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Diversity-dependent effects probably influenced the diversification of species-rich crown ant subfamilies during the Cenozoic

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Disentangling the influence of biotic interactions from abiotic environmental changes is a central challenge in macroevolution. While ants' evolutionary history has been widely studied, often in relation to abiotic factors or plant associations, the role of intra- and inter-lineage interactions, whether competitive or facilitative, remains poorly understood. In this study, we use birth–death models within a Bayesian framework, integrating fossil and extant data, to investigate how interactions between the five most species-rich crown ant subfamilies may have shaped their diversification during the Cenozoic. Our results suggest that negative intraclade interactions within Dolichoderinae, Dorylinae, Formicinae and Ponerinae probably affected their diversification. We detect a signal of interactions between Formicinae and Myrmicinae and Dolichoderinae and Dorylinae, possibly reflecting long-term co-evolutionary dynamics. Notably, contrary to earlier hypotheses suggesting competition between Ponerinae and Myrmicinae, our results indicate a facilitative interaction between these two groups, but also between Formicinae and Dolichoderinae and Ponerinae and Myrmicinae, suggesting that coexistence sometimes promotes rather than inhibits diversification. Overall, our study provides the first assessment of diversity-dependent effects on the evolutionary history of ants, establishing biotic interactions as a fundamental and quantifiable force in shaping macroevolutionary patterns of one of Earth's most successful animal groups.

1. Introduction

Over deep time, the diversity dynamics of lineages are shaped by biotic factors, such as changes in plant communities, resource competition and predation, and abiotic factors, including temperature and sea-level fluctuations [1–5]. This dichotomy is often conceptualized through two competing paradigms: the Red Queen (RQ) hypothesis, which posits that intrinsic biotic interactions are the primary engine of evolution, and the Court Jester (CJ) hypothesis, which argues that extrinsic abiotic perturbations drive major evolutionary shifts. While most research has traditionally emphasized the impact of abiotic changes on the rise and fall of clades (a focus on the CJ model), the role of biotic interactions (RQ dynamics), sometimes questioned, remains comparatively understudied, especially across large temporal and spatial scales, and using the fossil record [3,6–8]. However, recent macroevolutionary studies, drawing on a renewed interest in deep time ecological interactions within and between lineages, highlight the pivotal role of biotic factors in shaping diversification by affecting the rates of origination (i.e. speciation at levels higher than species) and extinction [4,9–12]. These studies have focused on quantifying the effects of two types of interactions: (i) diversity dependence, where changes in a clade's own diversity (i.e. accumulation of species) limit its origination and potentially increase its extinction rates; and (ii) interclade interactions, where changes in the diversity of one clade affect the diversification dynamics of other co-occurring clades [13–18].

Classically, diversity dependence has been attributed to a reduction in speciation rates or an increase in extinction rates as ecological niches become saturated [15,17,19,20]. This pattern is thought to result from the progressive filling of available ecological space, ultimately limiting opportunities for ecological speciation [15,21–25]. Such dynamics imply the existence of a clade-level carrying capacity, representing the maximum number of species that can coexist within a given lineage at a particular time. Interclade interactions encompass both negative interactions, such as competition (either by passive replacement and active displacement; [26]) or predation, which typically reduce origination and elevate extinction rates, and positive interactions, such as facilitation, where interactions between clades may enhance origination and buffer against extinction [4,10,27].

In deep time, both intraclade and interclade interactions can occur among taxa with similar ecology or under conditions of limited resources, particularly during or after key paleoevents (e.g. mass extinction events; ecosystem restructuring). These interactions may involve closely related species but can also arise between distantly related clades [4,12–14]. As a result, a lineage may diversify, decline or be replaced by another as ecological niches are created, vacated or filled [28,29]. While such dynamics have been mostly investigated in vertebrate groups, they remain poorly understood in invertebrates, particularly in insects. Yet insects represent the most diverse group of non-microbial organisms on Earth, with over one million described species [30]. Some lineages, such as ants (Formicidae), are not only ubiquitous but also function as keystone taxa and ecosystem engineers, contributing significantly to global biomass and influencing other species through biotic interactions [31,32].

With over 15 000 extant species, ants exhibit a remarkable range of ecological interactions, both competitive and cooperative, within and between lineages (figure 1) [33–36]. Negative interactions, potentially favouring extinction and limiting origination, are frequent among ants due to the tendency of many species to exploit similar ecological resources, such as nesting sites, prey or food sources [33,35,36]. This overlap often leads to intense competition within species or genera and among distantly related taxa [37,38]. These competitive dynamics give rise to diversity-dependent effects, which often manifest as constraints on spatial distribution, either during the establishment of new colonies (e.g. competition for nesting sites) or later in foraging areas (e.g. access to food resources such as aphids or extrafloral nectaries), and sometimes to the formation of well-defined colony territories [33,36]. These interactions have long been posited to act as mechanisms that shape ant diversification and community structure, even across deep time [11]. For instance, a recent study investigated potential diversity-dependent effects between stem and crown ants, examining their possible role in the extinction of stem ants during the Late Cretaceous, coinciding with and probably driven by the radiation of crown ants [11]. Similarly, researchers also hypothesized that during the Cenozoic, ponerine ants competed with myrmicines for prey and nesting sites, potentially constraining the diversification of ponerine ants [39]. From a macroevolutionary perspective, this would manifest as a

Figure 1. Ecological and morphological profiles of extant and extinct ants. (A) Formicinae: *Dinomyrmex gigas* (Latreille, 1802) (Sabah, Malaysia). (B) Formicinae: *Polyrhachis* sp. (Sabah, Malaysia). (C) Ponerinae: *Diacamma* sp. (Sabah, Malaysia). (D) extinct Myrmicinae (late Eocene, Baltic amber). (E) Formicinae: *Camponotus* sp. (mid-Miocene, Dominican amber). © Xavier Desmier (A–C); © Enrico Bonino (D,E).

decrease in origination rate and/or an increase in extinction rate of Ponerinae as Myrmicinae diversity increased—an expectation that can be explicitly tested using birth–death models [40]. It is also plausible that the diversification of generalist lineages occupying overlapping ecological niches—such as Formicinae and Dolichoderinae—led to negative interclade interactions. Similarly, the diversification of predatory lineages like Dorylinae may have negatively influenced the diversity trajectories of their prey lineages (e.g. Dolichoderinae). However, these hypotheses have yet to be empirically evaluated.

In contrast, complex mutualistic interactions (e.g. parabioses), potentially favouring origination and buffering against extinction, have been documented between certain ant species that share the same nest and may engage in interspecific trophallaxis or exploit common food resources [41]. At a more extreme level, some invasive ant species exhibit cooperative behaviours, which can enhance colony establishment and contribute to their dominance over native ant communities [42]. Such interactions are evident among the so-called 'big five' ant subfamilies (i.e. Myrmicinae, Formicinae, Ponerinae, Dolichoderinae and Dorylinae), most are generalist foragers (figure 1). However, if the evolutionary success of ants has long fascinated biologists [33,39], efforts to understand the drivers of this success in deep time have often focused on environmental factors, such as the diversification of flowering plants (e.g. [11,43]). In contrast, the potential role of diversity-dependent effects and interclade interactions within and between ant subfamilies has received comparatively little attention.

Using birth–death and diversity-dependent models within a Bayesian framework, and leveraging a combination of neontological and paleontological data, we aim to test for a macroevolutionary signal of Red Queen dynamics (i.e. competition and facilitation) among the five most speciose subfamilies of Formicidae—groups that together account for over 90% of ant diversity and possess the most complete fossil record. We investigated, *inter alia*, the long-standing hypothesis that links the diversity dynamics of ponerine ants to those of myrmicine ants [39]. Our analysis focused on the Cenozoic, a period marked by the rise and diversification of crown-group ants and dramatic abiotic change, providing a unique opportunity to assess the interplay of biotic and environmental forces [11,44,45].

2. Methods

2.1. Selection of ant subfamilies

Formicidae are highly diverse in modern ecosystems, but their species richness is unevenly distributed across subfamilies. Only five subfamilies are sufficiently speciose, in extant ecosystems (figure 2A) and the fossil record (figure 1D-E), to robustly investigate diversity-dependent effects: Dolichoderinae (approx. 5% of all extant species and approx. 5% of genera, 28 valid genera), Dorylinae (approx. 5% of species and approx. 8% genera, 27 valid genera), Formicinae (approx. 23% of species and approx. 16% of genera, 55 valid genera; figure 1A,B,E), Myrmicinae (approx. 50% of species and approx. 43% of genera, 148 valid genera; figure 1D) and Ponerinae (approx. 9% of species and approx. 14% of genera,

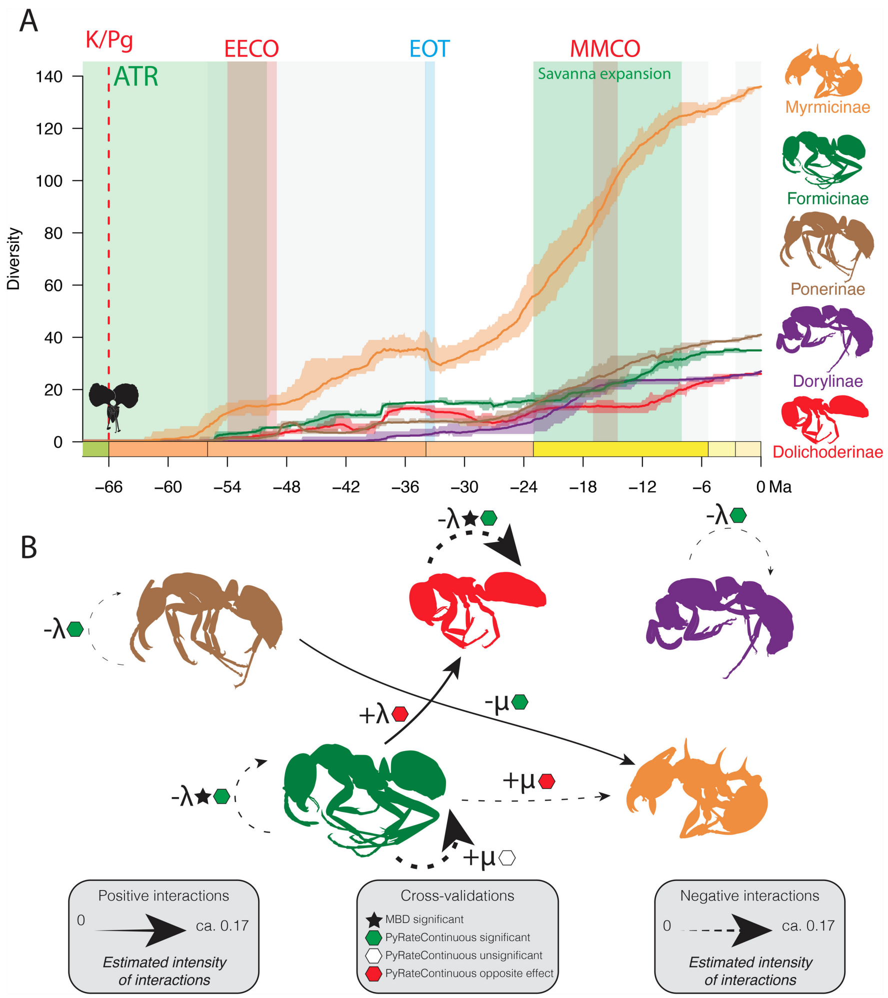

Figure 2. Diversity trajectories and the effect of diversity dependence or facilitation for the five most speciose ant subfamilies. (A) Diversity trajectories of five subfamilies, at the genus level, between the Cretaceous–Paleogene boundary and today. Reconstructions of diversity trajectories are from Jouault *et al.* [11] and have been replicated ten times, incorporating uncertainties around the ages of the fossil occurrences. For each plot, solid lines indicate mean posterior rates; shaded areas show 95% CI. (B) Network showing positive and negative interactions within and between ant subfamilies (only significant correlations are shown) reconstructed with the MCDD model. Each arrow indicates the intensity of interaction imposed by a given guild towards another one. Colour of the geological timescale follows Cohen *et al.* [46] and abbreviations are as follows: ATR: angiosperm terrestrial revolution, EECO: early Eocene climatic optimum, EOT: Eocene–Oligocene transition, K/Pg: Cretaceous–Paleogene boundary, MMCO: middle Miocene climatic optimum. Silhouettes by Corentin Jouault.

50 valid genera; figure 1C) (based on AntWeb data) (figure 2A). Other subfamilies, such as Paraponerinae (monospecific in both extant and extinct ecosystems; approximately 0.01% of all extant species and approximately 0.29% of genera), were excluded from our analyses due to their comparatively low species richness and abundance in ecosystems.

The diversity dynamics of these ant lineages were recently quantified using a Bayesian framework that integrates both fossil and neontological data from time-calibrated phylogenies [11,47]. This approach has proven effective for reconstructing lineage diversification patterns by incorporating taxa not preserved in the fossil record and mitigating some of its inherent limitations [11,48]. Specifically, birth–death models were employed to estimate origination (i.e. genus-level speciation) and extinction rates over time, while accounting for sampling biases such as uneven preservation and the Lagerstätte effect. These models also incorporate time-variable preservation rates and accommodate uncertainties associated with the age of fossil occurrences [49–51].

We based our downstream analyses on the outputs from Jouault *et al.* [11], generated using reversible jump Markov chain Monte Carlo (RJMCMC), the recommended model for estimating origination and extinction rates with PyRate. These RJMCMC analyses integrated both palaeontological and neontological data, mitigating limitations associated with each dataset, such as distributional bias or poor fossil representation of certain clades. The best-fitting preservation model was then selected after comparing non-homogeneous Poisson process, time-variable Poisson process and homogeneous Poisson process models, with a gamma model of rate heterogeneity incorporated to account for variation in preservation rates across lineages [11]. Origination (*Ts*) and extinction (*Te*) times were averaged across 10 independent analyses to reduce the influence of outliers, and these estimates were used to generate lineage-through-time trajectories (all input files are available in electronic supplementary material, file S1). Overall, these combined precautions and approaches provide confidence in the long-term stability and reliability of the results.

All analyses were conducted at the genus level, a common practice in macroevolutionary research. This taxonomic scale offers several methodological advantages: (i) it is less sensitive to stratigraphic binning effects, since most fossil insect species are known from a single deposit or locality, whereas genera typically include multiple species and thus span broader temporal and spatial ranges; and (ii) it also tends to be more taxonomically stable than species [52,53].

Moreover, conducting analyses at the genus level helps reduce the influence of singletons, taxa represented by only one occurrence, which can otherwise inflate perceived diversification or interaction signals [50,51]. By aggregating species within genera, this approach diminishes noise from poorly sampled lineages and enhances the robustness of macroevolutionary inferences. While this necessarily smooths out species-level heterogeneity, it represents a reasonable and often necessary trade-off when dealing with the incompleteness of the fossil record. Furthermore, analyses performed at higher taxonomic levels, such as genus, are also particularly valuable for diminishing the prevalence of singletons because genera typically encompass multiple species.

In ants, the relative proportions of subfamilies within total extant diversity remain remarkably consistent when expressed as percentages of either genera or species (electronic supplementary material, file S1). The five most species-rich subfamilies are also the five richest in genera, indicating a stable, relatively scaling relationship across taxonomic levels. Consequently, although this assumption should be explicitly tested in future work, we expect that the broad macroevolutionary patterns identified at the genus level are probably representative of species-level trends as well.

2.2. Multiple clade diversity-dependence model analysis

To assess the potential effect of diversity-dependence on the diversity dynamics of the five largest ant subfamilies, we used the multiple clade diversity-dependence (MCDD) model in which origination and extinction rates are correlated with the diversity trajectory of other clades [4]. This model, implemented in PyRate [49], postulates that competitive interactions linked with an increase in diversity result in decreasing origination rates and/or increasing extinction rates. The MCDD model allows for testing diversity-dependence between taxa of a given clade and interclade interactions between taxa of distinct clades potentially sharing a similar ecology [4,10].

We extract the past diversity dynamics of the five ant subfamilies (Dolichoderinae: 45 genera; Dorylinae: 27 genera; Formicinae: 51 genera; Myrmicinae: 165 genera; and Ponerinae: 50 genera) using the number of living species at every point in time based on the *Ts* and *Te* estimated under the RJMCMC model in Jouault *et al*. [40] (electronic supplementary material, file S1). We calculated ten diversity trajectories from the ten replicated analyses under the RJMCMC model. Because the fossil record of ants in the Mesozoic is much sparser than during the Cenozoic, and nearly exclusively composed of stem group lineages, we focused our study on the Cenozoic, which witnessed the rapid diversification of crown ants [11,44,47].

Our MCDD analyses were run and repeated on ten replicates (using the *Te* and *Ts* estimated under the RJMCMC model) with 1 billion MCMC generations and a sampling frequency of 50 000. For each of the five ant subfamilies, we computed the median and the 95% HPD of the baseline origination and extinction rates (λi and μi), the within-group diversity-dependence parameters gλi and gμi, and the between-groups diversity dependence parameters gλij and gμij. In the MCDD model, the median of the sampled diversity dependence parameters $g\lambda ij<0$ and $g\mu ij<0$ indicates a positive interaction between clades, so that increasing diversity of a clade j correlates with higher speciation rates and lower extinction rates in clade i. Oppositely, $g\lambda ij>0$ and $g\mu ij>0$ indicate a negative interaction between clades, so that increasing diversity of a clade j correlates with lower speciation rates and higher extinction rates in clade i. Finally, $g\lambda ij = 0$ and $g\mu ij = 0$ imply that no diversity-dependent effects are detected and the diversification dynamics of clade i are independent of the diversity of clade j [8]. The interactions were considered significant when their median was different from 0 and the 95%

highest posterior density (HPD) intervals did not overlap with 0. Output files are available as electronic supplementary material, file S2, and a summary of the results in electronic supplementary material, table S1.

We monitored chain mixing and effective sample size (ESS) by examining the log files in Tracer 1.7.2 [54] and considered the convergence of parameters sufficient when their ESSs were greater than 200.

2.3. Multivariate birth–death model analyses

We also explored diversity-dependent effects using the multivariate birth–death (MBD) model [55]. This dual-model approach was chosen to ensure the robustness of our findings; the MCDD model serves as a powerful exploratory tool for detecting a complex web of interactions simultaneously, while the MBD model, which employs a gamma prior to control for over-parameterization, acts as a more conservative, corroborative test of the key interactions (see [8,55]).

The MBD model allows for changes in origination and extinction rates through time in relation to variables so that origination and extinction rates depend on the temporal variations of each factor. Therefore, it can be used to run a multiple clade diversity-dependence analysis by providing the diversity trajectories of each of the other four ant subfamilies, interacting with a given subfamily, as continuous variables. The diversity trajectories of ant subfamilies were generated by PyRate using the lineages-through-time generated by the RJMCMC analyses (*-ltt* option).

An MCMC algorithm combined with a gamma prior (*-hsp 0*; recommended when testing only a few correlates), controlling for over-parameterization and for the potential effects of multiple testing, jointly estimates the baseline origination ($\lambda 0$) and extinction ($\mu 0$) rates and all correlation parameters ($G\lambda$ and $G\mu$) [8]. In the MBD model, a correlation parameter is estimated to quantify the impact of each variable on origination and extinction independently. The strength and sign (positive or negative) of the correlations are estimated for each variable. When their 95% CI overlaps with zero and their shrinkage weight is below or close to 0.5, the correlation is considered non-significant. The results of the MBD analyses were summarized by calculating the posterior mean and 95% HDP of all correlation parameters and the mean of the respective shrinkage weights (across ten replicates), as well as the mean and 95% HDP of the baseline origination and extinction rates.

We ran the MBD model using 100 million MCMC generations and sampling every 50 000 to approximate the posterior distribution of all parameters ($\lambda 0$, $\mu 0$, five $G\lambda$, five $G\mu$ and the shrinkage weights of each correlation parameter, ωG). We carried out five analyses, over the Cenozoic (*-maxT 66*), to estimate the effect of diversity-dependence between each of the five ant subfamilies of interest. We monitored chain mixing and ESS by examining the log files in Tracer 1.7.2 [54] and considered the convergence of parameters sufficient when their ESSs were greater than 200. Output files are provided as electronic supplementary material, file S2, and summaries of the results in electronic supplementary material, tables S2–S6.

2.4. Birth–death models with time-continuous correlates

To further assess the robustness of our results with respect to changes in the number and composition of clades included in the multivariate analyses, we employed a series of birth–death models with time-continuous correlates (*PyRateContinuous*) [49–51]. Compared with the multivariate MCDD and MBD frameworks, the *PyRateContinuous* analyses are inherently more conservative. PyRateContinuous fits a simplified birth–death process in which speciation and extinction rates are modelled separately as exponential functions of a single time-continuous covariate, using pre-estimated origination and extinction times (see §2.1) rather than the full occurrence data [49–51]. This greatly reduces the number of parameters and the amount of information available to detect subtle correlations. In addition, the use of an exponential link with broad, weakly informative priors on the correlation parameters ($G\lambda$ and $G\mu$) results in wider posterior distributions and significance is assessed strictly through the 95% HPD. Together, these factors cause weaker or marginal relationships identified in the more parameter-rich MCDD and MBD analyses to fall below the significance threshold in *PyRateContinuous*, making it a deliberately stringent tool for cross-validation rather than discovery.

We implemented these models in two complementary ways. First, we tested intraclade diversity dependence (option *-DD*) for the Dolichoderinae, Dorylinae, Formicinae, and Ponerinae, using an exponential model (*-m 0*), in which rates vary as exponential functions of the clades' own diversity. Second, we tested interclade diversity dependence, evaluating pairwise relationships between subfamilies (e.g. Dolichoderinae and Dorylinae, Dolichoderinae and Formicinae) by fitting birth–death models where speciation and extinction rates vary through time as exponential functions (*-m 0*) of a time-continuous variable—specifically, the diversity of another clade.

In the first implementation, correlations were considered significant when the estimated diversity-dependence parameters ($G\lambda$ for speciation and $G\mu$ for extinction) were significantly different from zero based on their 95% HPD. The sign of the parameters determined the direction of the correlation (positive or negative, depending on whether $G \gg 0$ or $G \ll 0$). Because *PyRateContinuous* rescales covariates to range from 0 (present) to 1 (oldest), we inverted the covariate series so that larger values correspond to more recent times, ensuring that positive correlation coefficients ($G\lambda$, $G\mu$) indicate higher speciation or extinction rates with increasing diversity toward the present. The estimated correlation parameters ($G\lambda$ and $G\mu$) were considered statistically significant when their 95% HPD intervals did not overlap zero and were significantly different from zero, indicating a consistent directional association between the diversification dynamics of the focal and predictor clades.

All PyRateContinuous models were run for 50 million MCMC generations, with sampling every 50 000 generations. We assessed chain mixing and ESS using Tracer v.1.7.2 [54], and considered parameter convergence adequate when ESS values exceeded 200. Output files are provided as electronic supplementary material, file S2, and summary of the results in table 1.

3. Results

Our MCDD analysis reveals a series of diversity-dependent effects and inter-subfamily associations among ants (figure 2B; electronic supplementary material, table S1). Among the negative associations, we find that increases in diversity within several subfamilies are associated with decreases in their own origination rates. This is particularly evident in Dolichoderinae, where higher diversity correlates with reduced origination (median: $g\lambda$ = 0.1782; 95% HPD interval: 0.0563–0.3). Similar trends are observed for Dorylinae ($g\lambda$ = 0.0374; 95% HPD: 0–0.2833), Formicinae ($g\lambda$ = 0.048; 95% HPD: 0–0.2072), and Ponerinae ($g\lambda$ = 0.0238; 95% HPD: 0–0.2567), suggesting that higher subfamily-level diversity tends to co-occur with reduced origination within each group (figure 2B; electronic supplementary material, table S1).

Our results also indicate that increasing diversity within Formicinae is positively correlated with their own extinction rates (median: $g\mu$ = 0.1659; 95% HPD: 0–0.2928), and correlates with a rise in extinction rates in Myrmicinae (median: $g\mu$ = 0.0483; 95% HPD: 0–0.2776), pointing to possible inter-subfamily competitive dynamics (figure 2B; electronic supplementary material, table S1).

In contrast, we also detect positive correlations across subfamilies. Notably, increasing Formicinae diversity is associated with higher origination in Dolichoderinae (median: $g\lambda$ = –0.0927; 95% HPD: –0.2466 to 0). Similarly, higher Ponerinae diversity co-occurs with reduced extinction rates in Myrmicinae (median: $g\mu$ = –0.0602; 95% HPD: –0.2825 to 0), suggesting potential stabilizing or facilitative correlations between these clades (figure 2B; electronic supplementary material, table S1).

Using the more conservative MBD model (figure 3A–J), we also detected statistically significant diversity-dependent correlations in both Dolichoderinae (median: $G\lambda$ = –7.68; 95% HPD: –14.6485 to –2.4175; figure 3A,B; electronic supplementary material, table S2) and Formicinae (median: $G\lambda$ = –8.1001; 95% HPD: –17.5549 to –0.7087; figure 3E,F; electronic supplementary material, table S3), indicating that increasing diversity within these subfamilies is statistically associated with lower origination rates (figure 3).

Although the correlations detected in other clades were not statistically significant, our MBD results broadly support a consistent pattern of diversity-dependent dynamics across all subfamilies. Specifically, we observe a negative correlation between diversity and origination in Dorylinae (figure 3C,D; electronic supplementary material, table S4), a positive correlation between diversity and extinction in Formicinae (figure 3E,F; electronic supplementary material, table S3), and a negative correlation between diversity and origination in Ponerinae (figure 3I,J; electronic supplementary material, table S5).

In terms of interclade associations, the MBD model also identifies a statistically supported negative correlation between Dorylinae diversity and Dolichoderinae origination (median: $G\lambda$ = –0.2317; 95% HPD: –0.4965 to –0.0021; figure 3A). Additionally, we recover similar (though not statistically significant) directional correlations as seen in our MCDD analysis with 1) an association between higher Formicinae diversity and increased origination in Dolichoderinae (figure 3A), 2) a correlation

Table 1. Results of PyRateContinuous analyses evaluating diversity-dependent relationships within and between pairs of clades (bold values indicate significant correlations).

		parameters	median	95% HPD	crossvalidations
diversity-dependent effects on Dolichoderinae	effect on origination (Dolichoderinae)	**$G\lambda$**	**−1.9865**	**[−3.1279, −0.9967]**	MCDD & MBD
	effect on origination (Dorylinae)	**$G\lambda$**	**−1.0272**	**[−1.7434, −0.2816]**	MBD
	effect on origination (Formicinae)	**$G\lambda$**	**−1.7688**	**[−2.8449, −0.7429]**	opposite MCDD
diversity-dependent effect on Dorylinae	effect on origination (Dorylinae)	**$G\lambda$**	**−3.28**	**[−4.5457, −2.094]**	MCDD
diversity-dependent effects on Formicinae	effect on origination (Formicinae)	**$G\lambda$**	**−1.4853**	**[−2.3716, −0.4017]**	MCDD & MBD
	effect on extinction (Formicinae)	$G\mu$	−1.0171	[−2.3385, 0.3042]	not significant
diversity-dependent effects on Myrmicinae	effect on extinction (Formicinae)	**$G\mu$**	**−1.9158**	**[−3.3213, −0.7638]**	opposite MCDD
	effect on extinction (Ponerinae)	**$G\mu$**	**−2.235**	**[−3.4359, −1.1737]**	MCDD
diversity-dependent effect on Ponerinae	effect on origination (Ponerinae)	**$G\lambda$**	**−1.6274**	**[−2.5707, −0.7262]**	MCDD

between higher Ponerinae diversity and reduced extinction in Myrmicinae (figure 3H), and 3) negative associations between Formicinae diversity and Myrmicinae extinction (figure 3H; electronic supplementary material, table S6).

Cross-validation of the correlations obtained with the MCDD and MBD models using the *PyRateContinuous* birth–death framework provided significant statistical support for several intra-subfamily effects. Negative diversity-dependent effects on speciation were detected for Dolichoderinae (median: $G\lambda = -1.9865$; 95% HPD: –3.1279 to –0.9967), Dorylinae ($G\lambda = -3.28$; 95% HPD: –4.5457 to –2.094), Formicinae ($G\lambda = -1.4853$; 95% HPD: –2.3716 to –0.4017) and Ponerinae ($G\lambda = -1.6274$; 95% HPD: –2.5707 to –0.7262). In contrast, the intra-subfamily effect on Formicinae extinction was not statistically significant (table 1). Regarding inter-subfamily interactions, the effect of Dorylinae on Dolichoderinae origination displayed the same direction as the MBD model ($G\lambda = -1.0272$; 95% HPD: –1.7434 to –0.2816), and the effect of Ponerinae on Myrmicinae extinction the same direction as the MCDD model ($G\mu = -2.235$; 95% HPD: –3.4359 to –1.1737). The effect of Formicinae on Dolichoderinae origination ($G\lambda = -1.7688$; 95% HPD: –2.8449 to –0.7429), and Formicinae on Myrmicinae extinction ($G\mu = -1.9158$; 95% HPD: –3.3213 to –0.7638) are inverted when compared to the MCDD analyses.

4. Discussion

This study builds upon a recent broad-scale analysis of potential diversity-dependent effects in ants, which identified a significant signal when examining the entire evolutionary history of the clade based solely on palaeontological data (excluding singletons), thereby laying the groundwork for the present research [11]. However, that earlier study did not deeply investigate diversity-dependent interactions within or among crown ant lineages.

Expanding on these dynamics, our MCDD and MBD analyses reveal that most interclade effects are asymmetric, with significant correlations detected in only one direction (figures 2 and 3). We interpret this pattern as reflecting biological asymmetry, potentially arising from directional predation/competitive dominance or facilitative influences—such as those exerted by ecologically broader, more diverse or earlier-radiating clades on others. At local ecological scales, frameworks such as competition hierarchies (e.g. [56]) demonstrate that interspecific interactions are frequently unidirectional, with

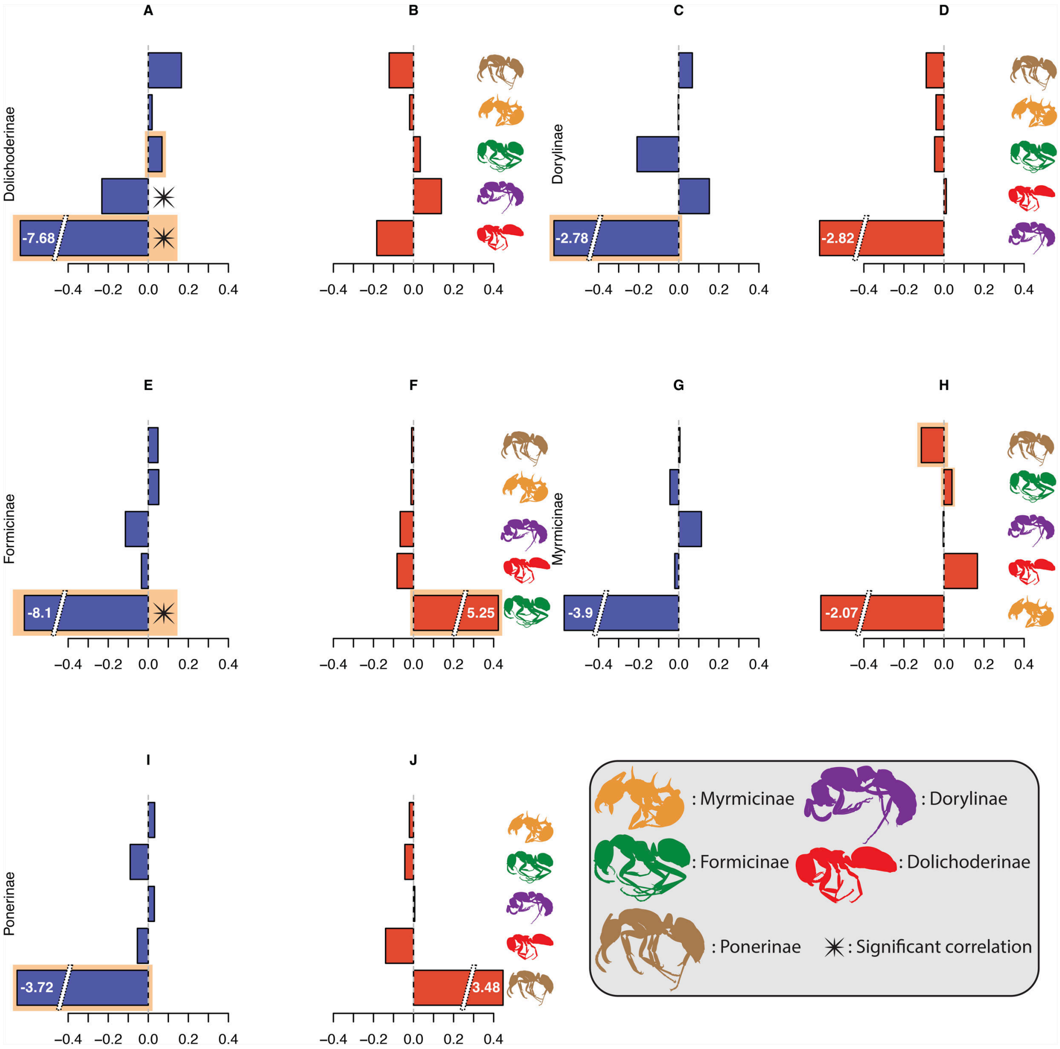

Figure 3. Correlations between changes in diversity of ant subfamilies and their diversification estimated with the MBD model. Bayesian inferences of correlation parameters on origination (blue: A,C,E,G,I) and extinction (red: B,D,F,H,J) with biotic factors. Stars indicate a significant correlation parameter for a given variable (shrinkage weights (*w*) > 0.5). The orange highlight shows correlations that were also recovered as statistically significant in the MCDD model analysis, underscoring the robustness of these findings. Silhouettes by Corentin Jouault.

dominant taxa suppressing subordinate ones. When these asymmetric dynamics are projected over geological timescales, they correspond to active displacement—a process in which the rise of one clade directly alters the diversification parameters of another, ultimately contributing to its decline [4,27,57,58]. Such asymmetry aligns with scenarios of predation, putative hierarchical competition, unidirectional diversity dependence, or facilitative interactions among ant lineages that we discuss below (see §4.2).

Our MBD analyses also tend to yield stronger correlation values for intraclade interactions than for interclade interactions (figures 2 and 3). Biologically, competitive interactions are generally expected to be stronger within subfamilies—where species often occupy overlapping ecological niches and compete directly for similar resources—than between subfamilies [36–38]. As a result, interclade effects may genuinely be smaller in magnitude.

Our *PyRateContinuous* analyses broadly corroborated the results obtained with the MBD and MCDD models, with two main exceptions: (i) the effect on extinction in Formicinae was not statistically significant, and (ii) the correlations between Formicinae and Dolichoderinae, as well as between Formicinae and Myrmicinae, exhibited opposite signs compared to those inferred from the MCDD analyses. *PyRateContinuous* evaluates each interclade relationship independently using rescaled time-continuous covariates, whereas MCDD estimates multiple interdependent correlations jointly within a hierarchical Bayesian framework, potentially capturing shared variance that reverses direction when the relationship is tested alone. These structural differences can lead to divergences in both the direction and magnitude of inferred effects, potentially emphasizing different temporal components of the relationship, particularly for weak or borderline-significant interactions, which *in fine* reflects the greater sensitivity of MCDD to shared diversification dynamics and the more conservative, pairwise nature of *PyRateContinuous* analyses. The MBD analyses appear to support this hypothesis. As an intermediate model in terms of sensitivity, it reveals the same trends observed in the MCDD analyses, albeit without statistical significance. At present, it is not possible to fully rule out these two interactions, as they are also biologically plausible (see §4.2), but they will require further investigation in future studies.

4.1. Intraclade negative interactions in crown ants

Our MCDD analysis captures a pattern of intraclade negative interactions among Dolichoderinae, Ponerinae, Dorylinae and Formicinae (figures 2B and 3). These results are statistically supported by the more conservative MBD model for Dolichoderinae and Formicinae, and detected for Dorylinae and Ponerinae, but not statistically significant (figure 3A,C,E,I). In our analysis, Dolichoderinae and Formicinae exhibit the strongest intraclade negative effects on diversification ($g\lambda$ = 0.1782 and $g\mu$ = 0.1659, respectively). Notably, Formicinae show a unique pattern, with negative effects on both origination and extinction (statistically significant only for origination in our MBD analysis), whereas in other clades, the negative effect is observed only on origination (figures 2B and 3E,F). However, no significant intraclade negative effect was found for Myrmicinae, which are apparently more impacted by interclade interactions (figures 2B and 3G,H).

We propose that the stronger intraclade effects observed in Dolichoderinae and Formicinae can be explained by their ecological ubiquity and higher global abundance compared to Dorylinae or Ponerinae (e.g. [32,59–61]). This superabundance is particularly pronounced in arboreal communities. For instance, in the tropical lowland rainforests of the Peruvian Amazon, sampling over 62 000 ants revealed that a single Dolichoderinae species, *Dolichoderus bispinosus* (Olivier, 1792), dominated both the biomass (64.2%) and the individual counts (69%) [62]. A similar dominance pattern is observed in tropical Colombian lowland rainforests, where Dolichoderinae and Formicinae together represent approximately 60% of total ant abundance [60], and in Australian temperate rainforests as well [63,64]. Along altitudinal gradients in Europe or in local site studies in North America, Dolichoderinae and Formicinae likewise constitute the majority of both species diversity and abundance (e.g. [65,66]). Additionally, species within these subfamilies generally exhibit less specialized diets, which probably increases the probability of resource overlap and competition among closely related species. This notable absence of a negative signal in the hyper-diverse Myrmicinae suggests a distinct macroevolutionary dynamic that will be explored in detail below (see §4.4).

The unique pattern observed in Formicinae, characterized by both elevated extinction rates and slowed speciation rates as diversity increases, may be a result of markedly strong competition within certain lineages of this clade. *Formica* species in particular are noted to display high levels of intraspecific and interspecific aggression towards other members of the genus [67–69]. This genus is highly diverse, comprising around 180 extant species, and is hyper-abundant in most temperate ecosystems, where it often accounts for more than 50% of all collected specimens and has a biomass comparable to that of large mammalian predators [66,70]. They are also diverse and abundant in the fossil record, with 58 extinct species described to date, representing approximately 28% of all known extinct Formicinae (AntWeb). Battles between colonies occur frequently; during the spring, aggression is especially high and workers from other colonies comprise a significant proportion of a colony's diet [71]. Moreover, many *Formica* species are facultatively dulotic, relying on kidnapped workers from other congeneric colonies to favour their colony's survival and expansion [72]. Such behaviour directly reduces the targeted colony's fitness, and over macroevolutionary timescales, may be one of the plausible mechanisms contributing to elevated extinction rates within the subfamily. Additionally, in high northern latitudes, assemblages are frequently dominated by Formicinae, fostering interactions among species and increasing the likelihood of intraclade competition.

Evidence for intraclade negative interactions is observable in modern ecosystems and can provide insight into how ecological limits constrain diversification. For example, dolichoderine species of the ant genus *Azteca*, which commonly nest in *Cecropia* trees, often establish numerous incipient colonies on a single tree [73,74]. However, such coexistence is typically short-lived, culminating in intense intra- and interspecific competition. Ultimately, only one colony tends to dominate, eliminating others through direct fight [74,75]. This competition occurs both within species, where colonies race to grow rapidly and monopolize space, and between closely related species, as multiple *Azteca* species may attempt to colonize the same tree simultaneously [73,74]. In the Formicinae subfamily, *Lasius niger* (Linnaeus, 1758) engages in pastoral behaviour, tending aphids to harvest honeydew. This activity often brings it into direct competition with other ant species, such as *Formica japonica* (Motschulsky, 1866). Conflicts frequently occur when these species encounter each other while tending aphids [76].

In predatory lineages such as the Dorylinae or some Ponerinae, the observed negative intraclade diversity dependence in diversification ($g\lambda$ = 0.0374; $g\lambda$ = 0.0238) probably reflects escalating competition over food resources as species richness increases. Within Dorylinae, particularly among army ants, many species exhibit varying degrees of dietary specialization, often preying predominantly on other ant species [77–79]. For example, studies in the La Selva Biological Station (Costa Rica) show that *Eciton burchellii* (Westwood, 1842) primarily targets *Camponotus*, *Neivamyrmex pilosus* (Smith, F., 1858) focuses on *Crematogaster*, and *Eciton dulcium* (Forel, 1912) preys on *Pachycondyla*. Other prey genera, such as *Pheidole*, are attacked by multiple species, including *Neivamyrmex gibbatus* Borgmeier, 1953, *Eciton vagans* (Olivier, 1792), and *Eciton mexicanum* Roger, 1863 [78], suggesting overlapping foraging niches. Despite some degree of ecological differentiation across prey identity, foraging strata (ground versus arboreal), and temporal activity (diurnal versus nocturnal), interspecific overlap remains common. When species such as *E. vagans* and *E. mexicanum* forage simultaneously in the same habitat and target the same prey (e.g. *Pheidole rugiceps* Wilson, 2003), direct competition becomes inevitable due to spatial and temporal limits on prey availability. While niche partitioning may buffer some interspecific conflict, it does not eliminate competition entirely and may instead concentrate competitive pressures among species [80–82]. Indeed, the significant dietary overlap on key, abundant prey resources like the genus *Pheidole* probably represents the specific ecological pressure point that manifests as a negative diversity-dependent signal over macroevolutionary time. Fossil evidence suggests that these behaviours have deep evolutionary origins, with signs of antagonistic interactions among stem ants, as evidenced by two species of *Gerontoformica* trapped while fighting in Kachin amber, dating back to the mid-Cretaceous [83].

While these are localized ecological interactions, they reflect a broader dynamic: as ant diversity increases, the intensity of competition for limited nesting sites (e.g. *Cecropia* tree) or ecological resources (e.g. prey or aphids) rises, reducing or constraining opportunities for the establishment and persistence of new lineages. Over evolutionary timescales, such niche saturation can slow diversification by decreasing speciation rates or increasing extinction risk, key features of diversity-dependent diversification. Similar mechanisms may operate across other taxa, especially those with tightly defined resource requirements and life-history constraints, illustrating how ecological limits can shape macroevolutionary patterns.

4.2. Interclade negative interactions in crown ants

Our results indicate that, over macroevolutionary timescales, intraclade interactions exert a stronger influence on diversification dynamics than interclade effects, which are often asymmetric. Among the eight significant diversity-dependent interactions we detected, five involved negative intraclade effects, while only one reflected a negative interclade interaction (figures 2B and 3). This pattern suggests that as diversity increases within a lineage, competition and other antagonistic interactions may sometimes increasingly constrain further diversification in another. Nonetheless, negative ecological interactions across taxonomic boundaries, whether between species, genera or subfamilies, remain frequent and ecologically consequential [84]. These include territorial aggression, chemical exclusion, competition for shared resources, predation and even social parasitism [33,85,86].

Interestingly, the asymmetry observed in our interclade effects, under both the MCDD and MBD models, probably reflects genuine ecological patterns consistent with the feeding behaviours of the lineages (figures 2 and 3). For instance, our MBD analysis reveals a significant negative correlation between the origination of Dolichoderinae and the increasing diversity of Dorylinae, potentially mirroring a unidirectional predator–prey dynamics (figure 3A). Dorylinae ants are predators that frequently target other ants, including Dolichoderinae, whereas the reverse scenario is less probable [78]. Thus, the directional interactions documented in modern ecosystems are plausibly echoed in our macroevolutionary results.

As highlighted in the *Azteca–Cecropia* case, competition among closely related ants for nesting sites and food resources is common. However, competition is not limited to close relatives; interclade competition also occurs when distantly related species exploit overlapping niches. For instance, *Cecropia* trees are inhabited not only by *Azteca*, but also by *Camponotus*, *Crematogaster*, *Neoponera*, *Pachycondyla* and *Pseudomyrmex* [87], all of which compete for nesting space and access to glycogen-rich Müllerian bodies. The correlation observed in our *PyRateContinuous* analyses, in which increasing Formicinae diversity is associated with a reduction in Dolichoderinae origination rates, may reflect competitive interactions between these two generalist clades. Both share overlapping ecological niches and have a high abundance in past and present ecosystems (table 1). Our analyses further suggest that increasing diversity in Formicinae is associated with elevated extinction rates in Myrmicinae ($g\mu$ = 0.0483), pointing to a long-term macroevolutionary signal of interclade antagonism, potentially driven by competition or even predation. Modern dominance hierarchies, generally driven by differences in foraging and aggression, are frequently dominated by formicines and dolichoderines, with myrmicines often being subordinate species. Such formicine-dominant hierarchies are especially pronounced in northern latitudes: taiga ant communities are dominated by Formica species, with *Myrmica* and *Leptothorax* being subordinate [88]; similarly, northern European island communities are dominated by *Formica* and *Lasius* species [89]. Interestingly, myrmicine species are more likely to be dominant in disturbed habitats today [36], making it possible that in the future the direction of this diversity-dependent interaction may switch. While our models do not detect the timing or biogeographic locality of diversity-dependent interactions, it is possible that across geological timescales, competitive suppression by dominant formicine species in formicine-rich latitudes could produce the macroevolutionary pattern of increased myrmicine extinction rates detected by our model (figures 2B and 3).

4.3. Facilitative interactions in crown ants

While our results highlight the significant role of negative interactions in shaping ant evolutionary history over time, they also reveal evidence of positive interactions between Formicinae and Dolichoderinae—also detected under the more conservative MBD model, but not statistically significant (figure 3A)—as well as between Ponerinae and Myrmicinae. Ants are well known not only for their competitive behaviours but also for their facilitative interactions, including complex forms of cooperation observed both within and between closely or distantly related species [33]. Our finding of a positive interaction whereby increased Ponerinae diversity is associated with reduced extinction in Myrmicinae is particularly noteworthy, as it runs counter to previous hypotheses of competition [39]. Although not statistically significant under the more conservative MBD model, the correlation was estimated in the same direction, supporting the robustness of this effect (figure 3H). A compelling ecological mechanism for this macroevolutionary pattern can be found in documented cases of commensalism or even parabiosis. For example, the tiny myrmicine ant *Strumigenys maynei* is known to form compound nests within the hollow-branch nests of the much larger ponerine ant *Platythyrea conradti* [90,91]. In this relationship, the *Strumigenys* workers scavenge on small prey thriving in the organic nest material collected by *P. conradti*, gaining a reliable food source and a protected environment [90,91], which would directly reduce their extinction risk. In this interaction, the ponerine host benefits from the nest defence capabilities of *S. maynei*. This specific, documented case of facilitation provides a powerful microevolutionary model for the large-scale pattern of reduced extinction detected by our analysis (figures 2B and 3). Moreover, such cases of facilitation also provide examples of effective niche 'construction', where the diversification of one clade leads to the creation of new microhabitats and niches for another, providing a mechanism that may buffer the latter against extinction and even drive its increased speciation. Ants are notable for shaping the biodiversity of many phylogenetically disparate taxa [31,92]; akin to myrmecophages and myrmecophiles, it is plausible that ecological diversification within a given clade leads to ecological diversification within others.

Another remarkable example of positive interactions among ants is found in ant–gardens, complex ant–plant mutualisms in which ants cultivate epiphytes in exchange for nesting space and nutritional rewards (e.g. [41,93–96]). These gardens typically involve species from the Formicinae, Dolichoderinae, Ponerinae and Myrmicinae subfamilies, though not all are necessarily present in every system. In Central and South America, ant–gardens are primarily maintained by genera such as *Crematogaster* and *Solenopsis* (Myrmicinae), *Azteca* and *Dolichoderus* (Dolichoderinae) and *Camponotus* (Formicinae), while *Anochetus* and *Odontomachus* (Ponerinae) are less commonly involved [97]. Within these ant-gardens, it is not uncommon to find two species exploiting the same food sources and cohabiting in non-obligatory, mixed colonies, where they tolerate each other and share a nest while maintaining separate brood chambers [98,99]. Both species actively defend their garden against a wide range of threats, including desiccation, invading ant species and phytophagous insects [100–104]. Such interactions can also reach a peak of complexity in mutualistic associations. For example, in the ant-gardens formed by

Crematogaster levior Longino, 2003 and *Camponotus femoratus* (Fabricius, 1804), the smaller *Crematogaster* species benefits from the nest-building activities of *Camponotus*, including seed-carrying behaviour and protection offered by the larger ants [94]. In return, *Camponotus* benefits from *Crematogaster*'s superior ability to locate food sources during foraging, which they often co-exploit or sometimes steal from the *Crematogaster* [94]. Our PyRateContinuous analyses, showing that increases in Formicinae diversity correlate with reduced extinction rates in Myrmicinae, may reflect such interactions, which could ultimately promote the persistence and survival of these clades (table 1). While this example focuses on interactions between formicine and myrmicine ants, similar cases of cohabitation and parabiosis have been documented between the Ponerinae (*Odontomachus panamensis* Forel, 1899 and *Neoponera goeldii* Forel, 1912) and the Myrmicinae (*Crematogaster limata parabiotica* Forel, 1904), with species from both subfamilies sharing the same nest and engaging in similar interactions [105]. Extended over long evolutionary timescales, these types of facilitative interactions offer a compelling ecological mechanism that could underlie the macroevolutionary pattern of increasing speciation or diminishing extinction rates detected by our models (figures 2B and 3).

4.4. The myrmicinae exception: diversification through niche partitioning and dispersion

The absence of a detectable negative intraclade signal in the Myrmicinae may represent a profound biological signal that speaks to the subfamily's exceptional evolutionary success [106]. As the most species-rich ant subfamily, accounting for roughly half of all described species (over 6000 extant species), Myrmicinae appear to have circumvented the diversity-dependent constraints that limit other clades. We propose that this is a direct consequence of their unparalleled adaptive radiation, which has facilitated niche partitioning and continuously expanded the available ecospace, but also the numerous dispersal events known for most of their genera [107–110].

Unlike the other subfamilies, which are sometimes more constrained in their ecology (e.g. predaceous Ponerinae ants), Myrmicinae have diversified along multiple niche axes (e.g. nesting strategies, feeding, colony size), thereby mitigating direct competition among their constituent lineages. First, while many myrmicines are generalists, the subfamily has produced remarkable trophic specialists. These include dedicated seed-harvesters in genera like *Pogonomyrmex* and *Messor* [33], and most famously, the tribe Attini, which evolved obligate fungus-farming—a unique agricultural strategy that created an entirely new trophic niche among ants [111,112]. Second, myrmicines occupy nearly every terrestrial habitat, from deep soil and leaf litter to the highest forest canopies [47,108,109,113,114]. This vertical and horizontal stratification allows different lineages to exploit different resources and avoid spatial overlap. Then, myrmicine colonies range from fewer than 50 individuals to massive supercolonies [115,116]. They exhibit a wide array of social structures (e.g. monogyny, polygyny), caste specializations (i.e. with or without dimorphism) and reproductive strategies (e.g. independent and dependent colony founding) [114,116–118]. This variation allows different species to adapt to different resource distributions and levels of habitat stability. Lastly, myrmicine ants possess an exceptional capacity for dispersal, achieved through a variety of strategies including long-distance nuptial flights, rafting across bodies of water and colony budding, each enabling the colonization of habitats far beyond their initial or native range [107,109,114,119]. This high dispersal ability probably facilitated the expansion of populations into novel or underexploited ecosystems rather than concentrating diversification within already saturated habitats. By continually accessing new ecological opportunities, myrmicines can circumvent the density-dependent constraints on speciation that often arise from competition in established communities. In other words, rather than intensifying resource overlap and competitive exclusion within the clade, dispersal-driven range expansion diffuses potential conflicts by spreading lineages across a broader array of environmental contexts. Over evolutionary time, this dynamic may contribute to both the clade's remarkable global distribution and the relatively weak signature of intraspecific diversity dependence detected in our analyses (figures 2B and 3).

Therefore, the absence of a negative intraclade signal is, paradoxically, strong evidence for the power of the diversity-dependence hypothesis. The model detects the 'filling' of available ecospace. For most subfamilies, this ecospace is a relatively contained niche that eventually becomes saturated. For Myrmicinae, however, constant dispersion and innovation have created a vast and expanding mosaic of semi-independent niches. A fungus-farming attine does not compete with a seed-harvesting *Messor*. The model correctly detects that, at the broad subfamily level, this mosaic is not 'full,' transforming a puzzling result into a powerful conclusion about the nature of adaptive radiation.

4.5. Future work

Our analyses are independent of phylogenetic framework, although they incorporate information derived from time-calibrated phylogenies, due to the nature of the models employed. Nonetheless, diversity-dependence models designed to detect similar effects using time-calibrated phylogenetic trees have been developed for over a decade. Early versions of these models were relatively simplistic, notably due to their assumption of zero extinction [15,120], but have since been refined to incorporate more realistic dynamics, including non-zero extinction rates [18,121].

While these methods have been predominantly applied to vertebrate or plant clades, they are equally applicable, and arguably underutilized, in the study of invertebrate evolution [15,122]. Specifically, exponential diversity-dependence (DDX) or diversity-dependence (DDL) models, either with or without a parameter model for extinction (e.g. DDL-E and DDL+E), could provide a powerful phylogenetic test of our findings. The main limitation to their application lies in the difficulty of achieving comprehensive sampling for extant species, particularly within highly diverse insect groups that can contain thousands of species. However, ants represent an 'exception' [121]. Thanks to the availability of molecular data, a significant proportion of ant diversity can be included in time-calibrated phylogenies [47], making them suitable candidates for such tree-based approaches. We therefore advocate for the development of a phylogeny-based counterpart to our study, which would allow for cross-validation of the trends and correlations identified through 'fossil-based' inferences.

Our study focuses on the most speciose ant subfamilies, which also possess the most temporally complete fossil records during the Cenozoic. However, other subfamilies that are ecologically significant in modern ecosystems, particularly in tropical regions, such as Ectatomminae, were not included in our analysis. This exclusion is due to the current limitations of their fossil record, which we consider insufficient to support robust temporal and statistical inferences [123]. Looking ahead, we hope that future discoveries and improvements in the fossil record of these subfamilies will enable the refinement of our hypotheses. In particular, efforts to redescribe and describe promising Cenozoic paleomyrmecofaunas (e.g. Fushun or Oise amber faunas) may help expand our understanding of their macroevolutionary dynamics.

5. Conclusion

Our findings demonstrate that the diversification of ants during the Cenozoic was not driven by biotic or abiotic factors in isolation, but by their continuous interplay. The persistent signals of competition and facilitation we detect are clear evidence of Red Queen dynamics, where the evolutionary fate of each subfamily was intrinsically linked to the diversity of its relatives and ecological counterparts. However, these biotic interactions played out on an environmental 'stage' that was constantly being reshaped by the Court Jester's abiotic forces.

The major paleoevents of the Cenozoic (figure 2A) probably modulated the intensity and nature of these interactions. For example, the global cooling and aridification associated with the Eocene–Oligocene transition drove the expansion of grasslands and savannas. This biome turnover would have created vast new ecological opportunities, potentially favouring generalist foragers common in Formicinae and Myrmicinae and thereby intensifying the competitive interactions our model detects between them. In this view, abiotic events (the Court Jester) periodically altered the ecological 'rules of the game,' which in turn altered the landscape of competition and facilitation (the Red Queen) that proximately shaped diversification rates. This study thus provides a compelling case study of how continuous Red Queen processes act as the engine of diversification, while the track is laid and periodically re-routed by the forces of the Court Jester.

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

Data accessibility. The original dataset is extracted from Jouault *et al.* [11] and available in the following Figshare digital repository: https://figshare.com/s/1d6a5e5639e797370c05 or as supporting information in the original paper. All the supplementary files used for the analyses are also available in the electronic supplementary material [124].

Supplementary material is available online [125].

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

Authors' contributions. C.J.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; A.S.: investigation, validation, writing—original draft, writing—review and editing; C.S.: conceptualization, investigation, 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.

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