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Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence

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Conservation biology can profit greatly from incorporating a phylogenetic perspective into analyses of patterns and drivers of species extinction risk. We applied such an approach to analyse patterns of bumblebee (*Bombus*) decline. We assembled a database representing approximately 43% of the circa 260 globally known species, which included species extinction risk assessments following the International Union fo Conservation of Nature Red List categories and criteria, and information on species traits presumably associated with bumblebee decline. We quantified the strength of phylogenetic signal in decline, range size, tongue length and parasite presence. Overall, about one-third of the assessed bumblebees are declining and declining species are not randomly distributed across the *Bombus* phylogeny. Susceptible species were over-represented in the subgenus *Thoracobombus* (approx. 64%) and under-represented in the subgenus *Pyrobombus* (approx. 6%). Phylogenetic logistic regressions revealed that species with small geographical ranges and those in which none of three internal parasites were reported (i.e. *Crithidia bombi*, *Nosema* spp. or *Locustacarus buchneri*) were particularly vulnerable. Bumblebee evolutionary history will be deeply eroded if most species from threatened clades, particularly those stemming from basal nodes, become finally extinct. The habitat of species with restricted distribution should be protected and the importance of pathogen tolerance/resistance as mechanisms to deal with pathogens needs urgent research.

1. Introduction

Consideration of evolution has proved to be useful in detecting patterns of species decline at higher taxonomic levels than species (e.g. mammals [1], lizards [2]). Because species belonging to some particular lineages can be more likely to decline, phylogeny can be *per se* a good predictor of extinction risk [3]. Moreover, as species show different degrees of relatedness, a phylogenetic approach is fundamental to test the influence of phylogenetically conserved species traits on decline [4].

There is a global consensus that pollinators, in general, and bees, in particular, are declining ([5] and references therein), with increasing evidence of decline within the genus *Bombus* [6], which comprises approximately 260 large and hairy charismatic bumblebee species grouped within 15 subgenera [7,8]. The bulk of evidence on bumblebee decline comes from studies at local or regional scales [9–11] with a few of them comparing patterns of decline across their complete geographical ranges [12], addressing predictors of decline in large bumblebee faunas [13,14] or, more recently, incorporating a phylogenetic perspective on the analysis of the decline pattern in the European

bumblebee fauna [15]. Despite this progress, the global picture of bumblebee decline is still fragmentary, as no previous study has evaluated worldwide patterns of bumblebee decline as well as their potential predictors within a phylogenetic framework.

The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species classifies each species into an extinction risk category according to rigorous and standardized criteria [16], thus providing the opportunity to explore patterns of decline and test hypotheses on drivers of decline across whole lineages. In 2009, Williams & Osborne [6] applied for the first time IUCN categories and criteria on bumblebees worldwide, identifying various causes of decline and highlighting gaps in knowledge. Although many bumblebee species have not been red-listed yet, particularly from Asia where new species are still being discovered, there have been recent advances in the red-listing process through the yearly contributions from the Bumblebee Specialist Group of the IUCN [17]. Moreover, the application of IUCN categories and criteria to continental assessments (for 46 North American species [18] and 68 European species [19]) is a first step that proved to be useful for the analysis of continental patterns of decline of bumblebee faunas [15].

Hypotheses aiming to explain differential extinction risk among bumblebees focus on extrinsic factors that threaten species' persistence, frequently called 'drivers', and on intrinsic susceptibility factors, also known as 'correlates' of decline. The main drivers of bumblebee decline that have been proposed are climate change, loss of flower abundance and/or diversity owing to agricultural intensification, pathogens and pesticides [20], whereas the most frequent correlates (i.e. intrinsic factors) are breadth of climatic range and food specialization [6,13,21]. Moreover, because some correlates may increase species susceptibility to certain drivers, the former can be used as proxy to test hypotheses on the influence of the latter on species decline [13,22].

Contraction of geographical range size related, among different factors, to climatic change can drive species population reductions [22]. Bumblebees, as cold-adapted organisms [7], are expected to be highly vulnerable to ongoing global warming. Thus, climate change could differentially jeopardize the survival of those species with small range sizes expected to inhabit narrow climatic niches that are not able to cope with a rapid rate of temperature increase [14,23].

In addition, habitat transformation and loss owing to agricultural intensification leads to a reduction or change of floral resources for bumblebees [24]. This may differentially affect species with more specialized diets or that are not able to switch to other floral resources when their preferred flowers become scarce [21,25,26], a response that may depend on species climatic requirements. A bumblebee's tongue length has been proposed as a proxy of trophic specialization, with species with long tongues being more restricted to feed on flowers with long corollas than species with short tongues, which are able to exploit nectar from a large diversity of flowers ([26], but see [27]), including those with long corolla via robbing [28]. Although a previous analysis did not support a positive association between decline and bumblebee tongue length [13], this is, to our knowledge, the first time that such relationship is addressed within a phylogenetic framework on a larger bumblebee fauna.

Finally, bumblebee pathogens can reduce the survival of individuals and the fecundity of colonies [29] with lethal and sublethal effects at the population level [30]. Therefore, some authors have suggested that susceptibility to the presence of internal parasites (e.g. *Crithidia bombi*, *Nosema* spp., *Locustacarus buchneri*) might explain population declines observed in some *Bombus* species [12]. A booming trade of commercial bumblebee colonies could be aiding in the spread of pathogens, increasing bumblebee decline [31].

By combining the conservation status data of more than 100 bumblebee species with a comprehensive phylogeny [32,33], here we conducted, to our knowledge, the first phylogenetically controlled analysis of patterns of global decline in the genus *Bombus*. First, we asked if declining species are non-randomly distributed among lineages, and whether the extinction of these species, or of those belonging to the most threatened *Bombus* subgenera, would imply a significant loss of phylogenetic diversity in the genus. Second, we explored whether existing hypotheses of *Bombus* decline related to range size, tongue length and parasite presence could explain the observed non-random phylogenetic pattern of decline. We predicted that those species with smaller ranges, longer tongues and/or harbouring parasites would be more prone to decline.

2. Material and methods

(a) Phylogeny and dataset

We performed all analyses using the most comprehensive *Bombus* chronogram (i.e. a phylogenetic tree with time-calibrated branch lengths) published up to date, which includes 219 *Bombus* species [32,33]. After removing synonyms [32], the 201 species phylogeny was further pruned to match our set of species with available assessments for extinction risk [6,18,19,34] and species traits chosen as predictors (i.e. range size, tongue length, and each parasite and overall parasite presence; electronic supplementary material, table S1).

We defined decline status as a categorical variable with two levels: 'declining' (coded as '1') and 'non-declining' (coded as '0'). Species classified in the IUCN Red List categories 'Critically Endangered' (CR), 'Endangered' (EN), 'Vulnerable' (VU) and 'Near Threatened' (NT) were assigned to the 'declining' group, whereas those species classified in the IUCN category 'Least Concern' (LC) were assigned to the 'non-declining' group (more detail on species classification is available in the electronic supplementary material). Species classified as 'Data deficient' (DD) were not included in our study (unlike [15]), because DD is not a threat category but rather an indication that more information is required to assign a given taxon to a reliable extinction risk category [16]. When extinction risk status for a given species did not agree among different assessment sources, we applied specific criteria to establish the risk status of such species (see more details on species classification in the electronic supplementary material).

We used unpublished data on bumblebee species global range size compiled by P.W. Range size was defined as the number of cells occupied by a given bumblebee species based on historical records, each cell covering approximately 611 000 km^2 (see more details on range size information in [6] and in the electronic supplementary material). Tongue length (i.e. the sum of glossa and prementum lengths in millimetres [35]) was obtained from the literature and averaged when multiple values were available for the same species (see the electronic supplementary material, appendix S1). We evaluated separately the effect of bearing just one out of three common

internal parasites (*C. bombi*, *Nosema* spp. or *L. buchneri*), and also the effect of bearing any of them, regardless of parasite identity (i.e. overall parasite presence). Thus, the presence of *C. bombi*, *Nosema* spp., *L. buchneri* and overall parasite presence were coded as '1' and absence as '0'. To reduce false negatives associated with extremely low sample sizes, the absence of parasites was considered only in species in which at least five individuals per study were screened for infection.

The database included 111 species with known extinction risk status that belonged to 14 of 15 accepted subgenera (electronic supplementary material, table S1). The complete database is available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.71q32 [36].

(b) Phylogenetic signal and the role of proposed predictors of decline

We assessed the presence of phylogenetic pattern (phylogenetic signal hereafter) in both species decline and species traits associated with decline. For continuous traits (range size and tongue length), we estimated Blomberg's K [37] using the function *phylosig* from the R package *phytools* [38]. Blomberg's K quantifies the amount of phylogenetic signal in the data relative to a Brownian motion model of trait evolution, so that $K = 1$ corresponds to a Brownian motion pattern and $K = 0$ corresponds to a random distribution of the trait across the phylogeny. Statistical significance of phylogenetic signal (i.e. departure from a random pattern) was assessed by randomizing tip values and generating a null distribution of 10 000 K-values from which a probability (p_{random}) could be estimated. Alternatively, phylogenetic signal in binary variables (i.e. decline status and parasite presence) was quantified with the D-statistic [3], which is a scaled sum of sister-clade differences in the state of a binary trait. For phylogenetically clumped traits: $D = 0$ for Brownian motion-like evolution [3] and $D < 0$ for extremely conserved traits; whereas for non-clumped traits: $D = 1$ for randomly distributed traits and $D > 1$ for phylogenetically overdispersed traits. Significant departures of D-values when compared with random ($D = 1$) and Brownian ($D = 0$) patterns were assessed by comparing the observed D-value with null distributions expected under random and Brownian motion patterns of trait evolution, respectively. The observed D-values and the null distributions based on 1000 simulations were estimated and plotted with the *phylo.d* function from the R package *caper* [39]. To compare the magnitudes of phylogenetic signal among continuous and binary traits, D-values were transformed as $K^* = 1 - D$, so that $K^* = 0$ indicates lack of phylogenetic signal, whereas $K^* = 1$ indicates an amount of phylogenetic signal comparable to that expected under a Brownian model of trait evolution [40]. Sensitivity of the estimation of phylogenetic signal in decline to incomplete sampling was assessed by resampling 1000 times at random a given number of bumblebee species, ranging from 20 to 110 out of the entire pool of 111 species (see below), and recalculating D for each randomly sampled dataset.

To assess whether the incidence of decline differed among subgenera, we calculated the proportion of species declining (p) for each subgenus together with its standard error estimated as $sqrt[p(1-p)/n)]$. Then, we compared graphically the proportion of species declining per subgenus with the overall proportion of species declining for the whole genus. We identified particular vulnerable (or stable) subgenera when the overall proportion of declining bumblebees was (or was not) included in the range of values delimited by the mean proportion ± 1 s.e. for each subgenus. Furthermore, we used the binomial test [41] to compare the overall proportion of declining species in the genus with the proportion of species declining in *Thoracobombus* and *Pyrobombus*, the two subgenera large enough to allow for statistical testing.

We analysed whether the extinction of the declining species would imply a significant loss of phylogenetic diversity (see [15] for a similar approach). We quantified phylogenetic diversity using Faith's phylogenetic diversity index (PD hereafter [42]), which is defined as the summed branch lengths connecting species across the phylogeny (i.e. total tree length). We estimated the loss of PD associated with the extinction of declining species by running 1000 simulations for a given number of declining species up to 38, which is the total number of threatened species, and assuming that all declining species had an equal probability of becoming extinct. This was then compared with the loss of PD expected if extinctions would occur randomly (i.e. independently of risk status). Furthermore, we performed a set of three similar analyses, but focusing on the three most susceptible subgenera (i.e. *Thoracobombus*, *Cullumanobombus* and *Alpinobombus*; see Results). This was done to assess whether the extinction of all or most of the species of these subgenera would imply a sudden decrease in phylogenetic diversity associated with the loss of deep branches in the phylogeny (i.e. a 'tipping point' [43]). For each target subgenus, we compared the decrease in PD arising from the extinction of an increasing number of species belonging to that subgenus with the expected decrease in PD assuming that the extinction probability was the same for all species, regardless of the subgenus they belong to. Again, we ran 1000 simulations for each number of extinct species. We used two datasets; a first including only the species with known risk status (111 species), and a second including all species represented in the phylogeny (201 species).

Finally, we evaluated the hypotheses of climate change, loss of bumblebee floral resources and diseases as drivers of decline by running phylogenetically controlled logistic regressions [44]. More specifically, these models assessed the influence of species range size, tongue length and parasite presence (i.e. *C. bombi*, *Nosema* spp., *L. buchneri* or overall parasite presence) on whether a species is declining or not. We ran phylogenetic regressions using the function *phyloglm* from the R package *phylolm* [45]. We performed separate tests for each of these predictors. However, predictors that showed a significant effect on decline when tested separately were also tested simultaneously to evaluate the independent effect of each of them on decline.

3. Results

(a) Overall declining trends

We found assessments on extinction risk for 115 (44%) out of the approximately 260 known *Bombus* species at the global ($n = 66$) or continental ($n = 49$) scale. Among these, 40 species (34.7%) were classified as declining. Similarly, 38 species (34.2%; 24 globally and 14 continentally assessed) out of the 111 species with known conservation status included in the *Bombus* phylogeny [32] were classified as declining. Hence, about one-third of global bumblebee fauna assessed for extinction risk is threatened.

(b) Phylogenetic signal and the role of the proposed predictors of decline

Declining species were non-randomly distributed across the *Bombus* phylogeny (figure 1). The phylogenetic signal of bumblebee decline was significantly higher than random expectations ($K^* = 0.41$ or $D = 0.59$, $p = 0.004$; see the electronic supplementary material, table S2), but less contagious than expected under a Brownian motion model of character evolution (electronic supplementary material, figure S1).
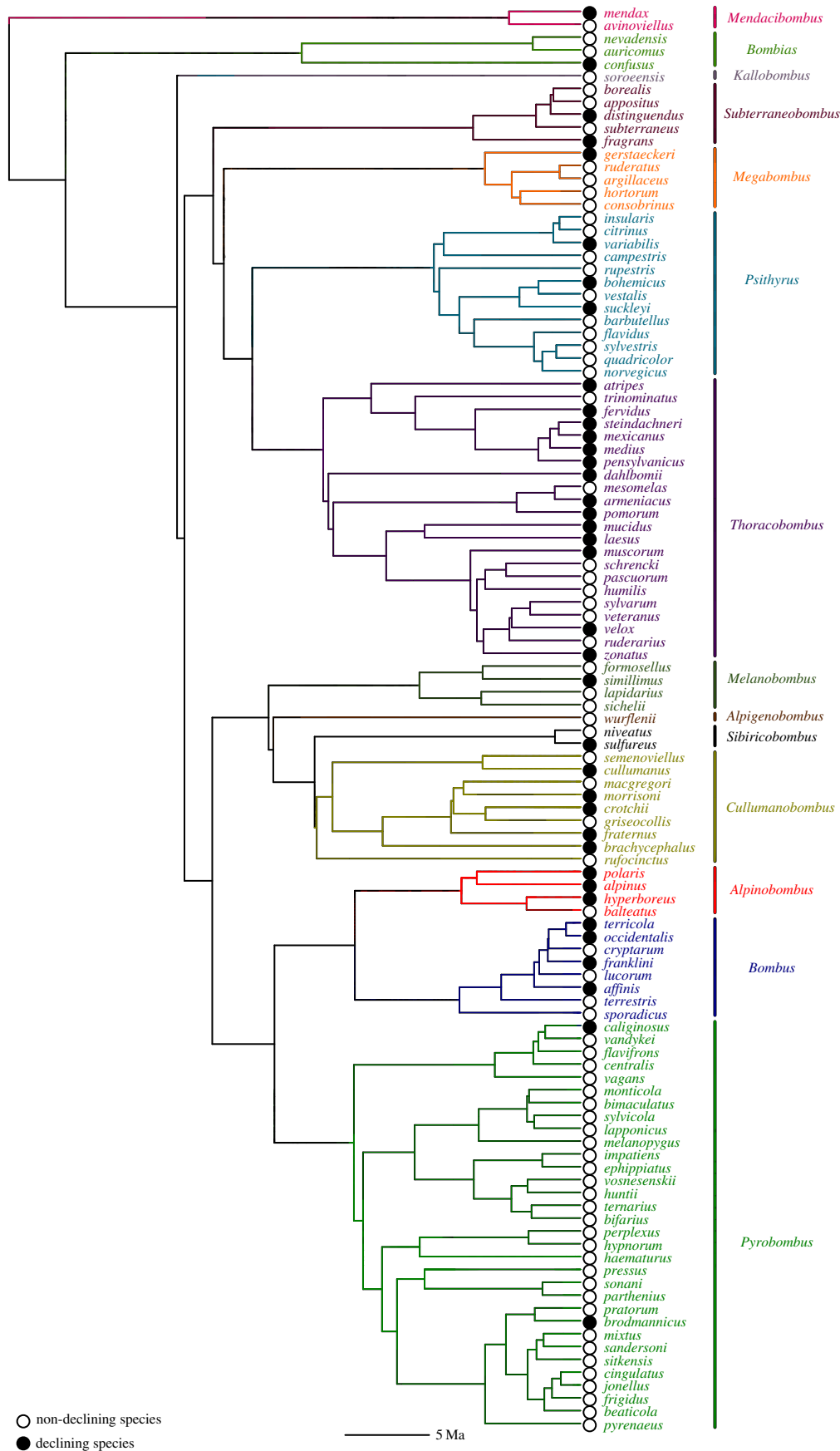
Figure 1. Phylogenetic relationships among *Bombus* species and decline status (binary-coded) for each species. The topology and divergence times were extracted from Cameron *et al.* [32] and Hines [33]. Declining and non-declining species are represented with closed and open symbols, respectively. Subgenera are indicated with different colours.

Owing to missing values in both declining status and the analysed phylogeny, we performed a sensitivity analysis which showed that our sample size was large enough to provide a robust estimation of phylogenetic signal in decline. Indeed, a subset of 80–90% of the species included in the analysis would have been sufficient to detect a significant,
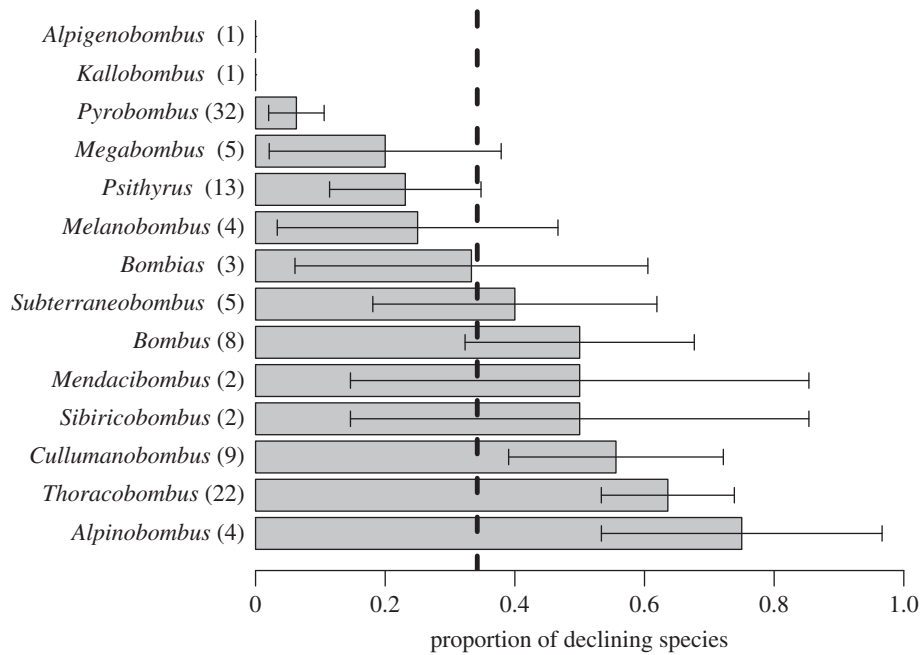
Figure 2. Proportion of species declining in each subgenus. Error bars represent the standard error of the proportion. The dashed vertical line represents the mean proportion of species declining for the whole genus (0.34). The number of species analysed is indicated between parentheses. The subgenus *Orientalibombus* was not included because of a complete lack of information on the conservation status for any of its species.

phylogenetically clumped pattern with approximately 100% certainty (electronic supplementary material, figure S2).

A significant phylogenetic signal in decline reflected the uneven distribution of declining species among subgenera. Figure 2 shows that the proportions of species declining in the subgenera *Alpinobombus, Thoracobombus* and *Cullumanobombus* were higher than the overall proportion across the whole genus. To the contrary, *Pyrobombus* showed the lowest proportion of declining species. Statistical tests confirmed that the proportion of species declining in *Thoracobombus* and *Pyrobombus* were significantly higher ($\chi^2 = 5.49$, $p = 0.019$) and lower ($\chi^2 = 8.32$, $p = 0.004$) than the overall proportion, respectively. Despite the significant amount of phylogenetic signal in decline (electronic supplementary material, table S2), the simulated extinction curves showed that the disappearance of the 38 threatened species would not imply a higher decrease in PD as compared to that expected after random extinctions (electronic supplementary material, figure S3). However, the analyses focusing on the most susceptible clades clearly show tipping points for the threatened and deep-rooted subgenera *Thoracobombus* and *Cullumanobombus*, but not for *Alpinobombus* (electronic supplementary material, figure S4) that stems from a more recent node (figure 1) [33]. Thus, the extinction of most species of *Thoracobombus* or *Cullumanobombus* would imply a higher loss of PD than expected if a similar number of species become extinct at random, which was evidenced either using the phylogeny that only included species with known decline status (electronic supplementary material, figure S4, left panels) or the complete phylogeny (electronic supplementary material, figure S4, right panels).

Range size, tongue length and overall parasite presence showed significant phylogenetic signal (electronic supplementary material, table S2). Species decline was significantly related to range size, with species with smaller ranges being more prone to decline (electronic

supplementary material, table S3). Also, species in which no internal parasites have been reported were more likely to decline (electronic supplementary material, table S3), but this trend was not detected when analyses were run for each parasite species separately, although all of them showed a negative trend (electronic supplementary material, table S3). The negative and significant influences of overall parasite presence and range size on decline susceptibility (electronic supplementary material, table S3) were not confounded by the positive (albeit weak) association between these two predictors ($\tau = 0.195$, $p = 0.046$; see also the electronic supplementary material, tables S4 and S5 and the Phylogenetically controlled multiple logistic regressions section in the electronic supplementary material). Furthermore, the effect of range size on decline was not influenced by the inclusion of species with decline status categorized according to the IUCN Red List criteria based on limited geographical ranges (i.e. five species, see Range size section in the electronic supplementary material for more detail on these analyses). Finally, the probability of decline was not significantly related to tongue length (electronic supplementary material, table S3).

4. Discussion

Pollinators are declining worldwide [5], and bumblebees are not an exception. To date, 44% of the known bumblebee species have been assessed for extinction risk either at the global or continental scale. About one-third of the species from this pool are declining across their ranges. Interestingly, our results showed that declining species are not randomly distributed across the *Bombus* phylogeny, suggesting the existence of differences among clades in their susceptibility to decline and that underlying evolutionarily conserved traits could be related to this differential susceptibility. Species occupying small geographical ranges were more prone to decline than species distributed over large ranges,

a prediction consistent with the hypotheses of climate change or habitat loss as drivers of decline [6,13,23]. In contrast with previous expectations, decline susceptibility increased in those species where none of the internal pathogens *C. bombi*, *Nosema* spp. or *L. buchneri* were reported.

A significant, albeit moderate, phylogenetic signal in decline status was related to an over-representation of declining species in the subgenera *Thoracobombus*, *Cullumanobombus* and *Alpinobombus*, although the low number of species in the latter two did not allow us to draw strong conclusions for these subgenera. Particularly, the global extinction risk status of many species in the *Alpinobombus* group is still not well established and populations of species in this subgenus might be declining in Europe but not elsewhere [46]. Similarly, *Bombus* (*Cullumanobombus*) *cullumanus* may be nearly extinct in Europe while remaining common in Asia [47]. In any case, these continental declines should raise an early warning for species with geographical ranges extending in more than one continent. In the case of *Thoracobombus*, 22 of the 52 recognized species in this subgenus (i.e. 42%) have a well-established extinction risk status and were included in the analysed phylogeny. From them, almost two-thirds of these 22 species (i.e. 14 species out of 22) are declining (figure 2). Moreover, six out of eight species in this subgenus are categorized as LC but already have a 'decreasing populations' trend, even though they do not qualify for a threatened category yet. This suggests that the number of species declining in this subgenus might increase in the near future if these trends continue. In fact, although *Bombus* (*Thoracobombus*) *rubriventris* has been assessed as CR, this species may be possibly extinct [48], which would represent the first documented extinction of a bumblebee species in historical times. To the contrary, the subgenus *Pyrobombus* was less prone to decline as compared to the overall proportion for the genus (figure 2). Out of the 50 species belonging to this subgenus, 32 species (64%) had well-established extinction risk status and were included in the analysed phylogeny, with only two species (*Bombus brodmannicus* and *Bombus caliginosus*), i.e. approximately 6%, being threatened. Sample sizes for most subgenera were clearly insufficient to draw robust conclusions on declining or not declining trends at this taxonomic level.

The state of knowledge on the biology of species of the genus *Bombus*, their phylogenetic relationships, their susceptibility to decline as well the species-specific drivers of decline, are far from being completely known. However, our results are robust to the existence of missing data, because we included 111 out of the approximately 260 known species of bumblebees representing 14 out of the 15 currently recognized *Bombus* subgenera. Furthermore, a sensitivity analysis demonstrated that the strength and significance of the phylogenetic signal in decline did not suffer from sample size limitations and did not depend on the inclusion or exclusion of any particular species (electronic supplementary material, figure S2). A recent study [15] reported a phylogenetic signal for European threatened species of $D \sim 0.7$, similar to our global $D \sim 0.6$, which was misinterpreted as implying phylogenetic overdispersion [15]. Indeed, the phylogenetic signal reported in that study was not significantly different from random expectations (i.e. $D = 1$), most likely because of working with half the species we included in our global analysis (see the electronic supplementary material, figure S2).

Despite the existence of a phylogenetic signal in decline and the large fraction of the bumblebee fauna currently declining, the extinction of all the species categorized as declining would not imply a higher decrease in PD than expected from random extinctions (see the electronic supplementary material, figure S3). This is because the two most threatened clades stemming from deeper nodes, i.e. *Thoracobombus* and *Cullumanobombus*, still retain a handful of non-threatened species (figure 1, [43]). However, the extinction of most or all the species of these two subgenera would imply a higher loss of PD than expected from random extinctions (electronic supplementary material, figure S4). Thus, from a phylogenetic perspective, species of these subgenera deserve the highest conservation priority, not only because a large proportion of their species are threatened, but also because the extinction of these clades will deeply erode the phylogenetic diversity of the whole genus.

Bumblebee species with small geographical ranges were particularly vulnerable (electronic supplementary material, table S3), a pattern that was already described for other taxa (e.g. [49]) and consistent with an earlier study relating decline susceptibility to narrow climatic specialization [13]. A recent study demonstrated severe range losses from species' southern limits and failures to track warming conditions at northern limits, both in European and North American bumblebees [14]. Therefore, our results raise an alarm on the conservation of bumblebee species with small ranges, which may thus be more susceptible to decline, as global warming is expected to further reduce their already limited ranges.

Tongue length affects food choice and access [35], which may increase susceptibility to reductions in availability of food plants [21,26], influencing bumblebee decline [50]. Although our study confirmed a strong phylogenetic structure in tongue length [51], this highly conserved trait was not significantly related to species decline. In the context of the hypothesis tested here, this result suggests that the loss of floral resources may not be a major driver of bumblebee decline at the global scale, as reported previously [13]. However, this lack of association might have alternative interpretations. First, species mean tongue length estimates used in analyses may obscure the high intraspecific variability in this trait existing within and among populations [52], and thus weaken the chance to detect a significant positive effect of tongue length on decline despite a relatively large effect size (electronic supplementary material, table S3). Second, the relationship between tongue length and specialization is more complex than assumed by this hypothesis, and strongly dependent on both the plant and bumblebee community [21,35]. For instance, an association between flower use and tongue length might exist in diverse bumblebee communities but not in simple ones. Hence, even if tongue length affected species performance at the community scale [53], this relationship would not scale up at the global or continental level, making tongue length a questionable proxy of species overall specialization at large spatial scales.

Susceptibility to decline increased in those species lacking internal pathogens, an unexpected result that seems to contradict previous hypotheses linking higher pathogen susceptibility to the current pattern of decline. However, our findings should be interpreted with caution, as opposing results are predicted depending on whether tolerance (i.e. host ability to deal with a given parasite load) or resistance (i.e. host ability to limit parasite establishment) is the

main mechanism explaining why some species may be more affected by pathogens than others. Indeed, our results suggest that non-declining species can carry internal parasites without large fitness costs, implying tolerance to these parasites rather than resistance. Accordingly, pathogens that are highly lethal in susceptible hosts should act as strong ecological filters, and thus those individuals, colonies and populations that still survive are expected to be mostly free of pathogens (supporting these results, see [54]). This will reduce the chance of detecting pathogens in wild populations of declining species, with sampling effects also mediating the negative relationship between parasite presence and decline. Given the increasing transport and usage of commercial bumblebee colonies, which may transmit parasites to novel bumblebee host species, the role of pathogens deserves the highest research priority.

Patterns and causes of *Bombus* decline have frequently been reported at a regional scale, but to our knowledge, this is the first phylogenetic global analysis within the genus. We conclude that bumblebee evolutionary history and associated genetic diversity could be deeply eroded if the threatened clades, especially *Thoracobombus* and *Cullumanobombus*, become extinct. A reduction in PD could be expected to affect evolutionary potential to cope with ongoing global change [55], also impairing current and future biodiversity uses derived from evolutionary processes [43]. Although the assumed links between phylogenetic diversity and both functional diversity and evolutionary potential remain unclear [56], our results suggest that the current bumblebee decline could have economic, ecological and evolutionary implications. In terms of traits, particularly vulnerable are those bumblebee species occupying small geographical ranges. Also, species from which none of the three most common *Bombus* internal parasites have been reported, were more prone to decline than those species harbouring at least one of these pathogens. This pattern could indicate reduced tolerance to infection in declining species, compared to non-declining species, but undoubtedly, further studies are needed to disentangle the meaning of this association. As the status of many of the species in the genus *Bombus* has not yet been assessed across their entire global range, but factors affecting bumblebee species keep acting, conservation efforts should particularly target those species belonging to the clades stemming from deeper nodes and/ or inhabiting narrow ranges.

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