

Relictual ant lineages (Hymenoptera: Formicidae) and their evolutionary implications

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Abstract

Due to their widespread distribution, range of adaptations, local abundance, and species diversity, ants are a major component of terrestrial communities worldwide. However, such high ecological prevalence is not shared among all ant lineages, with four ant genera – *Camponotus*, *Pheidole*, *Strumigenys*, and *Crematogaster* – accounting for a disproportionately large share of ant diversity. As a consequence, the study of variation in ant diversity has hitherto focused on testing whether more species-rich clades or regions are associated with disproportionately higher speciation and / or lower extinction rates. In this study, we investigate an intriguing but largely overlooked phenomenon in ants: the existence of ancient, species-poor lineages. We used both analytical and simulation results to assess evolutionary scenarios that could lead to current levels of ant diversity. We found that such relictual lineages are highly unlikely given constant-rate models of speciation and extinction. In particular, such old, species-poor lineages are much more likely to either go extinct, or to generate more species than currently observed. The possible mechanisms leading to such relictual lineages are discussed, particularly with respect to current scenarios of early ant evolutionary history.

Key words: Diversification, speciation, extinction, Formicidae.

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Introduction

Ants play a major ecological role in the most terrestrial biomes (HÖLLDOBLER & WILSON 1990, 2009). However, not all ants share the same level of ecological dominance. In a classic paper, WILSON (1976) asked "what are the most prevalent ant genera?", with prevalence being defined based on four criteria: species diversity, extent of geographical range, diversity of adaptations, and local abundance. Based on his results, Wilson concluded that three ant genera – *Camponotus*, *Pheidole*, and *Crematogaster* – are the most prevalent ant genera worldwide, being highly common in nearly all biogeographical regions. More recent phylogenetic and taxonomic work led *Strumigenys* to take the post of third most species-rich genus with ~ 840 species, but Wilson's main arguments are unaltered. Identifying the underlying causes of such high diversity, however, has been elusive. According to WILSON (1976), these three genera have "conquered the World" not because they share distinctive morphological or behavioural traits, but because they are sufficiently different from one another to allow for their coexistence (WILSON 1976). However, the ad hoc nature of this explanation merely pushes the problem one step back. Another explanation, particularly in the case of *Pheidole*, is the presence of polymorphism in the worker caste, including "cheap, expendable minor workers" that would provide its species a competitive advantage over their competitors (WILSON 2003), yet similar dimorphic worker castes have not generated corresponding prevalence in other ant genera (e.g., *Carebara*, *Acanthomyrmex*). One possible confounding factor in inter-

preting such differences is that comparing species richness among genera provides only a rough picture of discrepancies in diversification rates, both due to the considerable variations in the ages of ant genera, but also because many large genera might not be monophyletic, such that progress in this area necessarily involves an explicitly phylogenetic approach. For instance some studies explored heterogeneity in diversification rates among ant lineages (PIE & TSCHÁ 2009, MOREAU & BELL 2013) and focused more on the consequences of highly diverse clades (e.g., PIE & TRANIELLO 2007, MOREAU 2008), yet their causes such as variation in diversification rates are still poorly understood.

Although it is common to emphasize how impressive the most diverse ant clades are, a similar, but poorly explored issue involves the relictual ant lineages. We define a relictual lineage as a clade showing disproportionately low species richness (often including only one or two species) when compared with other, closely related lineages. There are several cases of this phenomenon in ants (i.e., *Agroecomyrmecinae*, *Paraponerinae*, *Aneuretinae*, *Martialinae*), which are represented by only one or two extant species. Given any stochastic diversification process, it is not surprising to find clades of different sizes, including those with few species. However, as we demonstrate in this study, the persistence of these ancient, species-poor lineages up to the present is highly improbable, given simple time-homogeneous models of diversification, suggesting that deterministic mechanisms are necessary to explain their persistence.

Material and methods

We simulated different scenarios for the diversification of ants based on a constant-rate birth-death process (YULE 1925, RAUP & al. 1973, PIE & WEITZ 2005). For each simulation, we chose parameter estimates that would, on average, generate species numbers comparable to the current levels of ant diversity. We ran two sets of simulations (N = 500 replicates for each combination of parameters) corresponding to 145 and 110 Mya, which correspond approximately with the ages of the ant crown lineages and the base of the Formicoid clade, respectively (WARD 2014). Given that it is widely believed that the current ant species richness of 13102 species (BOLTON 2014) is an underestimate, we used 20,000 and 15,000 species as the actual number of species for all ants and for the Formicoid clade, respectively. Sensitivity analyses using different estimates provided qualitatively similar results. We used four combinations of speciation (λ) and extinction (μ) rates. If we assume that both λ and μ are constant and $\lambda > \mu$, the expected total number of species after time t is simply $e^{(\lambda - \mu)t}$. Therefore, we chose combinations of λ and μ that would, on average, generate current ant diversity, but that involved different rates of lineage turnover (Tab. 1).

In addition, we used the equations provided in STRATHMANN & SLATKIN (1983) to calculate the probability of observing ant relictual lineages under scenarios of constant speciation and extinction rates. In particular, the probability of a clade surviving to time t and having 1 to k species is:

$$T_k(t) = [c(t) a(t)] [1 - a^k(t)]$$

where

$$c(t) = [(\lambda - \mu)^2 \exp(-(\lambda - \mu)t) / \lambda \cdot [1 - \exp(-(\lambda - \mu)t)] \cdot [\lambda - \mu \exp(-(\lambda - \mu)t)]$$

and

$$a(t) = [\lambda (1 - \exp(-(\lambda - \mu)t)) / [\lambda - \mu \exp(-(\lambda - \mu)t)]$$

Results

Regardless of the level of lineage turnover, all simulations failed to provide any instance of an ancient clade with less than ten species, suggesting that the probability of observing species-poor, ancient clades such as those recorded in ants is highly unlikely (zero cases in 500 simulations, $p < 0.002$). In particular, lineages either grew considerably or went extinct relatively early during their history (Fig. 1). It is important to note that there are multiple cases of relict lineages in the ant family, both at the level of crown lineages (e.g., *Martialis*, *Tatuidris*, *Paraponera*) and within Formicoids (e.g., *Aneuretus*), such that the probability of multiple events is even lower under scenarios of constant speciation and extinction rates, regardless of the level of lineage turnover. Finally, analytical results using the equations provided by STRATHMANN & SLATKIN (1983) are consistent with our simulations, with very low estimates for the probabilities of both persisting over such long periods of time while producing current species numbers below ten species ($p < 10^{-5}$).

Discussion

Much of the study on lineage diversification to date has focused on time-homogeneous Markov models of specia-

Tab. 1: Parameters used in diversification simulations.

Lineage turnover	Crown ants		Formicoid clade	
	λ	μ	λ	μ
0.00	0.068	0.000	0.087	0.000
0.33	0.102	0.034	0.131	0.044
0.50	0.137	0.068	0.175	0.087
0.67	0.205	0.137	0.262	0.175

tion and extinction (e.g., NEE & al. 1992, NEE 2006, PIE & TSCHÁ 2009). For instance, differences in the number of species between clades or regions are often interpreted as resulting from variation in speciation and extinction rates (RICKLEFS 1987, 2006, ROLLAND & al. 2014). However, as shown in the present study, models with constant speciation and / or extinction rates are unable to generate ancient, species-poor lineages such as those found in the ant tree because, according to these models, lineages should either increase in numbers or become extinct (STRATHMANN & SLATKIN 1983). The definition of what actually constitutes a relictual lineage, such as those investigated in this study, is necessarily arbitrary given that the topological properties of most phylogenetic trees include a wide variety of terminal nodes of different depths. However, such variation does not negate the conclusions of our analyses for the most ancient, species-poor branches of the ant tree, and might equally apply for some of the more recent, species-poor branches as well. In addition, although that there is uncertainty regarding estimates of divergence times, both for the ant crown group and for the Formicoid clade (see BRADY & al. 2006 and MOREAU & al. 2006 for different estimates and confidence intervals), all simulations involved rescaling speciation and extinction rates to generate, on average, the expected number of extant ant species. In other words, such variation would lead to small differences on the time axes of Figure 1, but the variation in species numbers would remain largely unaltered. Moreover, if our estimate for number of extant ant species is exceedingly conservative, that would necessarily involve increasing speciation and extinction rates, thus reducing even more the probability of observing relictual lineages.

It is important to note that simple changes in time-homogeneous models, such as decreasing turnover rates while maintaining constant speciation and extinction rates (Fig. 1) or allowing for fluctuations in speciation and extinction rates (STRATHMANN & SLATKIN 1983) are not sufficient and might make it even more difficult for species-poor lineages to persist. We propose two alternative (non-exclusive) explanations for the evolution of relict taxa. First, species might become adapted to fairly stable, but specialized niches, which might essentially buffer them from extinction while at the same time prevent them from further diversification. Examples of this syndrome might include the cryptobiotic *Martialis* (see LABELING & al. 2008), *Tatuidris* (see BROWN & KEMPF 1967), *Apomyrma* (see BROWN & al. 1971), *Opomyrma* (see YAMANE & al. 2008), *Aulacopone* (see ARNOL'DI 1930, TAYLOR 1980), and *Phalacroymyrmex* (see KEMPF 1960). Likewise, this explanation is similar to that of another "living fossil" – the coelacanth – which is thought to have escaped extinction by

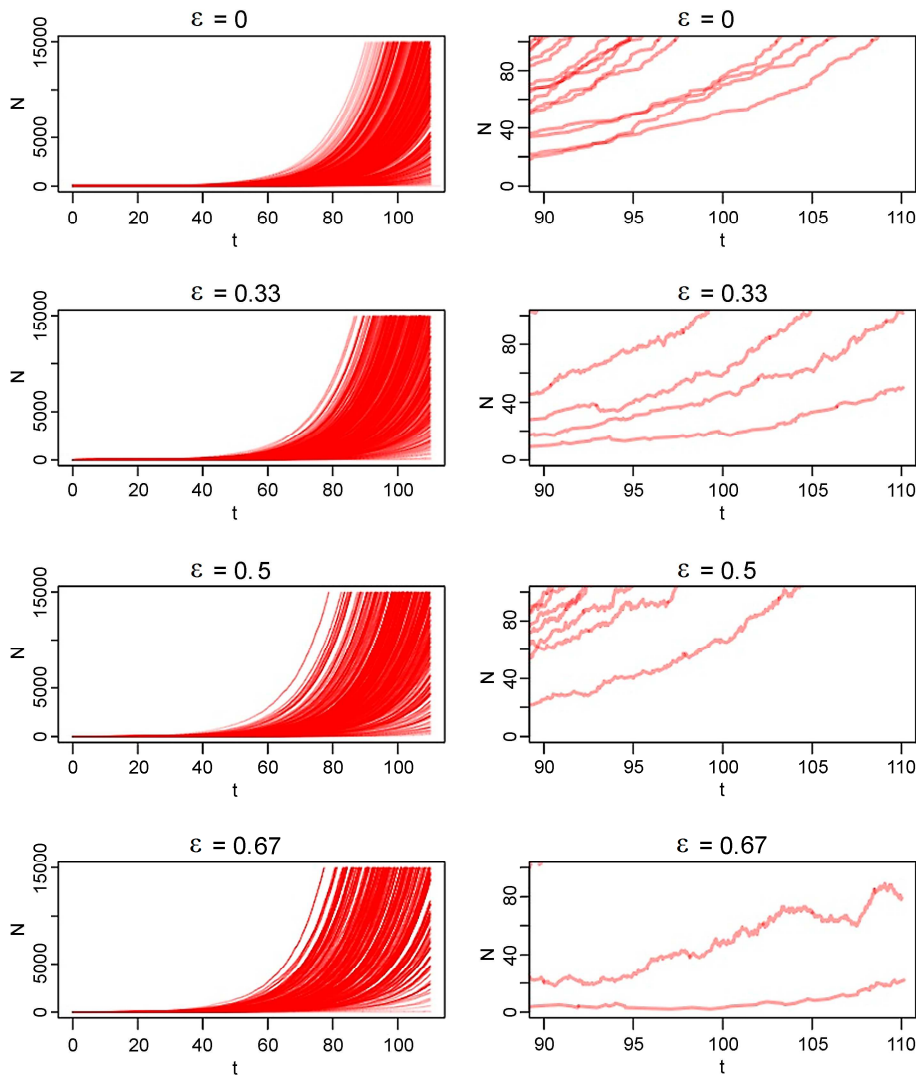


Fig. 1: Simulations of the diversification process of the formicoid clade based on different levels of lineage turnover (ϵ). Each simulation ($N = 500$) stopped when the number of lineages reached 0, the upper limit of 15,000 lineages, or after 110 My. Figures on the right show a detail of the original plot on the left, but focusing specifically on the region describing ancient, species-poor clades near the end of the simulation. The results for the crown-group of ants were qualitatively similar (not shown).

specializing in the highly stable deep waters of the Indian Ocean (FRICKE & PLANKE 1988, FRICKE & al. 1991). Second, lineages can remain in insular habitats, where the relatively depauperate local fauna and the reduced competition from other species might lead to long-term persistence. A potential instance of this syndrome is *Aneuretus simoni* EMERY, 1893, the sister-lineage to the Dolichoderinae subfamily (WARD & al. 2010) and the sole remnant of a clade that was widely distributed in the northern hemisphere throughout the Tertiary (DLUSSKY & RASNITSYN 2003). This species has remained in Sri Lanka and escaped the fate of the other members of the clade due to the relatively lower abundance of highly competitive genera such as *Pheidole* and *Crematogaster* (see WILSON 1956). Likewise, an analogous example outside Formicidae is the New Zealand *Sphenodon*, the only surviving genus of the order Sphenodontida of reptiles (REST & al. 2003). Elements of this alternative can be seen in the notion of "dynastic expansions" discussed by WILSON & HÖLLDOBLER (2005).

The two explanations indicated above have important implications for the interpretation of scenarios for the early stages of ant evolution. Given that most of the earliest branches in the ant tree involve rare, hypogaecic species (WARD & al. 2010), and based on the suite of morphological and ecological traits found in *Martialis heureka* (see

RABELING & al. 2008), it has been argued that the ancestral ant was a hypogaecic forager (e.g., LUCKY & al. 2013). However, the results obtained in the present study suggest that these relictual ant lineages experienced differentially low extinction rates in relation to other contemporaneous lineages with alternative ecologies. This could have caused a type of ascertainment bias that could severely mislead character reconstruction methods (MADDISON 2006). Future inferences on ant ancestral traits should therefore necessarily involve methods that could untangle the effect of character change and lineage diversification (PARADIS 2008).

Finally, there are some instances of a species-poor, ancient ant lineage that does not fit the two scenarios provided above, such as the bullet ant *Paraponera clavata* (FABRICIUS, 1775) (Paraponerinae). One might speculate that *P. clavata* represents a relict of regional extinctions of a previously diverse taxon, as suggested for the termite *Mastotermes darwiniensis* FROGGATT, 1897, the sole extant representative of the Mastotermitidae (GRANDCOLAS & al. 2014). However, contrary to the case of *Mastotermes*, despite the relatively extensive ant fossil record in amber, only one additional *Paraponera* species has been uncovered to date (BARONI URBANI 1994). Another possibility is that the currently recognized phylogenetic position of *Paraponera* is incorrect, possibly due to an artefact such as

long-branch attraction. Nevertheless, the contrast between the high ecological dominance and the relictual status of *Paraponera* is particularly intriguing and deserves further scrutiny, as well as other lineages in similar evolutionary conditions, such as *Oecophylla* and *Gigantiops*.

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