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A phylogenetic approach to conservation prioritization for Europe's bumblebees (Hymenoptera: Apidae: *Bombus*)

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ABSTRACT

Bumblebees are an essential component of our agroecosystems, and their decline represents a major threat for the sexual reproduction — and hence survival — of wild flowers and several important pollinator-dependent crops alike. The EU bumblebee fauna encompasses many highly imperiled species characterized by a relatively narrow range size and often restricted to high elevation mountain habitats where the threats of both current and future global warming are expected to be particularly severe. In this context, identifying how and where limited conservation resources should be targeted is a pressing priority to meet our fundamental biodiversity conservation targets in an economically-efficient way. Because classical taxonomic approaches to conservation can potentially overlook important alternative aspects of biodiversity such as the phylogenetic diversity, a key component for the maintenance of ecosystem processes and services, I used a multi-gene molecular phylogeny encompassing more than 85% of the EU species to combine categories of the IUCN Red List with the evolutionary legacy and range size of EU bumblebees. My results from phylogenetic generalized least squares (PGLS) and phylogenetic independent contrasts (PIC) analyses first indicate that, contrary to theoretical prediction, evolutionary relatedness explains none of the range size similarity or the probability of extinction risk in EU bumblebees. Furthermore, although the extinction of extant threatened EU bumblebee species is unlikely to have a significant effect on the expected phylogenetic dispersion of the remaining *Bombus* species at the EU scale, my results clearly illustrate that a significantly disproportionate amount of phylogenetic diversity/evolutionary history might be lost if the extant threatened EU bumblebee species would become extinct. Collectively, this study exemplifies the fact that the incorporation of a phylogenetic approach can increase the efficacy of the existing prioritization for the conservation of EU bumblebees (i) by capturing the phylogenetic diversity and its associated functions, as well as (ii) by better targeting species that are both evolutionarily unique (or non-redundant), threatened and restricted in their range size.

1. Introduction

As Darwin (1859) pointed out in his *magnum opus* “On the origin of species”, the tendency for closely-related species to exhibit similar habits, constitution and structure, is ubiquitous in nature. Evidence from modern-day phylogenetic trait mapping analyses across the tree of life supports — by and large — the idea that evolutionary relatedness explains the trait and sometimes ecological niche similarity between species, a pattern known as phylogenetic niche conservatism (Harvey & Pagel, 1991; Hansen & Martins, 1996; Revell et al., 2008; Wiens et al., 2010). This phenomenon has important implications, since it significantly impacts on a range of ecological and evolutionary processes and patterns, from fundamental aspects of e.g. co-occurrence probabilities of species, to the extent to which closely-related taxa of threatened species are expected to be more or less often at risk than their more distant relatives (Faith, 1992; Mace et al., 2003). While the IUCN Red List of Threatened Species represents a powerful tool for practical conservation planning (Rodrigues et al., 2006), conservation biologists today face the major challenge of setting conservation priorities in groups of sometimes highly diverse species for which a substantial part of the taxa evaluated are categorised as “Data Deficient (DD)”. In this context, the incorporation of species' contribution to phylogenetic diversity can successfully be taken into account for conservation planning, as it helps using alternative metrics of biodiversity to reach a better understanding of where and what diversity is at risk (Mace & Baillie, 2007; Mace & Purvis, 2008; Cadotte & Davies, 2010; Redding et al., 2010; Winter et al., 2013; Jetz et al., 2014; Nunes et al., 2015; Pollock et al., 2015).

With an estimated 20,000 species described worldwide (Ascher & Pickering, 2016) and their key role in the pollination of flowering plants (Ollerton et al., 2011), bees rank among the groups of species that are increasingly the focus of conservation actions following reports of

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large-scale declines. Like many other groups of wild bees, bumblebees have been reported to decline in developed regions such as in North America (Thorp & Shepherd, 2005; Cameron et al., 2011; Bartomeus et al., 2013) and in Western Europe where several authors have reported on apparent cases of widespread decline since the 1970's (Peters, 1972; Alford, 1973) and 1980's (Williams, 1982; Williams, 1986; Rasmont & Mersch, 1988; Goulson, 2003; Williams & Osborne, 2009). With the recent publication of the IUCN European Red List of Bees, Nieto et al. (2014) have provided an assessment of the status and trends of ca. 2000 species of wild bees, including all 68 species of EU bumblebee recorded of which an estimated 46% are thought to be threatened by extinction. Among the major causes of (bumble)bee decline, Nieto et al. (2014) have pointed out the intensification of agriculture, the increase of pollution from agricultural waste, the loss of habitat due to urban development and land use changes in agro-ecosystems such as the loss of permanent and unimproved grasslands as the main threats (see also González-Varo et al. (2013)). Climate change was also evoked as a significant explanatory variable in the equation by Nieto et al. (2014) and Rasmont et al. (2015) have stressed in their recent *Climatic Risk and Distribution Atlas of European Bumblebees* that the increasing temperatures and long periods of drought are severely threatening many of the EU bumblebee species, particularly those that live in high altitude habitats and characterized by very small range sizes (see also Kerr et al. (2015)). Indeed, although the geographic range of the world bumblebees spans a wide range of latitudes and habitat types, their tendency to be adapted to cold and temperate regions of the Northern Hemisphere (Williams, 1998; Hines, 2008) has led many species to be characterized by a relatively narrow range size, e.g. in high elevation mountain ranges where the threats of current and future global warming are particularly severe (Rasmont et al., 2015; Kerr et al., 2015). A narrow range size has therefore the potential to inflate the vulnerability of bumblebee species, a phenomenon also observed in other terrestrial animal and plant species with a smaller geographic range that are assumed to be comparatively more threatened by extinction, all other factors being equal (Cardillo et al., 2008; Harris & Pimm, 2008; Runge et al., 2015).

Bumblebees are an essential component of our agroecosystems, and their decline represents a major threat for the sexual reproduction — and hence survival — of wild flowers and pollinator-dependent crops alike. Furthermore, because *Bombus* is the only extant genus of the corbiculate bees in the tribe Bombini (Michener, 2007), it is of prime importance to assign priorities to conservation efforts by taking into account not only species as independent units, but also the fact that the extinction of more evolutionarily unique *Bombus* species would imply a greater loss of phylogenetic diversity (PD) (see also Isaac et al. (2007), Hidasi-Neto et al. (2013), Faith (1662), Forest et al. (2015), and Huang and Roy (2015)). PD is often used as a proxy for functional diversity (FD), an important component for the maintenance of ecosystem processes and services (Faith, 1662; Tilman et al., 1997a; Tilman et al., 1997b; Cadotte et al., 2008; Cadotte et al., 2009; Cadotte et al., 2012; Gravel et al., 2011; Rolland et al., 2011), particularly in the context of pollination services provided by wild bees (Hoehn et al., 2008; Albrecht et al., 2012; Fründ et al., 2013; Martins et al., 2015). Consequently, the conservation of higher PD is likely to safeguard the evolutionary legacy of bumblebees, their potential to face environmental changes, and can be anticipated to be pivotal for the maintenance of present and future ecosystem processes and services (Faith, 1662; Cadotte et al., 2012; McNeely, 1988; Faith et al., 2010). The time is now ripe for the incorporation of PD as an alternative biodiversity metric into conservation planning to avoid worst-case losses of long branches from the bumblebee tree of life (see e.g. Davies (2015) discussing this issue with a focus on the South African Cape flora) and their associated ecological/economic consequences (see also Kleijn et al. (2015) and Potts et al. (2016)).

To address this issue and to assess the relevance of a phylogenetically-informed conservation action of EU bumblebees compared to a scenario of conservation priorities based solely on the IUCN categories, I combined a molecular phylogeny with recent data on the distribution range (Nieto et al., 2014; Rasmont et al., 2015) and the conservation status of bumblebees (Nieto et al., 2014) in Europe. Using ancestral character estimation, phylogenetic independent contrasts (PIC) and phylogenetic generalized least squares (PGLS), I aim (i) to determine the extent to which the evolutionary legacy of bumblebees explains biogeographic patterns (range size in particular), and (ii) to test if IUCN Red Listed species that are threatened at the EU scale due to population declines are phylogenetically more closely-related or more evolutionarily unique than expected by chance alone. Next, I also computed the EDGE (Evolutionary Distinct, Globally Endangered) metric (iii) to analyse and combine the degree of evolutionary distinctiveness (ED) along with the extinction risk (weighted IUCN categories). Last, I discuss these results to assess conservation priorities by examining the extent to which the current IUCN Red List categories also captures alternative aspects of diversity such as the phylogenetic diversity of EU bumblebees, and how species that are both evolutionarily unique (or non-redundant), threatened and restricted in their range size (i.e., “evolutionary distinctiveness rarities”, EDR) can be better targeted for conservation action.

2. Materials & methods

2.1. Molecular phylogeny of EU bumblebees

To prepare a phylogenetic tree for the EU bumblebees whose first branch lengths capture the expected similarities and differences among species, I used the most likely Bayesian tree (Tree ID #Tr2906 on https://treebase.org) produced by (Hines, 2008) based on (Cameron et al., 2007) using mixed-model Bayesian analyses for a study on the historical biogeography, divergence times, and diversification patterns of bumblebees at the worldwide scale, including representatives of all 38 subgenera (Williams, 1998). This multi-gene molecular phylogeny encompasses 229 *Bombus* species; the sequence data include ~3745 amplified nucleotides, including both intron and exon regions from 5 genes: mitochondrial 16S rDNA, elongation factor-1α F2 copy (EF-1α), long-wavelength rhodopsin (opsin), arginine kinase (ArgK), and phosphoenolpyruvate carboxykinase (PEPCK) (Hines, 2008; Cameron et al., 2007).

I then pruned this tree with the *ape* package (Paradis et al., 2004), which yielded in a near-complete species-level phylogenetic tree comprising 59 *Bombus* species out of the 68 species listed at the EU scale, i.e. more than 85% of the EU bumblebee species count (Nieto et al., 2014). This phylogenetic tree was used for all statistical analyses in the present study by adjusting branch lengths with the rho parameter set to 1 using Grafen's (1989) method as implemented in the *ape* package (Paradis et al., 2004). The final tree had therefore scaled node heights so that the root height was equivalent to 1.

2.2. Phylogenetic diversity (PD) associated to threatened EU bumblebees

To estimate the taxonomic (TD) and phylogenetic diversity (PD) decline associated to a loss of Red Listed bumblebee species, I computed the TD and PD associated to 4 distinct communities: (i) all 58 EU bumblebee species, (ii) all 58 EU bumblebee species without species categorised as CR and EN on the IUCN Red List (Nieto et al., 2014), (iii) all 58 EU bumblebee species without species categorised as CR, EN and VU on the IUCN Red List (Nieto et al., 2014), and (iv) all 58 EU bumblebee species without species categorised as CR, EN, VU and NT on the IUCN Red List (Nieto et al., 2014). This analysis was performed with the *picante* package (version 1.6-2) (Kembel et al., 2010); calculations of PD are measured for each community as the total branch length of a tree linking all species represented in this particular community (Faith, 1992).