ROYAL SOCIETY
OPEN SCIENCE

royalsocietypublishing.org/rsos

Research

Testing tribe-specific macroevolutionary responses to palaeoenvironmental changes in ants, and the impact of taxon sampling on diversification analyses

Julie L. M. Campana[1,2], Corentin Jouault[3], Evan P. Economo[4,5] and Fabien L. Condamine[1]

[1]CNRS, Institut des Sciences de l'Évolution de Montpellier, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier, France
[2]Institut de Systématique, Évolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE-PSL, Université des Antilles, CP50, 57 rue Cuvier, 75005 Paris, France
[3]Oxford University Museum of Natural History, University of Oxford, Oxford OX1 3PW, UK
[4]Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Kunigami District, Okinawa Prefecture, Japan
[5]Department of Entomology, University of Maryland, College Park, MD, USA

JLMC, 0000-0001-8482-5699; CJ, 0000-0002-3680-5172;
EPE, 0000-0001-7402-0432; FLC, 0000-0003-1673-9910

Cite this article: Campana JLM, Jouault C, Economo EP, Condamine FL. 2026 Testing tribe-specific macroevolutionary responses to palaeoenvironmental changes in ants, and the impact of taxon sampling on diversification analyses. *R. Soc. Open Sci.* **13**: 251825.
https://doi.org/10.1098/rsos.251825

Received: 22 September 2025
Accepted: 16 April 2026

Subject Category:
Organismal and evolutionary biology

Subject Areas:
evolution

Keywords:
climatic change, diversification models, macroevolution, model selection, rate heterogeneity, taxon sampling

Authors for correspondence:
Julie L. M. Campana
e-mail: julie.campana@mnhn.fr
Corentin Jouault
e-mail: corentin.jouault@oum.ox.ac.uk

Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8451495.

The dynamics of speciation and extinction shape biodiversity over time. The Red Queen hypothesis attributes these dynamics to biotic factors, whereas the Court Jester hypothesis emphasizes abiotic drivers. We investigated how past environmental changes influenced ants (Formicidae) diversification using maximum-likelihood diversification models. We tested whether speciation and/or extinction rates were constant, time-dependent or shaped by variables such as angiosperm and gymnosperm diversities, temperature and sea level fluctuations. We expected biotic factors, particularly angiosperm diversity, to drive ant diversification. Through model selection across 22 diversification scenarios for 30 ant tribes, we found that the environment-dependent models explain nearly half (46%) of diversification patterns, providing comparable support for the Court Jester and Red Queen hypotheses. Angiosperm radiation was not the sole driver

THE ROYAL SOCIETY
PUBLISHING

of ant diversification, acting as a key factor only for several ant tribes. Instead, temperature and sea level fluctuations often emerged as stronger drivers. These findings suggest abiotic environmental changes played a greater role in shaping ant evolution than previously thought. Comparisons across grafted and non-grafted phylogenies further revealed that taxon sampling can strongly influence diversification analyses. By identifying potential causes of rate variation, this study offers testable hypotheses for understanding the eco-evolutionary processes underlying ant biodiversity.

1. Introduction

In macroevolution, the fates of clades and their species richness are shaped by the temporal dynamics of speciation and extinction rates [1]. Estimating how and why these rates vary is fundamental for understanding the biodiversity changes over long time scales and across different spatial scales [2–5]. Birth–death models are designed to model speciation and extinction rates, and their variations through time, allowing to explain the phylogenetic growth and its underlying causes [6–8]. When the fossil record is still too sparse to infer diversification rates, time-calibrated phylogenies become precious tools for inferring the evolutionary history of a clade. However, accurately estimating net diversification rates (i.e. speciation minus extinction) from phylogenies composed solely of extant species can be challenging [9–12]. Addressing these limitations and developing robust solutions have become a central objective in research on diversification dynamics based on time-calibrated trees of extant species. Importantly, several studies indicate that non-identifiability does not render current methods unusable [13,14]. By adopting hypothesis-driven approaches, implementing priors within Bayesian frameworks, and penalizing model complexity, it is possible to mitigate these challenges and effectively use existing diversification methods [14–17].

Birth–death models are effective tools to estimate diversification shifts over time and across clades using molecular-based phylogenies, which can mirror diversity dynamics observed in the fossil record [18,19]. Their integration into probabilistic frameworks, such as maximum likelihood and Bayesian inferences, allows analysing large datasets [7,20–22]. These models can also test the influence of environmental variables on speciation and extinction rates, help to infer evolutionary scenarios for clades and even project potential future trends under the influence of environmental changes [23,24]. As a result, these models can assess particular environmental factors that may be linked to major diversification events or even mass extinctions [25,26].

In macroevolution, two key hypotheses have been proposed to explain changes in diversity through time [27]. The Red Queen hypothesis [28] posits that diversification is primarily driven by biotic factors, such as species interactions, species ecology or life-history traits. In contrast, the Court Jester hypothesis [29] argues that diversification dynamics are mainly shaped by abiotic factors, such as abrupt climatic changes or tectonic events. These hypotheses, while not mutually exclusive, can explain rate heterogeneity within a phylogeny, unveil different clade-specific macroevolutionary dynamics [30–32] and declining diversity [18,19,33].

Explaining how diversification occurred is particularly challenging for organisms such as insects, which exhibit very specific biotic interactions like mutualism, symbiosis or parasitism with other species [34,35]. The extraordinary diversity and diversification of insects are presumed to be linked to the rise of flowering plants, the angiosperms [36,37]. The angiosperms underwent most of their radiation during the Late Cretaceous and the beginning of the Cenozoic. This period is often referred to as the Angiosperm Terrestrial Revolution (ATR; 100 to 50 Ma [38]) during which flowering plants became ecologically dominant (e.g. [39–43]) and crucial components of ecosystems, driving herbivore adaptation and diversification alongside their rise (e.g. [44–48]). Following the rise of angiosperms, a series of environmental upheavals occurred, which some studies suggest acted as catalysts for the diversification of both mammals and insects [3,49,50]. However, there is no consensus on the impact of these events on insect evolution [36,50–52].

Within this hyper-diverse group, ants (Formicidae) originated during the Jurassic or Early Cretaceous and diversified considerably during the ATR, with all major ant lineages emerging during the Cretaceous [53–59]. Today, ants are remarkably diverse in terms of ecology, behaviour [60], and species number, with 14,269 extant species (AntWeb). However, this diversity is unevenly distributed across major lineages (electronic supplementary material, additional file 10, and more details for the topology in [57]), suggesting different evolutionary trajectories among the clades. Ants possess a wide variety of morphological, biological and ecological traits [60,61]. Their near-ubiquity in terrestrial ecosystems, along with their ancient origin, makes them a highly interesting clade for evolutionary studies. Despite this, the extent to which their evolutionary history was influenced by past environmental changes remains unclear.

Previous studies suggested that ant diversification was likely synchronous or linked with the evolutionary radiation of angiosperms during the ATR [53,62] (figure 1). Alternatively, abiotic factors, such as temperature, may have played a key role in ant diversification. Indeed, as ectothermic animals, ants are particularly sensitive to environmental temperature fluctuations. Following the metabolic theory of biodiversity [64], the combined effects of body size and temperature significantly influence metabolic rates, which are thought to drive evolutionary rates [65]. Since higher temperatures may increase mutation rates in ectotherms [66], temperature fluctuations may have played a role in ant diversification, as observed in other insect groups [26]. Moreover, previous studies proposed that global geographical factors—such as the distinction between the Northern and Southern Hemispheres or tropical versus temperate regions— also significantly impacted diversification rates in the evolutionary history of ants [57,67,68]. While both biotic and abiotic factors have been proposed as key drivers of ant diversity, it remains unclear which ones have mostly influenced their diversification dynamics.

In recent years, considerable progress has been made in reconstructing the ant tree of life, including resolving the main internal nodes [53,58,69–72] and clarifying relationships between subfamilies and genera (e.g. [73–77]). However, as with many insect taxa, diversification patterns within ant genera remain a real challenge to explore, as not all genera present a complete and well-resolved phylogeny. Instead of a complete phylogeny, recent analyses have relied on methods that either incorporate taxa into trees with uncertainty or apply corrections for missing taxa. While these methods have their limitations [12], they offer an important starting point for understanding ant diversification patterns (e.g. [56,57,68]).

In this study, we investigate whether the Red Queen or the Court Jester hypothesis better explains ant diversification. Among the biotic factors tested, we hypothesize that angiosperm diversification will have the strongest influence on ant diversification [53,70,78,79]. Given the importance of ectothermy in insects, we also expect that temperature may have a major impact on ant diversification, with a predicted positive relationship between temperature and speciation rates. The main objective of our study is to propose hypothetical links between abiotic or biotic environmental changes and ant diversification processes using a maximum-likelihood framework of diversification models.

2. Material and methods

2.1. Ant time-calibrated phylogeny and delimitation into subclades

We used the time-calibrated phylogeny of ants from Economo *et al.* [57]. This phylogeny was reconstructed with the available nucleotide sequences mostly coming from nine different previous studies [53,54,69,80–85]. We chose the time-calibrated tree obtained with a traditional approach using node calibrations with uniform distributions of ages (uniform prior distributions for 51 fossil calibrations; more details in supplementary information of [57]). The ant tree included 14,594 extant species [57]. The tree was divided into subclades for the diversification analyses. Selecting the tribe level as subclades was preferred because it allowed: (i) comparing different evolutionary histories by potentially isolating heterogeneity of diversification, and (ii) working on a diversity of clade ages compatible with the environmental variables and defined over the geological time scale (see §2.2., §2.3. and §2.4.). Selecting genera rapidly proved to be difficult to achieve because of the presence of many para- and polyphyletic genera. Moreover, grouping into subfamilies resulted in too large subclades that can have high heterogeneity of diversification [56,70]. Ants were divided into 37 distinct tribes rather than 39 extant tribes officially described (www.antcat.org, 2020). Although most of the tribes were monophyletic, there were cases where tribes were not recovered as such. Instead of discarding these tribes or to avoid multiplying many small subclades, we made subclades composed of several tribes or tribes were split into several subclades (more details in electronic supplementary material, additional file 1).

The final selection included 30 subclades after excluding those that had less than 10 species (figure 1, in grey). The limited number of species in these tribes did not provide sufficient data for meaningful diversification analyses (more details of the final species assignments to a subfamily and a tribe in the electronic supplementary material, additional files 1 and 2).

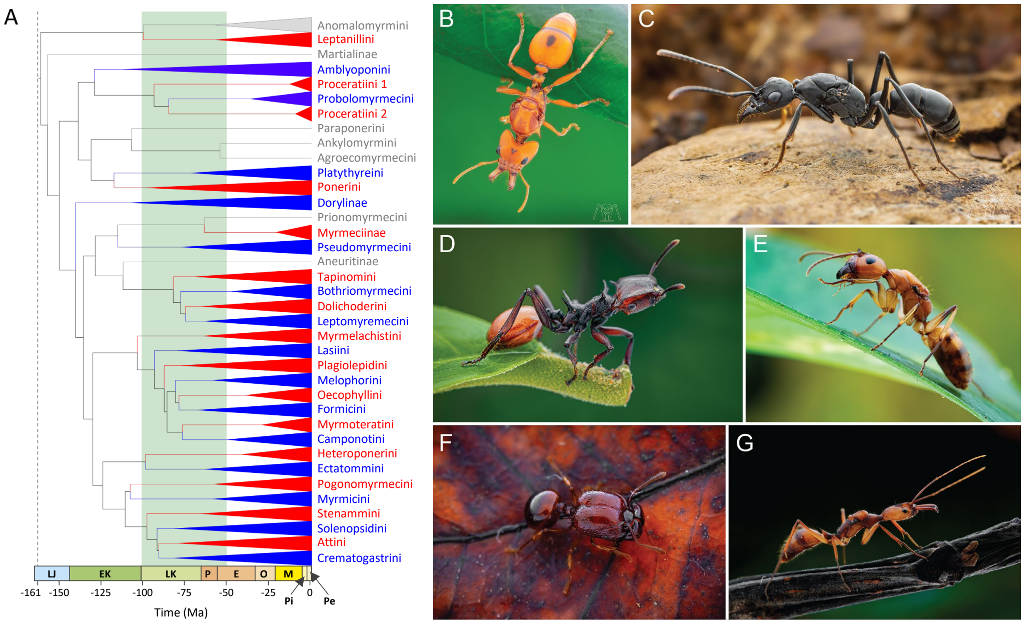

Figure 1. Phylogenetic distribution of ant biodiversity. (A) Simplified ant timetree showing the 37 tribes. The tribes with less than 10 species are represented in grey. The evolutionary radiation of angiosperms, called the Angiosperm Terrestrial Revolution, is highlighted in green. Morphological diversity in ants: (B) *Daceton armigerum* (Latreille, 1802), (C) *Neoponera apicalis* (Latreille, 1802), (D) *Cephalotes atratus* (Linnaeus, 1758), (E) *Camponotus* sp., (F) *Acanthomyrmex* sp. and (G) *Odontomachus hastatus* (Fabricius, 1804) (courtesy of © Baptiste Bentameur, used by permission). Abbreviations: Ma = million years ago; LJ = Late Jurassic; EK = Early Cretaceous; LK = Late Cretaceous; *p* = Palaeocene; E = Eocene; O = Oligocene; M = Miocene; Pi = Pliocene; Pe = Pleistocene. The phylogenetic tree was generated by using the FigTree 1.4.3 software [63].

2.2. Environmental variables

We selected two categories of environmental variables to model the diversification dynamics of ants based on biotic (Red Queen hypothesis) or abiotic (Court Jester hypothesis) factors.

For the biotic variables, we used the relative angiosperm and gymnosperm diversities through time [86,87]. These variables are relevant because they reflect the biological and ecological dynamics of terrestrial ecosystems [25].

For the abiotic variables, we chose past temperature variations [88] and past sea-level fluctuations [89,90] over the geological time scale. To reconstruct past temperature dynamics, we used δ^{18}O data derived from marine shells, capturing oceanic thermal records. The coupling between deep-ocean temperature and global mean surface temperature is well established, supporting the use of ocean-derived data as a robust and reliable proxy for global mean surface and continental temperatures within the temporal scope of our study [91,92]. These variables are commonly used to study the impact of environmental changes as they represent key aspects of climate change [3,5]. For instance, it is hypothesized that changes in sea level are a driver for island-dwelling clades, with rising seas potentially lowering speciation rates and/or increasing extinction rates [93].

All these four environmental variables are likely linked to climatic change and their data are available at the geological time scale, making them suitable for studying the impact of the environmental changes over time on ant diversification.

2.3. Diversification models

We fitted 22 diversification models to each of the 30 phylogenies (associated with the 30 selected tribes; see §2.1.) as well as to the whole phylogeny of the family. These models are birth–death models of cladogenesis, which account for speciation and extinction events and are fitted to reconstructed phylogenies using maximum likelihood [6,7].

The models were divided into three categories: those with constant diversification rates (two models), those with time-varying rates (four models) and those with environment-dependent rates based on angiosperms, gymnosperms, temperature and sea level dependencies (16 models, four models for each variable). Maximum likelihood fitting was performed using the *fit_bd* function (for the time-constant and time-varying models) and the *fit_env* function (for environment-dependent models) from the R package *RPANDA* 2.0 [94], which also uses the R packages *picante* 1.6 [95] and *pspline* 1.0-18 [96,97].

In the constant-rate models, both speciation rates λ and extinction rates μ are fixed and constant over time, and uniform across clades [98]. We tested two models: (i) constant speciation/no extinction, and (ii) constant speciation and extinction. These models were used to test the null hypothesis (H0), i.e. the ant diversification is constant over time.

In the time-dependent models, λ, μ or both vary as a continuous function of time t [18], where t progresses from the present to the past. We assumed an exponential variation of these functions as $\lambda(t) = \lambda_0 \times \exp(\alpha t)$ and/or $\mu(t) = \mu_0 \times \exp(\beta t)$ where λ_0 (μ_0) is the speciation (extinction) rate at present and α (β) is the correlation coefficient specific to λ (μ). These coefficients measure the sign and pace of the time-related changes, indicating how speciation and extinction rates have evolved. A positive α (β) suggests a slowdown in speciation (extinction) process towards the present, while a negative α (β) indicates a speed-up of speciation (extinction) process. The four time-dependent models tested were: (i) variable speciation/no extinction, (ii) variable speciation/constant extinction, (iii) constant speciation/variable extinction, and (iv) both variable speciation and extinction. They were used to test the first alternative hypothesis (H1), i.e. the ant diversification varies over time.

In the environment-dependent models, λ, μ or both vary as a continuous function of time t according to environmental variables [23]. The environmental data is first transformed into a continuous function of time by spline interpolation before being plugged into parametric functions describing how speciation and extinction rates vary with the environment. These models extend time-dependent diversification models to account for potential dependencies between speciation and/or extinction rates and one or several measured environmental variable(s). Here, relative angiosperm (A) and gymnosperm (G) diversities were used as the measured environmental biotic variables and, global fluctuations of temperatures (T) and sea level (S) as the measured environmental abiotic variables (see §2.2.). The same exponential dependencies as above were considered but with t replaced by A[t], G[t], T[t] or S[t] ($\lambda(E[t]) = \lambda_0 \times \exp(\alpha E[t])$ and/or $\mu(E[t]) = \mu_0 \times \exp(\beta E[t])$, with E[t]: A[t], G[t], T[t] or S[t]). In these cases, λ_0 (μ_0) is the expected speciation (extinction) rate under a E[t] of 0 and α (β) measures the sign and strength of the E[t] dependence. Hence, a positive α (β) indicates that speciation (extinction) rate is higher under high E[t] periods, while a negative α (β) indicates that speciation (extinction) rate is higher under low E[t] periods. Sixteen models corresponding to the four chosen variables for each of the four same models mentioned for the time-dependent models (see above) were used to test the second alternative hypothesis (H2), i.e. the ant diversification varies and is influenced by the variations of the environment over time. Each of the four environmental variables was considered as independent from each other, with no collinearity assumed between A[t], G[t], T[t] or S[t] in the tested environment-dependent models.

2.4. Estimating diversification of the ant family and tribes

Each model was optimized for each clade using the maximum likelihood method. For each clade, a sampling fraction (f) is specified as the ratio of sampled species over the total number of species described in this group. The maximum log-likelihood score (logL) was obtained, from which the corrected Akaike information criterion (AICc) and the Akaike weight (AICω) were calculated. The model best explaining the diversity dynamics of each tribe was selected based on the lowest AICc and the highest AICω. This approach allowed to avoid incorrectly favouring a more complex model (higher logL) over simple ones. All R scripts used for these analyses are provided in the data accessibility section. The manipulations and generations of datasets were made by using the R 4.4.1 software [99] and the R package *tidyverse* 2.0.0 [100].

2.5. Testing the effect of taxon sampling on diversification analyses

Given that the time-calibrated phylogeny of ants was partly reconstructed by grafting species in the phylogenetic tree, we tested the effect of taxon sampling on our diversification analyses. To do so, we compared our results with one alternative phylogenetic tree reconstructed using traditional approaches: node calibrations and uniform distributions of ages, without grafting missing taxa, also from [57]. After applying the same tribe selection criteria (discarded the tribes with less than 10 species) to the non-grafted tree, including 673 out of a total of 14,594, we identified 11 tribes in common. After adjusting the clade-specific sampling fractions, we then compared the best-fitting models for each tribe across the 'reduced' phylogenetic tree using the same analytical pipeline described above (see supplementary information of [57] for more details about phylogenetic trees).

3. Results

3.1. Diversification of ants over time

The diversity dynamics of the entire family (Formicidae) is best explained by a time-dependent model (figure 2A; electronic supplementary material, additional file 4A), where both speciation and extinction rates increase over time, though the variation is stronger for speciation ($\alpha = -0.0104$ and $\beta = -0.0098$).

When considering only constant-rate and time-dependent models (a total of six models), the diversity dynamics of 14 tribes are best explained by a constant-rate model (H0), while those of 16 tribes are best explained by a time-dependent model (H1) (electronic supplementary material, additional file 2).

Among the tribes supporting a time-dependent model, speciation rates vary as follows: Amblyoponini, Attini, Bothriomyrmecini, Crematogastrini, Dorylinae, Formicini, Melophorini, Plagiolepidini, Ponerini and Solenopsidini have increasing speciation rates through time ($\alpha < 0$), Lasiini shows decreasing speciation rates through time ($\alpha > 0$), and Camponotini, Heteroponerini, Leptanillini, Myrmelachistini, Myrmicini and Pseudomyrmecini have constant speciation rates ($\alpha = 0$). For extinction rates, Camponotini, Heteroponerini, Lasiini, Myrmelachistini, Myrmicini and Pseudomyrmecini have decreasing rates through time ($\beta > 0$), Crematogastrini has a constant extinction rate ($\beta = 0$), and Amblyoponini, Attini, Bothriomyrmecini, Dolichoderini, Formicini, Melophorini, Plagiolepidini, Ponerini and Solenopsidini have no extinction rate.

No tribe's diversity dynamics supports a model where the extinction rate increases over time ($\beta < 0$) (electronic supplementary material, additional file 2). The time-dependent models tend to have higher AICω (mean(AICω) = 0.596) compared to the constant-rate models (mean(AICω) = 0.404; figure 2A).

3.2. Influence of past climates on ant diversification

When incorporating models where rates vary with environmental changes, we find that the diversity dynamics of 14 tribes are best explained by environment-dependent models. However, these models have relatively higher AICω (mean(AICω) = 0.466) compared with constant-rate (mean(AICω) = 0.227) and time-dependent (mean(AICω) = 0.307) models for the same tribes (figure 2B; electronic supplementary material, additional file 3). Consequently, H0 (constant-rate models) and H1 (time-dependent models) are refuted for Dolichoderini, Leptanillini, Leptomyrmecini, Myrmoteratini and Pogonomyrmecini, and Amblyoponini, Crematogastrini, Dorylinae, Heteroponerini, Melophorini, Myrmelachistini, Plagiolepidini, Pseudomyrmecini and Solenopsidini, respectively. For the family (Formicidae), time-dependent diversification (H1) remains supported (AICω = 0.81; figure 2C; electronic supplementary material, additional file 3).

Including 22 models, the model selection (tables 1 and 2; figures 2C and 3) reveals the following distribution of best-fitting models among the tribes: the diversity dynamics of Ectatommini, Myrmeciinae, Oecophyllini, Platythyreini, Probolomyrmecini, Proceratiini1, Proceratiini2, Stenammini and Tapinomini are best explained by constant-rate models (figures 4 and 5A); Attini, Bothriomyrmecini, Camponotini, Formicini, Lasiini, Myrmicini and Ponerini by time-dependent models (figures 4 and 5B); Crematogastrini, Leptanillini and Leptomyrmecini by angiosperm-diversity-dependent models; Dolichoderini, Melophorini and Myrmoteratini by gymnosperm-diversity-dependent models; Amblyoponini, Heteroponerini and Pseudomyrmecini by temperature-dependent models; and Dorylinae, Myrmelachistini, Plagiolepidini, Pogonomyrmecini and Solenopsidini by sea-level-dependent models. Details about relative AICω for the models best explaining the diversity dynamics of both the entire family and the 30 tribes are provided in electronic supplementary material, additional files 4A and 5A.

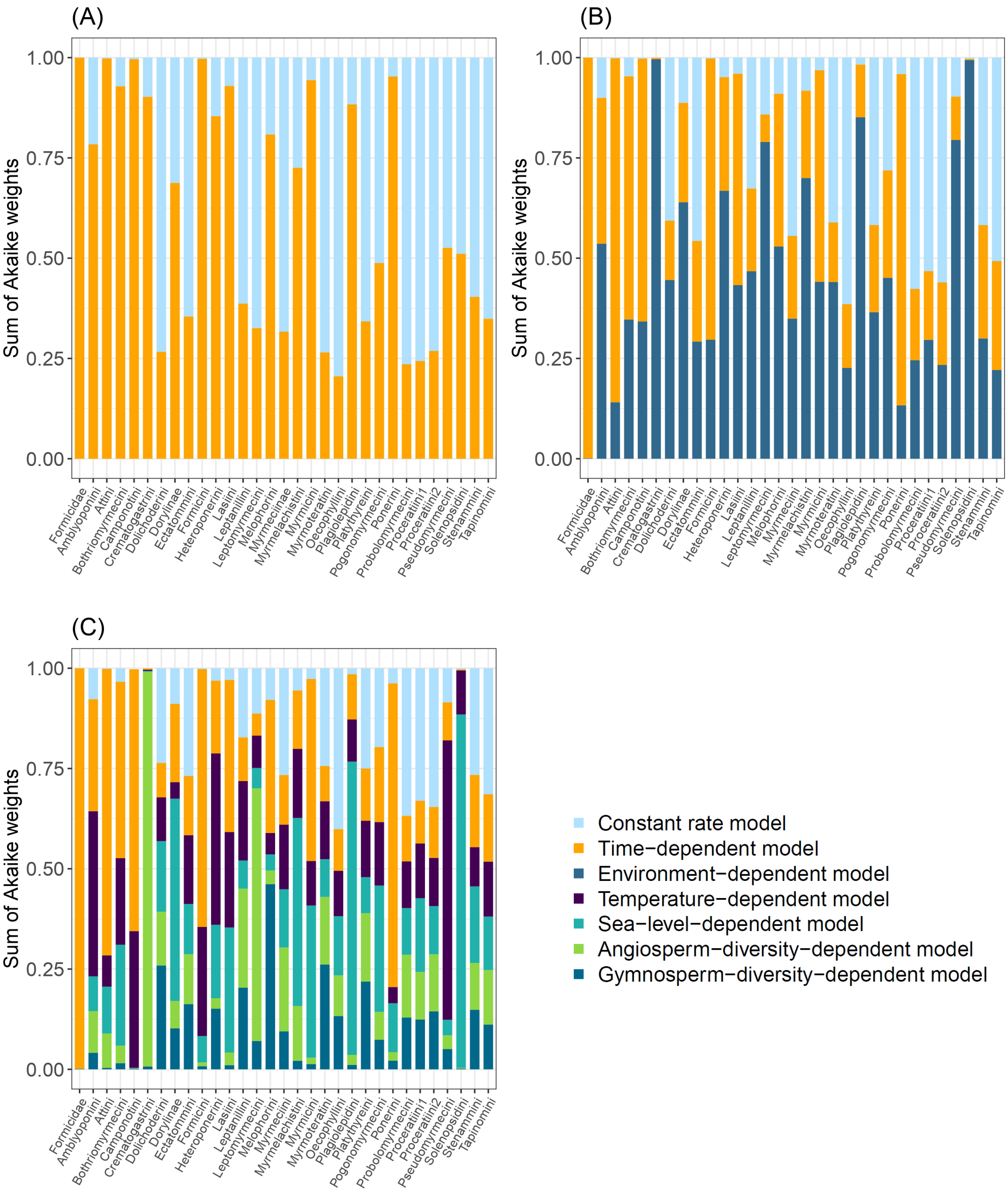

Figure 2. Model selection for the best-fitting diversification model based on AICω computed for the family as a whole and the 30 tribes independently. (A) Sum of AICω of best-fitting constant-rate and time-dependent models: mean(constant-rate models) = 0.404 and mean(time-dependent models) = 0.596 computed for the 30 tribes. (B) Sum of AICω of best-fitting constant-rate, time-dependent and environment-dependent models: mean(constant-rate models) = 0.227, mean(time-dependent models) = 0.307, mean(environment-dependent models) = 0.466 computed for the 30 tribes. (C) Sum of AICω of best-fitting constant-rate, time-dependent, temperature-dependent, sea-level-dependent, angiosperm-dependent and gymnosperm-dependent models: mean(constant-rate models) = 0.145, mean(time-dependent models) = 0.237, mean(temperature-dependent models) = 0.173, mean(sea-level-dependent models) = 0.205, mean(angiosperm-dependent models) = 0.138, mean(gymnosperm-dependent models) = 0.102.

3.3. Environment-dependent models: second alternative hypothesis (H2)

For the 14 tribes with the diversity dynamics best explained by environment-dependent models, the speciation and extinction rates and the AICω for these tribes, are as follows (tables 1 and 2; figure 2C; electronic supplementary material, additional file 6):

Table 1. Results of the best-fitting diversification model for each ant tribe and the family. Age: age of the clade in million years (Ma). Size: number of species. Type of model: best-fitting birth-death model. AICω: Akaike weight. λ: speciation rate defined for a value of 0 of the focal variable. α: correlation parameter for the evolutionary trend of λ in relation to the variable. μ: extinction rate defined for value of 0 of the interest variable. β: correlation parameter for the evolutionary trend of μ in relation to the variable.

tribe	age (Ma)	size	type of model	AICw	λ	α	μ	β	model description
Formicidae	161.1	14 594	time-dependent	0.81	0.1686	−0.0104	0.0737	−0.0098	speciation and extinction increase through time
Amblyoponini	116.5	120	temperature-dependent	0.228	0.14	−0.1037	—	—	speciation decreases as global temperatures increase
Attini	74.2	2649	time-dependent	0.397	0.1566	−0.0184	—	—	speciation increases through time
Bothriomyrmecini	40.5	44	time-dependent	0.268	0.3086	−0.0957	—	—	speciation increases through time
Camponotini	36.8	2353	time-dependent	0.416	0.3461	—	0.0288	0.0916	constant speciation and extinction decreases through time
Crematogastrini	74.7	2926	angiosperm-dependent	0.898	0.1488	—	0.0003	5.9947	constant speciation and extinction increases as angiosperm diversity increases
Dolichoderini	55	149	gymnosperm-dependent	0.152	0.0006	12.2068	—	—	speciation increases as gymnosperm diversity increases
Dorylinae	107.5	787	sea-level-dependent	0.301	0.0788	—	0.0198	0.0189	constant speciation and extinction increases as sea level increases
Ectatommini	57.2	267	constant-rate	0.126	0.0895	—	—	—	constant speciation through time
Formicini	44	337	time-dependent	0.315	0.3391	−0.0574	—	—	speciation increases through time
Heteroponerini	68.6	23	temperature-dependent	0.265	0.0314	0.2167	0.0088	0.3705	speciation and extinction increase as temperatures increase
Lasiini	58.3	405	time-dependent	0.227	0.1487	0.0926	0.1279	0.0975	speciation and extinction decrease through time
Leptanillini	85.7	45	angiosperm-dependent	0.156	0.102	−1.4555	—	—	speciation decreases as angiosperm diversity increases
Leptomyrmecini	55.3	418	angiosperm-dependent	0.372	21.6824	−5.7894	—	—	speciation decreases as angiosperm diversity increases
Melophorini	48.8	111	gymnosperm-dependent	0.254	0,0001	18.8755	0.0845	—	speciation increases as gymnosperm diversity increases and constant extinction
Myrmeciinae	42.5	93	constant-rate	0.153	0.102	—	—	—	constant speciation through time
Myrmelachistini	56.5	129	sea-level-dependent	0.244	0.0911	−0.0099	—	—	speciation increases as sea level increases
Myrmicini	46.8	196	time-dependent	0.292	0.1586	—	0.001	0.1916	constant speciation and extinction decreases through time
Myrmoteratini	42.1	41	gymnosperm-dependent	0.139	40.2629	−15.4465	—	—	speciation decreases as gymnosperm diversity increases
Oecophyllini	26.7	14	constant-rate	0.296	0.067	—	—	—	constant speciation through time
Plagiolepidini	56.7	130	sea-level-dependent	0.418	0.209	0.0087	0.1318	0.0446	speciation and extinction increase as sea level increases
Platythyreini	93.9	39	constant-rate	0.163	0.0262	—	—	—	constant speciation through time

(*Continued.*)

Table 1. (*Continued.*)

tribe	age (Ma)	size	type of model	AICw	λ	α	μ	β	model description
Pogonomyrmecini	78.3	90	sea-level-dependent	0.203	0.0404	0.0072	—	—	speciation increase as sea level increases
Ponerini	98.5	1271	time-dependent	0.445	0.0897	−0.0071	—	—	speciation increases through time
Probolomyrmecini	64.4	26	constant-rate	0.246	0.0406	—	—	—	constant speciation through time
Proceratiini1	50.5	33	constant-rate	0.206	0.0596	—	—	—	constant speciation through time
Proceratiini2	53.2	83	constant-rate	0.196	0.0709	—	—	—	constant speciation through time
Pseudomyrmecini	87.9	250	temperature-dependent	0.531	0.0414	0.1279	0.0229	0.16	speciation and extinction increase as temperatures increase
Solenopsidini	75.7	849	sea-level-dependent	0.831	0.224	0.0086	0.1666	0.0101	speciation and extinction increase as sea level increases
Stenammini	72.2	482	constant-rate	0.153	0.0925	—	—	—	constant speciation through time
Tapinomini	58.8	219	constant-rate	0.163	0.0929	—	—	—	constant speciation through time

Table 2. Fit of all the diversification models applied to the 30 tribe phylogenies. The number of phylogenies best explained by each model is reported based on AICω values.

type of model	model description	model acronym	number of tribes (phylogenies)	% of dataset
constant-rate models	constant speciation/no extinction	BCST	9	30%
	constant speciation/constant extinction	BCSTDCST	—	
time-dependent models	variable speciation/no extinction	BTimeVar_EXPO	4	24%
	variable speciation/constant extinction	BTimeVarDCST_EXPO	—	
	constant speciation/variable extinction	BCSTDTimeVar_EXPO	2	
	variable speciation/variable extinction	BTimeVarDTimeVar_EXPO	1	
temperature-dependent models	variable speciation/no extinction	BTempVar_EXPO	1	10%
	variable speciation/constant extinction	BTempVarDCST_EXPO	—	
	constant speciation/variable extinction	BCSTDTempVar_EXPO	—	
	variable speciation/variable extinction	BTempVarDTempVar_EXPO	2	
sea-level-dependent models	variable speciation/no extinction	BSeaVar_EXPO	2	16%
	variable speciation/constant extinction	BSeaVarDCST_EXPO	—	
	constant speciation/variable extinction	BCSTDSeaVar_EXPO	1	
	variable speciation/variable extinction	BSeaVarDSeaVar_EXPO	2	
angiosperm-dependent models	variable speciation/no extinction	BAngioVar_EXPO	2	10%
	variable speciation/constant extinction	BAngioVarDCST_ EXPO	—	
	constant speciation/variable extinction	BCSTDAngioVar_EXPO	1	
	variable speciation/variable extinction	BAngioVarDAngioVar_EXPO	—	
gymnosperm-dependent models	variable speciation/no extinction	BGymnoVar_EXPO	2	10%
	variable speciation/constant extinction	BGymnoVarDCST_EXPO	1	
	constant speciation/variable extinction	BCSTDGymnoVar_EXPO	—	
	variable speciation/variable extinction	BGymnoVarDGymnoVar_EXPO	—	
			30	

Among the three tribes supporting an angiosperm-diversity-dependent model as the best fit, speciation rates vary as follows: Leptanillini and Leptomyrmecini show negative associations with angiosperm diversity over time ($\alpha < 0$), while Crematogastrini exhibits a constant speciation rate ($\alpha = 0$) but has a varying extinction rate positively associated with angiosperm diversity ($\beta > 0$). Leptanillini and Leptomyrmecini show no dependence on extinction rates (table 1; figures 4, 5C and 5D; electronic supplementary material, additional file 6C).

Among the three tribes supporting a gymnosperm-diversity-dependent model as the best fit, speciation rates vary as follows: Dolichoderini and Myrmoteratini show positive associations with gymnosperm diversity ($\alpha > 0$), while Myrmoteratini exhibits a negative association ($\alpha < 0$). Melophorini has a constant extinction rate ($\beta = 0$), and Dolichoderini and Melophorini have no dependence on extinction rates (table 1; figures 4, 5E and 5F; electronic supplementary material, additional file 6E).

Among the three tribes supporting a temperature-dependent model as the best fit, Heteroponerini and Pseudomyrmecini show speciation rates positively associated with temperature variations over time ($\alpha > 0$), while Amblyoponini exhibits a speciation rate negatively associated with temperature variations ($\alpha < 0$). For extinction rates, Heteroponerini and Pseudomyrmecini have rates positively associated with temperature variations ($\beta > 0$), while Amblyoponini shows no extinction rate (table 1; figures 4, 5G and 5H; electronic supplementary material, additional file 6G).

Among the five tribes supporting a sea-level-dependent model as the best fit, four show varying speciation rates: positively associated with sea-level fluctuations over time for Plagiolepidini, Pogonomyrmecini and Solenopsidini ($\alpha > 0$), negatively associated for Myrmelachistini ($\alpha < 0$), and

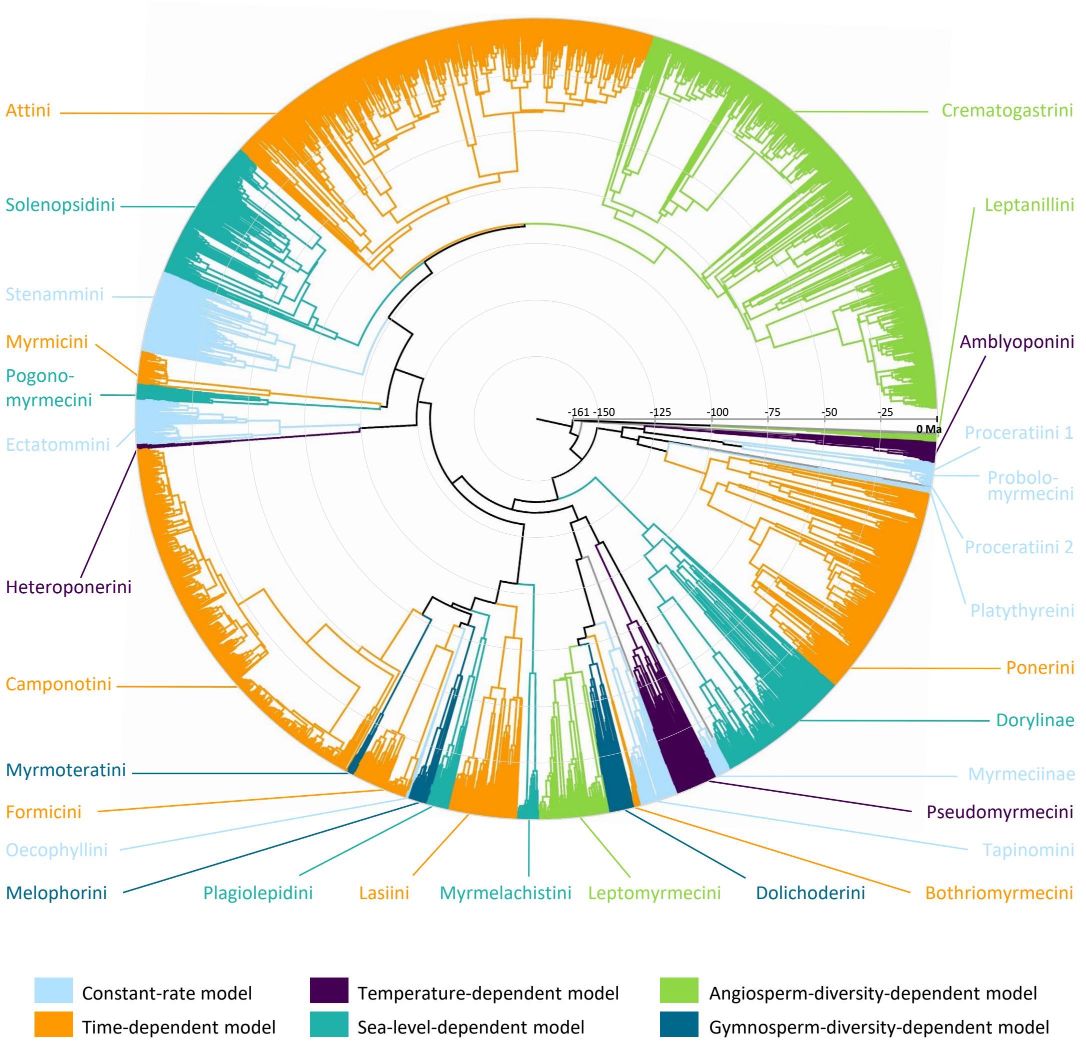

Figure 3. Phylogenetic distribution of the best-fitting model across the ant phylogeny. It shows that 30% of the tribes are best supported by a constant-rate model (9 out of 30), 24% by a time-dependent model (7 out of 30), 10% by a temperature-dependent model (3 out of 30), 17% by a sea-level-dependent model (5 out of 30), 10% by an angiosperm-dependent model (3 out of 30), and 10% by a gymnosperm-dependent model (3 out of 30). Interestingly, no single model explains all the tribes' diversification and there is no clustering of diversification models.

with a constant speciation rate for Dorylinae. Dorylinae, Plagiolepidini and Solenopsidini exhibit extinction rates positively associated with sea-level changes ($\beta > 0$), while none show negatively associated extinction rates ($\beta < 0$), and Myrmelachistini and Pogonomyrmecini have no extinction rate (table 1; figures 4, 5I and 5J; electronic supplementary material, additional file 6I).

3.4. Impact of taxon sampling on ant diversification results

Comparing the best-fitting models for the 11 common tribes across the grafted and non-grafted phylogenetic trees yields nuanced results (figure 6). The model that best explains the diversity dynamics of the Formicidae family varies across the trees. The non-grafted tree supports a sea-level-dependent model (AICω = 0.375; figure 6; electronic supplementary material, additional file 4B). By contrast, the best-fitting model for the grafted tree supports a time-dependent model (AICω = 0.81; table 1; electronic supplementary material, additional file 4A).

Second, no dominant pattern emerges for best-fitting models across the two trees, except for the tribes Crematogastrini, Stenammini, and Tapinomini. Indeed, Crematogastrini consistently supports an angiosperm-diversity-dependent model, Stenammini and Tapinomoni consistently support a

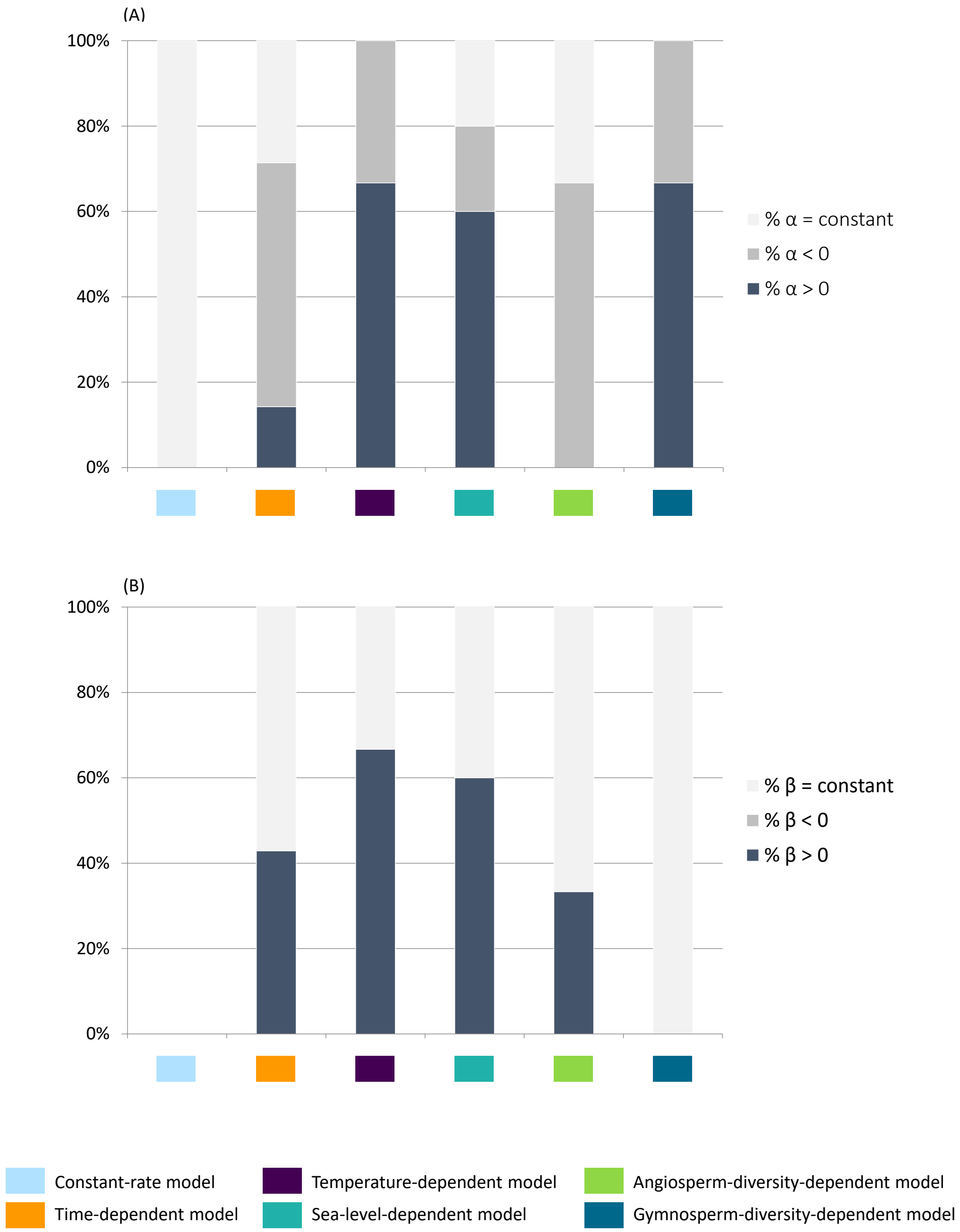

Figure 4. Correlation parameters of speciation (α) and extinction (β) for the best-fitting diversification models. For the 30 tribes, the histograms report the percentage of phylogenies best supported by a model with speciation (A) that is constant through time (light grey), varies negatively with the variable (dark grey), or varies positively with the variable (in blue). The same applies for extinction rate (B). Note that α (β) > 0 means that λ (μ) positively depends on the variable of interest, and the opposite when α (β) < 0.

constant-rate model in both grafted and non-grafted trees (figure 6; electronic supplementary material, additional file 5).

Third, some tribes show consistent support for an environment-dependent model, but according to different environmental variables across the trees. Respectively for the grafted and non-grafted trees, Amblyoponini supports a temperature-dependent and an angiosperm-diversity-dependent models, Dorylinae supports a sea-level-dependent and a gymnosperm-diversity-dependent models,

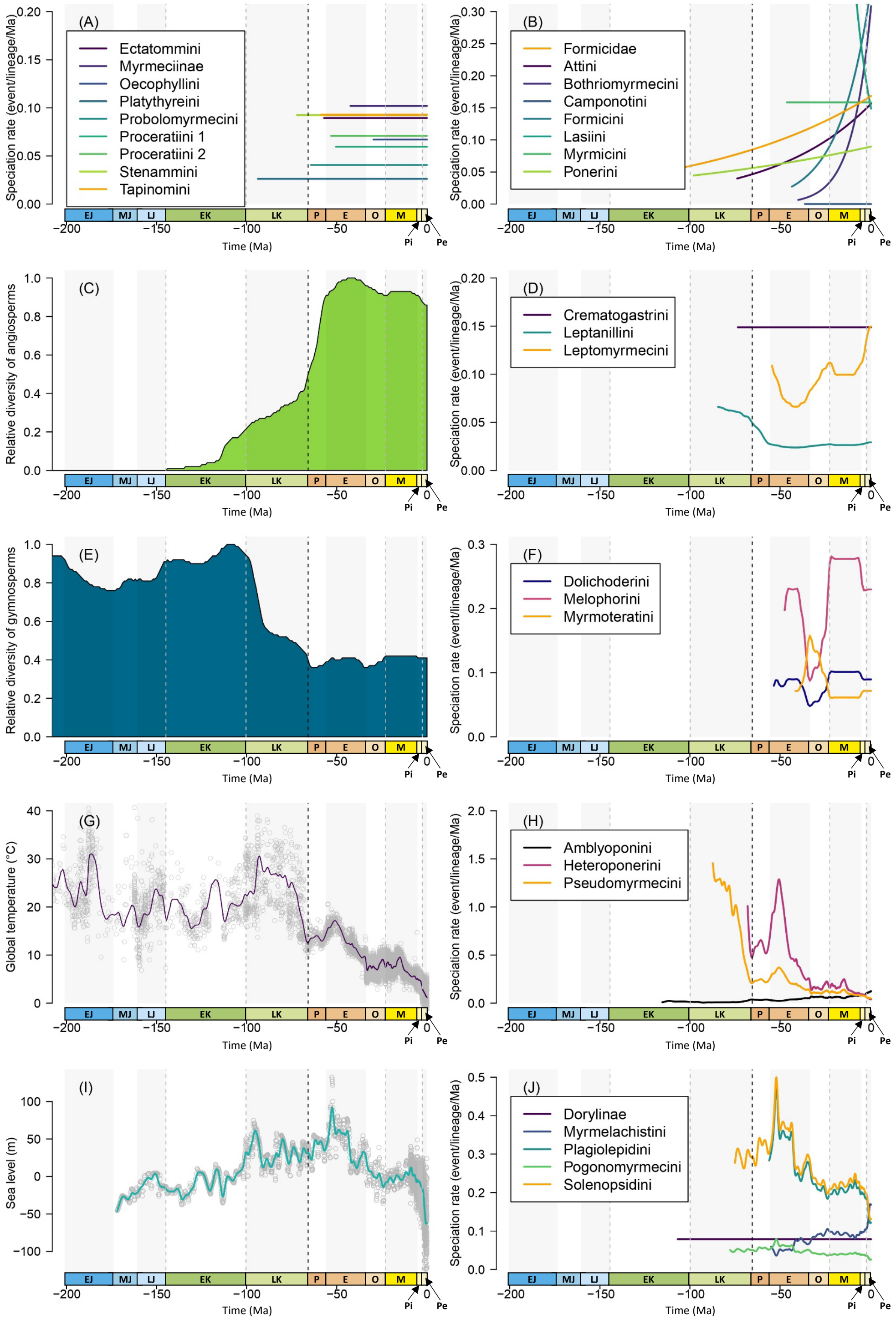

Figure 5. Temporal dynamic of speciation rates of ant tribes and of the family as a whole. (A) Tribes supporting a constant-rate model. (B) Tribes (and family) with a best-fitting time-dependent model. (C) Evolution of the relative diversity over time in angiosperms [86]. (D) Tribes with the best-fitting angiosperm-diversity-dependent model. (E) Evolution of the relative diversity over time in gymnosperms [86]. (F) Tribes with a best-fitting gymnosperm-diversity-dependent model. (G) Global temperature variations over time [101,102]. (H) Tribes with the best-fitting temperature-dependent model. (I) Sea-level variations over time [89]. (J) Tribes with the best-fitting sea-level-dependent model. Abbreviations: Ma = million years ago; EJ = Early Jurassic; MJ = Middle Jurassic; LJ = Late Jurassic; EK = Early Cretaceous; LK = Late Cretaceous; *p* = Palaeocene; E = Eocene; O = Oligocene; M = Miocene; Pi = Pliocene; Pe = Pleistocene.

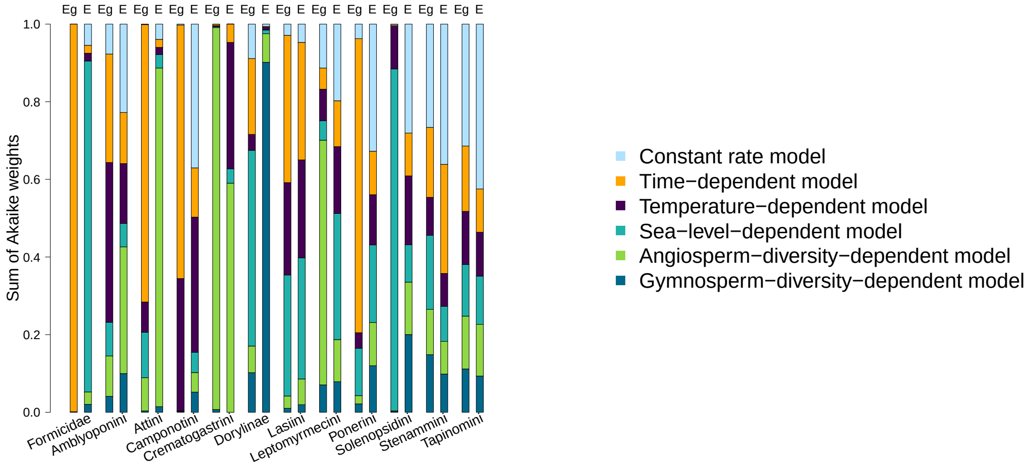

Figure 6. Comparison of the model selection for the best-fitting diversification model based on AICω computed for the family as a whole and the 11 tribes independently across the grafted and non-grafted phylogenetic trees. Sum of AICω of best-fitting constant-rate, time-dependent, temperature-dependent, sea-level-dependent, angiosperm-diversity-dependent and gymnosperm-diversity-dependent models. Abbreviations: Eg = grafted phylogenetic tree; E = non-grafted phylogenetic tree.

and Leptomyrmecini supports an angiosperm-diversity-dependent and sea-level-dependent models (figure 6; electronic supplementary material, additional file 5).

Finally, like for the family Formicidae, some tribes support models from different categories, especially time-dependent versus environment-dependent models for Formicidae, Attini and Lasiini, time-dependent versus constant-rate models for Camponotini and Ponerini, and environment-dependent versus constant-rate models for Solenopsidini (figure 6; electronic supplementary material, additional file 5). In particular, for the configuration time-dependent versus environment-dependent models, the tribes in the non-grafted phylogenetic tree mainly support environment-dependent models as the best fit (figure 6; electronic supplementary material, additional file 5). More detailed results for all tribes are provided in electronic supplementary material, additional files 5 and 7.

4. Discussion

This study aimed to determine whether environmental factors, both biotic and abiotic, influenced ant diversification dynamics over the geological time scales. If so, how did ants respond to these environmental changes?

4.1. Evidence for diversification rate heterogeneity in ants

Our results show significant heterogeneity in diversification patterns within Formicidae. Indeed, there is no single prevalent birth-death model that explains the diversification across all ant tribes. In fact, the six categories of birth–death models show an even distribution of tribes, with no clear pattern dominating (figure 3). Moreover, the best-fitting model for each tribe produces distinct rate estimates and correlations (table 1; figures 2 and 4), indicating clade-specific responses to environmental changes (figure 5).

Notably, we found that a time-dependent model with increasing speciation rates through time best explains the diversification of the entire family. A first hypothesis to explain this pattern is that environmental changes had a relatively weak influence on overall diversification dynamics, their diversification being rather driven by geographical factors and ecological traits of ants [103]. An alternative hypothesis to explain the overall increase in speciation rates is that radiating clades obscure the signal of differential diversification across clades. Indeed, when analysing the entire ant phylogeny, we implicitly assumed that diversification rates are homogeneous across lineages, which is likely inaccurate at this broad scale (almost 15,000 species diversifying over 160 Myr [57]). However, when we isolated individual radiating tribes from the phylogeny, we uncovered a range of birth–death models explaining ant diversification (see §3.). Once rate heterogeneity is accounted for, clade-specific drivers of diversification emerge, which would otherwise be hidden within the broad pattern of ant radiation.

The diversity dynamics of some tribes are best explained by constant-rate models with different speciation rates, ranging from 0.026 to 0.102 events per million years (figure 5; table 1). These tribes, relatively young overall (approx. 57.7 Myr on average), display a high heterogeneity in species richness, ranging from 26 species (Probolomyrmecini) to 482 (Stenammini) (table 1; electronic supplementary material, additional file 10), but there is no correlation between clade age and species richness ($R^2 = 0.0191$, p-value = 0.466, electronic supplementary material, additional file 8A). This suggests that tribe-specific traits would promote differential diversification at a consistent pace over time (e.g. cuticle investment in workers), implying that ants have independently evolved traits enabling this steady diversification [104–107]. Alternatively, constant-rate diversification could result from a spatially heterogeneous landscape that remains dynamic over time, providing favourable conditions for constant speciation. Indeed, the majority of these tribes are found in tropical regions [103], which probably serve as evolutionary arenas offering multiple niches in warm climates and favouring speciation at a steady pace [108–111]. On the other hand, these tribes may be less sensitive to environmental changes, allowing them to maintain a stable diversification dynamics over time [68]. This apparent low sensitivity to environmental change does not imply that these clades are entirely immune to environmental fluctuations. Rather, it suggests that environmental variation does not necessarily translate into immediate shifts in speciation or extinction rates, owing to biological, behavioural or ecological traits specific to these groups.

For example, Probolomyrmecini are rare and cryptic foragers inhabiting leaf litter and often foraging below the ground surface, with nests most of the time located in soil beneath rocks, within leaf litter, or in decaying wood [112,113]. As a result, gradual and moderate surface environmental changes are less likely to directly affect these species, which live in concealed microhabitats and are probably buffered against superficial or short-term external perturbations.

In the case of Stenammini, which are widely distributed, often abundant, and active above-ground foragers with relatively large nests, the situation is comparable. This tribe includes both relatively generalist omnivorous lineages (e.g. *Stenamma*) and more specialized ones (e.g. *Messor*), and exhibits good dispersal abilities [114]. It is therefore unlikely that gradual environmental changes had a strong macroevolutionary impact on the clade, as its ecological flexibility, dispersal capacity, and broad geographic distribution likely enabled it to track suitable habitats, exploit diverse resources, and persist across shifting environmental conditions. Such capacities to buffer or accommodate unfavourable conditions at local scales may, when integrated over macroevolutionary time scales, contribute to relatively stable diversification dynamics. More broadly, insect clades have also demonstrated resilience, continuously developing key innovations that allowed them to cope with the backdrop of global changes and survive extinction events [50,51,115,116].

It is hypothesized that the increase in fossil ants parallels their increasing abundance and ecological dominance from the Mesozoic to the Eocene [55], with clear evidence for shifts of diversification [62]. The increase in fossil ants can also be attributed to the growing number of favourable fossilization sites during the Cretaceous and Cenozoic, particularly due to the numerous amber deposits from this period [117]. Studying the fossil record and phylogeny of ants jointly could bring additional evidences for this constant diversification [118].

Rate heterogeneity is also observed within subclades with dynamics best explained by time-dependent models. It is interesting to find that speciation rates increase through time for the family as well as for seven out of nine tribes with dynamics best explained by time-dependent models (figure 5B; table 1). Typically, macroevolutionary patterns show that speciation rates decline through time [119], often explained by the 'ecological limits' hypothesis [120,121], which attributes this decline to negative diversity-dependent effects on diversification [122,123]. However, in ants, time appears to positively influence diversification in these seven tribes, suggesting that their diversification is not constrained by ecological limits (figure 5B; table 1). Instead, the 'diversity begets diversity' hypothesis might better explain the increasing diversification through time, as a positive diversity-dependent effect has been proposed for herbivorous insects [124]. Resource diversity, particularly for plant-dependent ants, may correlate with species richness, as ants expand their ecological niches by incorporating new plants into their repertoire and subsequently specializing. Our results align with the evidence that ants and plants increasingly relied on one another and incrementally evolved more intricate associations through time [62,70].

Nonetheless, the diversity dynamics of nearly half of ant tribes (14 out of 30) are better explained by environment-dependent models (figure 2C). A certain sensitivity ($\alpha < 0$) and/or adaptation ($\alpha > 0$)

to environmental variables has been highlighted (figure 4A). Thus, despite their resilience and high adaptive capacity, the ant diversification dynamics remain closely linked to environmental variations.

4.2. Has angiosperm evolutionary radiation influenced ant diversification?

Contrary to expectations, we did not find the angiosperm-diversity-dependent models as the most supported model across ant tribes: the diversity dynamics of three out of 30 tribes are best explained by this model (table 1; figures 2C, 5C and 5D). Moreover, two of these tribes (Leptanillini and Leptomyrmecini) show a negative correlation between the increase of angiosperm diversity and their speciation, suggesting that the rise of angiosperms limited the speciation of these groups (figures 5C, 5D and 4A). The third tribe (Crematogastrini) has extinction rates increasing when angiosperm diversity increases through time. Hence, the ATR does not seem to foster the diversification of these ant lineages (figures 5E and 5F), which challenges previous works [53]. This result may seem counterintuitive, especially for the tribe Crematogastrini, which benefits from their symbiosis with angiosperms such as Crematogaster ants forming the 'ant gardens' with Bromeliaceae [60]. However, the diversity dynamics of this tribe strongly support a positive angiosperm-diversity-dependent extinction and a constant speciation (AICω = 0.898; table 1).

The ATR, particularly the decline in gymnosperm diversity, may have significantly influenced the evolutionary history of ants by either promoting their diversification or contributing to their extinction, or through a buffer against the extinction effect [62]. Our results indicate that the diversity dynamics of three tribes, emerging during the early to middle Eocene, are best explained by a gymnosperm-diversity-dependent model with varying speciation rates (table 1; figures 5E and 5F). However, two of these tribes (Dolichoderini and Melophorini) exhibit a positive correlation between speciation rates and gymnosperm diversity, while one tribe (Myrmoteratini) correlates negatively with gymnosperm diversity. Therefore, the influence of the angiosperm and gymnosperm diversities on the ant diversification dynamics does not seem to be as straightforward as previously suggested.

Interestingly, it was demonstrated that living on and feeding on plants do not affect ant diversification [70]. This vegetation shift likely impacted ant diets and initiated new ant–plant interactions, but without leading to increasing speciation rates [70]. It remains possible that new species appeared due to adaptation to these changes without stimulating overall diversification. Previous study has shown that changes in diet alone do not appear to have spurred ant diversification, contrary to ant–plant symbiosis [125]. The influence of the angiosperm and gymnosperm diversities on ant diversification could therefore be studied in the context of these evolving mutualistic strategies and the changes in ant–plant symbioses initiated during ATR, which could have occurred with a certain time-lag between plant diversification and the ant response in terms of diversification. Future studies should go further in assessing the effect of the varying ant–plant relationships and trait evolution on ant evolutionary history (see [126,127] for examples).

4.3. Impacts of abiotic environmental changes

It is surprising that the diversity dynamics of only a few clades are best explained by temperature-dependent models (three out of 30 tribes; figures 3, 4 and 5G, 5H; table 1). Since ants are ectothermic organisms whose metabolic machinery is dependent on the environmental temperature, which can influence their diversification dynamics [65], we anticipated that the diversity dynamics of more tribes would be explained by temperature-dependent models, and have varying speciation rates positively associated with temperature.

This expectation is partially supported for two tribes (Heteroponerini and Pseudomyrmecini), which show positive temperature-dependent speciation and extinction rates. Amblyoponini exhibits a negative temperature-dependent speciation (figures 4A, 5G and 5H; table 1). These three tribes originated during periods of warm climate but at different times, suggesting they evolved in distinct environments or under high climatic heterogeneity. These results indicate that climate warming has not only favoured the origination of new species potentially adapted to these climatic changes, but also the extinction of species, as we observe a positive correlation between temperatures and extinction rates (figures 4B, 5G and 5H; table 1). Although the variability of both regional and local temperatures can depart significantly from global means, especially at the geological time scale [128,129], this suggests that the diversification of these ant tribes closely followed temperature fluctuations [4].

Our results show that for the five tribes with a diversity dynamics explained by sea-level-dependent models, with the exception of the tribe Myrmelachistini, speciation rates generally increase with rising sea levels (figures 4, 5I and 5J; table 1). This positive correlation between speciation and sea level may be explained by marine transgressions, which can isolate populations and limit gene flow, thereby promoting divergence and speciation through vicariance and dispersal [130,131]. Additionally, island connectivity cycles can lead to population divergence, but not necessarily to speciation [132]. Species within these tribes are primarily found in the tropical and insular regions (Caribbean Islands and those of Indonesia and Papua New Guinea), characterized by their numerous transgressive and regressive events [133,134]. Moreover, the divergence times of these five tribes (from 107.5 to 56.5 Ma; table 1) align with the continental fragmentation of Laurasia and Gondwana [135], which resulted in vicariance events. Future studies on the historical biogeography of these five tribes could further explore how biogeographic processes relate to our inferences on diversification (see [136] for an analysis of the global biogeographic regions for ants).

4.4. Limitations and perspectives

The study of macroevolution has become an increasingly complex field of evolutionary biology. When trying to reconstruct deep-time evolutionary histories, we need to keep in mind that macroevolutionary studies rely on numerous assumptions, starting with the taxonomy and species delimitation, passing through the building of a species-level dated tree, and culminating with the estimation of rates of species diversification and extinction. By doing so, we accumulate a cascade of assumptions at the expense of accuracy in macroevolutionary studies [13]. Hence, we are aware that our analyses and results remain in a hypothetical framework and the inferred clade-specific evolutionary histories are potential scenarios within a myriad of other scenarios [5,9,10,13,18,137–139]. Although the diversification rates were estimated using only one tree topology for the family and the subclades of each tribe, we think this study offers testable hypotheses for ant diversification. Indeed, confirming, refuting or nuancing the trend toward the Court Jester hypothesis to explain ants' evolutionary history could be re-evaluated in a stronger phylogenetic and ecological context.

Equally important is the phylogenetic data used in a macroevolutionary study. Here, the grafted ant tree includes 14,594 terminals, but most of them lack genetic data [57]. In the last decade, methods have been developed to place missing (unsampled) taxa in phylogenetic trees, using taxonomic information alone, and accounting for phylogenetic uncertainty. Several studies of vertebrate clades have used these approaches to generate dated phylogenetic trees that are complete at the species level, even in the absence of genetic data for many species (e.g. [140–142]). These comprehensive phylogenies, while not fully resolved, have proven to be very useful for evolutionary biology and applications in ecology (e.g. [57,143,144]). However, such a grafting procedure breaks down natural patterns of phylogenetic structure, which has been demonstrated to provide biased macroevolutionary inferences when trait data are used [12].

Our study revealed some divergences and congruences of results by comparing inferred clade-specific evolutionary histories relying on environmental factors varying over time across a selection of grafted and non-grafted species trees (see electronic supplementary material, additional files 4, 5 and 7). The divergences of results between the two phylogenies are likely linked to the differences in the total number of species included in each tribe subtree (electronic supplementary material, additional file 9). To our knowledge, the influence of a grafting procedure on macroevolutionary inferences from time-dependent and environment-dependent diversification models has not been tested. Our results suggest that 'manually added taxa' have important effects to be considered in macroevolution. Different methods and statistical tools are developed and continually improved to mitigate analytical biases associated with diversification models [13,145]. Additionally, using birth–death models assumes homogenous sampling fractions, whereas the sampling fraction is almost always heterogeneous, generally leading to some common biases in phylogenetic analyses such as under-representation of tropical clades. This is why in our study we studied diversification dynamics at the tribe level in an attempt to minimize this bias. Therefore, we remain cautious about potential issues in our model selection and corresponding diversification estimates, noting that more comprehensive molecular-dated trees could yield different results.

We performed a model selection with a limited set of diversification models: (i) our results may depend on our choice and availability of environmental and biological variables used as predictors; (ii) the use of global means of palaeo-environmental variables may not fully capture the ecological and evolutionary pressures shaping the diversification dynamics at finer spatial scales (e.g. regional or local levels); (iii) a single environmental variable is incorporated into each of the environment-dependent models, but it is widely assumed that diversification dynamics are influenced by a combination of abiotic and biotic variables [2,21]. It is worth mentioning that other variables, not included in this study, could be tested in a hypothetico-deductive approach [146]: past fluctuations of atmospheric carbon [41], volcanic episodes [147] or continental fragmentation [148,149]. In addition, biotic factors such as mutualism (symbiosis, parasitism) or competition may have also affected ant diversification [70,125,150], but their effects are difficult to estimate. Currently, diversification models have not been thoroughly tested for estimating the simultaneous effect of multiple variables on estimating speciation and extinction rates [23,24]. Finally, although it is not always feasible for certain global abiotic variables (e.g. sea-level fluctuations), incorporating regionally resolved environmental data represents an important direction of research on environmental dependencies of diversification [151].

Changes in traits and diversity-dependent effects are also classically invoked to explain changes in diversity dynamics through time, and their effect can be estimated using birth–death models where speciation and extinction are trait-dependent or diversity-dependent [152–157]. A recent study explored the impact of cuticular investment in workers, queens and males across different ant lineages and demonstrated a significant association between this trait and diversification rates [107]). Among ant subfamilies, the Dorylinae would be a relevant clade to test for trait-dependent diversification because of its important heterogeneity in life history traits across genera [71,80] and the wide distribution of its species [103]. Similarly, the extinction of stem ants in the Late Cretaceous might have been driven by traits that led to the decline of hyper-specialized lineages [62]. To date, no comprehensive study has explicitly tested for diversity dependence in ants using phylogenetic approaches. This gap is somewhat surprising given the well-documented inter- and intraclade competitive interactions within the group, as well as hypotheses suggesting that the rise of certain clades may have coincided with (e.g. Myrmicinae), or even contributed to, comparatively moderate diversification of others (e.g. Ponerinae) [78,158]. These hypotheses should be explored and validated through future studies using the latest advances in modelling extinction and diversification rates in relation to traits.

Interestingly, some of the best-fitting models estimate a non-zero extinction for several groups despite the fact that diversification models may underestimate the role of extinction [11]. While our results are not entirely immune to this limitation, the inclusion of an extinction parameter in our models shows that extinction can still be detected and its variation estimated through birth–death models. This underscores the potential for such models to capture extinction dynamics, despite known challenges.

At the geological time scale, effects of the climatic changes can be lineage- and taxonomic-level specific. For instance, a given genus within a tribe may not be affected in the same way as the rest of the tribe. Hence, it could be relevant to follow an approach similar to our study by focusing the analysis on genera instead of tribes. In addition, our results suggest that sea-level fluctuations would be a more substantial evolutionary driver than traditionally thought. We suggest that sea-level-dependent models should be tested more often when estimating diversification rates, especially since this factor is known to be closely linked to other key factors of evolutionary dynamics, such as temperature.

5. Conclusion

Estimating the underlying causes of variation in speciation and extinction rates through phylogenetic diversification models provides valuable insights into the evolution of biodiversity over long time scales. Our analysis focusing on ant diversification reveals significant heterogeneity in diversification rates, with no single dominant model explaining the diversification dynamics. However, environment-dependent models seem to better explain the diversity dynamics of nearly half of the ant tribes, indicating that abiotic factors have a comparable influence to biotic factors. It is also likely that these environmental variables were interacting jointly, which could explain why no single diversification model applies across the different phylogenetic trees. At the macroevolutionary scale, temperature variations and sea-level fluctuations, directly linked with climate change, appear to have impacted ant diversification, with warmer temperatures and higher sea levels fostering diversification.

Given these associations, one might predict that current global warming and rising sea levels could benefit ant biodiversity. However, the magnitude of current environmental changes surpasses that of the past [159], and we are instead witnessing local extinctions and a regional, if not global, decline of insect biodiversity [160–162]. Ongoing studies are improving our understanding of the ecological and microevolutionary mechanisms behind past, extant, and future diversification hotspots linked to these unprecedented environmental changes.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data and scripts to perform the analyses, and other additional files are available at Figshare [163].

Supplementary material is available online [164].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.L.M.C.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; C.J.: investigation, validation, visualization, writing—original draft, writing—review and editing; E.P.E.: investigation, validation, visualization, writing—original draft, writing—review and editing; F.L.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work has benefited from an 'Investissement d'Avenir' grant managed by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01). This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (project GAIA, agreement no. 851188).

Acknowledgements. We thank the associate editor, Dr. Adriana Mancuso, an anonymous reviewer, and Dr. Diogo B. Provete for their constructive comments on an earlier version of this manuscript. We greatly thank Prof. Corrie Moreau (Cornell University) for earlier comments on the study. We are grateful to Prof. Monique Gardes (Centre de Recherche sur la Biodiversité et l'Environnement) and Dr. Emilie Lecompte (Centre de Recherche sur la Biodiversité et l'Environnement) for their support on this work. We are also thankful to Dr. Arthur Weyna (Institut des Sciences de l'Évolution de Montpellier) for his help and comments about the presentation of results. The authors are extremely grateful to Baptiste Bentameur for providing and allowing the use of his magnificent photographs.

References

1. Jablonski D. 2008 Colloquium paper: extinction and the spatial dynamics of biodiversity. *Proc. Natl Acad. Sci. USA* **105**, 11528–11535. (doi:10.1073/pnas.0801919105)
2. Ezard THG, Aze T, Pearson PN, Purvis A. 2011 Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science* **332**, 349–351. (doi:10.1126/science.1203060)
3. Hannisdal B, Peters SE. 2011 Phanerozoic earth system evolution and marine biodiversity. *Science* **334**, 1121–1124. (doi:10.1126/science.1210695)
4. Mayhew PJ, Bell MA, Benton TG, McGowan AJ. 2012 Biodiversity tracks temperature over time. *Proc. Natl Acad. Sci. USA* **109**, 15141–15145. (doi:10.1073/pnas.1200844109)
5. Condamine FL, Rolland J, Morlon H. 2019 Assessing the causes of diversification slowdowns: temperature-dependent and diversity-dependent models receive equivalent support. *Ecol. Lett.* **22**, 1900–1912. (doi:10.1111/ele.13382)
6. Stadler T. 2013 Recovering speciation and extinction dynamics based on phylogenies. *J. Evol. Biol*. **26**, 1203–1219. (doi:10.1111/jeb.12139)
7. Morlon H. 2014 Phylogenetic approaches for studying diversification. *Ecol. Lett*. **17**, 508–525. (doi:10.1111/ele.12251)
8. Morlon H, Andréoletti J, Barido-Sottani J, Lambert S, Perez-Lamarque B, Quintero I, Senderov V, Veron P. 2024 Phylogenetic insights into diversification. *Annu. Rev. Ecol. Evol. Syst*. **55**, 1–21. (doi:10.1146/annurev-ecolsys-102722-020508)
9. Quental TB, Marshall CR. 2010 Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol*. **25**, 434–441. (doi:10.1016/j.tree.2010.05.002)
10. Louca S, Pennell MW. 2020 Extant timetrees are consistent with a myriad of diversification histories. *Nature* **580**, 502–505. (doi:10.1038/s41586-020-2176-1)
11. Burin G, Alencar LRV, Chang J, Alfaro ME, Quental TB. 2019 How well can we estimate diversity dynamics for clades in diversity decline? *Syst. Biol*. **68**, 47–62. (doi:10.1093/sysbio/syy037)
12. Rabosky DL. 2015 No substitute for real data: a cautionary note on the use of phylogenies from birth-death polytomy resolvers for downstream comparative analyses. *Evolution* **69**, 3207–3216. (doi:10.1111/evo.12817)
13. Helmstetter AJ *et al*. 2022 Pulled diversification rates, lineages-through-time plots, and modern macroevolutionary modeling. *Syst. Biol*. **71**, 758–773. (doi:10.1093/sysbio/syab083)
14. Morlon H, Robin S, Hartig F. 2022 Studying speciation and extinction dynamics from phylogenies: addressing identifiability issues. *Trends Ecol. Evol*. **37**, 497–506. (doi:10.1016/j.tree.2022.02.004)
15. Rabosky DL. 2017 Phylogenetic tests for evolutionary innovation: the problematic link between key innovations and exceptional diversification. *Phil. Trans. R. Soc. B* **372**, 20160417. (doi:10.1098/rstb.2016.0417)
16. Rabosky DL. 2018 BAMM at the court of false equivalency: a response to Meyer and Wiens. *Evolution* **72**, 2246–2256. (doi:10.1111/evo.13566)
17. Andréoletti J, Morlon H. 2023 Exploring congruent diversification histories with flexibility and parsimony. *Methods Ecol. Evol*. **14**, 2931–2941. (doi:10.1111/2041-210x.14240)

18. Morlon H, Parsons TL, Plotkin JB. 2011 Reconciling molecular phylogenies with the fossil record. *Proc. Natl Acad. Sci. USA* **108**, 16327–16332. (doi:10.1073/pnas.1102543108)
19. Mazet N, Morlon H, Fabre P, Condamine FL. 2023 Estimating clade-specific diversification rates and palaeodiversity dynamics from reconstructed phylogenies. *Methods Ecol. Evol*. **14**, 2575–2591. (doi:10.1111/2041-210x.14195)
20. Rabosky DL *et al*. 2018 An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395. (doi:10.1038/s41586-018-0273-1)
21. Condamine FL, Antonelli A, Lagomarsino LP, Hoorn C, Liow LH. 2018 Teasing apart mountain uplift, climate change and biotic drivers of species diversification. In *Mountains, climate and biodiversity* (eds C Hoorn, AL Perrigo, A Antonelli), pp. 257–272. Chichester, UK: John Wiley & Sons.
22. O'Hara TD, Hugall AF, Woolley SNC, Bribiesca-Contreras G, Bax NJ. 2019 Contrasting processes drive ophiuroid phylodiversity across shallow and deep seafloors. *Nature* **565**, 636–639. (doi:10.1038/s41586-019-0886-z)
23. Condamine FL, Rolland J, Morlon H. 2013 Macroevolutionary perspectives to environmental change. *Ecol. Lett*. **16**, 72–85. (doi:10.1111/ele.12062)
24. Lewitus E, Morlon H. 2018 Detecting environment-dependent diversification from phylogenies: a simulation study and some empirical illustrations. *Syst. Biol*. **67**, 576–593. (doi:10.1093/sysbio/syx095)
25. Lehtonen S, Silvestro D, Karger DN, Scotese C, Tuomisto H, Kessler M, Peña C, Wahlberg N, Antonelli A. 2017 Environmentally driven extinction and opportunistic origination explain fern diversification patterns. *Sci. Rep*. **7**, 4831. (doi:10.1038/s41598-017-05263-7)
26. Condamine FL, Rolland J, Höhna S, Sperling FAH, Sanmartín I. 2018 Testing the role of the Red Queen and Court Jester as drivers of the macroevolution of apollo butterflies. *Syst. Biol*. **67**, 940–964. (doi:10.1093/sysbio/syy009)
27. Benton MJ. 2009 The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**, 728–732. (doi:10.1126/science.1157719)
28. Van Valen L. 1973 A new evolutionary law. *Evol. Theory* **1**, 1–30.
29. Barnosky AD. 2001 Distinguishing the effects of the Red Queen and Court Jester on miocene mammal evolution in the northern rocky mountains. *J. Vertebr. Paleontol*. **21**, 172–185. (doi:10.1671/0272-4634(2001)021[0172:dteotr]2.0.co;2)
30. Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. 2009 Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA* **106**, 13410–13414. (doi:10.1073/pnas.0811087106)
31. Rabosky DL. 2013 Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annu. Rev. Ecol. Evol. Syst*. **44**, 481–502. (doi:10.1146/annurev-ecolsys-110512-135800)
32. Maliet O, Hartig F, Morlon H. 2019 A model with many small shifts for estimating species-specific diversification rates. *Nat. Ecol. Evol*. **3**, 1086–1092. (doi:10.1038/s41559-019-0908-0)
33. Chazot N, Willmott KR, Lamas G, Freitas AVL, Piron-Prunier F, Arias CF, Mallet J, De-Silva DL, Elias M. 2019 Renewed diversification following miocene landscape turnover in a neotropical butterfly radiation. *Glob. Ecol. Biogeogr*. **28**, 1118–1132. (doi:10.1111/geb.12919)
34. Raven PH, Berg LR, Hassenzahl DM. 2012 *Environment*, 8th edn. Hoboken, NJ: John Wiley & Sons.
35. Stork NE. 2018 How many species of insects and other terrestrial arthropods are there on earth? *Annu. Rev. Entomol*. **63**, 31–45. (doi:10.1146/annurev-ento-020117-043348)
36. Peris D, Condamine FL. 2024 The angiosperm radiation played a dual role in the diversification of insects and insect pollinators. *Nat. Commun*. **15**, 552. (doi:10.1038/s41467-024-44784-4)
37. Boderau M, Nel A, Jouault C. 2025 Diversification and extinction of *Hemiptera* in deep time. *Commun. Biol*. **8**, 352. (doi:10.1038/s42003-025-07773-x)
38. Benton MJ, Wilf P, Sauquet H. 2022 The angiosperm terrestrial revolution and the origins of modern biodiversity. *New Phytol*. **233**, 2017–2035. (doi:10.1111/nph.17822)
39. Coiffard C, Gomez B, Daviero-Gomez V, Dilcher DL. 2012 Rise to dominance of angiosperm pioneers in European cretaceous environments. *Proc. Natl Acad. Sci. USA* **109**, 20955–20959. (doi:10.1073/pnas.1218633110)
40. Magallón S, Gómez-Acevedo S, Sánchez-Reyes LL, Hernández-Hernández T. 2015 A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol*. **207**, 437–453. (doi:10.1111/nph.13264)
41. Foster GL, Royer DL, Lunt DJ. 2017 Future climate forcing potentially without precedent in the last 420 million years. *Nat. Commun.* **8**, 14845. (doi:10.1038/ncomms14845)
42. Coiro M, Doyle JA, Hilton J. 2019 How deep is the conflict between molecular and fossil evidence on the age of angiosperms? *New Phytol*. **223**, 83–99. (doi:10.1111/nph.15708)
43. Li HT *et al*. 2019 Origin of angiosperms and the puzzle of the Jurassic gap. *Nat. Plants* **5**, 461–470. (doi:10.1038/s41477-019-0421-0)
44. McKenna DD, Sequeira AS, Marvaldi AE, Farrell BD. 2009 Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl Acad. Sci. USA* **106**, 7083–7088. (doi:10.1073/pnas.0810618106)
45. Wiegmann BM *et al*. 2011 Episodic radiations in the fly tree of life. *Proc. Natl Acad. Sci. USA* **108**, 5690–5695. (doi:10.1073/pnas.1012675108)
46. Cardinal S, Danforth BN. 2013 Bees diversified in the age of eudicots. *Proc. R. Soc. B*. **280**, 20122686. (doi:10.1098/rspb.2012.2686)
47. Ahrens D, Schwarzer J, Vogler AP. 2014 The evolution of scarab beetles tracks the sequential rise of angiosperms and mammals. *Proc. R. Soc. B*. **281**, 20141470. (doi:10.1098/rspb.2014.1470)
48. Vea IM, Grimaldi DA. 2016 Putting scales into evolutionary time: the divergence of major scale insect lineages (Hemiptera) predates the radiation of modern angiosperm hosts. *Sci. Rep*. **6**, 23487. (doi:10.1038/srep23487)

49. Meredith RW *et al*. 2011 Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* **334**, 521–524. (doi:10.1126/science.1211028)

50. Labandeira CC, Sepkoski JJ Jr. 1993 Insect diversity in the fossil record. *Science* **261**, 310–315. (doi:10.1126/science.11536548)

51. Condamine FL, Clapham ME, Kergoat GJ. 2016 Global patterns of insect diversification: towards a reconciliation of fossil and molecular evidence? *Sci. Rep*. **6**, 19208. (doi:10.1038/srep19208)

52. Jouault C, Nel A, Legendre F, Condamine FL. 2022 Estimating the drivers of diversification of stoneflies through time and the limits of their fossil record. *Insect Syst. Divers*. **6**, 4. (doi:10.1093/isd/ixac017)

53. Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. 2006 Phylogeny of the ants: diversification in the age of angiosperms. *Science* **312**, 101–104. (doi:10.1126/science.1124891)

54. Rabeling C, Brown JM, Verhaagh M. 2008 Newly discovered sister lineage sheds light on early ant evolution. *Proc. Natl Acad. Sci. USA* **105**, 14913–14917. (doi:10.1073/pnas.0806187105)

55. LaPolla JS, Dlussky GM, Perrichot V. 2013 Ants and the fossil record. *Annu. Rev. Entomol*. **58**, 609–630. (doi:10.1146/annurev-ento-120710-100600)

56. Moreau CS, Bell CD. 2013 Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants: the tropics as museum and cradle of ant diversity. *Evolution* **67**, 2240–2257. (doi:10.1111/evo.12105)

57. Economo EP, Narula N, Friedman NR, Weiser MD, Guénard B. 2018 Macroecology and macroevolution of the latitudinal diversity gradient in ants. *Nat. Commun*. **9**, 1778. (doi:10.1038/s41467-018-04218-4)

58. Borowiec ML, Zhang YM, Neves K, Ramalho MO, Fisher BL, Lucky A, Moreau CS. 2025 Evaluating UCE data adequacy and integrating uncertainty in a comprehensive phylogeny of ants. *Syst. Biol*. **74**, 700–722. (doi:10.1093/sysbio/syaf001)

59. Jouault C, Oyama N, Álvarez-Parra S, Huang D, Perrichot V, Condamine FL, Legendre F. 2025 The radiation of *Hymenoptera* illuminated by Bayesian inferences from the fossil record. *Curr. Biol*. **35**, 2164–2174. (doi:10.1016/j.cub.2025.03.002)

60. Hölldobler B, Wilson EO. 1990 *The ants*. Cambridge, MA: Harvard University Press.

61. Bolton B. 2003 An online catalog of the ants of the world. See http://antcat.org.

62. Jouault C, Condamine FL, Legendre F, Perrichot V. 2024 The angiosperm terrestrial revolution buffered ants against extinction. *Proc. Natl Acad. Sci. USA* **121**, e2317795121. (doi:10.1073/pnas.2317795121)

63. Rambaut A. 2018 Figtree ver 1.4.4. Edinburgh, UK: Institute of Evolutionary Biology, University of Edinburgh.

64. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)

65. Allen AP, Gillooly JF, Savage VM, Brown JH. 2006 Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl Acad. Sci. USA* **103**, 9130–9135. (doi:10.1073/pnas.0603587103)

66. Gillooly JF, Allen AP, West GB, Brown JH. 2005 The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc. Natl Acad. Sci. USA* **102**, 140–145. (doi:10.1073/pnas.0407735101)

67. Dunn RR *et al*. 2009 Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecol. Lett*. **12**, 324–333. (doi:10.1111/j.1461-0248.2009.01291.x)

68. Pie MR. 2016 The macroevolution of climatic niches and its role in ant diversification. *Ecol. Entomol*. **41**, 301–307. (doi:10.1111/een.12306)

69. Brady SG, Schultz TR, Fisher BL, Ward PS. 2006 Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proc. Natl Acad. Sci. USA* **103**, 18172–18177. (doi:10.1073/pnas.0605858103)

70. Nelsen MP, Ree RH, Moreau CS. 2018 Ant-plant interactions evolved through increasing interdependence. *Proc. Natl Acad. Sci. USA* **115**, 12253–12258. (doi:10.1073/pnas.1719794115)

71. Borowiec ML. 2019 Convergent evolution of the army ant syndrome and congruence in big-data phylogenetics. *Syst. Biol*. **68**, 642–656. (doi:10.1093/sysbio/syy088)

72. Cai C. 2024 Ant backbone phylogeny resolved by modelling compositional heterogeneity among sites in genomic data. *Commun. Biol*. **7**, 106. (doi:10.1038/s42003-024-05793-7)

73. Economo EP, Huang J, Fischer G, Sarnat EM, Narula N, Janda M, Guénard B, Longino JT, Knowles LL. 2019 Evolution of the latitudinal diversity gradient in the hyperdiverse ant genus *Pheidole*. *Glob. Ecol. Biogeogr*. **28**, 456–470. (doi:10.1111/geb.12867)

74. Booher DB *et al*. 2021 Functional innovation promotes diversification of form in the evolution of an ultrafast trap-jaw mechanism in ants. *PLoS Biol*. **19**, e3001031. (doi:10.1371/journal.pbio.3001031)

75. Borowiec ML, Cover SP, Rabeling C. 2021 The evolution of social parasitism in *Formica* ants revealed by a global phylogeny. *Proc. Natl Acad. Sci. USA* **118**, e2026029118. (doi:10.1073/pnas.2026029118)

76. Barrera CA, Sosa-Calvo J, Schultz TR, Rabeling C, Bacci M Jr. 2022 Phylogenomic reconstruction reveals new insights into the evolution and biogeography of *Atta* leaf-cutting ants (Hymenoptera: Formicidae). *Syst. Entomol*. **47**, 13–35. (doi:10.1111/syen.12513)

77. Romiguier J *et al*. 2022 Ant phylogenomics reveals a natural selection hotspot preceding the origin of complex eusociality. *Curr. Biol*. **32**, 2942–2947.(doi:10.1016/j.cub.2022.05.001)

78. Wilson EO, Hölldobler B. 2005 The rise of the ants: a phylogenetic and ecological explanation. *Proc. Natl Acad. Sci. USA* **102**, 7411–7414. (doi:10.1073/pnas.0502264102)

79. Labandeira CC. 2014 Chapitre 13: why did terrestrial insect diversity not increase during the angiosperm radiation? Mid-mesozoic, plant-associated insect lineages harbor clues. In *Evolutionary biology: genome evolution, speciation, coevolution and origin of life* (ed. P Pontarotti), pp. 261–299. Switzerland: Springer International Publishing. (doi:10.1007/978-3-319-07623-2_13)
80. Brady SG, Fisher BL, Schultz TR, Ward PS. 2014 The rise of army ants and their relatives: diversification of specialized predatory doryline ants. *BMC Evol. Biol*. **14**, 93. (doi:10.1186/1471-2148-14-93)
81. Schultz TR, Brady SG. 2008 Major evolutionary transitions in ant agriculture. *Proc. Natl Acad. Sci. USA* **105**, 5435–5440. (doi:10.1073/pnas.0711024105)
82. LaPolla JS, Cheng CH, Fisher BL. 2010 Taxonomic revision of the ant (Hymenoptera: Formicidae) genus paraparatrechina in the afrotropical and malagasy regions. *Zootaxa* **2387**, 1. (doi:10.11646/zootaxa.2387.1.1)
83. Ward PS, Brady SG, Fisher BL, Schultz TR. 2010 Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Syst. Biol*. **59**, 342–362. (doi:10.1093/sysbio/syq012)
84. Ward PS, Brady SG, Fisher BL, Schultz TR. 2015 The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae): phylogeny and evolution of myrmicine ants. *Syst. Entomol*. **40**, 61–81. (doi:10.1111/syen.12090)
85. Schmidt C. 2013 Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). *Zootaxa* **3647**, 201–250. (doi:10.11646/zootaxa.3647.2.1)
86. Silvestro D, Cascales-Miñana B, Bacon CD, Antonelli A. 2015 Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol*. **207**, 425–436. (doi:10.1111/nph.13247)
87. Nyman T, Onstein RE, Silvestro D, Wutke S, Taeger A, Wahlberg N, Blank SM, Malm T. 2019 The early wasp plucks the flower: disparate extant diversity of sawfly superfamilies (Hymenoptera: 'Symphyta') may reflect asynchronous switching to angiosperm hosts. *Biol. J. Linn. Soc*. **128**, 1–19. (doi:10.1093/biolinnean/blz071)
88. Veizer J, Prokoph A. 2015 Temperatures and oxygen isotopic composition of phanerozoic oceans. *Earth Sci. Rev*. **146**, 92–104. (doi:10.1016/j.earscirev.2015.03.008)
89. Miller KG *et al*. 2005 The phanerozoic record of global sea-level change. *Science* **310**, 1293–1298. (doi:10.1126/science.1116412)
90. Miller KG, Browning JV, Schmelz WJ, Kopp RE, Mountain GS, Wright JD. 2020 Cenozoic sea-level and cryospheric evolution from deep-sea geochemical and continental margin records. *Sci. Adv*. **6**, eaaz1346. (doi:10.1126/sciadv.aaz1346)
91. Valdes PJ, Scotese CR, Lunt DJ. 2021 Deep ocean temperatures through time. *Clim. Past* **17**, 1483–1506. (doi:10.5194/cp-17-1483-2021)
92. Goudsmit-Harzevoort B *et al*. 2023 The relationship between the global mean deep-sea and surface temperature during the early eocene. *Paleoceanogr. Paleoclimatol*. **38**, e2022PA004532. (doi:10.1029/2022pa004532)
93. Condamine FL, Toussaint EFA, Clamens AL, Genson G, Sperling FAH, Kergoat GJ. 2015 Deciphering the evolution of birdwing butterflies 150 years after alfred russel wallace. *Sci. Rep*. **5**, 11860. (doi:10.1038/srep11860)
94. Morlon H, Lewitus E, Condamine FL, Manceau M, Clavel J, Drury J. 2016 RPANDA: an R package for macroevolutionary analyses on phylogenetic trees. *Methods Ecol. Evol*. **7**, 589–597. (doi:10.1111/2041-210X.12526)
95. Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010 Picante: r tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464. (doi:10.1093/bioinformatics/btq166)
96. Ramsay JO, Heckman N, Silverman BW. 1997 Spline smoothing with model-based penalties. *Behav. Res. Methods Instrum. Comput*. **29**, 99–106. (doi:10.3758/BF03200573)
97. Heckman NE, Ramsay JO. 2000 Penalized regression with model-based penalties. *Can. J. Stat*. **28**, 241–258. (doi:10.2307/3315976)
98. Nee S, May RM, Harvey PH. 1994 The reconstructed evolutionary process. *Phil. Trans. R. Soc. B* **344**, 305–311. (doi:10.1098/rstb.1994.0068)
99. R Core Team. 2024 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
100. Wickham H *et al*. 2019 Welcome to the tidyverse. *J. Open Source Softw*. **4**, 1686. (doi:10.21105/joss.01686)
101. Prokoph A, Shields GA, Veizer J. 2008 Compilation and time-series analysis of a marine carbonate δ18O, δ13C, 87Sr/86Sr and δ34S database through Earth history. *Earth Sci. Rev*. **87**, 113–133. (doi:10.1016/j.earscirev.2007.12.003)
102. Zachos JC, Dickens GR, Zeebe RE. 2008 An early cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283. (doi:10.1038/nature06588)
103. Janicki J, Narula N, Ziegler M, Guénard B, Economo EP. 2016 Visualizing and interacting with large-volume biodiversity data using client–server web-mapping applications: the design and implementation of antmaps.org. *Ecol. Inform*. **32**, 185–193. (doi:10.1016/j.ecoinf.2016.02.006)
104. Sarnat EM, Friedman NR, Fischer G, Lecroq-Bennet B, Economo EP. 2017 Rise of the spiny ants: diversification, ecology and function of extreme traits in the hyperdiverse genus *Pheidole* (Hymenoptera: Formicidae). *Biol. J. Linn. Soc*. **122**, 514–538. (doi:10.1093/biolinnean/blx081)
105. Branstetter MG, Longino JT, Reyes-López JL, Brady SG, Schultz TR. 2022 Out of the temperate zone: a phylogenomic test of the biogeographical conservatism hypothesis in a contrarian clade of ants. *J. Biogeogr*. **49**, 1640–1653. (doi:10.1111/jbi.14462)
106. Blanchard BD, Moreau CS. 2023 Defensive spines are associated with large geographic range but not diversification in spiny ants (Hymenoptera: Formicidae: *Polyrhachis*). *Syst. Entomol*. **48**, 328–340. (doi:10.1111/syen.12578)
107. Matte A, Guénard B, Gautam S, Azuma F, Katzke J, Garcia FH, van de Kamp T, Economo EP. 2025 The evolution of cheaper workers facilitated larger societies and accelerated diversification in ants. *Sci. Adv*. **11**. (doi:10.1126/sciadv.adx8068)
108. Jablonski D, Belanger CL, Berke SK, Huang S, Krug AZ, Roy K, Tomasovych A, Valentine JW. 2013 Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl Acad. Sci. USA* **110**, 10487–10494. (doi:10.1073/pnas.1308997110)

109. Saupe EE, Farnsworth A, Lunt DJ, Sagoo N, Pham KV, Field DJ. 2019 Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic. *Proc. Natl Acad. Sci. USA* **116**, 12895–12900. (doi:10.1073/pnas.1903866116)
110. Brown JH. 2014 Why are there so many species in the tropics? *J. Biogeogr*. **41**, 8–22. (doi:10.1111/jbi.12228)
111. Wiens JJ, Donoghue MJ. 2025 The origins of the latitudinal diversity gradient: revisiting the tropical conservatism hypothesis. *J. Biogeogr*. **52**, 15172. (doi:10.1111/jbi.15172)
112. Ito F. 1998 Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae). *Insectes Soc*. **45**, 79–83. (doi:10.1007/s000400050070)
113. Kikuchi T, Tsuji K. 2005 Unique social structure of *Probolomyrmex longinodus*. *Entomol. Sci*. **8**, 1–3. (doi:10.1111/j.1479-8298.2005.00094.x)
114. Juvé Y *et al*. 2025 Phylogenomics of *Messor* harvester ants (Hymenoptera: Formicidae: Stenammini) unravels their biogeographical origin and diversification patterns. *Syst. Entomol*. **50**, 1025–1040. (doi:10.1111/syen.12693)
115. Mayhew PJ. 2007 Why are there so many insect species? Perspectives from fossils and phylogenies. *Biol. Rev.***82**, 425–454. (doi:10.1111/j.1469-185X.2007.00018.x)
116. Rainford JL, Hofreiter M, Nicholson DB, Mayhew PJ. 2014 Phylogenetic distribution of extant richness suggests metamorphosis is a key innovation driving diversification in insects. *PLoS One* **9**, e109085. (doi:10.1371/journal.pone.0109085)
117. Delclòs X *et al*. 2023 Amber and the cretaceous resinous interval. *Earth Sci. Rev*. **243**, 104486. (doi:10.1016/j.earscirev.2023.104486)
118. Condamine FL, Nel A, Grandcolas P, Legendre F. 2020 Fossil and phylogenetic analyses reveal recurrent periods of diversification and extinction in dictyopteran insects. *Cladistics* **36**, 394–412. (doi:10.1111/cla.12412)
119. Moen D, Morlon H. 2014 Why does diversification slow down? *Trends Ecol. Evol*. **29**, 190–197. (doi:10.1016/j.tree.2014.01.010)
120. Rabosky DL. 2009 Ecological limits on clade diversification in higher taxa. *Am. Nat*. **173**, 662–674. (doi:10.1086/597378)
121. Pontarp M, Wiens JJ. 2017 The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate and carrying capacity. *J. Biogeogr*. **44**, 722–735. (doi:10.1111/jbi.12896)
122. Phillimore AB, Price TD. 2008 Density-dependent cladogenesis in birds. *PLoS Biol*. **6**, e71. (doi:10.1371/journal.pbio.0060071)
123. Etienne RS, Haegeman B, Stadler T, Aze T, Pearson PN, Purvis A, Phillimore AB. 2012 Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. R. Soc. B*. **279**, 1300–1309. (doi:10.1098/rspb.2011.1439)
124. Janz N, Nylin S, Wahlberg N. 2006 Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evol. Biol*. **6**, 4. (doi:10.1186/1471-2148-6-4)
125. Chomicki G, Renner SS. 2019 Climate and symbioses with ants modulate leaf/stem scaling in epiphytes. *Sci. Rep*. **9**, 2624. (doi:10.1038/s41598-019-39853-4)
126. Chomicki G, Ward PS, Renner SS. 2015 Macroevolutionary assembly of ant/plant symbioses: *Pseudomyrmex* ants and their ant-housing plants in the neotropics. *Proc. R. Soc. B* **282**, 20152200. (doi:10.1098/rspb.2015.2200)
127. Chomicki G, Renner SS. 2015 Phylogenetics and molecular clocks reveal the repeated evolution of ant-plants after the late Miocene in Africa and the early Miocene in Australasia and the neotropics. *New Phytol*. **207**, 411–424. (doi:10.1111/nph.13271)
128. Osman MB, Tierney JE, Zhu J, Tardif R, Hakim GJ, King J, Poulsen CJ. 2021 Globally resolved surface temperatures since the last glacial maximum. *Nature* **599**, 239–244. (doi:10.1038/s41586-021-03984-4)
129. Laepple T *et al*. 2023 Regional but not global temperature variability underestimated by climate models at supradecadal timescales. *Nat. Geosci*. **16**, 958–966. (doi:10.1038/s41561-023-01299-9)
130. Warren BH *et al*. 2015 Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecol. Lett*. **18**, 200–217. (doi:10.1111/ele.12398)
131. Delić T, Stoch F, Borko Š, Flot J, Fišer C. 2020 How did subterranean amphipods cross the Adriatic Sea? Phylogenetic evidence for dispersal–vicariance interplay mediated by marine regression–transgression cycles. *J. Biogeogr*. **47**, 1875–1887. (doi:10.1111/jbi.13875)
132. Papadopoulou A, Knowles LL. 2015 Genomic tests of the species-pump hypothesis: recent island connectivity cycles drive population divergence but not speciation in Caribbean crickets across the Virgin Islands: genomic tests of the species pump. *Evolution* **69**, 1501–1517. (doi:10.1111/evo.12667)
133. Losada IJ, Reguero BG, Méndez FJ, Castanedo S, Abascal AJ, Mínguez R. 2013 Long-term changes in sea-level components in Latin America and the Caribbean. *Glob. Planet. Change* **104**, 34–50. (doi:10.1016/j.gloplacha.2013.02.006)
134. Gold DP, White LT, Gunawan I, BouDagher-Fadel MK. 2017 Relative sea-level change in western New Guinea recorded by regional biostratigraphic data. *Mar. Pet. Geol*. **86**, 1133–1158. (doi:10.1016/j.marpetgeo.2017.07.016)
135. Seton M *et al*. 2012 Global continental and ocean basin reconstructions since 200Ma. *Earth Sci. Rev*. **113**, 212–270. (doi:10.1016/j.earscirev.2012.03.002)
136. Wang R, Kass JM, Chaudhary C, Economo EP, Guénard B. Global biogeographic regions for ants have complex relationships with those for plants and tetrapods. *Nat. Commun*. **15**, 5641. (doi:10.1038/s41467-024-49918-2)
137. Steeman ME *et al*. 2009 Radiation of extant cetaceans driven by restructuring of the oceans. *Syst. Biol*. **58**, 573–585. (doi:10.1093/sysbio/syp060)
138. Rabosky DL, Goldberg EE. 2015 Model inadequacy and mistaken inferences of trait-dependent speciation. *Syst. Biol*. **64**, 340–355. (doi:10.1093/sysbio/syu131)
139. Moore BR, Höhna S, May MR, Rannala B, Huelsenbeck JP. 2016 Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures. *Proc. Natl Acad. Sci. USA* **113**, 9569–9574. (doi:10.1073/pnas.1518659113)

140. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
141. Tonini JFR, Beard KH, Ferreira RB, Jetz W, Pyron RA. 2016 Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biol. Conserv*. **204**, 23–31. (doi:10.1016/j.biocon.2016.03.039)
142. Stein RW, Mull CG, Kuhn TS, Aschliman NC, Davidson LNK, Joy JB, Smith GJ, Dulvy NK, Mooers AO. 2018 Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nat. Ecol. Evol*. **2**, 288–298. (doi:10.1038/s41559-017-0448-4)
143. Rolland J, Condamine FL, Jiguet F, Morlon H. 2014 Faster speciation and reduced extinction in the tropics contribute to the Mammalian latitudinal diversity gradient. *PLoS Biol*. **12**, e1001775. (doi:10.1371/journal.pbio.1001775)
144. Burin G, Kissling WD, Guimarães PR, Şekercioğlu ÇH, Quental TB. 2016 Omnivory in birds is a macroevolutionary sink. *Nat. Commun*. **7**, 11250. (doi:10.1038/ncomms11250)
145. Morlon H, Hartig F, Robin S. 2020 Prior hypotheses or regularization allow inference of diversification histories from extant timetrees. (doi:10.1101/2020.07.03.185074)
146. Jouault C, Condamine FL, Legendre F, Perrichot V. 2024 Reply to Vermeij: challenges and opportunities in macroevolution. *Proc. Natl Acad. Sci. USA* **121**, e2408795121. (doi:10.1073/pnas.2408795121)
147. Grasby SE, Them TR II, Chen Z, Yin R, Ardakani OH. 2019 Mercury as a proxy for volcanic emissions in the geologic record. *Earth Sci. Rev*. **196**, 102880. (doi:10.1016/j.earscirev.2019.102880)
148. Zaffos A, Finnegan S, Peters SE. 2017 Plate tectonic regulation of global marine animal diversity. *Proc. Natl Acad. Sci. USA* **114**, 5653–5658. (doi:10.1073/pnas.1702297114)
149. Rolland J, Condamine FL. 2019 The contribution of temperature and continental fragmentation to amphibian diversification. *J. Biogeogr*. **46**, 1857–1873. (doi:10.1111/jbi.13592)
150. Jouault C, Swain A, Sosiak C. 2026 Diversity-dependent effects likely influenced the diversification of species-rich crown ant subfamilies during the Cenozoic. *R. Soc. Open Sci* **13**, 252318. https://doi.org/10.1098/rsos.252318
151. Tardif D, Condamine FL, Streiff SJR, Sepulchre P, Couvreur TLP. 2025 Generating spatialised and seasonal deep-time palaeoclimatic information: integration into an environmental-dependent diversification model. *Glob. Ecol. Biogeogr*. **34**, e70024. (doi:10.1111/geb.70024)
152. Maddison WP, Midford PE, Otto SP. 2007 Estimating a binary character's effect on speciation and extinction. *Syst. Biol*. **56**, 701–710. (doi:10.1080/10635150701607033)
153. FitzJohn RG. 2012 Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol*. **3**, 1084–1092. (doi:10.1111/j.2041-210X.2012.00234.x)
154. Beaulieu JM, O'Meara BC. 2016 Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Syst. Biol*. **65**, 583–601. (doi:10.1093/sysbio/syw022)
155. Etienne RS, Pigot AL, Phillimore AB. 2016 How reliably can we infer diversity-dependent diversification from phylogenies? *Methods Ecol. Evol*. **7**, 1092–1099. (doi:10.1111/2041-210X.12565)
156. Etienne RS, Haegeman B, Dugo-Cota Á, Vilà C, Gonzalez-Voyer A, Valente L. 2023 The phylogenetic limits to diversity-dependent diversification. *Syst. Biol*. **72**, 433–445. (doi:10.1093/sysbio/syac074)
157. Pannetier T, Martinez C, Bunnefeld L, Etienne RS. 2021 Branching patterns in phylogenies cannot distinguish diversity-dependent diversification from time-dependent diversification. *Evolution* **75**, 25–38. (doi:10.1111/evo.14124)
158. Cerdá X, Arnan X, Retana J. 2013 Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? *Myrmecol. News* **18**, 131–147. (doi:10.25849/myrmecol.news_018:131)
159. Zeebe RE, Ridgwell A, Zachos JC. 2016 Anthropogenic carbon release rate unprecedented during the past 66 million years. *Nat. Geosci*. **9**, 325–329. (doi:10.1038/ngeo2681)
160. García-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ. 2016 Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. *Proc. Natl Acad. Sci. USA* **113**, 680–685. (doi:10.1073/pnas.1507681113)
161. Seibold S *et al*. 2019 Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674. (doi:10.1038/s41586-019-1684-3)
162. Sánchez-Bayo F, Wyckhuys KAG. 2019 Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv*. **232**, 8–27. (doi:10.1016/j.biocon.2019.01.020)
163. Campana JLM, Jouault C, Economo EP, Condamine F. 2026 Testing tribe-specific macroevolutionary responses to palaeoenvironmental changes in ants, and the impact of taxon sampling on diversification analyses. Figshare. (doi:10.6084/m9.figshare.30128773)
164. Campana JL, Jouault C, Economo EP, Condamine FL. 2026 Supplementary material from: Testing tribe-specific macroevolutionary responses to paleoenvironmental changes in ants, and the impact of taxon sampling on diversification analyses. Figshare. (doi:10.6084/m9.figshare.c.8451495)