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The Angiosperm Terrestrial Revolution buffered ants against extinction

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With ~14,000 extant species, ants are ubiquitous and of tremendous ecological importance. They have undergone remarkable diversification throughout their evolutionary history. However, the drivers of their diversity dynamics are not well quantified or understood. Previous phylogenetic analyses have suggested patterns of diversity dynamics associated with the Angiosperm Terrestrial Revolution (ATR), but these studies have overlooked valuable information from the fossil record. To address this gap, we conducted a comprehensive analysis using a large dataset that includes both the ant fossil record (~24,000 individual occurrences) and neontological data (~14,000 occurrences), and tested four hypotheses proposed for ant diversification: co-diversification, competitive extinction, hyper-specialization, and buffered extinction. Taking into account biases in the fossil record, we found three distinct diversification periods (the latest Cretaceous, Eocene, and Oligo-Miocene) and one extinction period (Late Cretaceous). The competitive extinction hypothesis between stem and crown ants is not supported. Instead, we found support for the co-diversification, buffered extinction, and hyper-specialization hypotheses. The environmental changes of the ATR, mediated by the angiosperm radiation, likely played a critical role in buffering ants against extinction and favoring their diversification by providing new ecological niches, such as forest litter and arboreal nesting sites, and additional resources. We also hypothesize that the decline and extinction of stem ants during the Late Cretaceous was due to their hyper-specialized morphology, which limited their ability to expand their dietary niche in changing environments. This study highlights the importance of a holistic approach when studying the interplay between past environments and the evolutionary trajectories of organisms.

birth–death models | Formicoidea | flowering plants | macroevolution | paleoenvironment

Understanding how clades wax and wane, delving into the factors that spurred the diversification of flourishing lineages or sealed the fate of now-extinct ones, is of prime interest in evolutionary biology (1, 2). Combining paleontological—the primary source of information on biodiversity in the distant past—and neontological data, together with advances in analytical methods, have shed light on the intricate dynamics of diversification across various lineages and through time (3–7). Abiotic factors like continental fragmentation and temperature fluctuations have been suggested as significant drivers of diversification (8, 9), as well as key innovations or biotic changes, such as the Angiosperm Terrestrial Revolution (ATR, 100 to 50 Ma) (10–13). All these factors have been primarily associated with bursts of diversification (i.e., the difference between origination and extinction). Extinction has not been ignored but, beyond mass extinctions, it has received comparatively less attention (14–18).

The Cretaceous (145 to 66 Ma) period witnessed a surge in insect diversification (19), a phenomenon undeniably linked to the ATR. The ATR marked a shift from gymnosperm-dominated ecosystems to angiosperm-dominated ecosystems (17, 20, 21). This transition led to profound alterations in ecological niches, and many novel opportunities for ecological relationships to evolve (13, 22, 23). Thus, many examples correlated the diversification of angiosperms with that of speciose insect lineages, even when they were offset in time (24–29). Such a co-diversification is a frequent explanation in diversification studies. Competitive extinction is another common hypothesis when one lineage diversifies while another one with similar features goes extinct (sometimes dubbed a double-wedge pattern (17, 30–33)). However, co-diversification and competitive extinction represent only a fraction of diversification phenomena, most of which can be tested with process-based diversification and diversity-dependent models.

Ants (Formicoidea) represent a relevant group to dwell further into these hypotheses. They are ubiquitous keystone taxa in many habitats, constitute a major component of the Earth's biomass, and directly or indirectly support or threaten other species through complex biotic interactions (34, 35). Ants have both their phylogenetic relationships thoroughly investigated (36, 37) and a rich fossil record spanning 100 My (38, 39). A distinctive

Significance

All lineages have experienced changes in their diversity dynamics, sometimes leading to their complete disappearance from Earth. The underlying causes of these extinctions or diversifications often remain puzzling, particularly when delving into deep time. Using an unprecedented combination of paleontological and neontological data, we investigate the past diversity dynamics of stem and crown ants. Our results challenge one of the most common hypotheses explaining ant extinction: the competitive exclusion of stem ants by crown ants. Instead, the Angiosperm Terrestrial Revolution acted as a buffer against extinction and a driver of diversification in ants. Our approach clarifies one of the most widely accepted patterns in insect–plant diversification.

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double-wedge pattern has been derived from this data, where stem ants have coexisted alongside crown ants before being fully replaced by them (38, 39). This intriguing pattern has sparked the formulation of several hypotheses (40), which are not necessarily mutually exclusive. Stem ants may have failed to adapt to the ATR perhaps due to hyper-specialization leading to high extinction level for specialized lineages during the ATR (Fig. 1*A*); or they may have been outcompeted by crown ants through a competitive extinction (Fig. 1*B*). Besides, it is likely that the ATR played a critical role in the diversification dynamics of these insects via a co-diversification history (24, 41, 42): Fig. 1*C*). Finally, the ATR may have buffered crown ants against extinction, leading to reducing their probability to go extinct (40; Fig. 1*D*).

Here, we tested these hypotheses and compiled a genus-level fossil record of Formicoidea that spans the entire existence of the superfamily since their first records in the mid-Cretaceous (ca. 100 Ma). We combined fossil data with neontological data extracted from recent time-calibrated phylogenies (43). We used birth–death models in a Bayesian framework (*Materials and Methods*) to estimate extinction and origination (speciation at the genus level) rates of Formicoidea and constitutive lineages through time, while accounting for biases in the fossil record (e.g., heterogeneous preservation, Lagerstätte effect) by incorporating a time-variable preservation process and mitigating uncertainties associated with the age of fossil occurrences (3, 4, 6). From these diversification estimates, including those derived from diversity-dependent analyses, we also assessed the support for four different hypotheses commonly proposed to explain ant diversification: hyper-specialization, competitive extinction, co-diversification, and buffered extinction (Fig. 1). We finally examined the putative role of past environmental changes (e.g., changes in the relative abundance of angiosperms and gymnosperms in ecosystems, temperature) to better evaluate the role of the ATR in ant evolution.

Results and Discussion

Macroevolutionary Scenarios for Ants. Using both the fossil record and a combination of fossil and neontological data, we estimated the temporal variation in the rates of origination and extinction (Fig. 2 and *SI Appendix*, Figs. S1–S32). These estimates were used to elucidate past diversity dynamics and present-day diversity of ants using different birth–death models. Our results reveal that ant evolution has been punctuated by episodes of major origination and extinction (Fig. 2*A*). We found evidence for three distinct periods of ant diversification: after the K/Pg boundary (66 Ma), the Priabonian (37.7 to 33.9 Ma), and the Oligo-Miocene (33.9 to 23.03 Ma); and one period of major extinction (the Late Cretaceous, 100.5 to 66 Ma), all with significant shifts in net diversification rates (origination minus extinction rate, Fig. 2*B*).

Ants belonging to both the crown and stem groups have been documented in amber deposits dating back to the mid-Cretaceous (Fig. 2*C*; French amber and Kachin amber, Myanmar; ca. 99 Ma) (44–47). Stem ants were already well diversified at this period (38, 39, 45, 46). This suggests that they diversified earlier even though the fossil record is depauperate before the mid-Cretaceous. The decline of stem ants during the Late Cretaceous marks a first critical period in the evolutionary history of ants. While our understanding of ant diversity during the latest Campanian–Paleocene interval is limited, the few identified taxa exclusively belong to the crown group (48–50), indicating that stem ants did not survive the K/Pg event or the last stages of the ATR. The extinction rate of ants during the Late Cretaceous (≈2.9 times the background extinction rate for fossil-based analysis) is higher than the origination rate (Fig. 2 *A*, *B*, *D*, *E*, *G* and *H*). Not surprisingly, this extinction mainly affected stem ants (background extinction rate ≈0.16 events/My/lineage), whose diversity declined strongly during the Late Cretaceous (Fig. 2 *C*, *F*, and *I* and *SI Appendix,*

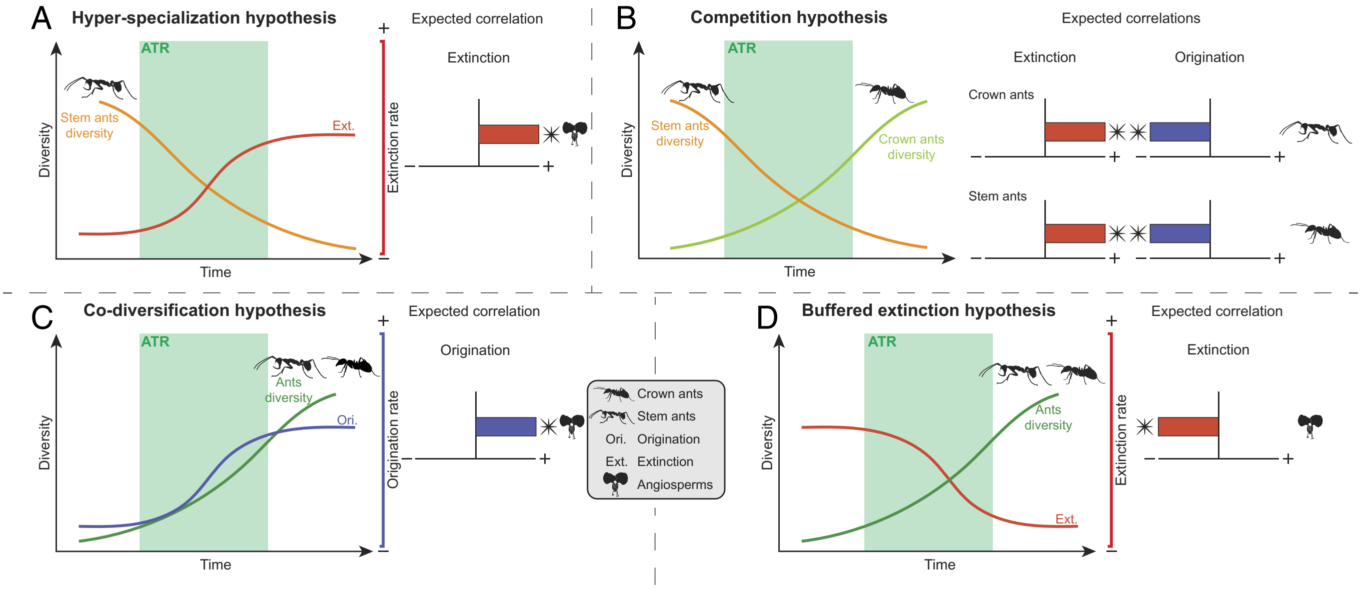

Fig. 1. Main hypotheses to explain the past diversity dynamics of ants. (*A*) Hyper-specialization hypothesis, with the diversity of stem ants decreasing during the ATR while their extinction increased due to their inability to adapt to environmental changes. As a result, a significant positive correlation is expected between the extinction of stem ants and the rise of angiosperms. (*B*) Competitive extinction hypothesis with a double-wedge pattern. The expected results for this hypothesis are a significant positive correlation between the extinction of stem ants and the increase of diversity in crown ants (the same for crown ants) and a significant negative correlation between the origination of stem ants and the increase of diversity in crown ants (the same for crown ants). (*C*) Co-diversification hypothesis, with the diversity and origination of ants increasing synchronously to angiosperms diversification. The expected result for this hypothesis is a significant positive correlation between ant origination and the rise of angiosperms. (*D*) Buffer hypothesis, with the diversity of ants increasing synchronously with angiosperm diversification and extinction decreasing oppositely. The expected result for this hypothesis is a significant negative correlation between ants extinction and angiosperm diversification (i.e., angiosperms tend to decrease ants extinction). The green block represents the ATR. Silhouettes from http://phylopic.org/. Licenses at https://creativecommons.org/publicdomain/zero/1.0/ or by Corentin Jouault.

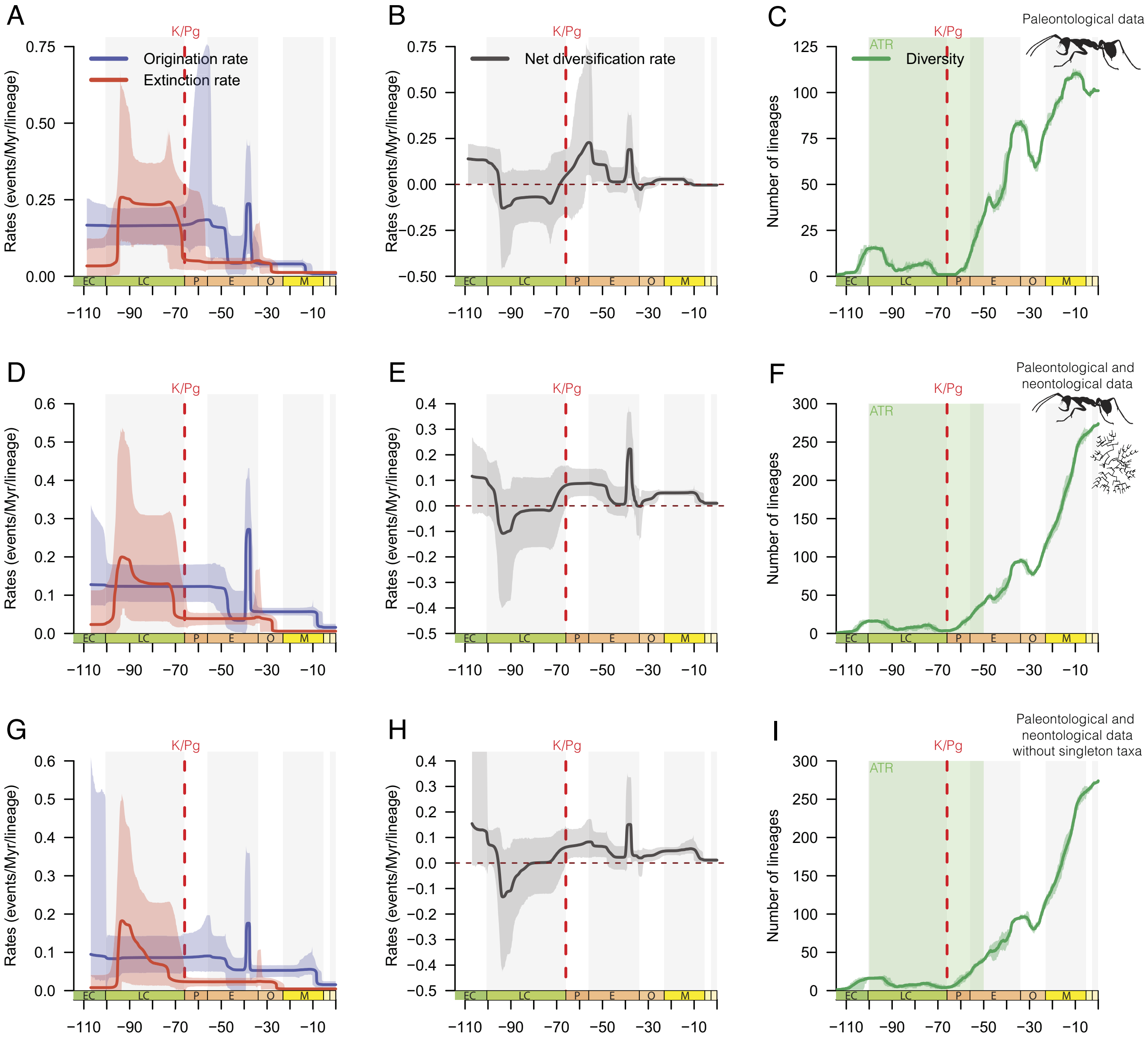

Fig. 2. Diversification and diversity dynamics of ants. Bayesian estimates of origination (blue), extinction (red), net diversification (black, origination minus extinction) rates, and diversity of all ants inferred from paleontological data (*A–C*), from the combination of paleontological and neontological data (*D–F*) and from the combination but without singletons (*G–I*). Net diversification decreased during the Late Cretaceous. Ants diversified during the latest Cretaceous, the Eocene, and the Oligo-Miocene. The diversity of ant genera greatly increases just after the K/Pg, with a rebound after the Eocene (partially due to the Baltic amber). Reconstructions of diversity trajectories replicated to incorporate uncertainties around the age of the fossils. Solid lines indicate mean posterior diversity, and the shaded areas show 95% credibility intervals. The red vertical line indicates the Cretaceous–Paleogene boundary (K/Pg). The green period represents the ATR. Time is in millions of years. The color of each geological period in the chronostratigraphic scale follows that of the International Chronostratigraphic Chart (v2022/02). Silhouettes and other items by Corentin Jouault. EC, Early Cretaceous; LC, Late Cretaceous; P, Paleocene; E, Eocene; O, Oligocene; M, Miocene.

Fig. S13). Either obtained with the fossil record alone (Fig. 2 *A–C*) or in conjunction with phylogenetic data (Fig. 2 *D–I*), these results confirm that stem ants went predominantly extinct during the Late Cretaceous, with a negative net diversification rate (≈−0.1). Our results are further supported by various sensitivity analyses, excluding singletons (Fig. 2 *G–I* and *SI Appendix*, Figs. S2–S11), changing predefined times of rate shifts (*SI Appendix*, Fig. S5), removing occurrences from the fossil-rich Baltic amber (*SI Appendix*, Fig. S12), and using an alternative birth–death model (*SI Appendix*, Figs. S2 and S3).

The period around the K/Pg boundary marks the second significant phase in ant evolution, characterized by the diversification of crown ants, leading to a sharp increase in the number of genera (Fig. 2*C*). After the K/Pg event, the net diversification rate of crown ants is consistently positive, indicating continuous diversification of this group (Fig. 2*B*). Notably, their origination rate reaches approximately ≈1.75 times the extinction rate shortly after the K/Pg, and the highest rate is just before the Eocene (*SI Appendix*, Fig. S14). The onset of the crown ant diversification can be traced back to the mid/Late Cretaceous, when some of the most diverse lineages emerged, such as Dolichoderinae, Formicinae, and Ponerinae (47, 48).

The diversification of crown ants pursues into the Eocene, as indicated by a positive net diversification rate, representing the third significant period of ant diversification (Fig. 2*B*). During this time, a peak in origination rate is observed (≈6.5 times the background net diversification rate; Fig. 2*A*), which is likely related to the combined effects of Baltic amber and the diversification of Myrmicinae, Formicinae, Dolichoderine, and lineages of Dorylinae and Ponerinae (41, 43, 51, 52). This diversification peak is evident in the diversity of ant genera (Fig. 2 *C*, *F* and *I*) and also observed when all occurrences from the Baltic amber are removed from the analysis (*SI Appendix,* Fig. S12). Ants maintained their diversification trajectory throughout the Oligocene and Miocene (≈1.2 and ≈1.45 times the background net diversification rate, respectively), which corresponds to a fourth significant phase in ant evolution. This result is consistent with net diversification rates estimated from phylogenetic analyses (41, 43, 51, 52).

The presence of both crown and stem ants in mid-Cretaceous amber supports an Early Cretaceous or even pre-Cretaceous origin of ants. However, the parallel decline of stem ants and rise of crown ants during the Late Cretaceous and Paleogene suggest a transition in dominance within ant lineages. These events overlap with the ATR (100 to 50 Ma), suggesting that this ecosystem shift was a critical phase in ant evolution, marked by the diversification of crown ants. To gain deeper insights into the evolutionary history of ants, we explore various hypotheses that have traditionally been proposed to explain the extinction of their stem group and the expansion of their crown group.

Diversity Dependence between Stem and Crown Ants: Competitive Extinction Hypothesis. Our analysis of the ant fossil record reveals the coexistence of the crown and stem groups in the same Cretaceous forests, likely exploiting similar resources (47), and a parallel diversification for at least 20 My (36, 47, 53, Fig. 2). However, stem ants experienced a decline and eventual extinction during the Late Cretaceous, while crown ants persisted into the present. Such contrasted patterns of diversity dynamics, potentially interpreted as evidence of competitive or negative interactions between the lineages (54), illustrate a putative clade replacement event during the ATR and Late Cretaceous (40). In the fossil record, two patterns are typically observed for such a phenomenon: the double-wedge pattern, in which one clade declines while the other thrives (30), and the mass extinction pattern, which suggests an extinction event that eliminates one group allowing another to diversify (55). Surprisingly, no study to date has specifically investigated this hypothesis for ants with diversity-dependent analyses.

Among stem ants, Haidomyrmecinae were likely leaf-litter foragers or epigaeic ground-nesting predators (56), while Zigrasimeciinae and Sphecomyrminae were likely more generalists (40). Among contemporaneous crown subfamilies, similar ecological features are observed in Ponerinae (56, 57), suggesting the possibility of competitive interactions between crown and stem ants in deep time (i.e., effect of diversity of multiple co-occurring clades on origination and extinction rates: diversity dependence). However, and although it may be due to the limited fossil material from the Late Cretaceous to the Paleocene, our analyses do not support this scenario (*SI Appendix,* Tables S1 and S2). We find no significant correlations between the origination and extinction rates of crown ants and the stem-ant diversity (*SI Appendix,* Tables S1 and S2). Similarly, the decline of stem ants does not correlate with the diversification of crown ants (*SI Appendix,* Tables S1 and S2).

While our current understanding of the feeding habits of ants during the Cretaceous is limited (44), it would be intriguing to incorporate and contrast the feeding behaviors of stem and crown ants in future studies. The high degree of specialization observed in many stem ants suggests that they might have preyed upon distinctly different organisms compared to crown ants. This would further corroborate that there was no competition between stem and crown ants.

Hyper-Specialization and Age-Dependent Extinction (ADE) in Ants. Since the decline of stem ants cannot be directly attributed to the diversification of crown ants, we assessed the role of other factors, like the taxon age (58). Recently, it has been demonstrated that, in the context of a changing environment, the probability of extinction can increase with the age of a lineage (18). Therefore, during the environmental changes of the ATR, it is plausible that the old stem-ant lineages, compared to the recently originated crown-ant lineages, may have been more prone to extinction. We tested this phenomenon with the ADE model (58) in the context of ant evolution, encompassing both the Cretaceous (115 to 66 Ma) and the Cenozoic (66 Ma to the present).

For stem ants, we found no evidence for an interdependence between extinction and genus age during the Cretaceous ($\phi = 1.19$; *SI Appendix,* Table S3). This supports Van Valen's hypothesis of constant extinction (59), indicating that the age of stem-ant lineages did not influence their decline. If not their age, the hyper-specialization of stem ants may have hampered their ability to alter their dietary niche in response to the collapse of the bottom–up trophic network of the ATR (40, 60), ultimately leading to their decline during the Late Cretaceous. This hyper-specialization is evidenced by the unprecedented morphological features observed in many stem ants, including vertically articulated mandibles and horn-like cranial appendages, which indicate an extreme degree of dietary specialization (44, 46, 56, 61). This hypothesis parallels the scenario proposed to explain the decline of hyper-specialized vertebrates during the Pleistocene (62). Therefore, the specialization, particularly in terms of morphology, appears to elevate the risk of extinction.

For crown ants, a correlation between taxon age and extinction is recovered during the Cenozoic ($\phi = 0.37$; *SI Appendix,* Table S3), even when considering runs with partial convergence ($\phi = 0.51$; *SI Appendix,* Table S3), which contrasts with Van Valen's hypothesis of constant extinction. These results suggest that, during the Cenozoic, recently originated genera had a higher probability of extinction, which decreases with the age of genera ($\Phi < 1$). Similar outcomes were found for planktonic foraminifera and Carnivora (58, 63, 64). Our analyses also reveal a diversity-dependence effect when the singleton taxa were removed (Fig. 3 and *SI Appendix,* Tables S4 and S5). The diversity dependence is negatively correlated with origination ($\omega > 0.91$), which indicates that the increase in ant diversity during the Cenozoic tends to slow their diversification (Fig. 3*C*). This can be explained by competition between taxa with a similar ecology: the oldest and more diversified genera would have a better chance of survival than the youngest and maybe less diversified genera. For crown ants, these results are consistent with their fossil record: Many genera that emerged during the Paleogene persist today (39). These extinction-resistant genera, while experiencing species-level extinctions, have demonstrated an ability to adapt to global change, often by migrating to new geographic regions (65, 66). This could be attributed to their relatively less specialized morphology, which allowed them to be more opportunistic.

Angiosperm Diversification and Gymnosperm Decline Buffered Ants against Extinction. Abiotic and biotic factors, such as temperature fluctuations or vegetational changes, have been recognized as important drivers of animal diversification in both modern and ancient ecosystems (17, 18, 67, 68). These factors likely played a role in shaping the origination and extinction rates of Formicoidea and influenced the success or decline of ant

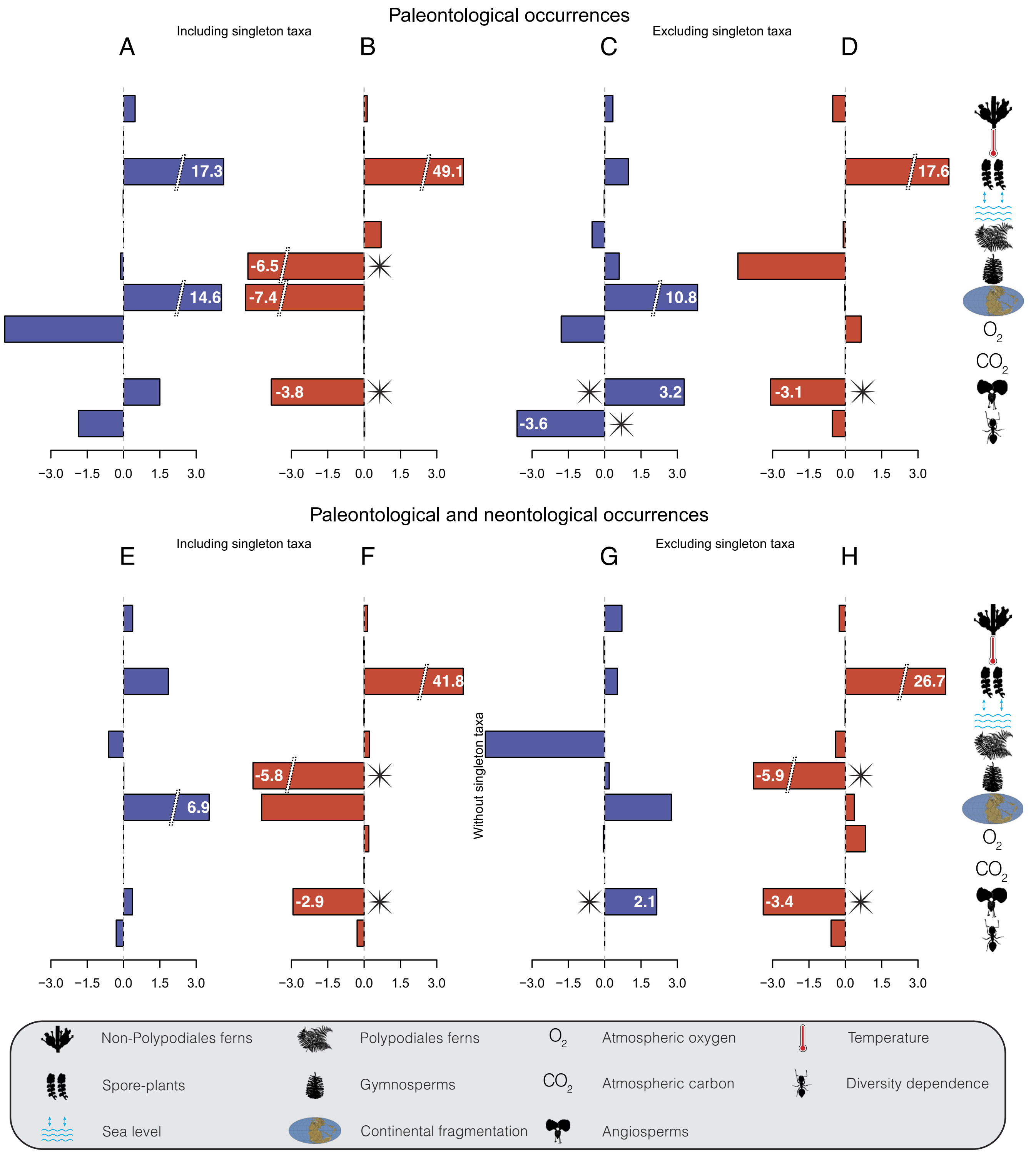

Fig. 3. Paleoenvironmental correlates and potential drivers of the diversification dynamics of ants. Bayesian inference of correlation parameters on origination (blue: *A*, *C*, *E*, and *G*) and extinction (red: *B*, *D*, *F*, and *H*) with abiotic factors like global temperature, continental fragmentation, sea level fluctuations, global variation of atmospheric CO_2 and O_2; and with biotic factors like relative diversity through time of Polypodiales ferns, non-Polypodiales ferns, gymnosperms, spore-plants, and angiosperms; and diversity-dependence factors with diversity through time of ant lineages. (*C* and *D*) 19.11% of genera removed (singletons); (*G* and *H*) 11.22% of genera removed (singletons). Stars indicate a significant correlation parameter for a given variable [shrinkage weights (ω) > 0.5]. Silhouettes from http://phylopic.org/. Licenses at https://creativecommons.org/publicdomain/zero/1.0/ or by Corentin Jouault.

lineages (69). To explore the drivers of ant diversification, we used a multivariate birth–death (MBD) model (70) to analyze the effects of ten potential factors (*SI Appendix*) on the diversification patterns of Formicoidea.

Among the variables examined, the rise of angiosperms during the ATR is one of the main drivers of ant diversification dynamics (ω > 0.85; Fig. 3 and *SI Appendix,* Tables S4–S7). The diversity of flowering plants promoted ant origination, supporting the co-diversification hypothesis, and reduced ant extinction, supporting the buffering hypothesis. When analyzing the fossil record alone, ant extinction showed a strong negative correlation with angiosperm diversification (Fig. 3 *B* and *D*). The same results were obtained when the fossil record was combined with phylogenetic data (Fig. 3 *F* and *H*). When removing singleton taxa, ant origination showed a significant strong positive correlation with angiosperm diversification (Fig. 3 *C* and *G*). Further analysis of the diversity dynamics revealed that the extinction of crown ants showed a strong negative correlation ($\omega > 0.94$) with the diversity of angiosperms (*SI Appendix,* Table S1). These results suggest that the rise of angiosperms had a dual role in shaping the diversity dynamics of ants, favoring their diversification, and buffering ants against extinction (Fig. 1 *C* and *D*).

The decline of gymnosperms during the ATR is also a significant driver of ant diversity dynamics ($\omega > 0.90$; Fig. 3 and *SI Appendix,* Tables S4–S7). When analyzing the fossil record alone, we observed a negative correlation between ant extinction and the decline of gymnosperms (Fig. 3*B*). Similar results were obtained when the fossil record was combined with phylogenetic data (Fig. 3*F*) and when singleton taxa were removed (Fig. 3*H*).

During the ATR, characterized by major global changes (i.e., global cooling, shift in vegetational composition, asteroid impact), many lineages declined or went extinct (13, 71, 72). The expansion and diversification of angiosperms coupled with the decline of gymnosperms have played an intricate role in shaping the ecosystems (e.g., litter composition: 73). Our analyses support a dual role for the ATR, promoting ant diversification and buffering them against extinction. The diversification of flowering plants introduced new food sources and habitats, particularly in open-canopy biomes such as deserts and dry grasslands (13, 41). These environmental changes have spurred ant diversification. Notably, the emergence of structures, such as elaiosomes, extrafloral nectaries, and domatia, aligns chronologically with periods of ant diversification (Fig. 2 *B*, *E*, and *H*). Origin of elaiosome-bearing plant lineages trace back to the Late Cretaceous (74, 75), clades forming extrafloral nectaries evolved by the Eocene (76, 77), and the domatia originated during the Neogene (78). These novelties, used by ants in modern ecosystems, not only facilitated their diversification but also ensured their survival by offering alternatives to diminishing gymnosperms food sources, thereby reducing their extinction risk (41).

Interestingly, ant nesting strategies and their independence from aboveground ecosystems (i.e., niche spaces: epigaeic or hypogaeic) have been proposed as critical traits in buffering against extinction (40, 41, 79). Stem ants were primarily leaf litter or ground-nesting and hyper-specialized foraging predators (56). Oppositely, the most recent common ancestor of crown Formicidae was likely either subterranean (79) or had strict predatory, ground-foraging, and ground-nesting behaviors (41). Therefore, changes in litter or soil conditions could have significantly affected stem and early crown ants, but in different ways. Ancestral state estimations support this hypothesis with an ecomorphological turnover across the K/Pg boundary in temporally and phylogenetically distinct lineages (56).

The decline of gymnosperm forests triggered a turnover in litter composition, resulting from angiosperm decomposition known to be more favorable structurally, chemically, and microclimatically for ant colonies compared to gymnosperms (69). During the K/Pg event and the profound ecosystem changes of the ATR, living in a less favorable gymnosperm litter may have been disadvantageous for ants, potentially leading to an increase in extinction. In contrast, as the dominance of gymnosperms declined, this effect on extinction is expected to diminish over time, which can be in line with the negative correlation recovered by the MBD model (Fig. 3 and *SI Appendix,* Tables S4–S7). Conversely, the angiosperm litter may have favored the survival of ants by providing shelter against predators (insectivorous lizards: 80; mammals: 81), allowing them to adapt to and colonize different ecological niches and occupy different habitats over time (82). At the same time, the rise of angiosperms allowed ants to colonize new shelters, favoring their survival during the end-Cretaceous events and the drastic environmental upheavals of the ATR (13). This colonization is evident in the shift to arboreal nesting strategies around the K/Pg associated with the stratification of nesting sites, which have probably reduced interspecific competition, thus limiting ant extinction (42). The importance of such shelters is also highlighted in another lineage of eusocial insects, termites, in which unique defensive morphological adaptations have been documented in reproductives during the Cretaceous (83).

Overall, changes in floral assemblages likely influenced ant diversity dynamics, with the diversification of angiosperms and the decline of gymnosperms that worked in tandem to buffer ants against extinction (Figs. 1*D* and 3 *A*–*H*). This interplay between plants and ants highlights the intricate ecological relationships and the importance of considering the broader context of plant diversification for understanding the evolutionary history of ants, and possibly of other lineages (84, 85).

Limitations and Perspectives. Studying deep-time diversity dynamics inevitably implies certain limitations associated with the data and analytical methods. First, the fossil record may be biased for certain ant lineages because of their biology, morphology (e.g., Leptanillinae, Martialinae), or geographic distribution. This taphonomic bias is well documented for certain groups and can hinder our understanding of the past dynamics of ants (*SI Appendix,* Fig. S33). While we cannot overcome this limitation, new discoveries (i.e., fossil deposits or specimens) can provide valuable information about the diversity of both fossil ant lineages. It should be noted that PyRate adequately accounts for incomplete taxon sampling when assessing past dynamics (3, 5, 6, 54). Second, the geologic periods around the K/Pg boundary exhibit a paucity of fossil ants (38, 39), a pattern that holds for many insect lineages dating back to the Cretaceous (19). Overcoming this issue will also require the discovery of new fossil deposits (9). Third, like any process-based model, PyRate is based on assumptions about the processes underlying a clade's evolutionary history that may not fully capture real evolutionary processes. For instance, we did not account for geographic bias in fossil sampling when modeling the diversification rates (86). However, we have partially addressed this issue by combining paleontological and neontological data (*SI Appendix,* Fig. S33) and including unpublished data from recently found deposits (e.g., Miocene ambers from Ethiopia and China, preliminary surveyed in refs. 87 and 88). Fourth, our results depend on the selection and availability of environmental and biological variables used as potential diversification drivers. We focused on ten candidates (excluding diversity dependence) that reflect widespread environmental changes likely to have influenced ant diversification (24). Additional factors, such as trait evolution and the diversification of scale insects, treehoppers, or honeydew-secreting butterflies (engaged in symbiotic interactions with ants) could also play a role and should be considered in future studies (69). Nonetheless, given the size of our dataset and the conservative nature of our analyses, our results are relatively robust and lead to testable conclusions with future extended datasets or new models accounting for the above-mentioned biases. Finally, we adopted a multi-model and multi-data approach, in line with recent recommendations and best practices for investigating past diversity dynamics (89).

This comprehensive approach integrates all currently available information on fossil ants, providing a more accurate reflection of past ant diversity dynamics.

Lineage-through-time curves are often used to investigate correlations between environmental changes and periods of rapid diversification or abrupt extinctions. Nevertheless, these diversity curves can arise from a complex interplay of macroevolutionary processes, making it challenging to untangle their underlying causes. In this study, we demonstrate that various hypotheses proposed in the literature can be discerned by considering several factors, encompassing both origination and extinction rates, as well as correlation outcomes. Consequently, it becomes feasible to assess which of the hypotheses is the most plausible explanation for the observed diversity curves.

Conclusion

Our study of the past diversification dynamics of ants, a highly ecologically important and diverse group of insects, provides valuable insights into the periods that have either favored or hindered their past diversity. Through the integration of paleontological and neontological data, we have identified four strongly supported phases of ant diversification or extinction, specifically, the Late Cretaceous, the K/Pg transition, the Priabonian, and the Oligo-Miocene. This approach refines our analyses beyond what can be achieved by relying solely on time-calibrated phylogenies. This combined methodology holds the potential to enhance our understanding of the evolutionary trajectories of numerous insect groups. Our findings challenge the hypothesis of competition between stem and crown ants. Instead, we provide an alternative scenario with substantial evidence supporting the hypothesis that the decline of gymnosperms and the concomitant rise of angiosperms played a critical role as a buffer against extinction and favored ant diversification during a period marked by profound environmental changes, known as the ATR. These results shed light on the pivotal role of the ATR in shaping the diversity dynamics of ants, and likely of other insect lineages.

Materials and Methods

Additional data and details about the methodology are described in the *SI Appendix*.

Paleontological and Neontological Data. We compiled all species-level fossil occurrences of ants from the literature and private and institutional collections, resulting in an unprecedented database for the Formicoidea (*SI Appendix*). We cleaned the synonyms, outdated combinations, *nomina dubia*, and other erroneous and doubtful records, based on revisions provided in the literature and/or on the expertise of the authors. For instance, we removed most occurrences of ants from the Ypresian Fushun amber because the descriptions and placements need revision (90). This extensive work resulted in a genus-level dataset spanning the Early Cretaceous to the Recent interval (Dataset S1). We extracted neontological data from recent time-calibrated phylogenies (Dataset S2) reconstructed with molecular data and the fossilized birth–death process (43) and combined it with the fossil record (7). Our final dataset encompasses 38,367 occurrences.

Dynamics of Origination and Extinction. We analyzed the fossil datasets with PyRate 3 (6) under the BDCS (5) and the RJMCMC (6) models to simultaneously estimate the preservation process, the times of origination (*Ts*) and extinction (*Te*) of each taxon, the origination (λ) and extinction (μ) rates, and their variation through time. Under the BDCS model, the temporal placement of rate shifts is fixed a priori, while the RJMCMC estimates the number of rate shifts. In our case, shifts were constrained within geological stages. This BDCS model focuses on the difference between the rate shifts estimated between the predefined time intervals. This model assumes half-Cauchy prior distributions for λ and μ between shifts, with a hyper-prior on the respective scale parameter to reduce the risk of over parameterization. The RJMCMC model "jumps" across different models and uses the posterior ratio to avoid under- and overparameterization. The result of RJMCMC is a posterior sample of λ and μ through time averaged over model uncertainty and posterior probabilities associated with each model, while incorporating the uncertainties associated with the preservation process. In the RJMCMC framework, the number and temporal placement of rate shifts are considered an unknown variable and are estimated from the data. We ran PyRate for 100 or 200 million Markov chain Monte Carlo (MCMC) generations with time bins of 5 My or geological ages (*SI Appendix*). For each analysis, we tested for the best-fitting preservation process by comparing the homogeneous Poisson process, the non-homogeneous Poisson process, and the time-variable Poisson process (*SI Appendix*). We also accounted for varying preservation rates among taxa using the Gamma model (3). We replicated the analyses on 10 randomized datasets of each clade and combined the posterior estimates of λ and μ across all replicates to generate rates-through-time plots (mean λ, μ, and net diversification rates, and their 95% HPD). We also obtained 10 posterior estimates of the time of speciation (*Ts*) and time of extinction (*Te*) for all taxa. We estimated the past diversity dynamics by calculating the number of living taxa at every point in time based on the *Ts* and *Te*. For the subsequent analyses, we used the estimated *Ts* and *Te* of all taxa, which avoids remodeling the heterogeneity of preservation, and re-estimated times of speciation and extinction. We monitored chain mixing and effective sample sizes (ESS) by examining the log files in Tracer 1.7.1 (91). The parameters are considered as converged when their ESS are greater than 200. All these analyses were performed with the original datasets with and without singletons. Although PyRate accounts for known biases in the fossil record, we also performed the same Bayesian inferences by excluding all occurrences from the Baltic amber, which resulted to a substantial reduction in the number of occurrences, from 23,795 to 11,481, and removed 15 genera from the analysis.

Selection of Abiotic Variables. We examined the relationship between past environmental changes and origination/extinction rates over the evolutionary history of ants. We focused on the role of 10 variables that have been linked to changes in biodiversity of terrestrial invertebrates and that span the full temporal range of ants (Dataset S3). The diversification of several insect lineages is believed to be correlated with changes in biotic and abiotic factors, whose fluctuations drive clades to thrive or decline. Among the most notable are the changes in atmospheric CO_2 and O_2 concentrations (92, 93), changes in continental fragmentation over time (9), fluctuations of the global temperature (18, 94) and sea levels–a factor that influences insect dispersal capacities–(95, 96), and most notably changes in flora assemblages through time (i.e., in the relative diversity of gymnosperms, non-Polypodiales ferns, Polypodiales ferns, spore-plants, and of angiosperms) (18, 97, 98).

MBD Model. We used the MBD model to assess whether multiple factors explain temporal variations in ant speciation and extinction rates (70). Under the MBD model, speciation and extinction rates can vary through correlations with time-continuous variables, and the strength and sign of the correlations are estimated jointly for each variable (70). PyRate estimates the baseline speciation ($\lambda 0$) and extinction ($\mu 0$) rates and all correlation parameters ($G\lambda$ and $G\mu$) jointly, using a horseshoe prior to control for over-parameterization and for the potential effects of multiple testing. Under the MBD model, origination and extinction rates were modeled through an exponential correlation with the diversity trajectories of the selected variables (53). We ran the MBD model with 50 million MCMC iterations and sampling every 50,000 to approximate the posterior distribution of all parameters ($\lambda 0$, $\mu 0$, $G\lambda$, $G\mu$, and the shrinkage weights of each correlation parameter). We summarized the results of the MBD analyses by calculating the posterior mean and 95% HPD of all correlation parameters and the mean of each shrinkage weight, as well as the mean and 95% HPD of the baseline speciation and extinction rates. We monitored chain mixing and ESS by examining the log files in Tracer 1.7.1 (91). The parameters are considered as converged when their ESS are greater than 200.

ADE Model. We fitted the ADE model (58) to calculate the probability of a lineage going extinct as a function of its age (the elapsed time since its origin). We ran PyRate for 100 million MCMC iterations and sampling every 50,000 with a time-varying Poisson process of preservation, while accounting for different preservation rates across taxa using the Gamma model. We replicated the analyses on 10 randomized datasets for the Mesozoic and for the Cenozoic and combined the posterior estimates across all replicates. We focused on the shape (Φ) of the Weibull distribution, knowing that $\Phi < 1$ indicates an extinction rate that is higher for young species and decreases with species age, and $\Phi > 1$ indicates an extinction rate that increases with species age (no effect of age when $\Phi = 1$). We monitored chain mixing and ESS by examining the log files in Tracer 1.7.1 (91). The parameters are considered as converged when their ESS are greater than 200.

Data, Materials, and Software Availability. Outputs and code data have been deposited in FigShare (https://figshare.com/s/1d6a5e5639e797370c05) (99). All study data are included in the article and/or supporting information.

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