and Russia; (v) *vogtianus* from Shetland; (vi) *yarrowianus* from Pyrenees and Cantabrian mountains; (vii) *alboanalis* in North America, (viii) *jonellus* from British Islands, Germany, Belgium, Netherlands, North of France, Massif Central, Alps, Balkan peninsula, Tatra mountains, Northern Russia.

Sequencing protocol

We obtained new sequences of the barcoding fragment of the cytochrome c oxidase subunit I (*COI*) from 41 specimens of *B. jonellus* (Online Resource 1). Extraction, purification and polymerase chain reactions (PCR) were performed from legs of fresh killed specimens using a standard DNA extraction kit (NucleoSpin Tissue, Macherey–Nagel). Based on primers which amplify the classic *COI* barcode fragment (LepF1/LepR1, Hebert et al. 2003), we designed specific primers for *B. jonellus* (Forward GGTCTGGAATAATTG GTTCATCA/Reverse GGATTGGATCACCTCCTCCT). For each PCR samples, the mix contained approximately 200 ng of total cell DNA (1 µl), 10 pmol of each primer (2 × 1 µl), 2.5 µl of dNTP (2 mM), 7.5 µl of PCR buffer (5 µl GoTaq Flexi Buffer with 2.5 µl MgCl₂ 25 mM), 0.125 µl Taq DNA polymerase (5 units/µl, Sigma-Aldrich) and H₂O was added for a final volume of 25 µl. For temperature cycling, PCR conditions were as follows: 94 °C (1 min), 6 cycles of 94 °C (1 min), 45 °C (90 s), 72 °C (75 s), 36 cycles of 94 °C (1 min), 51 °C (90 s), 72 °C (75 s) and a final extension at 72 °C (5 min). *COI* amplicons were Sanger sequenced by Eurofins Genomics (Ebersberg, Germany) and manually edited in Bioedit v.7.2.5 (Hall 1999). Newly obtained genetic

Table 1 COI nucleotide polymorphisms in *Bombus jonellus*

Collecting sites	96	112	147	149	163	204	222	232	282	300	331	333	335	366	382	408	432	435	438
Belgium (3)	C	G	T	T/C	T	A	C	T	C	T/C	T	A	T	C	G	C	A	C	T
Germany (4)	–	–	–	C	–	–	–	–	–	T	–	–	–	–	–	T/C	A/G	–	A/T
Pyrenees (6)	–	A	–	C	–	–	–	–	–	T	–	–	–	–	–	–	A/G	–	–
Ireland (1)	–	–	–	C	–	–	–	–	–	T	–	–	–	–	–	–	G	–	–
Hebrides (10)	–	–	–	C	–	–	–	–	–	T	–	–	–	–	–	–	–	–	–
Iceland (6)	–	–	–	C	–	–	–	–	–	T	–	–	–	–	–	–	G	–	–
Norway (1)	–	–	–	C	–	–	T	–	–	T	A	T	A	–	–	–	G	–	–
Khanymey (5)	C/T	G/A	T/A	C	–	–	–	–	C/T	T	–	–	–	C/T	A/G	–	–	–	–
Mongolia (3)	T	–	A	C	–	–	–	C	T	T	–	–	–	T	–	–	–	–	–
Kolyma (1)	T	–	A	C	–	T	–	C	T	T	–	–	–	T	–	–	–	–	–
Chokurdakh (9)	T	–	A	C	–	–	–	C	T	T	–	–	–	T	–	–	–	–	–
N-W Canada (3)	T	G/A	A	C	–	–	–	C/T	T	T	–	–	–	T	–	–	–	C/T	–
Alaska (7)	T	–	A	C	T/C	–	–	C	T	T	–	–	–	T	–	–	–	–	–
N-E Canada (1)	T	–	A	C	–	–	–	C	T	T	–	–	–	T	–	–	–	–	–

Numbers in the top row refer to nucleotide positions within a condensed alignment of the sequences with minimal gaps (455 base pairs), letters are FASTA codes for nucleotides but with additional polymorphisms shown explicitly. Traits indicate a nucleotide matching the first sequence. Numbers next to species' names are the numbers of sequences examined

sequences were deposited on GenBank (Accession numbers in Online Resource 1).

Phylogeographic analyses

The alignment of the *COI* sequences was performed using the ClustalW algorithm implemented in Bioedit v.7.2.5 (Hall 1999). Each *COI* sequence was trimmed to a 455-bp fragment with no missing data following Potapov et al. (2018). We investigated the genetic differentiation within *B. jonellus* through haplotype network analyses and phylogeographic inference. We used the median-joining method to produce haplotype networks with Network 4.6.1.3 software (www.fluxus-engineering.com, Bandelt et al. 1999), weighting transversions twice as high as transitions to reconstruct the network (Lecocq et al. 2015; Brasero et al. 2020). Genetic divergences and nucleotide substitutions were estimated in MEGA6 (Tamura et al. 2013) using similar settings as Potapov et al. (2018). We calculated the *p*-distance as the proportion of nucleotide sites at which two sequences being compared are different by dividing the number of nucleotide differences by the total number of nucleotides compared (Nei and Kumar 2000).

Results

We found 14 different *COI* haplotypes (Fig. 4) amongst 60 *COI*-samples of *Bombus jonellus* (accession numbers listed in Online Resource 1). These *COI* data are information rich, with 19/455 nucleotide sites phylogenetically informative (Table 1). The phylogeographic haplotype network analysis unveiled 19 segregating sites and nine parsimony-informative sites (Fig. 4). Two main lineages appear with four unique Single Nucleotide Polymorphisms (SNPs) separating the two groups (0.8% *COI* divergence): (i) a first one comprising North-West American (three haplotypes), North-West Siberian (one unique haplotype) and North-East Siberian (two haplotypes) samples; (ii) a second one including European (eight haplotypes including one unique haplotype in Norway with four unique SNPs separating this group) and North-West Siberian samples (two haplotypes). In Europe, populations from the Pyrenees ($n=2$), Norway ($n=1$), Belgium ($n=3$) and Germany ($n=2$) include unique haplotypes (i.e. haplotypes shared by no other population). Specimens from the Hebrides share a common *COI*-haplotype with specimens from Belgium and Khanymey (W-Siberia) whilst specimens from Iceland are in the same haplogroup as specimens from Germany and Ireland. Only a few SNPs separating individuals within these groups. The mean uncorrected *COI p*-distance amongst the lineages is $1.2 \pm 0.3\%$. Globally, the haplotype network of *B. jonellus* reveals two geographically distinct clades, the European lineage (including

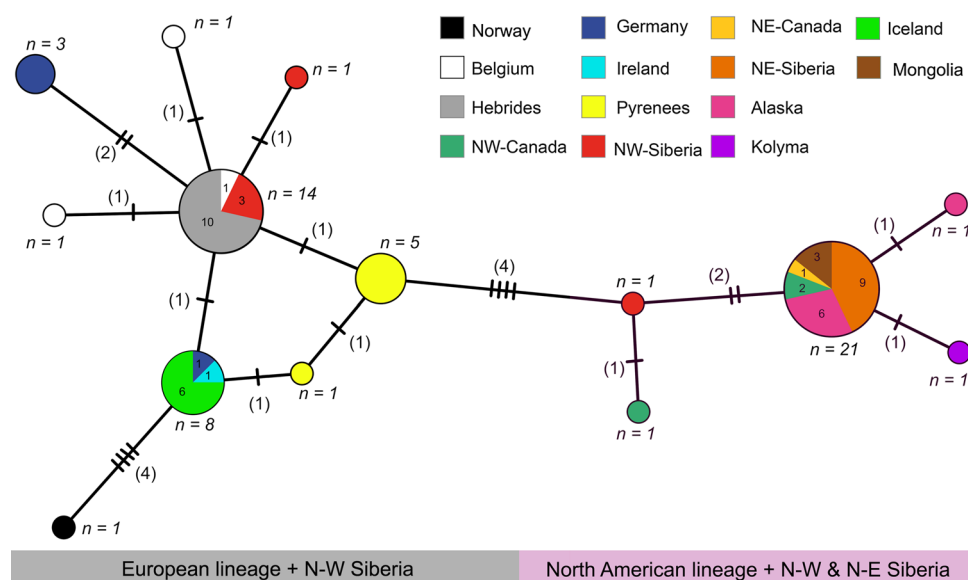


Fig. 4 Haplotype network analysis. Median-joining networks based on a fragment of the Cytochrome oxidase I (*COI*). Each sequenced haplotype is represented by a circle, the size of which is proportional to its overall frequency in the dataset (Online Resource 1). Black lines and numbers on the branches are used to indicate the number

of mutational changes between two different haplotypes. n = number of sequences per haplotypes and numbers in circles correspond to the number of sequences per sampling sites and per haplotypes. Haplotype colours correspond to the sampling localities displayed on the map (Fig. 2) and annotated on the legend

its relictual populations) and the North-West American + North-East Siberian one.

Discussion

The evolutionary processes between allopatric populations around the Arctic Circle and their connections with populations from glacial refugia have been a central topic in the field of polar biogeography and Arctic ecology (Reinig 1937; Irwin and Geoghegan 2001; Irwin et al. 2005; Päckert et al. 2005; Monahan et al. 2012; Alcaide et al. 2014; Martinet et al. 2019). Circum-boreal distribution can involve chains of intergrading populations, eventually leading to reproductively isolated taxa (Stresemann and Timofeeff-Ressovsky 1947; Irwin and Geoghegan 2001; Brunke et al. 2020; Combe et al. 2021). However, some species with a priori distant circum-Arctic populations could remain connected and still considered as conspecific (Martinet et al. 2019; Lhomme et al. 2021).

We explored the genetic relationships amongst circum-boreal populations of *B. jonellus* across three continents within the Holarctic region. Despite the very large distribution of the species and the presence of both isolated and phenotypically distant populations, *B. jonellus* appears especially poorly variable on the analysed gene fragment (*COI*) across a large part of its distribution range. In particular, the well differentiated population of the Hebrides (ssp. *hebridensis*) shows an identical haplotype to that of other European populations that are not phenotypically divergent from the typical *B. jonellus*, contrary to the hypothesis of Potapov et al. (2018). Strikingly, the Hebrides haplotype is even identical to that of some specimens from W-Siberia, and only one nucleotide differentiated from samples from the distant and isolated French Pyrenees.

The distribution of *B. jonellus* is especially wide for a non-managed bumblebee species: from Iceland and the Sierra Cantabrica in the west to the Anadyr on the Pacific and even beyond the Arctic Circle in the north. However, it is likely that the Icelandic population was introduced from mainland Europe by humans after the last glaciation (Potapov et al. 2018). In Russia, the distribution of *B. jonellus* is continuous north of the 55th parallel and rather patchy south of this latitude (Rasmont et al. 2015). In the south of Europe, the range of *B. jonellus* is restricted to higher-altitude biotopes, reaching one of the highest mountain ranges of the Iberian Peninsula where it is very rare (Genoud and Rasmont 2009; Rasmont et al. 2015). Whilst *B. jonellus* is common in the North of its distribution, it is considered as rare and localized in its southern relictual refugia.

The present haplotype network analysis suggests the presence of several populations of *B. jonellus* connected along a widespread boreal distribution (Fig. 4). Based on a more

restricted dataset, Potapov et al. (2018) highlighted two main lineages in the global phylogeography of *B. jonellus*, corresponding to two different postglacial recolonization patterns, the latter having resulted in the presence of one European lineage (including Southern relictual populations) and a second one in the East-Palearctic and North-West Nearctic regions. However, as hypothesized (Potapov et al. 2018), the intermediate *COI* sequences from Siberia analysed here narrow the expected gap between European and Nearctic haplogroups (Fig. 4). These may reflect two glacial refugia with intermediate haplogroups from W-Siberia (Yamalo-Nenets region) which display haplotypes of both lineages. From the three newly obtained haplotypes from West Siberia (Khanymey), two are from the Palearctic group (including one unique haplotype) and one is associated with the Nearctic samples. Based on hypothetical reconstructions of the paleogeography of Northern Eurasia in the Quaternary period, NW Siberia could have served as a glacial refugium for bumblebees during the Late Pleistocene (Panfilov 1957; Potapov et al. 2019). From this region, postglacial recolonization could have taken place towards both the east and west Palearctic regions. This could explain why we found haplotypes similar to those of Yamalo-Nenets region (NW Siberia) both in the Palearctic and the Nearctic + East-Siberia groups.

Alternative hypotheses exist about Central Siberia as a potential glacial refugium for animals and plants during the last Ice Ages. For instance, the presence of a large swamp area in the North-Center of Siberia (de Lattin 1967) may have resulted in an unsuitable zone for terrestrial organisms during the Würm glaciation. At that time, a huge freshwater lake is thought to have formed in the south of the glacier due to water accumulation (Berg 1959). Following this hypothesis, post-glacial recolonizations could have taken place in this region from European and North-Eastern Siberian refugees (Habel et al. 2010). Although we are not aware of studies that have focussed on this hypothesis as an important parameter in biogeographic reconstructions of boreal species, the authors have observed a relatively low diversity of bumblebee species in Yamalo-Nenets region, which could partly support this hypothesis. Further work on several model species would be useful to disentangle the impact of this possible glacial ecological barrier on the patterns of recolonization of mobile organisms such as bumblebees.

The haplogroup from Europe seems to be more structured than previously suggested by Potapov et al. (2018). Whilst isolated populations with a non-differentiated colour pattern display of a unique haplotype (e.g. from Pyrenees ssp. *yarrowianus*, Kolyma, Norway ssp. *subborealis*), differentiated and isolated taxa such as the red-tailed subspecies *hebridensis* share their *COI*-haplotype with other European taxa. This finding challenges the hypothesis of a single, compact haplogroup in Europe (Potapov

et al. 2018). The presence of two unique haplotypes in the Pyrenees (ssp. *yarrowianus*) could reflect the role of these mountains as a relictual glacial refugium in Southern Europe in the Late Pleistocene or Early Holocene. Whilst the unique Norwegian haplotype might be the inheritance of a glacial refugia (Habel et al. 2010) in North of Europe, the diversity (three haplotypes) in Belgium (ssp. *martes* and ssp. *jonellus*) could reflect an interbreeding zone between different subspecies (Rasmont and Iserbyt 2014).

Unveiling the phylogeographic patterns of widespread yet relatively specialized pollinators such as *B. jonellus* is crucial to identify where genetically differentiated taxa occur within the species' range. Locating such original populations is of utmost interest in conservation biology, especially for species that are endangered at least in some parts of their range. Our global overview of *B. jonellus* suggests an unexpected cryptic diversity and that conservation efforts would be especially relevant in regions presenting unique haplotypes (e.g. the Pyrenees, Norway, Siberia, Belgium or Kolyma). However, despite the singularity of these haplotypes often defined only based on a gene fragment (i.e. *COI*), it is on a global scale that the species could be threatened by environmental changes requiring local but also global conservation plans. In addition, although the population *hebridensis* from the Hebrides does not present a unique haplotype separating it from the mainland populations, its original combination of a unique colour pattern, subtle morphological and presumable ecological differences (Alford 1975; personal observations) would make it an interesting model to investigate the intraspecific radiation of colour patterns within morphologically monotonous bumblebee species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-021-02937-x>.

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Author contributions Conceived and designed the experiments: BM, GP. Conducted experiments: BM, GG, KP, GP. Analysed the data: BM, GG, KP, GP. Wrote the paper: BM, GG, KP, EZ, NB, AVK, AAT, YSK, INB, PR, GP.

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Data availability All data are available in the main text or the supplementary materials including full data sets with the global sampling. Genetic sequences are available on Genbank (Accession Number in Online Resource 1).

Declarations

Conflict of interest The authors declare no competing financial interests.

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