Opinion paper

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Can biogeography help bumblebee conservation?

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Abstract. Bumblebees (*Bombus* Latreille, 1802), because of their large body size, bright colours and activity at times and places that coincide with biologists, are an example of a group of insects that is particularly well represented in museum collections. This is important if taxonomic revisions are to achieve greater comparability among species. Bumblebees have also attracted particular attention because they are especially ecologically and economically valuable for pollination in north temperate regions, where they are now becoming increasingly threatened. I argue that the what, the where, and the how of effective conservation management may be informed by understanding the divergent characteristics that have affected their biogeographical past: by helping us to see 'the woods', not just 'the trees', of their habitat needs. Identifying suitable habitat should be part of reconstructing historical biogeography within taxonomic revisions. For bumblebees, for example, biogeographical analysis associates major taxonomic groups either with flower-rich lowland grasslands or with flower-rich montane grasslands, highlighting their contrasting requirements for: nest sites, flowers of different depths, pollen-plant families, and especially the differing importance of early spring and late summer flowers for breeding success. This broad view of species groups helps filter the less important idiosyncrasies from local case studies in order to focus conservation actions.

Keywords. Biogeography, bumblebee, conservation, distribution, phylogeny.

The what, the where, and the how of bumblebee conservation

Taxonomy is at the root of everything we do in trying to discover, document, and understand life on Earth. For every scientist working on biodiversity, taxonomy is fundamental, as taxa and their standardised name labels are essential to retrieve and relate previously published information (Borowitzka 2016). These taxa and names also enable the information we have on organisms to be understood (and interpolated) within a framework of heredity, evolution, and 'trees' (Darwin 1859; Huxley 1942; Baum & Smith 2012). Discovery and reconstruction of this framework is one of the greatest achievements of biology (Dobzhansky 1973; Lander & Weinberg 2000). Now, in the midst of an unprecedentedly rapid and man-made biodiversity decline and mass extinction (Hallmann *et al.* 2017; Cowie *et al.* 2022), taxonomy has become an urgent and central part of our efforts to know the 'what' and the 'where' for conservation management (Vane-Wright 1996; Dubois 2003; Mace 2004; Braby & Williams 2016), providing the species names that are typically the legal and practical focus for conservation actions. Museums, with

global collections of representative specimens, are uniquely well placed to fulfil this role for society and the planet (Winston 2007).

How could biogeographical insights help inform conservation? Biogeographic analyses have often been part of taxonomic revisions in recent years. When applied to bumblebees (genus *Bombus* Latreille, 1802), biogeographic analyses have depended on identifying the habitat requirements of not just all bumblebees, but also the differences in habitat preferences between the major subgroups, in order to identify suitable corridors for, and barriers to, dispersal (Williams *et al.* 2022b). This focus on more broadly shared habitat characteristics has the potential to highlight overlooked requirements important for the conservation of groups of species, contributing, in addition, to informing differences in the 'how' of conservation management.

## Revising bumblebee taxonomy with a consistent species concept and delimitation methods

Faced with nearly 3000 bumblebee names for probably around 300 species at the beginning of my research career (more than 40 years ago), along with many others, I have been seeking to understand the different bumblebee species and to map the extent of their distributions world-wide (Williams 1998; updated in Fig. 1). Bumblebee taxonomy is challenging because their morphology is relatively homogeneous among species (giving few clues) when compared with many other bees (Michener 2000). In contrast, bumblebee colour patterns show very obvious patterns of variation, both within and among species, although these can be misleading because of an impressive degree of convergence among the species in any particular region (Vogt 1909, 1911; Reinig 1939; Plowright & Owen 1980; Williams 2007). My research programme has been able to benefit not just from museum collections, but also from field work across all of the northern continents and especially across Asia, where the largest number of bumblebee species occurs (Williams *et al.* 2017a; Fig. 1 inset). New taxonomic revisions are an opportunity to apply a uniform theoretical concept of what species are, and it follows that all species revised using the same species concept should be more nearly comparable in kind (even if not identical).

Species-taxon concepts for bumblebees have been changing in recent decades as taxonomists have shifted, from a paradigm of a species concept focussed on interbreeding, to viewing species as 'evolutionarily independent lineages' (EILs, de Queiroz 2007). Museum collections remain important for accountability, for conserving the 'hypodigm' samples of the specimens on which each species-taxon concept is based (Simpson 1940; Mayo 2022). The evidence used has expanded over recent decades from morphology to draw increasingly on molecules (Williams *et al.* 2022b). There is also now a widespread adoption of an array of quantitative methods for species 'delimitation' (or more precisely for EILs, recognition) within an integrative framework (Schlick-Steiner *et al.* 2010), which is improving the transparency, accountability and, it is hoped, predictive value and stability, of taxonomic decisions (Williams 2022b).

To help achieve this greater comparability among species-taxon concepts, several bumblebee subgenera (Williams *et al.* 2008) have had their species revised formally world-wide, applying a consistent approach to morphology and to species' coalescents in the fast-evolving COI gene (Zhang *et al.* 2013). These revisions, carried out with the essential help of many collaborators internationally, cover (in an order corresponding to Fig. 6) the subgenera *Mendacibombus* Skorikov, 1914 (Williams *et al.* 2016), *Subterraneobombus* Vogt, 1911 (Williams *et al.* 2011), *Alpinobombus* Skorikov, 1914 (Williams *et al.* 2019), and *Melanobombus* Dalla Torre, 1880 (Williams *et al.* 2020), with other revisions in progress (*Alpigenobombus* Skorikov, 1914; *Sibiricobombus* Vogt, 1911). Further subgenera have had all of their species and their species' relationships reviewed, including *Megabombus* Dalla Torre, 1880 (Hines & Williams 2012; Huang *et al.* 2015), *Orientalibombus* Richards, 1929 (Williams 1991; Williams *et al.* 2009b), and *Bombus* s. str. (Williams *et al.* 2012b; Williams 2021). Some of the other subgenera have had

only a few of the more problematic species-groups reviewed or new species described, including, e.g., *Thoracobombus* Dalla Torre, 1880 (Brasero *et al.* 2021), *Pyrobombus* Dalla Torre, 1880 (Williams *et al.* 2009b, 2014, 2022a, 2022c; Martinet *et al.* 2018b; Sheffield *et al.* 2020; Potapov *et al.* 2021; Williams 2022a), and *Cullumanobombus* Vogt, 1911 (Williams *et al.* 2012c). In contrast, some recent studies continue to give more emphasis to an interbreeding concept of species, for example in regarding male pheromones as decisive for recognising species (Martinet *et al.* 2018a; Lecocq *et al.* 2019), rather than regarding male pheromones as just one more source of information for integrative analyses (Williams *et al.* 2019, 2020).

One of the concerns for conservation in general has been that complexes of closely related species may include unrecognised cryptic species that could be overlooked. The bumblebee subgeneric revisions should provide clarification on this issue. Cryptic species have been a particular problem within the subgenus *Bombus* s. str. (Krüger 1951; Kullenberg *et al.* 1970; Rasmont 1984; Williams *et al.* 2012b; Williams 2021), which is also the most important group commercially for crop pollination (Goulson 2010; Williams *et al.* 2012a; Orr *et al.* 2022). These global studies report previously unsuspected cryptic
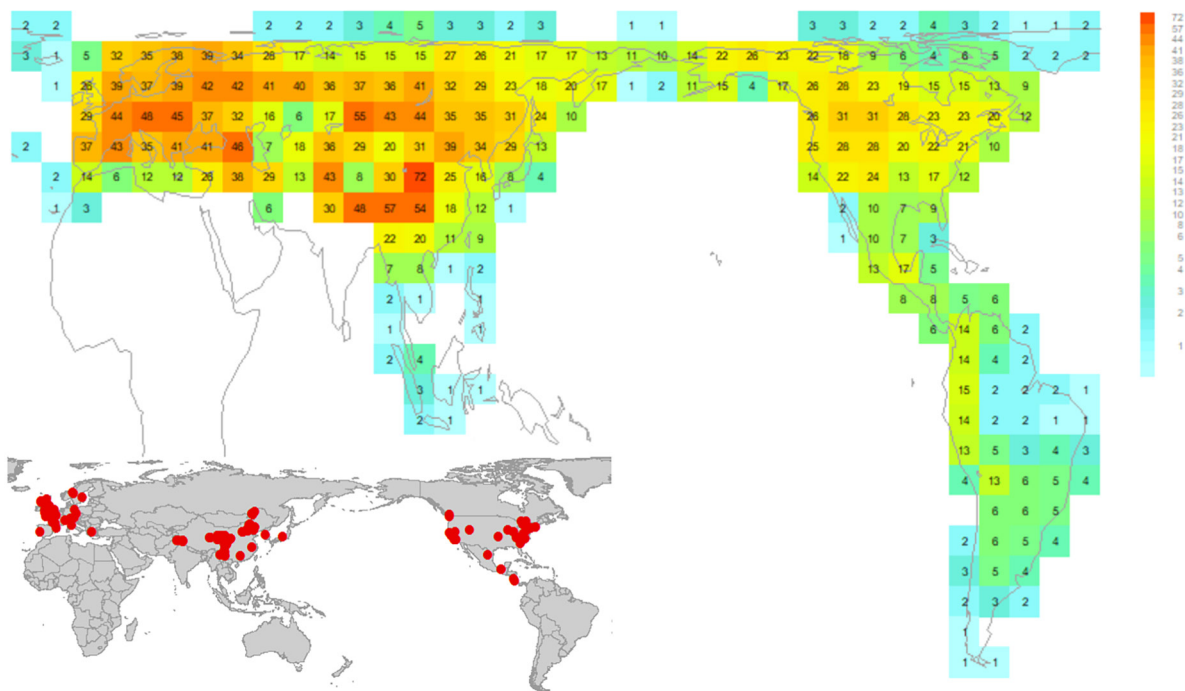
Fig. 1. Revising bumblebee species world-wide. The total bumblebee (indigenous) species richness is highest in Asia, especially in the Himalaya and Hengduan Mountains on the southern and eastern fringes of the Qinghai-Tibetan Plateau (Williams 1998, data updated). There are no indigenous bumblebees in sub-Saharan Africa, lowland India, or in Australia and New Zealand (and Antarctica). Species numbers peak in the region of Xining, Qinghai. Even when mapping such a globally well-sampled group as bumblebees, using a coarse-scale equal-area grid reduces species-area effects, reduces the effects of sampling heterogeneity (species-accumulation curves for these large grid cells are more nearly asymptotic than for many smaller grid cells), and smooths the effects of local habitat variation. The grid is based on intervals of 10° longitude, which are used to calculate graduated latitudinal intervals so as to provide equal-area cells (each cell has an area of approximately 611 000 km²). The colour scale has equal-frequency richness classes. Cylindrical orthomorphic equal-area projection (excluding Antarctica) with north at the top of the map. Lower left, inset: field-work sites sampled for bumblebees by the author 1971–2018 (red spots).

species that are already in commercial use for crop pollination within glasshouses in Asia, ringing alarm bells for the need for care when moving bumblebees among areas (Williams *et al.* 2012a).

From taxonomy to biogeography to habitat suitability

A hundred years have now passed since a great leap in our understanding of the diversity, distribution, and history of bumblebees. Aleksandr Skorikov of the Zoological Museum (now the Zoological Institute of the Russian Academy of Sciences) in St Petersburg, in his *Palaearctic Bumblebees* (Skorikov 1923), mapped out both taxonomically and geographically the outline of much of our current understanding of these animals. Considering patterns in only the morphology and distribution of the different taxonomic groups, he inferred that bumblebees originated in Asia, and then spread to Europe, North America, and South America. By considering geology, Skorikov even inferred a timeline for this history that is not so very different to that accepted today.

The development of techniques for sequencing and interpreting DNA over the last two decades has added much new evidence for improving our understanding of the evolutionary relationships among bumblebee species (Kawakita *et al.* 2004; Cameron *et al.* 2007; Sun *et al.* 2020). Nonetheless, dating the events on phylogenetic trees remains probably the most challenging and uncertain part of this process, with few informative fossils available for the calibration of models of DNA-sequence evolution (Hines 2008; Dehon *et al.* 2019; Santos Junior *et al.* 2022; Williams *et al.* 2022b). In interpreting information on dates, most recent studies (Williams 1985; Kawakita *et al.* 2004; Hines 2008; Dehon *et al.* 2019) have agreed with Skorikov (1923) that the strong climatic cooling outside of the tropics at the beginning of the Oligocene (around 34 Ma) is likely to have been a significant factor favouring the early diversification of bumblebees. Cooling would have favoured bumblebees at high latitudes and high elevations more than the other corbiculate bees, especially in comparison with their tropical sister-group, the stingless bees (Cameron *et al.* 2007; Bossert *et al.* 2019). This is because of the more effective thermoregulatory abilities of bumblebees (Heinrich 1979) and their ability to survive predictable, long adverse seasons at low energy cost by queens hibernating alone.

Crucially for biogeography, although bumblebees are strong fliers and can travel long distances (Haeseler 1974; Mikkola 1984; Prys-Jones *et al.* 2016), the weight of evidence is that they are surprisingly poor at dispersing very long distances and then establishing new populations when crossing the wide barriers posed by, e.g., seas and deserts (reviewed by Williams *et al.* 2022b; including differing opinions and possible explanations for these), especially when compared with groups such as butterflies and dragonflies. This conclusion has been shared by other bumblebee biogeographers (Skorikov 1923; Panfilov 1957; Ito & Sakagami 1980; Ito 1987; Pekkarinen & Teräs 1993; Estoup *et al.* 1996; Lecocq *et al.* 2017). This explains why bumblebee species don't occur everywhere in the world that has a suitable habitat and climate for them (as evidenced by their 'successful' introduction into, e.g., New Zealand: Gurr 1957; Macfarlane & Gurr 1995). It also means the effects of ancient barriers and corridors can still be traced within their distributions. But the intriguing part is that some of these barriers have changed through deep time – with the rise and fall of mountains, with changes in sea levels, and with changes in climate (Williams *et al.* 2017b).

Habitats that are likely to be either suitable, or else a barrier, for a particular taxonomic group can often be identified from species-richness maps for the group, by considering the shared characteristics of (parts of) the map areas with correspondingly high, or low, species richness (e.g., for bees, Michener 2000). Just as with habitat-suitability modelling, this approach requires bold assumptions about populations being at equilibrium with causal factors, about monotonic responses, and about interactions among factors and species (Lee *et al.* 2019). Nonetheless, the principle is still considered to have value at coarse spatial scales. Such inferences can be 'ground-truthed' at finer spatial scales through field surveys (Fig. 1 inset).

Early bumblebees divided by the Oligocene deserts

One insight to come from this 40-year taxonomy and mapping project is that the expansion of the desert region across Central Asia, China, and Mongolia from the beginning of the Oligocene around 34 Ma (Dupont-Nivet *et al.* 2007; Yin *et al.* 2008; Barbolini *et al.* 2020) may have been especially important for the evolution of bumblebees (Williams *et al.* 2017b, 2022b).

It is most likely that bumblebees as we know them today originated in Asia, because that is where most of the early-diverging extant bumblebee species occur and where biogeographic reconstructions place their ancestors (Skorikov 1923; Williams 1985; Kawakita *et al.* 2004; Hines 2008; Williams *et al.* 2017b, 2022b; Santos Junior *et al.* 2022). However, one of the strongest patterns that has been hidden within the global distribution of bumblebee species richness (Fig. 1) is the deep biogeographic boundary between the north Asian and south Asian bumblebee faunas (Williams 1996; Williams *et al.* 2022b: figs 2–3). This boundary coincides closely with the broad stretch of desert across 'Central Asia', including China and Mongolia (Barbolini *et al.* 2020) (Fig. 4), which in its broad arid centre is severely unsuitable to bumblebees (Fig. 5). Some of the earliest-diverging subgenera of bumblebees (34–21 Ma, Fig. 6) have few extant species, although these remain concentrated immediately on either side of this Central Asian desert region, either in the mountains to the south (*Mendacibombus*), or in the hills to the north (*Bombias* Robertson, 1903; *Kallobombus* Dalla Torre, 1880) (Williams *et al.* 2017b). Elsewhere in the world, deserts and tropical lowlands also appear to have blocked bumblebee dispersal, for example into sub-Saharan Africa, into the mountains of southern India, and into Australia (Fig. 1) (Williams 1998).

Subsequently, early Miocene re-activation of the uplift of the Tian Shan and Pamir mountain ranges (after 21 Ma, Yin *et al.* 2008; Yin 2010; Miao *et al.* 2012; Barbolini *et al.* 2020) may have bridged the Central Asian deserts in the west, providing a high, cooler, wetter, vegetated corridor for dispersal and faunal interchange of lineages of ancestral bumblebees (Fig. 4). Dispersal of their descendants (Fig. 6) then spread the principal groups of species that we see in bumblebee faunas throughout most of the world today.

The two largest sister groups of bumblebees in Fig. 6 now have modern descendant species concentrated either more to the north or more to the south of the Central Asian deserts (Figs 7–8) (even though the most recent common ancestors of both groups appear to have been distributed initially to the south of the desert). These groups have been described variously as: (1) the long-faced or long-tongued bumblebees, which are now most species-rich in 'Lowland Grassland' ('LG') habitats to the north (Figs 6 (in green), 7); and (2) the short-faced or short-tongued bumblebees, which are now most species-rich in 'Montane Grassland' ('MG') habitats to the south (Figs 6 (in blue), 8) (Kawakita *et al.* 2004; Cameron *et al.* 2007; Williams *et al.* 2022b). Early last century these two groups were given the formal, sectional names *Odontobombus* and *Anodontobombus* (Krüger 1917; although sectional names no longer have nomenclatural status (ICZN 1999), and were later reduced to synonyms of the subgeneric names *Megabombus* and *Pyrobombus* respectively in Milliron 1961). These two large groups, with their tendency to association with flower-rich grassland habitats at different elevations, now make up the bulk of most modern bumblebee faunas. Nonetheless, the effect of this faunal division is now very much in evidence in the composition of the different bumblebee faunas of northern and southern Asia (Figs 2–3). (Note that although bumblebees are often abundant along forest edges (Mola *et al.* 2021), few bumblebee species live entirely within closed-canopy dense forest, where bumblebee densities are usually much lower than in neighbouring flower-rich grasslands (Williams 1988, 1991).)

Different habitats and dispersal corridors for the two principal bumblebee groups

To the north of the Central Asian deserts, spreading out from the north Asian hills through the broad Siberian and north European flower-rich grassland plains (Fig. 7), ancestors of many LG bumblebees tended to have longer tongues and often nested on the surface of the ground amongst tall grass. Many

of these species have more uniformly yellow or grey colour patterns that may provide protection by camouflage when flying among drying grasses in summer (Williams 2007; Fig. 7 inset).

To the south of the Central Asian deserts, spreading out from the high mountains around Tibet through the flower-rich mountain corridors of Iran and southern Europe (Fig. 8), ancestors of many MG bumblebees tended to have shorter tongues and often nested among rocks or in cavities underground. Many of these
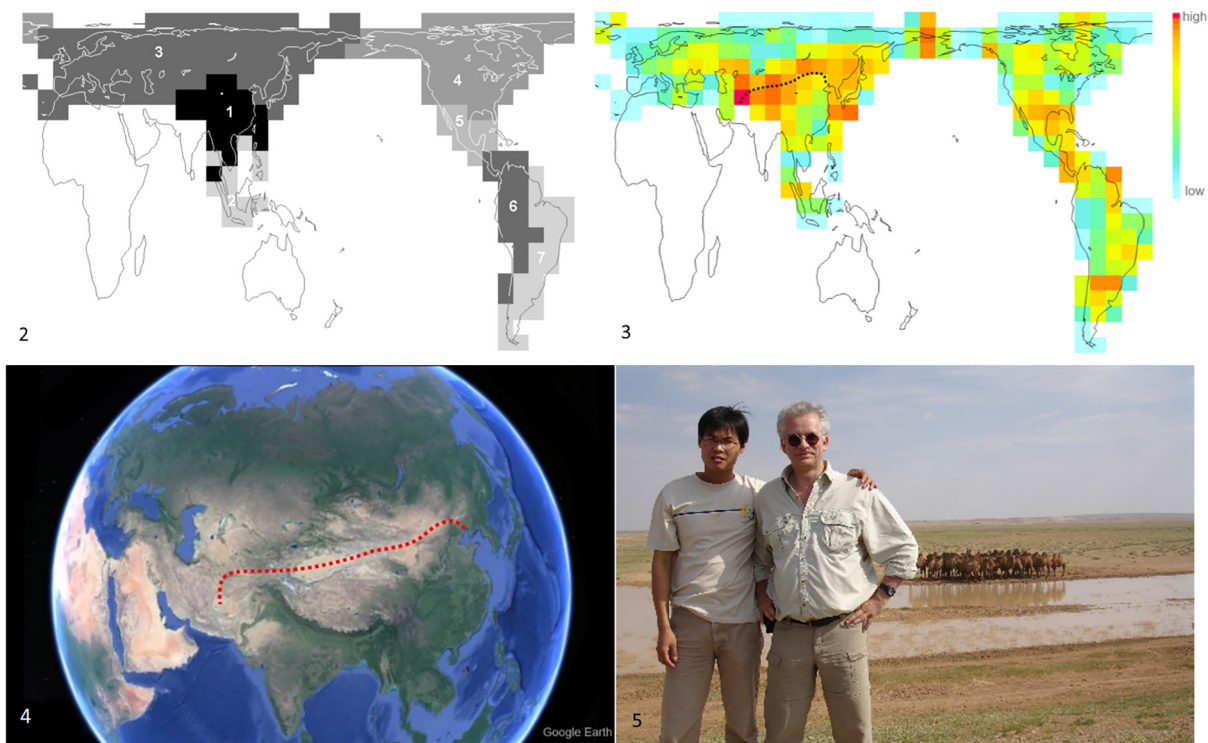

Figs 2–5. Biogeographic boundaries and the Central Asian deserts. **2**. Principal faunal (biogeographic) regions world-wide derived directly from bumblebee data, include an Oriental Region (1, black), a Southeast Asian Region (2, light grey), a Palaearctic Region (3, dark grey), a North American Region, (4, mid grey), a Mesoamerican Region (5, light grey), an Andean Region (6, dark grey), and a Lowland South American Region (7, light grey). Principal faunal regions are identified from grid-cell bumblebee faunas (Fig. 1) using the TWINSPAN procedure that combines ordination with classification (Williams 1996, data updated). Background map as in Fig. 1. **3**. One of the most marked transition zones between bumblebee faunas globally (in orange) corresponds to the arid zone of the Central Asian deserts (the centre of this arid belt is traced by the dotted black line). The map scores measure the differences in species composition among bumblebee faunas within neighbourhoods of grid cells (Fig. 1) using the *β*-3 spatial turnover index (Williams 1996; Williams *et al.* 2022b). Background map and colour scale as in Fig. 1. **4**. Image of Asia based on satellite images shows wet (green) and arid (yellow) regions, with the Central Asian desert belt, its centre traced out with a dotted red line (cf. Fig. 3). Image (without line) from GoogleEarth. **5**. Searching for bumblebees across the Central Asian arid belt of Inner Mongolia with Huang Jiaxing – in the northern wooded/grassland edge zones finding some old favourites from Europe, including *Bombus distinguendus* Morawitz, 1869, *B. subterraneus* (Linnaeus, 1758), *B. consobrinus* Dahlbom, 1832, *B. muscorum* (Linnaeus, 1758), *B. humilis* Illiger, 1806, *B. pascuorum* (Scopoli, 1763), *B. lucorum* (Linnaeus, 1761) and *B. cryptarum* (Fabricius, 1775), as well as some striking local species in the desert-edge zones (north and south), such as *B. sibiricus* (Fabricius, 1781) and the large *B. amurensis* Radoszkowski, 1862, but finding no bumblebees here nearer the middle (An *et al.* 2014; Williams *et al.* 2017a).

species have colour patterns with bands of strongly contrasting, aposematic colours, which appear to have converged regionally to provide protection through Müllerian (for females) or Batesian (for males) mimicry (Williams 2007) – so that they include more of the archetypal 'stripy' bumblebees (Fig. 8 inset; e.g., E. Shepard in Milne 1926).

Changing barriers and corridors for dispersal through time

Over the last 20 Ma, some lineages of both principal groups of bumblebees (LG, MG) have dispersed back to overlap over most of Asia and Europe (Figs 7–8), following corridors to both the east and the west of the Central Asian desert barrier. They have also dispersed out from Asia to North America when land connections and suitable climatic conditions in Beringia allowed (Fig. 9) (Williams 1985; Kawakita *et al.* 2004; Hines, 2008; Santos Junior *et al.* 2022; Williams *et al.* 2022b). They may have reached Central America around 8–12 Ma, but were probably prevented from reaching South America
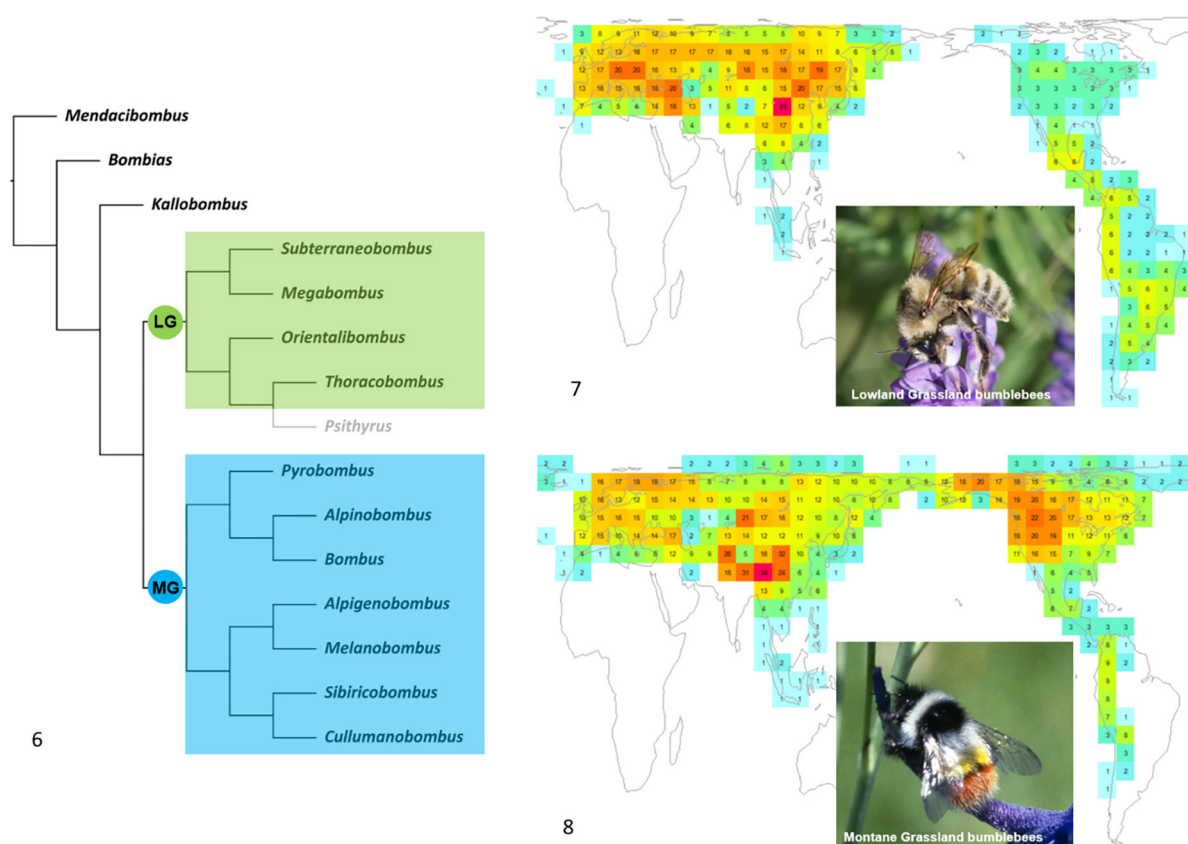

Figs 6–8. Distribution of the two principal bumblebee groups. **6**. Bumblebee subgenera world-wide as revised (Williams *et al.* 2008) based on an estimate of phylogeny from five genes (Sanger sequencing, trees estimated using models of DNA-sequence evolution fitted with Bayesian methods: Cameron *et al.* 2007), updated from estimates from broad genomic data (Illumina sequencing of ca 10 000 genes, trees from maximum likelihood analysis: Sun *et al.* 2020) and shown as a non-metric tree. Lowland Grassland (LG) group highlighted in green and Montane Grassland (MG) group highlighted in blue. **7**. Bumblebee species richness (see Fig. 1) for the Lowland Grassland (LG) group (excluding the subgenus *Psithyrus* Lepeletier, 1832, with its divergent parasitic habit), showing an example (inset) of *Bombus pseudobaicalensis* Vogt, 1911, from the grasslands of north-eastern Inner Mongolia (Williams *et al.* 2022b). **8**. Bumblebee species richness (see Fig. 1) for the Montane Grassland (MG) group, showing an example (inset) of *Bombus kashmirensis* Friese, 1909, from the mountains of the eastern Tibetan plateau (Williams *et al.* 2022b). Background maps and colour scale of 7 and 8 as in Fig. 1.

by a sea. There then seems to have been a period with a burst of diversification of extant lineages centred on the mountains of southern Mexico (Williams *et al.* 2022b). Discussion of the precise date continues (Hines 2008; Santos Junior *et al*. 2022), but perhaps only as late as 3 Ma were bumblebees able to reach South America via the emerging Panama land bridge, most likely during periods when the climate was also cooler (Williams *et al.* 2022b). Although there has been further speciation within South America, there has been less time for speciation there than nearer their origins in Asia, where by far the greatest diversity of bumblebees has had time to accumulate and still survives today.

Regional centres of bumblebee diversity and endemism

In the Old World, the greatest concentration of bumblebee subgenera, and of species (Fig. 1), is in the mountains of Asia south of the Central Asian desert belt. The MG bumblebees are not only especially species-rich but predominate to the south, around the Tibetan plateau, as well as in the Arctic (Figs 10–11, in light grey-blue). Most of the MG subgenera (Fig. 6) are likely to have originated around the Tibetan plateau (Williams *et al.* 2022b). In contrast, the LG bumblebees are not only especially species-rich but predominate in the steppes in the north and east of Eurasia (Figs 10–11, in light, grey-green). Among the LG subgenera, *Megabombus* has early-diverging lineages to the north-east of the Central Asian desert belt, but with a secondary centre of diversity in China just to the east of Tibet. The subgenus *Psithyrus* Lepeletier, 1832 is less comparable to the other LG subgenera, because the species are social parasites of both LG and MG bumblebees throughout the northern hemisphere (Skorikov 1923; Lhomme & Hines 2018), although they are absent from South America (it may be that these parasites are especially poor at dispersing across barriers into regions with low host densities). LG groups that have left especially many species concentrated in northern Asia and Europe are the subgenera *Subterraneobombus* (Williams *et al.*
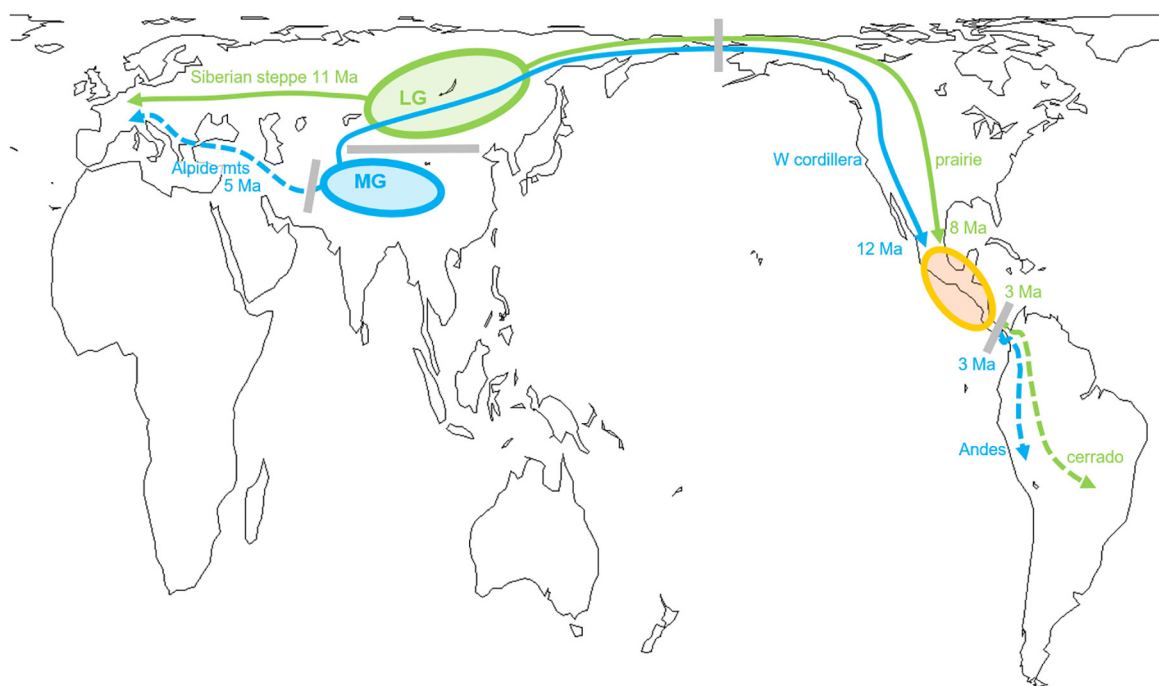

Fig. 9. History of dispersal for the two principal bumblebee groups. Principal outward dispersal corridors for Lowland Grassland (LG, green) and Montane Grassland (MG, blue) bumblebees (groups as in Fig. 6), showing some of the changing barriers as grey rectangles (Williams *et al*. 2017b; Williams *et al.* 2022b) (dispersal patterns estimated using DIVALIKE+J in BioGeoBEARS fitted with Bayesian methods). For simplicity, dispersals in the reverse directions are not shown. Background map as in Fig. 1.

2011) and *Thoracobombus*. Southern Asia has few species of *Thoracobombus,* although *Orientalibombus* is a small group that could be regarded as a Himalayan extension of *Thoracobombus* (Fig. 6). The subgenus *Thoracobombus* is one of the few groups to have shown a lot of speciation in Europe (Fig. 7; Williams *et al.* 2022b).

As bumblebees have spread further around the world, some groups have left more extant species in particular regions of the other continents (Williams *et al.* 2022b). In the New World, the MG bumblebees predominate much more strongly in the Arctic and especially in north-western North America (Fig. 10, in darker, saturated blue), while the LG bumblebees predominate much more strongly in south-eastern South America (Fig. 10, in darker, saturated green). As MG bumblebees reached North America,
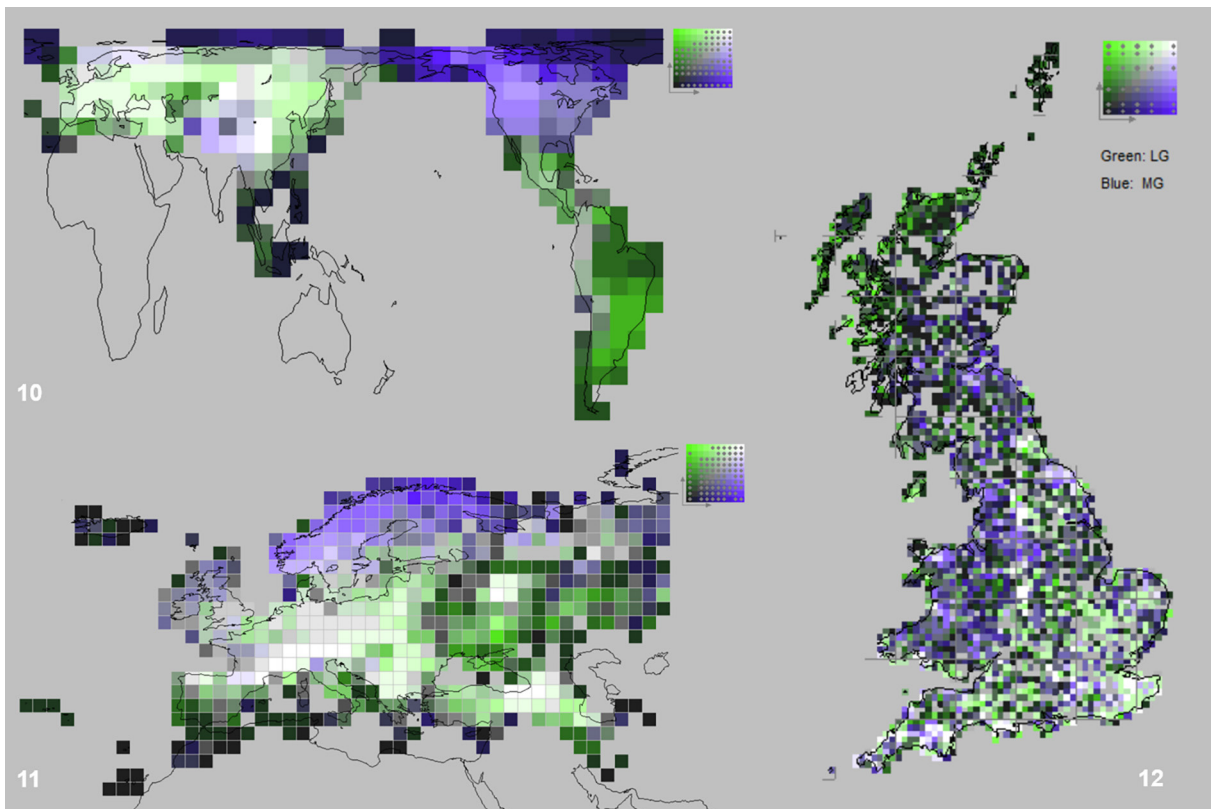
Figs 10–12. Current regional preponderance of the two principal bumblebee groups. **10**. Comparison of species richness for Lowland Grassland (LG: in green) and Montane Grassland (MG: in blue) bumblebees (groups as in Fig. 6). The map overlays numbers of species (Figs 7–8) in green and blue (Williams & Gaston 1998) within equal-area grid cells (Fig. 1). Both colour axes are transformed to give near-uniform frequency distributions among classes along both axes (so that the scales differ among the figures, see the colour-scale boxes to the upper right of each map). Cells with high richness on both green and blue axes appear white, whereas cells with low richness on both axes appear black, with areas of intermediate and precisely covarying richness appearing in shades of grey. By contrast, deviations from an overall positive relationship appear as increasingly saturated green or blue, showing an 'excess' richness of one axis over the other (the colour values represented on the map are indicated in the scale box with grey spots). Background map as in Fig. 1. **11**. Similar comparison of LG (in green) and MG (in blue) bumblebee richness across Europe from the European guide data (Rasmont *et al.* 2021) on a 2°×2° grid (not equal-area grid cells) with north at the top of the map. **12**. Comparison of LG (in green) and MG (in blue) bumblebee richness across Britain from the bumblebee atlas data (Alford 1980) on a 10×10 km grid with north at the top of the map.

there is a particular concentration of *Alpinobombus* species centred in Beringia and most especially of *Pyrobombus* species centred in the western mountains (Fig. 7) (Williams *et al.* 2019). As LG bumblebees reached Mesoamerica and South America, there is a particular concentration of species of *Thoracobombus* centred in southern Mexico, on the lower slopes of the Andes, and especially in the cerrado (savanna) region of South America (Figs 7, 10). The MG species of *Cullumanobombus* are centred on southern Mexico and in the high Andes (Figs 8, 10). Some lineages of *Thoracobombus*, *Pyrobombus* and *Cullumanobombus* appear, in addition, to have dispersed back northwards from Mexico, contributing some of the most familiar and widespread components of the North American fauna (*B. fervidus* (Fabricius, 1798) s. lat., *B. pensylvanicus* (DeGeer, 1773) s. lat., *B. impatiens* Say, 1837, *B. griseocollis* (DeGeer, 1773), *B. morrisoni* Cresson, 1878 and *B. fraternus* (Smith, 1854); Williams *et al.* 2022b).

In Europe (Fig. 1 1), both principal groups of bumblebees are now widespread. There is a tendency for LG species to predominate (green cells) in the North European Plain and the Russian Steppes, for the MG bumblebees to predominate (blue) in the Arctic, and for both groups (white) to be relatively species-rich in the southern mountains of the Alps and Armenian highlands, with low richness for both (black) in the Mediterranean lowlands and islands. Even within Britain (Fig. 12), we still tend to see more of the LG species (e.g., *B. humilis* Illiger, 1806, *B. sylvarum* (Linnaeus, 1761)) in our southern and coastal grasslands (e.g., *B. muscorum* (Linnaeus, 1758) and *B. distinguendus* Morawitz, 1869 in the north-western coastal fringe), but more of the MG species (e.g., *B. monticola* Smith, 1849, *B. jonellus* (Kirby, 1802)) in our northern and western hill moors.

How can biogeography help conservation?

The last 40 years have seen a growing awareness of the need to conserve bumblebees with the elucidation of a variety of threats (e.g., Williams 1982; Colla & Packer 2008; Goulson *et al.* 2008; Williams & Osborne 2009; Cameron & Sadd 2020; Rasmont *et al.* 2021; Orr *et al.* 2022). From early on, there has been an appreciation that habitat degradation has played a major role for many bumblebee species (Williams 1986). Understandably, the response has often been to identify the most threatened species (Nieto *et al.* 2014) and to seek to identify and model particular threatening factors (Rasmont *et al.* 2015; Lee *et al.* 2019). A review of the habitat characteristics of bumblebees important for conservation in relation to their larger evolutionary groups and biogeographic history would be useful, but is too broad a subject for this article (a Google Scholar search for bumble+conservation+habitat found 19 200 articles, 12 600 of them within the last decade).

A problem with focussing on the conservation needs of individual bumblebee species is that potentially it could lead to a myriad of disparate individual case studies that become difficult to integrate. For example, *B. distinguendus* is associated in Britain with machair vegetation (Redpath-Downing *et al.* 2013), in Sweden with red clover seed farms (Mossberg & Cederberg 2012), whereas in Inner Mongolia it is found visiting sunflowers in agricultural fields on the edge of the desert (pers. obs.). Summarising this information in their book, which includes many valuable contributions on conservation, Rasmont *et al*. (2021: 372) wrote "it is not easy to understand the ecological requirements that make the species [*B. distinguendus*] so fragile." However, considering the broader group of related species to which it belongs may help by clarifying the shared habitat and behavioural characteristics that are associated with their shared biogeographic history. Biogeographic analysis shows *B. distinguendus* to be one of the LG species that is likely to have dispersed westwards through the Russian steppes and North European Plain (Fig. 9), implying that flower-rich tall grassland with many suitably deep-corolla food plants flowering during the late-summer season may be a more general requirement.

The importance of taxonomic (evolutionary) groups and their association with habitat characteristics affecting conservation is clearly apparent in the phylogenetic patterns detected in bumblebee Red-List threat status (Arbetman *et al.* 2017). Comparing the biogeographic distinction between LG and MG groups (Figs 6–8) has highlighted diverging trends (Williams *et al.* 2022b) in several characteristics important for bumblebee conservation, including: (1) in preferences for nesting sites (Sladen 1912; Sakagami 1976; Williams *et al.* 2008); (2) in preferences for nectar diets from flowers of different corolla depths (Heinrich 1979; Harder 1983); (3) in preferences for pollen diets (Wood *et al.* 2021); and (4) in their seasonal activity patterns (Williams 2005; Fitzpatrick *et al.* 2007; Williams *et al.* 2009a). For example, some MG bumblebees may be especially susceptible to loss of rewarding food sources early in their, sometimes short, nesting seasons. In contrast, knowing that LG bumblebees tend to have longer colony-development periods implies that encouraging a long annual flowering succession including late-flowering plants and avoiding the cutting of grassland during the late summer (Williams & Osborne 2009; Timberlake *et al.* 2019) may be especially important for their reproductive success, something that has been under-appreciated in conservation management. These requirements may be important not just for *B. distinguendus* (above), but also for several declining LG species of the subgenus *Thoracobombus*, so that management benefits may also be shared by other, non-target LG bumblebee species (Sears *et al.* 2016).

The emphasis above is on the LG and MG groups of species. But habitat characteristics can be examined for groups of species at any level in the phylogenetic tree. For example, one of the most divergent and best-known cases is the relatively extreme arctic and alpine specialisation of species of the subgenus *Alpinobombus* (Skorikov 1923; Williams *et al.* 2019). The strength of considering a biogeographic analysis is in its broad-brush view of habitat suitability across closely related groups of species, not just for bumblebees, but for any organisms. Biogeographic analyses also have the potential to inform us about how populations have been affected by major climate changes in the distant past (Williams *et al.* 2017b), which may help to inform our expectations for the future.

We need museums and taxonomy more than ever, not just to know which parts of biodiversity we are looking at, but also to discover whether there are groups that may have different needs for conservation management. This is the kind of work that can only be done with the large museum collections of specimens to provide both accountable genetic and spatial data (not just images) that can provide this vital source of information. Anyone who cares about biodiversity should be calling for more, not fewer, taxonomists and for properly funded natural history museums to focus resources on taxonomy and collections.

Acknowledgements

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