

Research



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Evolutionary biology

Historical species losses in bumblebee evolution

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Investigating how species coped with past environmental changes informs how modern species might face human-induced global changes, notably via the study of historical extinction, a dominant feature that has shaped current biodiversity patterns. The genus *Bombus*, which comprises 250 mostly cold-adapted species, is an iconic insect group sensitive to current global changes. Through a combination of habitat loss, pathogens and climate change, bumblebees have experienced major population declines, and several species are threatened with extinction. Using a time-calibrated tree of *Bombus*, we analyse their diversification dynamics and test hypotheses about the role of extinction during major environmental changes in their evolutionary history. These analyses support a history of fluctuating species dynamics with two periods of historical species loss in bumblebees. Dating estimates gauge that one of these events started after the middle Miocene climatic optimum and one during the early Pliocene. Both periods are coincident with global climate change that may have extirpated *Bombus* species. Interestingly, bumblebees experienced high diversification rates during the Plio-Pleistocene glaciations. We also found evidence for a major species loss in the past one million years that may be continuing today.

1. Introduction

The fossil record shows successive extinction and replacement of species, with diversification periods that have been linked with global climate change and drastic geological reorganizations. Episodes of extinction have punctuated the evolutionary history of clades [1,2], during which exhibit extinction rates and magnitudes that far exceed those observed elsewhere in the geological record. Extinction is a dominant feature of biological evolution as 99.9% of all species that ever lived are now extinct [3]. Today, approximately one-fifth of animal and plant species are threatened or face extinction, and we may be entering one of the largest extinction events ever [4]. As environmental changes and extinctions are part of the history of life, studying the past can shed light on the current crisis [4,5]. Analysing past extinction events allows us to distinguish background from exceptional extinction rates and provides a better understanding of the causes of extinctions, such as climatic or geological events [1,6,7].

Present-day terrestrial ecosystems harbour approximately 250 species of bumblebees (Hymenoptera: Apidae: *Bombus*), an ecologically important pollinator clade vital for numerous native and agricultural plant species [8,9]. This lineage has been subjected to considerable species decline in the past century attributed to agricultural practices, climatic conditions and increased spread of pathogens [10]. Their susceptibility raises questions of how the ancestors of modern bumblebees coped with crises during their evolutionary history. Bumblebees, a predominantly cold-temperate and alpine group, evolved against a backdrop of radical alterations of their ecological niches. Phylogenetic evidence from a nearly complete sampling of bumblebee species supports modern diversity originating during the Oligocene in the Palaearctic with colonization events to the

New World in the early Miocene and to South America in the late Miocene and early Pliocene [11] (figure 1a). Their evolutionary expansion throughout these periods may be described as an episodic process, apparently affected by large-scale environmental changes such as the Plio–Pleistocene glaciations [11]. The episodic patterns of diversification observed in the bumblebees should be expected if bumblebees living in these periods were sensitive to and went extinct with environmental change or if they radiated in response to post-extinction niche vacancy.

Fossil data indicate the presence of bumblebees during the mid-Miocene, yet, because of the incompleteness of this record, fossils shed little light on the time and rate at which modern taxa attained their diversity [11–14]. Molecular divergence time estimates based on extant taxa can instead provide information on historical extinction rates as they retain signatures of historical shifts in diversification [15–17]. Teasing apart speciation and extinction from phylogenies remains challenging [18,19]. However, diversification models applied to several bee clades have provided good examples in which extinction or population decline is inferred [20–23]. Molecular phylogenetic analyses of *Bombus* have resulted in a taxonomically well-sampled time-calibrated tree especially suited for examining their diversification dynamics [9,11]. We use this chronogram combined with more recent approaches for examining shifts in speciation and extinction rates to more thoroughly investigate the macroevolutionary history of bumblebees. We examine whether the clade has experienced episodic pulses of speciation and/or extinction and how these pulses associate with environmental fluctuations.

2. Material and methods

Time-dependent diversification analyses were conducted on the chronogram of Hines [11], which comprises 219 of the 250 known *Bombus* species. Analyses were performed with two primary methods: TREEPAR [16] and the Morlon *et al.* [17] approach. These methods provide separate estimates for speciation and extinction rates through time and relax the assumption of constant diversification rates by allowing either discrete changes in rates at estimated points in time [16] or continuous changes through time [17]. We also performed Bayesian analysis of macroevolutionary mixtures [19], which allows shifts in rates among/within clades, but has the disadvantage of treating extinction as constant. All of these methods allow for diversification rates to be negative, that is to say periods of declining diversity, and account for under-sampled phylogenies. For details and settings for each analysis, see the electronic supplementary material, text S1.

As taxon sampling in the tree did not include all species, we adjusted the sampling fraction accordingly. Although there is some phylogenetic clustering of missing species, missing taxa tend to be distributed fairly evenly across the phylogeny, thus not deviating much from random sampling.

Models were fitted to the timetree and also repeated on 100 phylogenies of the dating analyses in order to take into account phylogenetic and dating uncertainties.

3. Results and discussion

The best-fitting diversification models for *Bombus* were models with variable rates (electronic supplementary material, table S1 and figures S1–S5). Results were congruent among all methods, although some inherent differences exist owing to the way in which speciation and extinction rates are estimated.

The three methods recovered an important role of extinction in shaping the bumblebee tree: the extinction rate increased towards the present (electronic supplementary material, table S1 and figures S1–S5). Using TREEPAR, the best model supported four shift times, thus five distinct diversification periods (figure 1b). According to this model, bumblebees diversified with an initial net diversification rate of 0.05 lineages Myr^{−1} (turnover 0.99), resulting in very close speciation and extinction rates (*period 1*).

Over the first 20 Myr, bumblebees diversified with no detectable change of diversification. We inferred that diversification rate and turnover first changed in the mid-Miocene (*period 2*). This period corresponds to the mid-Miocene extinction (14.8–14.5 Ma), a wave of extinctions of terrestrial and aquatic organisms [24]. A major cooling step occurred at this time, associated with major growth of the Antarctic ice-sheets [25]. We estimated diversification rate to be negative after the shift and turnover to be slightly above 1, meaning that bumblebee diversity declined, because extinction was slightly higher than speciation, consistent with expectations during an extinction event. Given the small difference between speciation and extinction, species diversity at that time might be also explained by a stasis, with no species formation or loss.

This diversification decline remained steady until the late Miocene. While the diversification rate continued to decrease (−0.24 lineages Myr^{−1}), the overall diversification rate declined even further (*period 3*). This was not because of increased extinction, which actually decreased twofold (1.4738 to 0.5618 events lineages Myr^{−1}), but because of a stronger fourfold decrease in speciation (1.4714 to 0.3246 events lineages Myr^{−1}). At this time, the cooling trend had eliminated warm–temperate-mixed forests and had formed mid-latitude cool temperate habitats [26]. These environments were likely favourable to these primarily cold–temperate bees, which may have undergone an ‘evolutionary lag’ in speciation because of increased gene flow in an expanding niche.

The third diversification shift occurred in the late Pliocene (*period 4*), when diversification rate became positive again (0.68 lineages Myr^{−1}) owing to a concomitant twofold increase in speciation (from 0.3246 before the shift to 0.679 events lineages Myr^{−1} after) and an important decrease in extinction (from 0.5618 before the shift to 6.10^{−8} events lineages Myr^{−1} after). Thus, bumblebee species richness bounced back during the Plio–Pleistocene glaciations. Climatic oscillations are likely to have isolated populations in refugia, leading to allopatric differentiation during glacial periods and recolonizations during post-glacial periods [11]. The stochasticity of glaciation periods did not act as a trigger of extinction for these already cold-adapted bees, but likely acted as an opportunity to break up continuous populations into new species. This may have been especially facilitated by the largely alpine distribution of bumblebees, which may have become isolated on mountain-tops in warm phases and moved down into valleys and expanded their ranges in cold periods. Diversification owing to more opportunities for allopatric speciation was also suggested by temperate allodapine bee diversifications driven by aridification [20].

Bumblebees diversified until a last shift of diversification occurred in the late Pleistocene, when a strong negative diversification rate is inferred (−2.036 lineages Myr^{−1}), explained by a ninefold decrease in speciation rate and a spectacularly

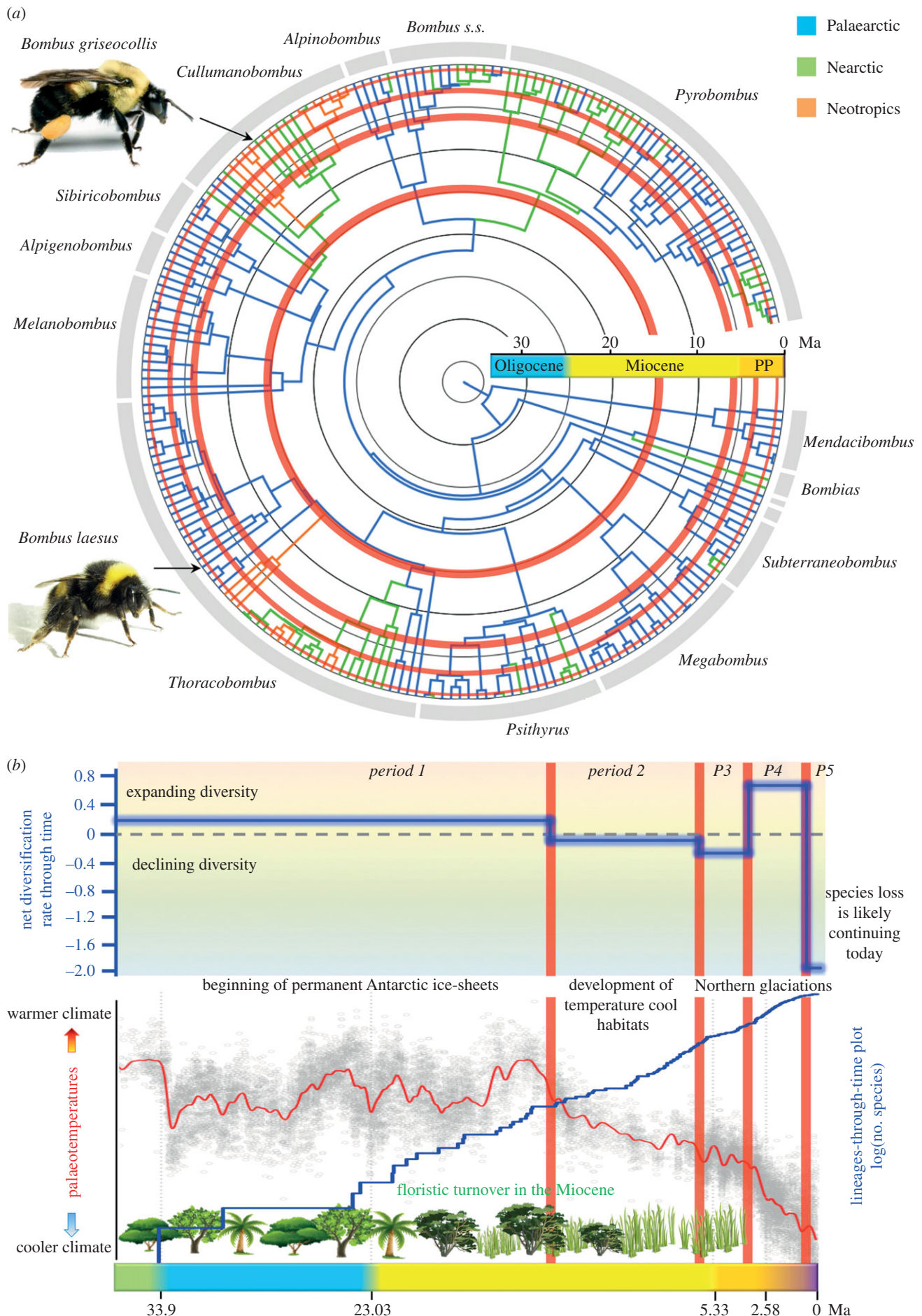


Figure 1. Diversification pattern of bumblebees. (a) A circular tree showing the evolutionary timeline of the clade with the inferred shifts of diversification rates through time indicated with circles. PP, Plio-Pleistocene. Biogeographic reconstructions from Hines [11]. (b) A synthetic view is provided for the possible evolutionary and ecological determinants of the *Bombus* diversification. P, period. Picture from Alex Surciă. (Online version in colour.)

high extinction rate (*period 5*). The cause of this trajectory is unclear, although three factors are of note. First, climatic oscillations are more pronounced in the past million years, with rapid and extreme climatic shifts [25]. Facing those short-term and abrupt conditions, bumblebee species may have gone extinct. Comparable patterns have been observed in halictine bees, which demonstrate reduced population sizes in tropical regions only with recent glaciation events [23]. Second, bumblebees may have been affected more recently by human impacts on their environment, such as agricultural intensification, even before our record of bumblebee diversity. Third, and as a caveat, inferences regarding the past million years may be confounded by our knowledge of what comprises a species. Recent molecular data support some species that we thought were separate being conspecific [9] and others as complexes of several related species [27].

Few studies have suggested that macroevolutionary estimates of extinction rates may be relevant to present-day conservation. Yet, similar drivers influenced both ancient extinctions and modern extinctions, suggesting that extinction risk may be phylogenetically conserved [4,5]. We found

evidence of past shifts in extinction rates and a potential ongoing extinction period in bumblebees, each synchronous with environmental shifts. These findings are not isolated: exceptional extinction patterns were also found in other bee clades [22]. Altogether, these results demonstrate how bees have experienced drastic periods of extinction during environmental changes. As bumblebees are sentinel organisms strongly affected by current environmental changes [10], understanding what caused ancient extinctions can inform what may be affecting modern species. Such information about the past vulnerability of related species might provide meaningful predictions of current and future risks.

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