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Out of the temperate zone: A phylogenomic test of the biogeographical conservatism hypothesis in a contrarian clade of ants

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Abstract

Aim: The standard latitudinal diversity gradient (LDG), in which species richness decreases from equator to pole, is a pervasive pattern observed in most organisms. Some lineages, however, exhibit inverse LDGs. Seemingly problematic, documenting and studying contrarian groups can advance understanding of LDGs generally. Here, we identify one such contrarian clade and use a historical approach to evaluate alternative hypotheses that might explain the group's atypical diversity pattern. We focus on the biogeographical conservatism hypothesis (BCH) and the diversification rate hypothesis (DRH).

Location: Global.

Taxon: Ants (Hymenoptera: Formicidae: Stenammini).

Methods: We examined the shape of the LDG in Stenammini by plotting latitudinal midpoints for all extant, described species. We inferred a robust genome-scale phylogeny using UCE data. We estimated divergence dates using BEAST2 and tested several biogeographical models in BioGeoBEARS. To examine diversification rates and test for a correlation between rate and latitude, we used the programs BAMM and STRAPP, respectively.

Results: Stenammini has a skewed inverse LDG with a richness peak in the northern temperate zone. Phylogenomic analyses revealed five major clades and several instances of non-monophyly among genera (*Goniomma*, *Aphaenogaster*). Stenammini and all its major lineages arose in the northern temperate zone. The tribe originated ~51 Ma during a climatic optimum and then diversified and dispersed southward as global climate cooled. Stenammini invaded the tropics at least seven times, but these events occurred more recently and were not linked with increased diversification. There is evidence for a diversification rate increase in Holarctic *Aphaenogaster* + *Messor*, but we found no significant correlation between latitude and diversification rate generally.

Main Conclusions: Our results largely support the BCH as an explanation for the inverse latitudinal gradient in Stenammini. The clade originated in the Holarctic and likely became more diverse there due to center-of-origin, time-for-speciation

and niche conservatism effects, rather than latitudinal differences in diversification rate.

KEYWORDS

ants, biogeography, boreotropics hypothesis, contrarian clade, diversification, Formicidae, latitudinal diversity gradient, phylogenomics, ultraconserved elements

1 | INTRODUCTION

The observation that species richness decreases from the equator to pole is the oldest and best-known pattern in biogeography (Hawkins, 2001; Willig et al., 2003). Although not a consistent pattern throughout the history of life on Earth, the current latitudinal diversity gradient (LDG) has existed for at least the last 30 million years and is pervasive (Mannion et al., 2014; Meseguer & Condamine, 2020). The standard LDG occurs in most fauna and flora, in both terrestrial and marine realms, and across a range of spatial and temporal scales (Brown, 2014; Field et al., 2009; Hillebrand, 2004; Willig et al., 2003). Hypotheses attempting to explain the standard LDG abound, yet a broad consensus as to which hypothesis, or set of hypotheses, best predicts the gradient remains a topic of active debate (Brown, 2014; Jablonski et al., 2006; Pianka, 1966; Rohde, 1992; Wiens & Donoghue, 2004; Willig et al., 2003).

A challenge to understanding the standard LDG has been the discovery of a small but growing number of lineages that exhibit inverse diversity gradients, in which species richness peaks in extratropical regions and decreases toward the equator. These contrarian clades occur in a variety of marine and terrestrial groups, including marine bivalves (Krug et al., 2007), pelagic seabirds (Chown et al., 1998), ichneumonid wasps (Owen & Owen, 1974), bees (Orr et al., 2020) and lampropeltine snakes (Pyron & Burbrink, 2009). Seemingly problematic, discovery of these groups has improved our understanding of diversity gradients by making it necessary to explain these non-standard cases using the same fundamental mechanisms (i.e., speciation, extinction and dispersal) that underlie the standard LDG. These cases have also illuminated the fact that the LDG is a property of clades and that diversity patterns are likely to be different for clades of varying age and inclusivity, with older, more diverse clades being more likely to follow the standard pattern, and younger less diverse clades more likely to diverge. Thus, a worthwhile objective in biogeography should be to identify contrarian clades and to understand the ecological and evolutionary processes that have caused them to be different. Here, we demonstrate that a major group of ants is a contrarian clade, and we infer a robust phylogeny of the group to test several hypotheses that might account for the group's atypical diversity pattern.

Ants (Hymenoptera, Formicidae) are the most successful group of eusocial insects on Earth. They occur in most terrestrial ecosystems and are often ecologically and numerically dominant (Hölldobler & Wilson, 1990). As a whole, ants exhibit the standard LDG (Economio et al., 2018; Kaspari et al., 2003), with the Neotropics

being particularly important in the group's evolutionary history (Moreau & Bell, 2013). Several ant lineages, however, are predominantly temperate in distribution and exhibit obvious adaptations to living in colder, seasonal environments. One of the largest of these groups is the myrmicine ant tribe Stenammini (Ward et al., 2015).

Stenammini is a monophyletic tribe that includes seven genera and about 450 extant species (Bolton, 2020; last accessed on July 6, 2020). It is distributed across the globe, being absent from only Amazonia, temperate South America, and permanently frozen regions. Considering type localities, the majority of the tribe's diversity occurs in the temperate zone of the northern hemisphere, with less than one quarter of the species known from the New and Old World tropics, a pattern that strongly suggests an inverse latitudinal gradient. Ecologically, the tribe exhibits a variety of life history strategies, but the group is best known for several genera that have radiated in arid landscapes as seed harvesters. These lineages are the genera *Messor* (126 spp.), *Veromessor* (9 spp.), *Novomessor* (3 spp.), *Goniomma* (10 spp.), and *Oxyopomyrmex* (12 spp.). The remaining two genera in the tribe, *Stenamma* (84 spp.) and *Aphaenogaster* (205 spp.), are less specialized in their diets and are more strongly associated with mesic forest habitats.

Currently, the phylogeny of Stenammini is not well resolved. A few studies have focused on species-level relationships within particular genera (Branstetter, 2012; DeMarco & Cognato, 2016), and a few broader studies on ants have incorporated several divergent stenammine lineages (Brady et al., 2006; Demarco & Cognato, 2015; Moreau et al., 2006; Ward et al., 2015), but no single study has thoroughly sampled the group's diversity on a global scale. Consequently, there is uncertainty about the monophyly of genera, in particular the genus *Aphaenogaster*, as well as the group's evolutionary history.

To explain the diversity pattern observed in Stenammini, we evaluate two alternative "umbrella" hypotheses, which have been proposed to explain latitudinal diversity gradients generally. These are the biogeographical conservatism hypothesis (BCH; Pyron & Burbrink, 2009), and the diversification rate hypothesis (DRH; Cardillo et al., 2005; Rohde, 1992; Weir & Schluter, 2007). A third possibility, the ecological regulation hypothesis (ERH; Currie, 1991; Kaspari et al., 2000; Rabosky & Hurlbert, 2015), is not considered here. The BCH is a generalized version of the tropical conservatism hypothesis (TCH; Wiens & Donoghue, 2004), which proposes that the standard LDG is the consequence of the combined effects of niche conservatism, center-of-origin and time. Under the TCH, it is posited that most higher-level lineages originated in the tropics at a time when tropical environments were much more extensive (65–34 Ma), and ecological range shifts



from tropical to temperate environments were both limited and more recent, providing less time for species to accumulate. The BCH uses the same argumentation as the TCH, except that it applies to groups with either standard or inverse LDGs.

The DRH also assumes niche conservatism, but in contrast to the TCH, it proposes that differences in speciation and extinction rates, rather than center-of-origin and time, are most important. Under the DRH, and assuming a standard LDG, observed higher species richness in the tropics is explained by most lineages having higher diversification rates in the tropics as compared to the temperate zone. In a more general sense, this hypothesis predicts a correlation between diversification rate and latitude, with the directionality of the relationship dependent on the type of diversity gradient observed.

To differentiate between the BCH and DRH for a particular clade, it is necessary to evaluate global richness for a group and then infer the group's biogeographic history and lineage specific diversification rates. Under the BCH, and assuming an inverse LDG, we would predict that Stenammini originated in the temperate zone and dispersed to the tropics both relatively infrequently and more recently in time. Alternatively, under the DRH, and again assuming an inverse LDG, we would predict there to be a positive correlation between latitude and diversification rate, with species and clades at higher latitudes diversifying more rapidly than species at lower latitudes. We also suppose that both hypotheses together could explain the Stenammini diversity pattern, given that each hypothesis is just weighting different aspects of fundamental processes, namely speciation, extinction and dispersal.

2 | MATERIALS AND METHODS

2.1 | Assessing the diversity gradient

To examine the latitudinal diversity gradient in Stenammini, we estimated the latitudinal midpoint for all extant, described species in the tribe as of July 6, 2020 (see Appendix S1: Table S1.1; Bolton, 2020). This was carried out by inspecting species' distributions using an online database (www.antmaps.org; Guénard et al., 2017) and recording the northernmost and southernmost points for each species. In cases where only an administrative district was reported (country, state, etc.), rather than a point record, we estimated latitude. In a few cases, we also used point data available from AntWeb (www.antweb.org). Using midpoint latitudes, we classified species as having either tropical or extratropical distributions (cutoff set at 23.5° N/S) and we generated a histogram of all points in R 3.6.2 (R Core Team, 2019). Our list of species and distribution records was last updated on July 6, 2020. We did not include new species described after this point in time or morphospecies.

2.2 | Taxon selection for phylogenomics

We selected eight outgroup and 92 ingroup species for inclusion in our molecular dataset (Appendix S1: Table S1.2). Within Stenammini,

we included all genera and a selection of exemplar species from all regions where each genus occurs. For *Stenamma*, we included 23 species from the Neotropics and 14 species from the Holarctic, including a rare species from Morocco (*S. punctiventre*) that has not yet been sampled in a molecular study. We sampled all three species of the genus *Novomessor* and eight out of the nine valid species of *Veromessor*. We sampled five out of 10 species of *Goniomma* and three out of 12 species of *Oxyopomyrmex*. For *Messor*, we only sampled six species, but these included taxa from southern Africa, Europe and Asia. For *Aphaenogaster*, we sampled 12 tropical species, nine Nearctic species and nine Palearctic species. The tropical species included three from the Neotropics, four from Madagascar, one from Borneo, two from New Guinea and one from Australia.

2.3 | UCE data generation

To generate a robust phylogeny, we employed a phylogenomic method that combines targeted enrichment of ultraconserved elements (UCEs) with multiplexed next-generation sequencing (Branstetter, Longino, et al., 2017; Faircloth et al., 2012, 2015). To enrich UCE loci, we used the original Hymenoptera probe set that targets 1510 UCE loci (hym-v1; Faircloth et al., 2015). The protocols are outlined in Faircloth et al. (2015) and described in Appendix S2. We extracted published sequence data for 16 species from Faircloth et al. (2015) and Branstetter, Ješovnik, et al. (2017) and generated new sequence data for the remaining taxa.

2.4 | Bioinformatics and DNA matrix preparation

Starting with FASTQ files, we performed all initial bioinformatics steps, including read cleaning, assembly, and alignment, using the software package PHYLUCE 1.5 or 1.6 (Faircloth, 2016; Faircloth et al., 2012). Raw reads were cleaned and trimmed using ILLUMIPROCESSOR (Faircloth, 2013) and cleaned reads were assembled de novo using TRINITY v2013-02-25 (Grabherr et al., 2011). After assembly, we mapped contigs to UCE loci and then aligned all loci using MAFFT (Katoh & Standley, 2013). After alignment, we used GBLOCKS (Talavera & Castresana, 2007) with reduced stringency settings, to trim poorly aligned regions. Finally, we filtered all alignments for taxon occupancy, requiring alignments to have some data for at least 75% of samples. For additional details, see Appendix S2.

2.5 | Phylogenetic Inference

We employed maximum likelihood (ML), Bayesian (BI) and species tree (ST) inference methods. For ML analyses, we used the program IQ-TREE 2.0.6 (Minh et al., 2020) and examined the effects of partitioning on phylogenetic reconstruction, testing no partitioning, by locus partitioning, and partitioning with the Sliding-Window Site Characteristics based on Entropy method (SWSC-EN; Tagliacollo &

Lanfear, 2018). After running the SWSC-EN algorithm, which splits individual loci into left flank, core and right flank subsets, we merged the subsets using MODELFINDER2 within IQ-TREE. The resulting best-fit partitioning scheme reduced the number of data subsets from 2919 to 804 subsets. Using IQ-TREE we then inferred phylogenetic trees for each partitioning scheme, selecting GTR+G4 as the substitution model and performing 1000 Ultrafast Bootstrap replicates (UFB; Hoang et al., 2018) and 1000 replicates of the SH-like approximate likelihood ratio test (SH-aLRT) (Guindon et al., 2010) to assess support.

For BI, we used EXABAYES 1.5 (Aberer et al., 2014) and we analysed the concatenated dataset without partitioning and with the SWSC-EN partitioning scheme. For the no partitioning analysis, we executed three independent runs, each with two coupled chains (one cold and two heated chains), for 1 million generations each. For the partitioned analysis, we performed two runs, each with four coupled chains (one cold and three heated chains), for 1 million generations. For both analyses, we assessed burn-in, convergence among runs, and run performance with the program TRACER 1.7.1 (Rambaut et al., 2018). We made sure that most parameter ESS values were above 200 and all were above 100.

We performed ST estimation using the summary method implemented in ASTRAL-III 5.7.8 (Zhang et al., 2017). To carry out the analysis, we first estimated individual gene trees with IQ-TREE. We then combined gene trees into a single file and collapsed all nodes with less than or equal to 10% UFB support using NEWICK UTILITIES 1.6 (Junier & Zdobnov, 2010). We input the collapsed gene trees into ASTRAL-III and ran a standard analysis, with support measured using local posterior probabilities.

We further examined our data for signs of systematic error by filtering or modifying the dataset in different ways and then performing tree inference using IQ-TREE. We created a total of seven alternative datasets, constructed to control for variation in evolutionary rate and base composition across loci and to remove data subsets that violated common model assumptions of stationarity, reversibility, and homogeneity (SRH). For the SRH datasets we employed the symtest method implemented in IQ-TREE 2 (Naser-Khdour et al., 2019).

For additional details see Appendix S2.

2.6 | Divergence dating

To infer divergence dates for the evolution of stenamine ants, we used node dating and the Bayesian program BEAST2 2.6 (Bouckaert et al., 2014). To calibrate the analysis, we used two calibration points, a secondary calibration applied to crown Myrmicinae, and a single fossil calibration applied to crown Stenammini. The secondary calibration was taken from a large study on myrmicine ants (Ward et al., 2015) and the fossil calibration was selected based on the oldest known stenamine fossil, *Aphaenogaster dluskyana*, which is from Sakhalin amber (Radchenko & Perkovsky, 2017). Although many additional stenamine fossil species have been described (Bolton, 2020; accessed on

July 6, 2020), we view the placement of these fossils within the tribe as dubious given that there has been instability in generic boundaries over time and many fossils are of wings only.

For the root node calibration, we selected a normal distribution and set the mean and sigma parameters to 98.6 Ma and 7.0, respectively (95% CI 87.9–110 Ma), which corresponds to the mean age and 95% highest posterior density (HPD) reported by Ward et al. (2015). The fossil is from the Naibuchi Formation and has been dated to the Lutetian age of the Middle Eocene (Baranov & Perkovsky, 2013; Kodrul, 1999; Radchenko & Perkovsky, 2017). For this fossil, we applied a log normal distribution and used a minimum age offset of 41.2 Ma, corresponding to the lower age of the Lutetian, a mean of 2.46 and a sigma of 0.81 (95% CI 44.3–85.6 Ma).

Due to computational constraints, we made the BEAST2 analysis possible by using a fully resolved constraint tree, turning off tree search operators, and using a subset of available UCE loci rather than the full dataset. For the constraint tree, we used the tree inferred from the SWSC-EN partitioned ML analysis, and we made it ultrametric using the chronos function in the R package 'ape' (Paradis et al., 2004) before input into BEAST. For the sequence data, we tested two different strategies: 300 random loci from a 90% taxon-filtered locus set, and 300 clock-like loci selected using the program SORTA DATE (Smith et al., 2018). To root gene trees for input into SORTA DATE, we used the program PHYX (Brown et al., 2017). To evaluate the performance of BEAST2 runs we inspected run parameters using TRACER 1.7.1 (Rambaut et al., 2018).

To check for the influence of assigning informative prior distributions (i.e., normal and lognormal distributions) to calibration nodes, we repeated the above analyses using more diffuse uniform prior distributions for each calibration. For the root node calibration, we used an age range of 87.9–109.6 Ma and for the crown Stenammini calibration we used an age range of 41.2–98.6 Ma. We analysed both the 300 random and clocklike loci using these priors. For additional details see Appendix S2.

2.7 | Biogeographic reconstruction

We inferred the biogeographic history of Stenammini using three different models, available as part of the R package 'biogeobears' (Matzke, 2013). These are the DEC model (dispersal-extinction-cladogenesis; Ree & Smith, 2008), the dispersal-vicariance model (DIVA-like; Ronquist, 1997), and the Bayesian Analysis of Biogeography model (BayArea-like; Landis et al., 2013). The DIVA and BayArea models are likelihood interpretations of the original models. We chose not to use the jump dispersal (+j) parameter available in BioGeoBEARS, because of recent criticisms (Ree & Sanmartín, 2018). The best-fitting biogeographic model was selected using AICc scores.

We coded terminal taxa using the seven classic biogeographic realms (Olson et al., 2001) plus the Malagasy region: Nearctic (A), Neotropic (B), Palearctic (C), Afrotropic (D), Malagasy (E), Indomalay (F) and Australasia (G). Based on the observation that most extant species occupy one area, and only a few two adjacent



areas, we set max areas to two regions. We also excluded several implausible ancestral areas (AD, AE, AF, AG, BC, BD, BE, BF, BG, CE, CG, DF, DG, EF, EG). For the dispersal multipliers, we tested three alternative schemes: (1) equal rates, (2) different rates, with 0.5 used for adjacent areas and 0.1 used for non-adjacent areas or transoceanic dispersal, and (3) different rates following the strategy proposed by Condamine et al. (2013), in which adjacent areas without major separating barriers received a probability of 0.5, adjacent areas with barriers received 0.25, areas separated by one area received a probability equal to the multiple of the two dispersal probabilities, long-distance oceanic dispersal events were given a probability of 0.01, and a few unlikely events (e.g. long-distance dispersal to Madagascar from the Nearctic) were given a probability of 0.001. We used a single time slice for the analysis given the time frame under consideration (<60 Ma). See Appendix S1: Table S1.3 for sample coding.

For the input tree, we used the BEAST2 chronogram generated from clock-like loci, with all outgroups and two ingroup species pruned using R. We pruned one sample of *Aphaenogaster* from Madagascar, originally thought to be a separate morphospecies (this group was recently revised by Csösz et al., 2021), and one sample of *Oxyopomyrmex* cf. *magnus*.

2.8 | Diversification rates

We investigated diversification dynamics in Stenammini using the Bayesian program BAMM 2.5 and the accompanying R package 'bammtools' (Rabosky, Donnellan, et al., 2014; Rabosky, Grundler, et al., 2014; Rabosky et al., 2013; Shi & Rabosky, 2015). For the input tree, we used the same pruned tree used for the BioGeoBEARS analysis. To account for non-random, incomplete taxon sampling we input a sampling probability file, in which we assigned all terminals to clades roughly corresponding to genera ("Aphaenogaster", "Deromyrma", "Goniomma", "Novomessor", "Stenamma", "Veromessor"; see Figure 3) and we gave each clade a sampling probability based on the number of species sampled and the number of both described and undescribed, extant species in that clade (0.08, 0.39, 0.32, 1.00, 0.43, and 0.89, respectively; see also Appendix S1: Table S1.4). To select appropriate priors for the BAMM analysis, we used the "setBAMMpriors" function in BAMMTOOLS on the input time tree. Using the prior settings, we then ran the BAMM analysis with four chains for 10,000,000 generations, sampling event data every 2000 generations. After the analysis, we assessed burn-in, run convergence, and ESS values for all parameters using the R package 'coda' (Plummer et al., 2006). We then explored the post-burn-in output using BAMMTOOLS and selected the best rate-shift configuration by assessing posterior probabilities and Bayes Factors. Although the documentation recommends using a prior of 1.0 for datasets with <500 tips, we repeated the analysis using rate shift priors (= "expectedNumberOfShifts") of 1, 5 and 10 to explore the sensitivity of the results to the prior setting.

After estimating diversification rates and rate shifts using BAMM, we tested for trait-dependent diversification in Stenammini using

the STRAPP method (Structured Rate Permutations on Phylogenies; Rabosky & Huang, 2016), implemented in BAMMTOOLS. We specifically tested for a correlation between speciation rate, as estimated with BAMM, and midpoint latitude for all taxa in our pruned time tree.

3 | RESULTS

3.1 | Diversity gradient

Using a cutoff of 23.5°N/S latitude, we found that 371 species are extratropical and 78 species are tropical (Figure 1). The tribe ranges from roughly 30°S to 50°N and has an obvious diversity peak in the northern hemisphere between 35°N to 40°N latitude. The diversity distribution is strongly left-skewed, with richness dropping below 10 species from 10°N to 35°S (binned at 5° intervals). This distribution is concordant with Stenammini having an inverse LDG.

3.2 | UCE sequencing and matrix assembly

We recovered an average of 987 UCE contigs per sample, with a mean length of 909 bp and a mean coverage per base of 85X (Appendix S1: Table S1.5). The final aligned locus set included 973 loci, with a mean locus length of 763 bp, resulting in a concatenated dataset of 741,994 bp and 247,377 informative sites (Appendix S1: Table S1.6).

3.3 | UCE phylogeny

We recovered completely congruent results at key nodes, with only slight differences in support values across ML, BI, and ST analyses, or the modified/filtered datasets (Figure 2 and Appendix S3: Figures S3.1–3.14). There was slight topological variation within groups of closely related species, but none of these changes were of importance to the main conclusions reported here.

We recovered Stenammini as monophyletic and comprising five major clades: (1) the genus *Stenamma*, (2) the genera *Novomessor* + *Veromessor* (the "Novomessor" clade), (3) a group of tropical "Aphaenogaster" (the "Deromyrma" clade), (4) the genera *Goniomma* + *Oxyopomyrmex* (the "Goniomma" clade) and (5) the genus *Messor* plus all Holarctic members of *Aphaenogaster* (the "Aphaenogaster" clade). Within the "Goniomma" clade, the genus *Goniomma* was found to be paraphyletic with respect to *Oxyopomyrmex*, and within the "Aphaenogaster" clade, the genus *Messor* was found to be nested within Holarctic *Aphaenogaster*. Distributions are provided in Appendix S4.

3.4 | Historical biogeography

The two different datasets used for divergence dating returned nearly identical age estimates without any major discrepancies (Figure 3, Appendix S3: Figures S3.13–3.14). Using uniform prior distributions

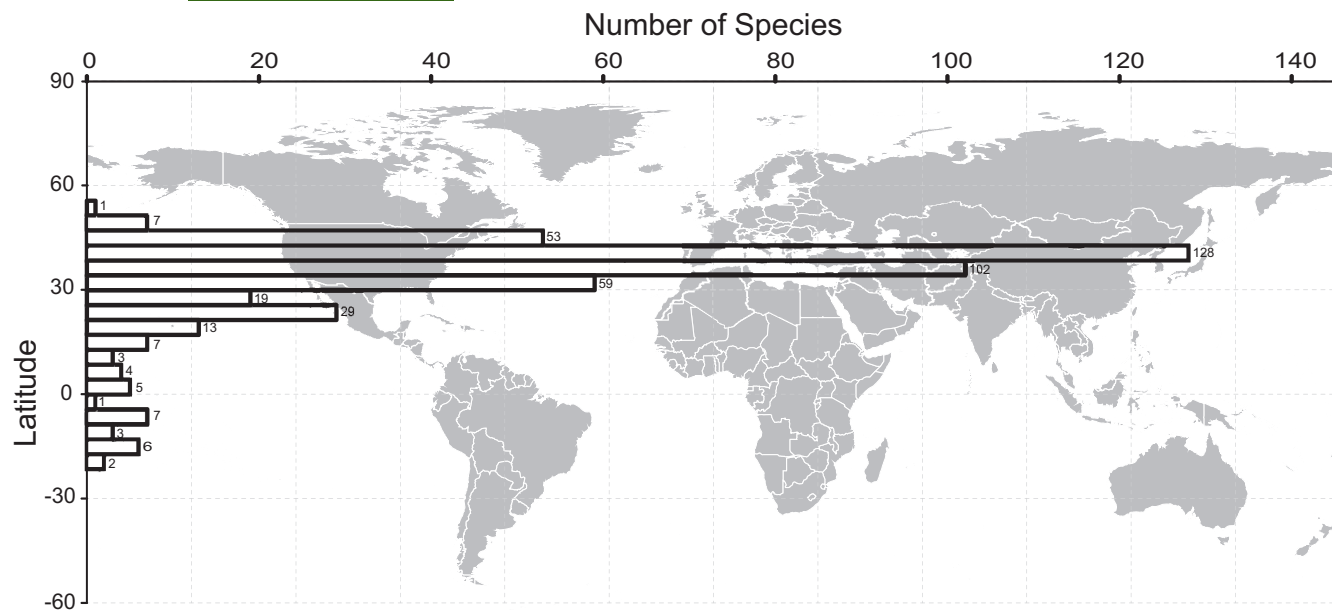


FIGURE 1 Midpoint latitude of all extant, described species of *Stenammini* binned into 5° intervals. The plot shows an inverse latitudinal diversity gradient, with a strong richness peak in the northern temperate zone. The base map was acquired from www.simplemapper.net and is a pseudo Plate Carrée projection.

instead of the more informative normal and lognormal prior distributions to calibrate nodes had little to no effect (Appendix S3: Figures S3.15–S3.18). Similarly, the different schemes used for assigning dispersal multipliers in the biogeographic analyses returned very congruent results and in all cases the DEC model was favoured over the alternative DIVA-like or BayArea-like models (Appendix S1: Table S1.7; Appendix S5: Figures S5.1–S5.16). Because the second dispersal multipliers scheme returned the best likelihood among the different DEC reconstructions, we focus on this reconstruction, integrated with the clock-like divergence dates, below. Dates are presented as mean ages and ancestral ranges are presented as the most likely states.

The tribe *Stenammini* evolved 50.5 Ma (42.6–60.1 Ma 95% highest posterior density [HPD]) in the Holarctic region. Among the major clades, most have an origin in the northern temperate zone. The genus *Stenamma* originated in the Holarctic 40.6 Ma (51.2–29.9 Ma). The “*Goniomma*” and “*Aphaenogaster*” clades both originated in the Palearctic region 17.9 Ma (12.5–23.6 Ma) and 42.2 Ma (33.9–51.5 Ma), respectively. The “*Novomessor*” clade was inferred to have had a temperate origin, evolving in the Nearctic 23.6 Ma (16.2–31.4 Ma). Within the “*Novomessor*” clade, the DEC model inferred a Nearctic plus Neotropical origin for *Novomessor* and a Nearctic-only origin for *Veromessor*, 15.4 Ma (9.8–22.2 Ma) and 13.0 Ma (9.4–16.8 Ma), respectively. Unexpectedly, the “*Deromyrma*” clade, which includes mostly tropical taxa (a few species occur in temperate Australia), was also found to have had a temperate origin, with the ancestor inhabiting the Holarctic 40.3 Ma (32.1–49.3 Ma).

Across the tribe there were a total of seven separate dispersal events into the tropics and three separate dispersal events out of the tropics (Figure 3). Most notably, the “*Deromyrma*” clade dispersed into the tropics four separate times. Between the Nearctic and Palearctic regions, there were two dispersal events, one in each direction.

3.5 | Diversification rates

We found support for an increase in diversification rate in the branch leading to the completely Holarctic “*Aphaenogaster*” clade (Figure 3; Appendix S6). With the rate shift prior set to 1, BAMM produced posterior probabilities for six rate-shift models. Of these, the single rate-shift model received the highest posterior probability (78%) and was favoured over all other sampled models based on Bayes Factors (Appendix S1: Table S1.8). The “*Aphaenogaster*” clade is dated to 17 Ma with the rate shift inferred to have occurred along the stem lineage prior to the origin of the crown group. Increasing the rate shift prior from 1 to 5 and 10 did not significantly change the results.

Despite there being evidence for rate differences among lineages in the tree, the STRAPP analysis used to test for a correlation between latitude and speciation rate did not find a significant correlation ($p = 0.942$).

4 | DISCUSSION

4.1 | The latitudinal diversity gradient

We found that *Stenammini* has a strong inverse diversity gradient, with most species inhabiting the northern temperate zone between 30 and 45°N latitude (Figure 1). Separating results by clade and biogeographic region, the diversity peak is mainly attributable to *Aphaenogaster* and *Messor* species in the Palearctic; however, even with this clade removed, there is still a peak in the northern temperate zone. This pattern is likely not due to specimen collection bias, given that there has been extensive ant sampling by the authors and

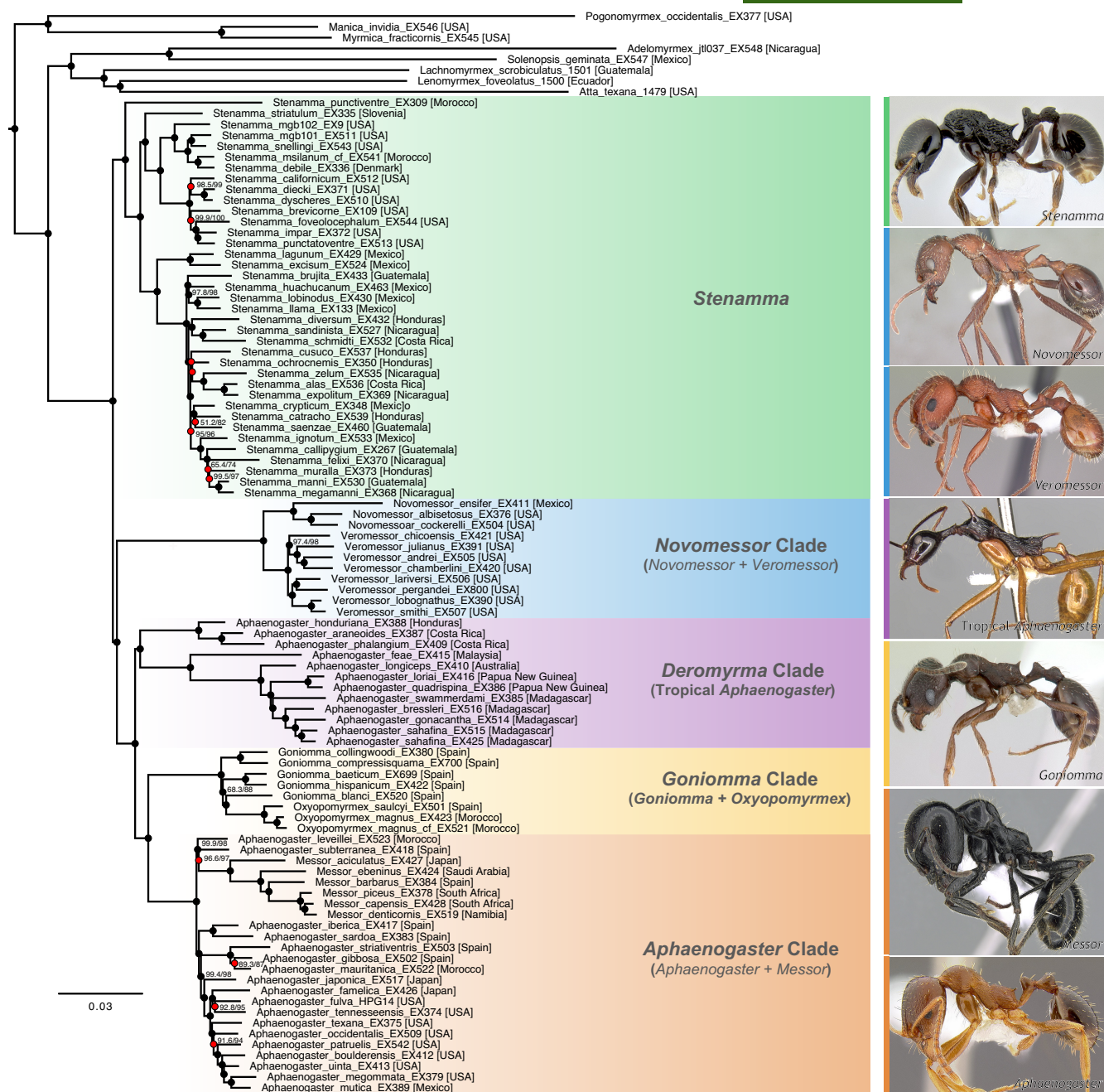


FIGURE 2 Maximum likelihood phylogeny depicting relationships among 92 Stenammini species and eight outgroups. Analysis performed with IQ-TREE using 973 concatenated UCE loci (75% taxon filtering) and SWSC-EN partitioning. Support values on nodes indicate UFB/SH-aLRT scores and are only shown for nodes with values below 100/100. Red dots mark clades that were not recovered in all analyses. Sample names include a unique extraction code and the country where the sample was collected. Ant images from www.antweb.org. From top to bottom: *Stenamma lobinodus* (CASENT0102824, credit: M. Branstetter), *Novomessor albisetosus* (CASENT0102824, credit: A. Nobile), *Veromessor lobognathus* (CASENT0104781, credit: A. Nobile), *Aphaenogaster loriai* (CASENT0900358, credit: W. Ericson), *Goniomma hispanicum* (CASENT0178839, credit: A. Nobile), *Messor barbarus* (CASENT0281546, credit: E. Ortega), and *Aphaenogaster occidentalis* (CASENT0106090, credit: M. Branstetter).

colleagues in many tropical regions and few additional morphospecies have been identified. In contrast, there have been several recent taxonomic revisions focusing on Palearctic taxa and these studies have all added species to overall diversity (Bolton, 2020).

An interesting characteristic of the inverse gradient observed in Stenammini is its skewed distribution. Even though the group

extends into the southern temperate zone, the diversity peak is only found in the northern hemisphere. This pattern of a northern temperate species peak has been observed in other animal lineages (Chown et al., 1998; Owen & Owen, 1974; Pyron & Burbrink, 2009; Smith et al., 2005; Stephens & Wiens, 2003; Wiens, 2007). Bimodal, amphitropic distributions are also known (Dixon et al., 1987; Krug

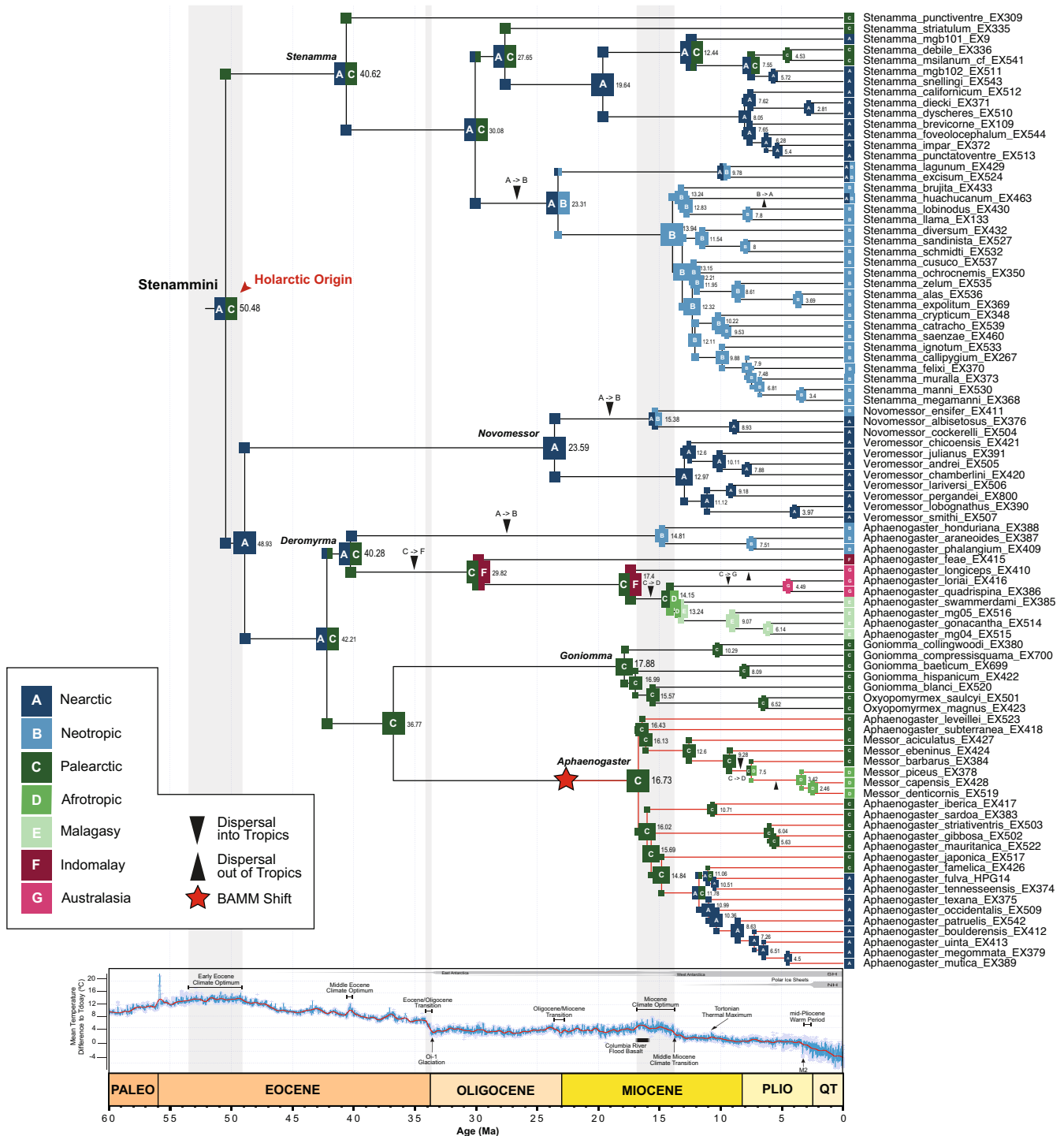


FIGURE 3 The biogeographic history of Stenammini. Chronogram inferred with BEAST2 using 300 clock-like UCE loci and a relaxed lognormal clock model. Ancestral areas inferred with BioGeoBEARS using the best-fitting DEC model and the second dispersal multipliers scheme. Coloured squares on nodes and branches indicate most likely ancestral areas and range inheritance scenarios, respectively. The red star and subsequent red branches indicate the diversification rate shift inferred by BAMM. Numbers on nodes are divergence times in millions of years. The graph underneath the chronogram shows global temperature differences over the last 60 Ma as compared to current temperature and is modified from Westerhold et al. (2020).

et al., 2007; Orr et al., 2020), but no clade-based studies have shown a skewed distribution in which diversity peaks in the southern temperate zone, although at least one assemblage-based study has shown this pattern (Rivadeneira et al., 2011).

4.2 | Evaluating alternative LDG hypotheses

The BCH (Pyron & Burbrink, 2009) proposes that the ancestral biogeographic range of a group should be the area where that group is



most diverse due to the combined effects of center-of-origin, time-for-speciation, and niche conservatism. Given that *Stenammini* is most diverse in the northern temperate zone, we predicted that this region would be the group's inferred ancestral area. Our results support this prediction of the BCH. We found that *Stenammini* most likely evolved in the Holarctic region 51 Ma and that all major clades originated in the northern temperate region as well. Although the group dispersed into the tropics seven times, these lineages are generally younger and have fewer species. Additionally, the Middle American clade of *Stenamma*, while tropical, has radiated in montane Middle America, possibly because of its ancestral adaptation to more northern environments (Branstetter, 2012, 2013). Thus, while the tribe has shifted into the tropics multiple times, it has not been very successful at radiating into niches occupied by most tropical ants. The BCH is further supported by the observation that *Stenammini* is not only species poor in the tropics, but it is also species poor in the extratropics of the southern hemisphere. The modal rather than bimodal species richness pattern is the consequence of *Stenammini* having originated in the Holarctic biogeographic region and not the southern extratropical region.

The DRH (Cardillo et al., 2005; Rohde, 1992; Weir & Schluter, 2007), in contrast, predicts that latitudinal differences in species richness are the result of differences in diversification rate across latitude. In the context of the standard LDG, the idea is that tropical lineages will have higher speciation and/or lower extinction rates compared to temperate lineages. However, in the case of an inverse LDG the opposite should be true. Thus, for *Stenammini*, we expected to see higher diversification rates in temperate lineages. In general, this hypothesis is rejected: we did not find a correlation between latitude and diversification rate, as would be predicted under the DRH, and most temperate lineages have diversification rates similar to tropical lineages. The one exception to this is the "Aphaenogaster" clade, which predominately includes extratropical species and shows evidence of increased diversification relatively recently in time. Although this finding indicates that a diversification rate increase has contributed to the inverse latitudinal diversity gradient, it was not the most important factor in shaping the gradient. This is supported by the observation that if the "Aphaenogaster" clade were to have diversified at a similar rate to other lineages, there would still be an inverse diversity gradient.

Given that there is considerable debate about the validity of diversification rate analyses (Helmstetter et al., 2022; Louca & Pennell, 2020), particularly when taxa have been incompletely sampled (Chang et al., 2020), these results should be viewed cautiously and tested with more data. With this caveat in mind, we conclude that the BCH and its component hypotheses are best supported by the results presented here. This conclusion is consistent with similar evolutionary studies on ants (Economo et al., 2018, 2019) and several other organismal groups, such as snakes (Pyron & Burbrink, 2009), mammals (Buckley et al., 2010) and birds (Duchêne & Cardillo, 2015).

It is worth noting, however, that some studies investigating the standard LDG have identified diversification rate differences as being more significant, including in swallowtail butterflies

(Condamine et al., 2012), mammals (Rolland et al., 2014), and amphibians (Pyron & Wiens, 2013), and at least one study in carnivores has identified dispersal combined with range contraction as being the primary mechanism (Rolland et al., 2015). The swallowtail butterfly example is an interesting contrast to *Stenammini*, because the clade has similar diversity and evolved in the Holarctic at about the same time (Condamine et al., 2012). Unlike *Stenammini*, the group split into a pair of sister clades, one tropical and one temperate, and the tropical clade diversified more rapidly than the temperate clade.

4.3 | Biogeography and evolution of *Stenammini*

Crown-group *Stenammini* originated in the Holarctic during the Early Eocene approximately 51 Ma. This period corresponds to the early Eocene climatic optimum (EECO) when temperatures were roughly 12–16°C warmer than today (Westerhold et al., 2020; Zachos et al., 2001) and broad-leaved evergreen forest and paratropical rainforest were greatly expanded (Graham, 1993, 2011). Fossil records indicate that broad-leaved, evergreen forest extended above 70°N latitude (Eberle & Greenwood, 2012; Harrington et al., 2012) and that relatives of animals with present-day tropical affinities, such as the tapir, inhabited these forests (Eberle & Greenwood, 2012). It is also known that the vegetation in North America and Eurasia was more homogeneous during this time, likely due to the lack of polar glaciation and the existence of two major land bridges, the Bering Land Bridge (75°N) and the North Atlantic Land Bridge (45–65°N) (Wing, 1987).

Stenammini thus originated in the Holarctic at a time when wet forest habitat dominated the northern hemisphere and significant connections between northern continents existed, facilitating inter-continental dispersal. Considering our evaluation of the BCH, one criticism might be that the dominant ancestral environment in the northern latitudes was tropical, in the climatic sense, and very different from the more seasonal habitats that exist today in the same region. If *Stenammini* originally occupied a "tropical" niche, it would suggest that the tribe underwent a climatic niche shift after originating. Although tropical and paratropical habitats were more widespread during the EECO, temperate floras like those present today also existed (Harrington et al., 2012). Considering that most modern *stenammine* species occupy temperate niches, we conclude that *Stenammini* likely originated as a cold-adapted clade.

After the EECO there was a gradual decrease in global temperature culminating in a sharp decrease 33.9 Ma at the Eocene–Oligocene boundary. During the cooling, evergreen forests retracted, and more seasonal habitats expanded (Graham, 2011; Wing, 1987). This period is important because many modern plant and animal lineages originated (Bininda-Emonds et al., 2007; Jaramillo et al., 2010; Pellmyr & Leebens-Mack, 1999; Wing, 1987). For plants, the homogeneous nature of the vegetation between North America and Eurasia began to disappear, suggesting that dispersal via the northern land bridges became increasingly less likely, especially for species adapted to warm, wet environments. Many wet-adapted species that were once

widespread across Eurasia retracted into tropical refugia, creating disjunct distributions between the Old and New World tropics. This pattern, often recognized in plants, is known as the Boreotropics hypothesis (Donoghue, 2008; Lavin & Luckow, 1993; Tiffney, 1985; Wolfe, 1975), and we believe it applies to the “Deromyrma” clade.

The “Deromyrma” clade is primarily a tropical group and our phylogenetic results show that the clade originated ~40 Ma at about the time of the middle Eocene climatic optimum, and it bifurcated into New and Old World lineages. Contrary to expectations, we found that the clade originated in the Holarctic and dispersed into the tropics four times, once into Middle America, once into Indomalaya, once into the Afrotropics, and once into Australasia. This reconstruction is concordant with the Boreotropics hypothesis. The ancestor of the “Deromyrma” clade was widespread and adapted to warm, wet evergreen forest habitat. When the wet forest contracted and no longer extended across the northern land bridges, “Deromyrma” separated vicariantly into the New and Old World lineages. Both lineages then followed the retraction of wet forest into the tropics, where they have persisted into the present. This scenario is concordant with the fossil record, which includes a species from Dominican Amber (*Aphaenogaster amphiocenica*) that has been suggested to be closely related to tropical *Aphaenogaster* (De Andrade, 1995), although an exact placement of the fossil based on morphology is difficult.

In the Old World tropics, the “Deromyrma” clade has penetrated into Indomalaya, Australasia, and Madagascar (Afrotropics). How the clade arrived in Madagascar is interesting to consider, since it is not known from mainland Africa. Our biogeographic reconstruction suggests that the clade dispersed into the Afrotropics from the Palearctic rather than from Indomalaya or Australasia. This scenario suggests dispersal through Africa to reach Madagascar with later extinction from the mainland. A “through Africa” hypothesis is supported by the fact that most extant Malagasy taxa have African origins (Yoder & Nowak, 2006) and rainforest was once more extensive in Africa during the Eocene (Burgess, 1998; Couvreur et al., 2008).

Global cooling after the EECO explains another intriguing diversification event within Stenammini. The ant genus *Stenamma* includes three clades, the relict Palearctic taxon *S. punctiventre*, a Holarctic clade, and a Middle American clade. The species *S. punctiventre* is included in a molecular phylogeny for the first time in this study. Unexpectedly, the species was placed as sister to all remaining *Stenamma*, pushing the age of the crown group back to 41 Ma. Previous work inferred the origin of *Stenamma* to be Nearctic (Branstetter, 2012), but with *S. punctiventre* included, we inferred the origin of the genus to be Holarctic. The two major clades in the genus each contain about 40 species, with the Holarctic clade including a mix of Nearctic and Palearctic lineages and the Middle American clade including predominately Central American species, with only a couple of species reaching northern Mexico/southern USA and a few reaching northern South America. The timing of the split for these two clades is 30 Ma. This date overlaps very closely with the sharp cooling event at the Eocene–Oligocene boundary at 33.9 Ma, which caused the mesic

forests that once stretched between North and Central America to become fragmented due to aridification in the southwestern USA and northern Mexico (Wing, 1987). Given that *Stenamma* is generally associated with wet forest leaf litter, this aridification event is potentially what caused the nearly complete split between northern and southern clades.

The strong association of Stenammini with the northern temperate zone is further exemplified by the “Goniomma”, “Aphaenogaster” and “Novomessor” clades having ancestral areas in the temperate zone. The “Goniomma” clade originated 18 Ma and is completely restricted to the Mediterranean region. The “Aphaenogaster” clade is about the same age (17 Ma) but has spread more widely across the globe. It is distributed across the Holarctic, and with the genus *Messor*, has penetrated arid regions in Africa, extending all the way down into South Africa. The “Novomessor” clade also had a temperate origin. This group is arid-adapted and likely evolved in the Nearctic with later dispersal into the Neotropics. The age of the clade is 24 Ma and is split into the two monophyletic genera *Novomessor* and *Veromessor*. The former is distributed more southerly into Mexico, whereas the latter is more diverse in the western USA. It is possible that these two genera separated into northern and southern lineages during periods of increased aridification, similar to the pattern observed in *Stenamma*.

We found a significant increase in diversification rate leading to the “Aphaenogaster” clade. This is the most diverse group of stenammine ants with 305 species included. In comparison, its sister clade only has 22 species and all other groups combined have 143 species. Why did the “Aphaenogaster” clade diversify significantly faster than the other lineages? We believe the answer can be linked to the group's ecological diversity and its ties to the Mediterranean region. The clade includes two major genera, *Messor* and *Aphaenogaster*. *Messor* is a specialist seed-harvester that is well adapted to desert and grassland habitats. It is currently widespread, occurring throughout the Palearctic and into arid Africa. The genus *Aphaenogaster* is more varied in its habits but tends to consist of medium-sized epigeic ants that are omnivorous. It does well in temperate forests and seasonally dry areas around the Mediterranean. Given the ability of both genera to do well in seasonally dry areas, increasing aridification over the last 20 Ma may have promoted diversification by fragmenting forested habitats and expanding arid environments.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Raw Illumina reads and contigs representing UCE loci are available in the NCBI Sequence Read Archive and GenBank, respectively (BioProjects #PRJNA820050, PRJNA248919, PRJNA379607). A complete list of relevant NCBI accession numbers is available in Appendix S1: Table S1.9. The concatenated UCE matrix, TRINITY contigs, UCE alignments, tree files, and the UCE bait file have been deposited in Dryad (<https://doi.org/10.5061/dryad.2280gb5tv>).

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BIOSKETCH

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SUPPORTING INFORMATION

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