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RESEARCH ARTICLE

Spatial phylogenomics of acrobat ants in Madagascar—Mountains function as cradles for recent diversity and endemism

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Abstract

Aim: A crucial step to protecting biodiversity is assessing species diversity and endemism. We delineate spatial patterns of diversity in Malagasy ants on a phylogenetic and taxonomic level to identify centers of diversity and endemism, and evaluate the 'museum vs. cradle' hypothesis with regard to ant endemism.

Location: Madagascar.

Taxon: Ants, genus *Crematogaster*.

Methods: We estimated distribution models for 33 *Crematogaster* species and generated a phylogeny based on ultraconserved elements. We calculated species richness (SR), phylogenetic diversity (PD), weighted (WE), phylogenetic endemism (PE), randomized phylogenetic diversity (PD-sig), and relative phylogenetic diversity (RPD) and endemism (RPE). Categorical analyses of neo- and paleo-endemism (CANAPE) and the phylo-jaccard index were used to delineate centers of neo- and paleo-endemism. We correlated these measures with elevation metrics to investigate the role of mountains in generating ant endemism.

Results: We found extensive phylogenetic clustering (significantly low PD-sig) and short branches (low RPD) at higher elevations in central and south-central to southern Madagascar. In contrast, phylogenetic overdispersion (significantly high PD-sig) and long branches (high RPD) predominate at lower elevations in eastern humid and northern western dry forests. CANAPE and phylo-jaccard estimated five centers of endemism, whereby neo- and mixed endemism were significantly correlated with higher elevations, and paleo-endemism with lower elevations.

Main conclusions: Centers of ant endemism are located in western dry and humid forests of northern Madagascar, eastern humid forests, and in the southern Central Highland region. Mountainous areas appear to be cradles of recent diversification for acrobat ants, whereas lower elevations may be regarded as centers of paleo-endemism and thus museums for relict lineages. Species diversification among acrobat ants may have coincided with the arrival of a new biome in the central highlands of Madagascar.

KEYWORDS
CANAPE, centers of endemism, Formicidae, neo-endemism, paleo-endemism, phylogenetic diversity, phylogenetic endemism

1 | INTRODUCTION

The first step in protecting biodiversity and its associated ecosystem functions is assessing and quantifying measurable units of biodiversity. The two key elements of measuring biodiversity across space and time are species diversity, which includes alpha (species richness in a habitat), beta (species turnover between habitats), and gamma diversity (regional diversity = alpha + beta); and endemism. Over the last decade, it has become common practice in conservation to assess phylogenetic (lineage) diversity alongside taxonomic species richness when assessing alpha diversity (Tucker et al., 2017; Winter et al., 2013). Phylogenetic diversity, usually measured as the sum of branch lengths integrated across a focal clade (Faith, 1992), is insufficient to prove lineage rarity. Therefore, conservation assessments often lend credence to a complementary measure and phylogenetic endemism (Rosauer et al., 2009). High phylogenetic endemism occurs when long phylogenetic branches (i.e., species or clades) are restricted to a small geographic range, with total phylogenetic endemism increasing with the number of restricted species or clades occurring in the area (Rosauer & Jetz, 2015). Rarity and endemism are of particular concern in conservation planning that takes into account global climate change, as range shifts are expected to have more drastic consequences for endemic species (Fordham & Brook, 2010).

While identifying spatial distribution patterns of endemism and diversity is the basis for conservation practice, most researchers are also interested in deciphering the evolutionary processes that created present-day distributions of diversity. High species richness in tropical regions has frequently been attributed to greater origination or speciation rates in this evolutionary "cradle" of diversity, or conversely, to low extinction rates and greater antiquity in tropical "museums" of evolutionary history (Chown & Gaston, 2000; Gaston & Blackburn, 1996). This "cradle vs. museum" hypothesis is often tested by estimating species diversification rates from global phylogenies (e.g. Dornburg et al., 2017; Moreau & Bell, 2013). However, the cradle vs. museum hypothesis can also be investigated from a spatial angle focusing on endemism, which is the approach used in our study. When considering the evolutionary history of endemism, we can distinguish, at least conceptually, between "new" or neo-endemics and "old" or paleo-endemics (Gillespie & Roderick, 2002; Mishler et al., 2014). Neo-endemics are recently diverged species which have not (yet) dispersed from their geographic cradle of origin, while paleo-endemics are presumed to have been more widespread in the past and have since become isolated in a smaller geographic area due to, for example, continental fragmentation and relictualization, or a changing climate.

A derivative statistical framework for phylogenetic diversity (PD) and phylogenetic endemism (PE) has been designed to distinguish between these two different origins while identifying centers of endemism. This approach uses "Categorical Analysis of Neo- and Paleoendemism" (CANAPE) (Mishler et al., 2014), which relies on the novel diversity measure of relative phylogenetic endemism (RPE). A center of endemism here is defined by a cluster of grid cells that show significantly high endemism as measured by relative phylogenetic endemism (RPE), whether in the RPE numerator, denominator, or both. CANAPE permits further distinctions between paleo-endemic centers that harbor many endemic long-branched species (i.e., long terminal branches) and neo-endemic centers that consist of many endemic species subtended by short branches in the phylogeny. Moreover, centers of mixed endemism are regions statistically significant for RPE but containing a mix of endemic taxa on short and long branches (Mishler et al., 2014). In this context, centers of neo-endemism can be seen as centers of recent diversification, or "cradles" of diversity. By contrast, centers of paleo-endemism are areas where taxa persisted over time, creating "museums" of diversity (Dagallier et al., 2019), and can be the source of hypotheses about historical processes that shaped biodiversity (Thornhill et al., 2016).

In Madagascar, a long history of isolation from other landmasses and the stochasticity of long-distance dispersal (Yoder & Nowak, 2006) have created a unique pool of species (Goodman & Benstead, 2005). The geography of the island supports diverse and complex biomes (Figure 1a). Precipitation patterns are strongly influenced by north-to-south mountain ranges (Figure 1b), which block rain-laden trade winds from the Indian Ocean. These rainfall patterns have produced humid forests along Madagascar's east coast and mountains, and more seasonal habitats, such as western dry forest, in the northernmost parts of the island and throughout the west, transitioning toward extremely arid regions in the south and endemic dry spiny forest in the southwest (Moat & Smith, 2007). Wooded grassland–bushland and plateau grasslands, which currently cover the majority of the central highland region in Madagascar, were suspected to be anthropogenic habitats (Burney, 1987). Recent evidence has indicated that these plant communities were established long before the arrival of humans by climate, natural grazing and other natural factors (Bond et al., 2008; Vorontsova et al., 2016), although human action may have contributed to the expansion of the grasslands (Vorontsova et al., 2016).

Madagascar's exceptional levels of endemism have largely been estimated based on taxonomic species and vertebrate data (Goodman & Benstead, 2005; Wilmé et al., 2006). Such scholarship often highlights the role of mountains as refugia during climatic shifts and as centers of endemism and species diversification (Brown et al., 2014, 2016; Everson et al., 2020; Wollenberg et al., 2008). Exploring the evolution of diversity and endemism within a more diverse clade such as the arthropods is essential to unravel the processes that generated the island's thousands of specialized endemics. Ants make good models for this endeavor given their general ecological importance and abundance in all terrestrial habitats (Holldobler & Wilson, 2008). Inventories for ants have been completed at more than 200 field sites across a broad array of habitats and elevation ranges (Fisher, 2005), yielding a remarkably complete distribution dataset. In addition, updated taxonomy now exists for many speciose ant groups (e.g. Blaimer & Fisher, 2013b; Rakotonirina & Fisher, 2018; Salata & Fisher, 2020).

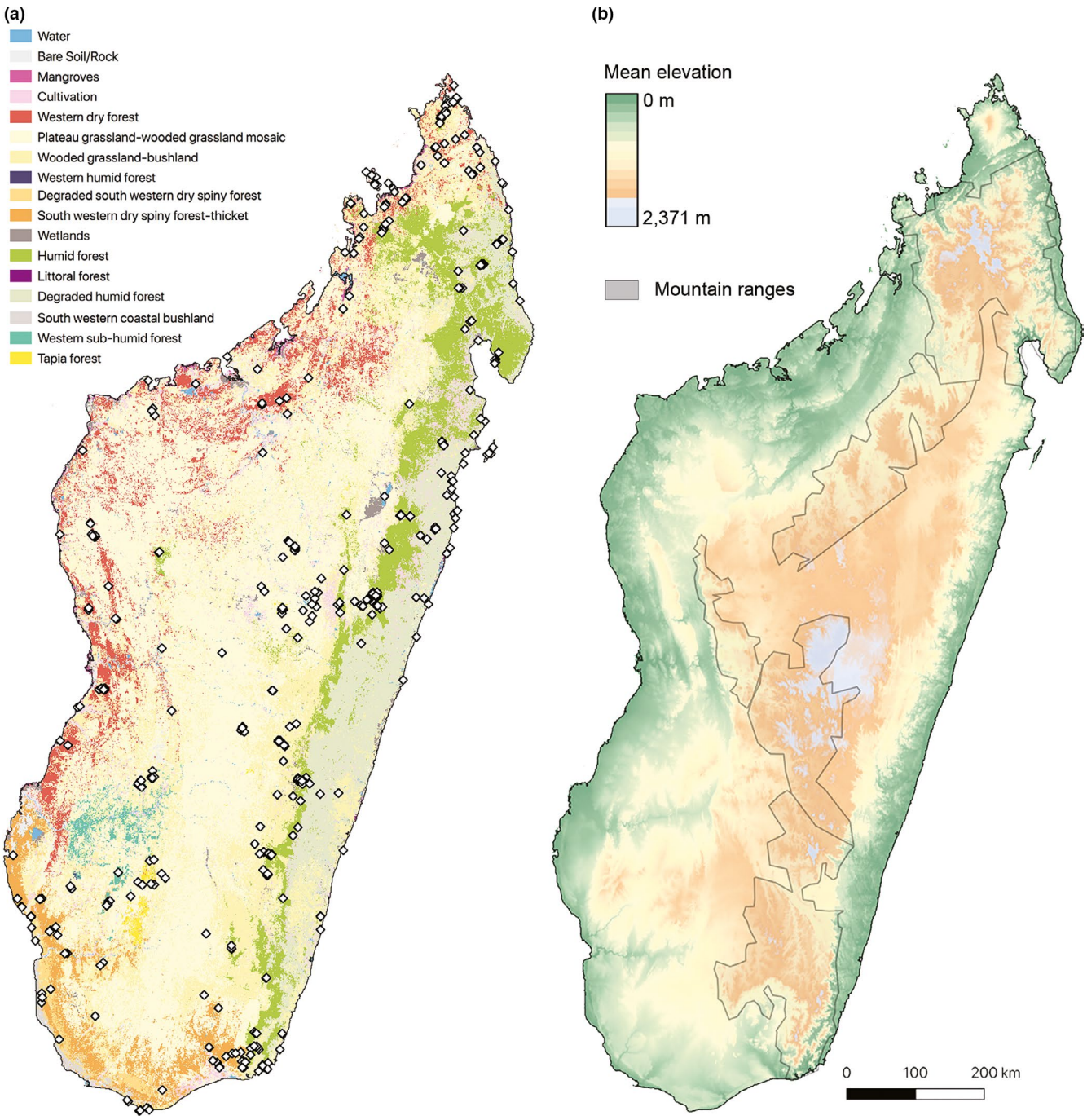

FIGURE 1 Map of Madagascar depicting: a) the vegetation types occurring across the island, as defined by Moat and Smith (2007), with the collection localities for *Crematogaster* represented by white diamonds. A full list of collection records, including locality information and vegetation type, is available in Table S1.1; b) the mean elevation across the island, in meters, where grey shading delineates "montane areas" as defined by the GMBA mountain inventory_v1.2 (Körner et al., 2011, 2016). Elevation data were downloaded from MadaClim (https://madaclim.cirad.fr/)

In this study, we use Malagasy acrobat ants (genus *Crematogaster*) as surrogates to unravel phylogenetic diversity and endemism across ants in Madagascar to improve understanding of insect diversity patterns and their evolution across this biodiversity hotspot. Acrobat ants are among the most species-rich clades worldwide and their taxonomy has been recently revised (e.g. Blaimer, 2012b; Blaimer & Fisher, 2013a, 2013b). *Crematogaster* ants have colonized the island several times from the African mainland throughout the Miocene. Today, there are seven evolutionarily distinct *Crematogaster* lineages in Madagascar, as investigated in Blaimer (2012a) based on a global phylogeny. The clades representing independent colonizations are indicated in Appendix 4, Figure S.4.9. We use ecological niche modeling to complement the extensive, yet potentially still biased, distribution data for these ants in Madagascar. We correlate this

comprehensive spatial analysis with a newly generated phylogeny based on phylogenomic data with the following aims:

(a) We measured spatial patterns of taxonomic species richness and phylogenetic diversity, as well as weighted and phylogenetic endemism for *Crematogaster*. (b) We identified regions where phylogenetic diversity is significantly elevated or lower than expected compared to a null model. (c) Applying relative phylogenetic endemism (RPE) and Categorical Analysis of Neo- and Paleo-endemism (CANAPE) (Mishler et al., 2014) methodology for the first time in insects, we identified centers of endemism (COEs) for *Crematogaster* and tested the museum versus cradle hypothesis. (d) We further correlated significant phylogenetic diversity and endemism with elevation, expecting to find evidence for mountains functioning as refugia or museums for diversity and endemism. We discuss our results in the context of Madagascar's biogeography and delineate several hypotheses for future testing via expanded sampling for ants and other insects.

2 | MATERIALS AND METHODS

2.1 | *Crematogaster* occurrence records

We used 3,890 georeferenced occurrence records for *Crematogaster* in Madagascar that are available publicly from AntWeb (www.antweb.org), a database of georeferenced occurrences and photos of ants from around the globe. After subsequent cleaning for taxonomic consistency (i.e., removing species codes not assigned to a described or undescribed species, or morphospecies only known by males) and spatial consistency (i.e., removing duplicated records (-Res, -D01, and -M after an existing CASENT specimen identifier)), the resulting dataset comprised 3,356 records for 34 species of *Crematogaster* in Madagascar (AntWeb-cleaned). The full dataset containing all the collection records used in our analysis is available in Table S1.1 in Supporting Information. Ecological niche modeling (ENM) was used to estimate species geographic range, with AntWeb-cleaned data as input. The distributions estimated by the ENM analysis (see detailed methods below) were then used as input for biodiversity analyses.

2.2 | Species geographic range estimation

Geographic ranges were estimated using ecological niche modeling (ENM) for 31 species with at least three unique occurrence records at the 30 arc-second spatial resolution based on the *Crematogaster* dataset. As predictor variables, we used environmental data downloaded from MadaClim (https://madaclim.cirad.fr/). After removing highly correlated variables (Pearson correlation coefficient ≥0.8), we selected 14 to build the models: nine climatic variables related to temperature and water availability, and five non-climatic variables (slope, aspect, solar radiation, soil, and watershed). To account for sampling bias, we used all collecting events of ants in Madagascar recorded on AntWeb (33,295 collection events) to build a sampling density map at QGIS 3.12, using a quartic kernel shape and 10 km radius of influence.

Models were estimated using Maxent 3.4.1 (Phillips et al., 2006) implemented in the R package 'dismo' (Hijmans et al., 2017), with 10,000 background points sampled with a probability proportional to the kernel cell's values. We used Maxent's default auto-features and a regularization multiplier of 1. To convert continuous ENM maps in a binary map of species occurrence, we used a 10th percentile training presence logistic threshold. For a more detailed methodology, a species list, and a description of selected variables for ENM analyses, refer to Appendix S2 (Figure S2.1–3, Table S2.2–3). For *Crematogaster sisa* and *C. hafahafa*, species with fewer than three unique occurrence records (i.e., not included in the ENM analyses), we estimated the geographic range using a 10 km radius buffer around each occurrence point. *Crematogaster marthae* (a species only known from the holotype) was not included in our geographic range estimation given its imprecise and old collection label data. For maps of each species habitat suitability and occurrence estimation, see Figure S2.4–8.

2.3 | Phylogenetic data generation

We selected 33 specimens of *Crematogaster* for DNA sequencing, one for each species that occurs in Madagascar (with the exception of *C. marthae*) and outgroup specimens from the species *Terataner alluaudi*, *Meranoplus mayri*, and *Meranoplus radamae* (Table S3.4 in Supporting Information). All data were newly generated for this study except in the cases of *C. alafara*, *C. telolafy*, *M. mayri*, and *M. radamae*, for which published data were available (Blaimer et al., 2018).

To examine phylogenetic relationships among species, we employed a method combining target enrichment of ultraconserved elements (UCEs) with multiplexed, next-generation sequencing (Branstetter et al., 2017). UCE molecular work was performed following the methodology first described for ants in Branstetter et al. (2017). Sequence data were trimmed, assembled, and aligned using PHYLUCE v1.6 (Faircloth, 2016), which includes wrapper scripts that facilitate batch processing of large numbers of samples. We inferred phylogenetic relationships of *Crematogaster* with the likelihood-based program IQ-TREE v1.6.8 (Nguyen et al., 2015), and the resulting tree, as well as the sequenced data alignment used to generate it, were then used to carry out a dating analysis using MCMCTree and BASEML programs, which are part of the PAML software package for phylogenetic analysis (Yang, 2007). For detailed methodology, refer to Appendix S3 in Supporting Information.

2.4 | Spatial analyses of phylogenetic diversity and endemism

All spatial analyses of phylogenetic and endemism were conducted using 10 × 10 km grid cells and Coordinate Reference System EPSG

29738. Spatial data (inferred using ENM at 30 arc-second spatial resolution) were first correlated with the chronogram (inferred in the MCMCTree analysis), then converted into presence within 10 × 10 km grid cells for optimal visualization, resulting in 6,161 grid cells.

2.4.1 | Biodiversity analyses

Using methods and metrics described by Mishler et al. (2014) and Thornhill et al. (2016), we calculated taxonomic and phylogenetic indices for each grid across both our datasets. The taxonomic indices used were **Species Richness (SR)**, defined as the number of distinct species present in each grid cell, and **Weighted Endemism of taxa (WE)** (Crisp et al., 2001)), defined as a range-weighted richness score, such that the contribution of each species is weighted to be proportional to the fraction of its range across each grid cell (Laffan et al., 2016). The phylogenetic indices used were **Phylogenetic Diversity (PD)** (Faith, 1992), the sum of branch lengths connecting the root of the phylogenetic tree to all species within each grid cell; and **Phylogenetic Endemism (PE)** (Rosauer et al., 2009), defined as the degree to which branches found in each grid cell are restricted to those locations (Laffan et al., 2016). We also calculated two additional metrics, **Relative Phylogenetic Diversity (RPD)** and **Relative Phylogenetic Endemism (RPE)**, indices that compare the PD/PE observed on the actual phylogenetic tree in the numerator to the PD/PE observed on a theoretical comparison tree in the denominator. The theoretical tree has the same topology as the original tree, but identical length branches (Mishler et al., 2014). All metrics were calculated using the 'Biodiverse Pipeline' (https://github.com/NunzioKnerr/biodiverse_pipeline) to run Biodiverse v.2.0 (Laffan et al., 2010) directly from R v.3.6.3.

2.4.2 | Randomization tests

To assess the statistical significance of phylogenetic diversity (PD), phylogenetic endemism (PE), relative phylogenetic diversity (RPD), and relative phylogenetic endemism (RPE) (i.e., which grid cell had significantly higher or lower observed values than expected given the species richness in that grid cell and the geographical range of the species), we ran 999 randomizations using the 'Biodiverse Pipeline' in R. This method randomly reassigns species occurrences in grid cells to grid cells without replacement, keeping the original number of species in each grid cell and the original number of grid cells in which the species occurs. Then, for each metric, the observed value is compared with the 999 randomization values. Values significantly higher or lower than expected are defined as being >97.5% or <2.5% of random, respectively (two-tailed test, $a = 0.05$) (Thornhill et al., 2017). This randomization test was carried out for PD (PD-sig), PE, RPD, and RPE, resulting in assignment of a significance class for each metric for each grid cell: significantly very low (<0.01), significantly low (<0.025), not significant, significantly high (>0.975), or significantly very high (>0.99). Significantly high phylogenetic diversity (PD-sig) indicates grid cells with species less closely related than expected by chance (phylogenetic overdispersion), whereas significantly low phylogenetic diversity (PD-sig) indicates grid cells with species more closely related than expected by chance (phylogenetic clustering). Significantly high RPD indicates over-representation of long-branched species, whereas significantly low RPD indicates over-representation of short-branched species (Mishler et al., 2014).

2.4.3 | Categorical analysis of neo- and paleo-endemism (CANAPE)

For grid cells that were significantly high in phylogenetic endemism (PE), we assessed contribution to PE by branches longer or shorter than expected, a two-step process named CANAPE described in detail by Mishler et al. (2014). The first step identifies grid cells showing significantly high phylogenetic endemism (one-tailed test, $a = 0.05$) in the relative phylogenetic endemism (RPE) numerator, RPE denominator, or both (as calculated by the randomization tests above). In the second step, grid cells that passed one of those tests were divided into meaningful, non-overlapping categories as: (a) centers of paleo-endemism (endemic long-branched taxa, with significantly high RPE ratios using a two-tailed test); (b) centers of neo-endemism (endemic short-branched taxa, with significantly low RPE ratios using a two-tailed test); or (c) centers of mixed endemism (mixture of endemic long and endemic short branches, not significant for RPE) (Thornhill et al., 2016).

2.4.4 | Comparisons among identified areas of endemism

Grid cells identified as statistically significant centers of endemism (relative phylogenetic endemism (RPE) significantly high, one-tailed test, $a = 0.05$) were then compared using phylogenetic diversity (PD) dissimilarity using the phylo-jaccard index visualized using cluster analyses in the program Biodiverse v2.0. The phylo-jaccard index measures the proportion of PD shared between two grid sets (the PD of the intersection of the grids divided by the PD of the union of the grids) (Laffan et al., 2016).

2.5 | Correlation with elevation, montane areas, and habitat

We compared the distribution of the mean, minimum, and maximum elevation of the grid cells, as well as their standard deviance, and the overlap with "montane areas" (see below) across results for: (a) the three categories of phylogenetic diversity (PD) (significantly high; not significant; significantly low); (b) the three categories of relative phylogenetic diversity (RPD) (significantly high

or very high; not significant; significantly low or very low); and (c) the four categories of categorical analysis of neo- and paleo-endemism (CANAPE) (neo-endemism; paleo-endemism; mixed-endemism; not significant). Elevation data were downloaded from MadaClim. To define montane areas, we used shapefiles provided by the Global Mountain Biodiversity Assessment (GMBA mountain inventory_V1.2; (Körner et al., 2016)). As normality of the residuals (one of the fundamental assumptions for ANOVAs) was not fulfilled for the three comparisons (results not shown), we used a non-parametric Kruskal–Wallis test. If at least one of the distributions was significantly different from the others ($p < 0.05$), then a Wilcoxon pairwise comparison (two-tailed tests with Holm's correction) was performed to disentangle which categories were significantly different ($p < 0.05$). To understand how species richness and phylogenetic diversity would differ across different habitats that occur in Madagascar, we tested the correlation between SR and PD per habitat, considering the habitat types defined by Moat and Smith (2007).

3 | RESULTS

3.1 | Tree topology

Our maximum likelihood analysis recovered a robust and well-supported phylogeny, with most nodes having 100% bootstrap support (Figure S4.9), similar to the results of Blaimer (2012a). Our dating analysis recovered *Crematogaster* in Madagascar with a crown age between 39 and 27 Ma. All ages with 95% confidence intervals are shown in Figure S4.10.

3.2 | Patterns of species richness and phylogenetic diversity

3.2.1 | Species Richness (SR) and phylogenetic diversity (PD)

Patterns of species richness and phylogenetic diversity for *Crematogaster* are very similar. Eastern humid forests and the humid and western dry forests throughout the Ampasindava peninsula and the Tsaratanana massif in the Greater Sambirano region in the north of the island have the highest richness and phylogenetic diversity (Figure 2a, b). Higher-elevation humid forests around Ranomafana in central Madagascar have high expected species richness, but less estimated PD than similarly species-rich areas (Figure 2a, b). Areas with similar medium–high SR and PD values are the eastern humid forest regions where about 58–76% of the branches of the entire phylogeny present for PD. The Greater Sambirano region also shows corresponding areas of high SR and high PD. Overall, the northern, eastern, and to a lesser extent western regions of Madagascar host most of the phylogenetic diversity for *Crematogaster*. We found PD to be moderately correlated with species richness across the island (Figure 2c, $R^2 = 0.65$).

3.2.2 | Significant Phylogenetic Diversity (PD-sig) and Relative Phylogenetic Diversity (RPD)

Assessment of statistical significance shows extensive phylogenetic clustering (significantly low PD-sig) (Figure 3a, in blue) for higher-elevation forests and wooded grassland–bushland habitat in the central (Antananarivo region) and south-central to southern parts of Madagascar (Ranomafana, Midongy du Sud, and Andringitra forests). In contrast, we see extensive phylogenetic overdispersion (significantly high PD-sig) (Figure 3a, in red) in eastern humid forests and northwestern dry forests. These results were mirrored by RPD metrics, which also indicated a significant concentration of short branches (i.e., significantly low RPD), in the central, south-central, and southern part of Madagascar (Figure 3b, in blue), similar to areas with very low PD. There was a significant concentration of long branches in eastern humid forests and western dry forests (Figure 3b, in red).

3.3 | Patterns of endemism

Patterns of endemism for *Crematogaster* ants show that two areas in northern Madagascar have the highest weighted endemism (WE) (Figure 4a) and phylogenetic endemism (PE) (Figure 4b): Montagne d'Ambre and Manongarivo. The categorical analysis of neo- and paleo-endemism (CANAPE) identified 486 grid cells as centers of endemism. These were compared to identify areas that share the most similarity in phylogenetic diversity (PD). Most grid cells were not highly distinct from each other and formed a geographically continuous cluster with other adjacent cells, allowing us to highlight five distinct centers of endemism (COEs). We used existing regional names to define COEs where possible, and otherwise derived names from the most prominent included protected areas or forests: (a) Greater Sambirano region in the north, (b) Melaky in western Madagascar, (c) eastern humid forests, (d) Midongy du Sud/Andringitra, and (e) Ranomafana in south-central Madagascar. Figure 4c illustrates that some areas in the Greater Sambirano, Ranomafana, and Midongy du Sud/Andringitra are centers of neo-endemism, that is, they support a high number of species that have arisen recently (Figure 4c, in red). The majority of the Greater Sambirano region, however, is recovered as a center for paleo-endemism, with formerly widespread "old" species now restricted to a smaller area (Figure 4c, in blue). The remaining areas represent mixed endemism (Figure 4c, green) and include both endemic short and long branches. The phylo-jaccard dissimilarity analysis of CANAPE cells recovered a number of major, geographically distinct clusters within which the endemic *Crematogaster* fauna is united by a unique evolutionary history (Figure 5a, b). COEs 1, 2, and 3 are hereby grouped together with higher PD similarity, while COEs 4 and 5 are most similar to each other.

3.4 | Correlation of diversity and endemism with elevation and montane areas

Mean elevation (Figure 6a, S4.11a) differs significantly between the relative phylogenetic diversity (RPD) randomization categories

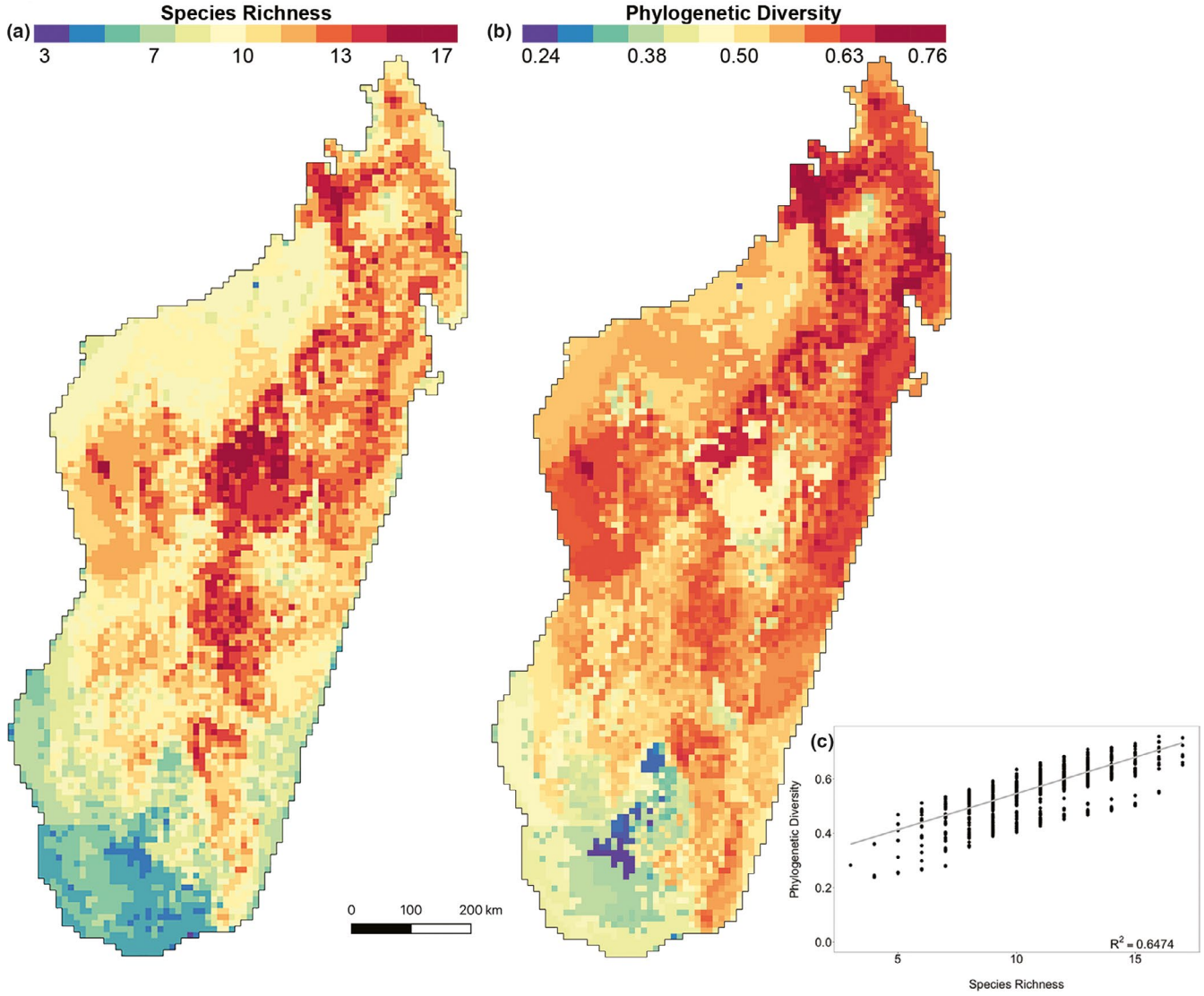

FIGURE 2 Species Richness (SR) and Phylogenetic Diversity (PD) maps, and the relationship between SR and PD, for 33 species of *Crematogaster* ants in Madagascar. Grid cells are 10 × 10 km squares. a) Observed values of SR; b) observed values of PD; c) scatter plot illustrating the relationship between species richness and phylogenetic diversity across the island; the trend of the data points follows a regression line (R^2 = 0.6474)

(Kruskal–Wallis test, p < 0.05; Table S5.5). The same pattern is also recovered when considering the minimum (Figure S4.11b), maximum (Figure S4.11c), and standard deviation (Figure S4.11d) elevation within the grid cells (Kruskal–Wallis test, p < 0.05; Table S5.6, S5.7, S5.8, respectively). The grid cells that have significantly low RPD are significantly higher in elevation than non-significant and high RPD grid cells (Wilcoxon pairwise comparison, p < 0.05; Table S5.5–8). Elevation (Figure 6b, S4.12) also differs significantly between the categorical analysis of neo- and paleo-endemism (CANAPE) categories (Kruskal–Wallis test, p < 0.05; Table S5.9–12). The elevation of mixed- and neo-grid cells is significantly higher than the elevation of non-significant cells (Wilcoxon pairwise comparison, p < 0.05; Table S5.9–12), whereas the elevation of paleo-grid cells is significantly lower. Similarly, elevation (Figure S4.13) differs significantly between the significant phylogenetic diversity (PD-sig) randomization categories (Kruskal–Wallis test; p < 0.05, Table S5.13–16). Grid cells with significantly low PD-sig are significantly higher in elevation, while grid cells with significantly high PD-sig are significantly lower in elevation, than non-significant PD-sig grid cells (Wilcoxon pairwise comparison, p < 0.05; Table S5.13–15) for mean, minimum, and maximum elevation values (Figure S4.13a–c). When considering the standard deviation of elevation within grid cells, cells with significantly low and significantly high PD-sig are both significantly higher in elevation than non-significant PD-sig grid cells (Figure S4.13d) (Wilcoxon pairwise comparison, p < 0.05; Table S5.16). The overlap of grid cells with montane areas considering the different CANAPE categories is 70% for neo-grid cells, 48.4% for paleo-grid cells, and 59.6% for mixed-endemism grid cells (Table S5.17). When analyzing overlap with the RPD significance classes, 41.3% of the significantly low RPD and 14.6% of significantly high RPD grid cells correspond

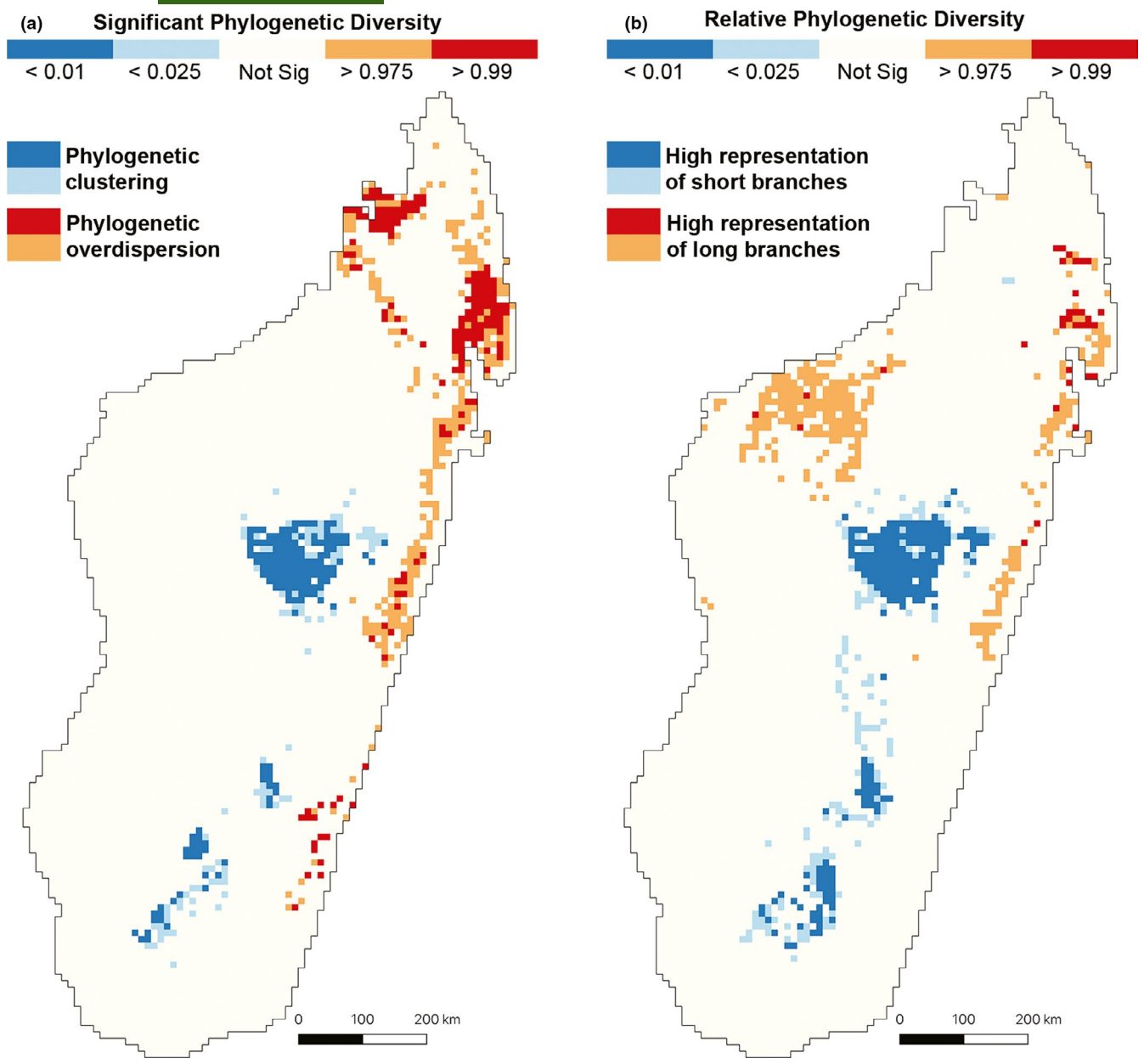

FIGURE 3 Maps of significant phylogenetic diversity (PD-sig) and relative phylogenetic diversity (RPD) of 33 species of *Crematogaster* in Madagascar. Grid cells are 10 × 10 km squares. a) Randomized phylogenetic diversity (PD-sig). Cells in blue have a significant under-representation of the phylogeny diversity. Cells in red have a significant over-representation of the phylogeny diversity. b) Randomized relative phylogenetic diversity (RPD). Cells in blue have a significant concentration of short branches. Cells in red have a significant concentration of long branches. Cells in beige are not significant

to montane areas (Table S5.18). Species richness (Figure S4.14a) and phylogenetic diversity (Figure S4.14b) of *Crematogaster* are significantly different between most habitat types (Kruskal–Wallis test, $p < 0.05$; Table S5.19–20).

4 | DISCUSSION

This research provides a first glimpse into emerging patterns of both taxonomic and phylogenetic diversity and endemism among ants in Madagascar, using a comprehensive empirical dataset to model species distributions in the widespread and ecologically dominant ant genus *Crematogaster*. Our results generate hypotheses to be tested with extended datasets on Malagasy ants and other insect groups. It is our hope that these findings can ultimately guide future research in insect diversity and actions in conservation. In the following, we discuss our results in the light of previous research and known limitations of our methodology, and also aim to formulate a series of predictions for further investigation.

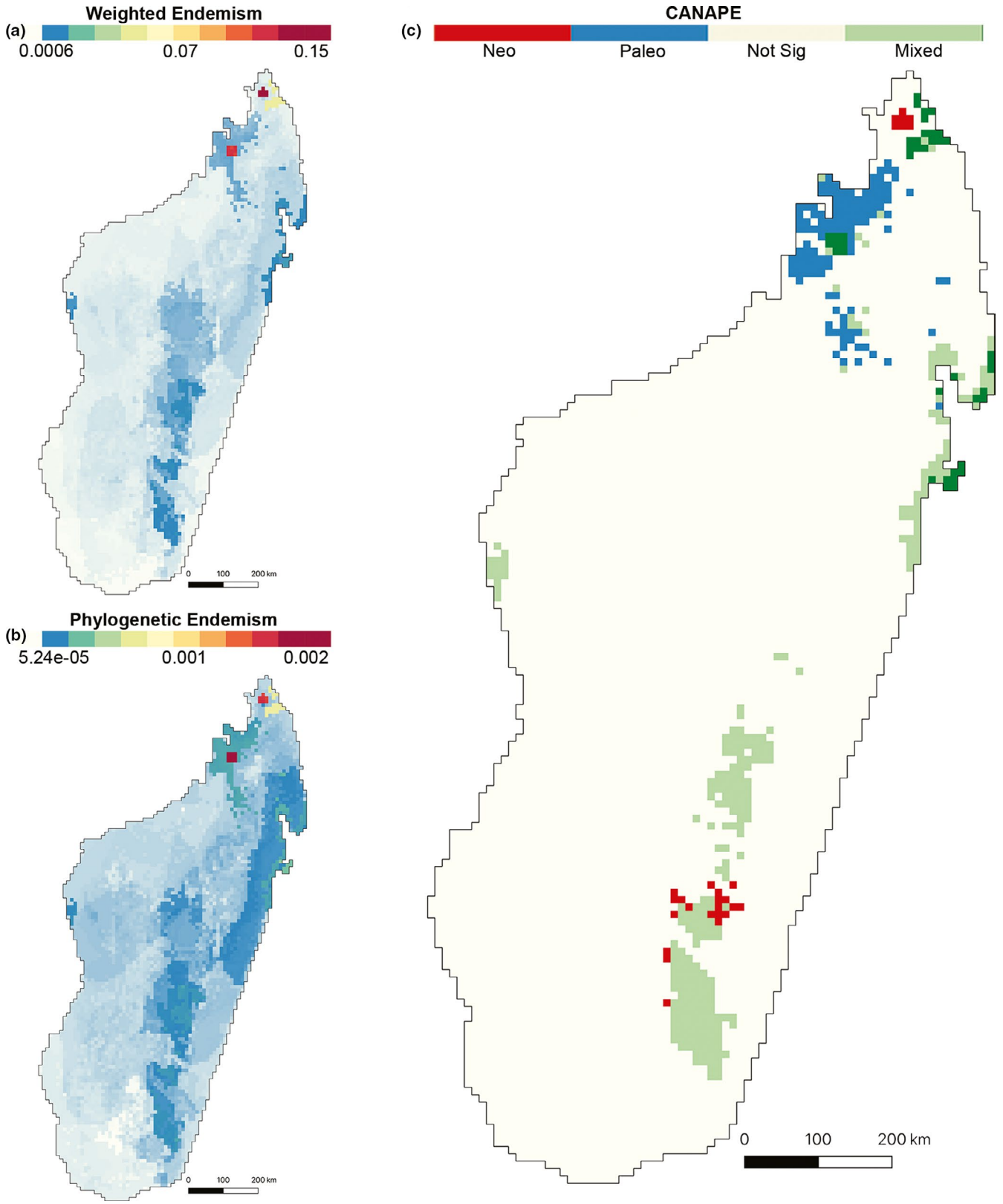

FIGURE 4 Weighted Endemism (WE), Phylogenetic Endemism (PE), and Categorical analysis of neo- and paleo-endemism (CANAPE) maps of 33 species of *Crematogaster* ants in Madagascar. Grid cells are 10 × 10 km squares. a) Observed values of WE; b) observed values of PE; and c) CANAPE results, showing cells having significantly high PE (>0.95), with centers of neo-endemism in red, centers of paleo-endemism in blue, and centers of mixed endemism in green. Beige cells are not significant

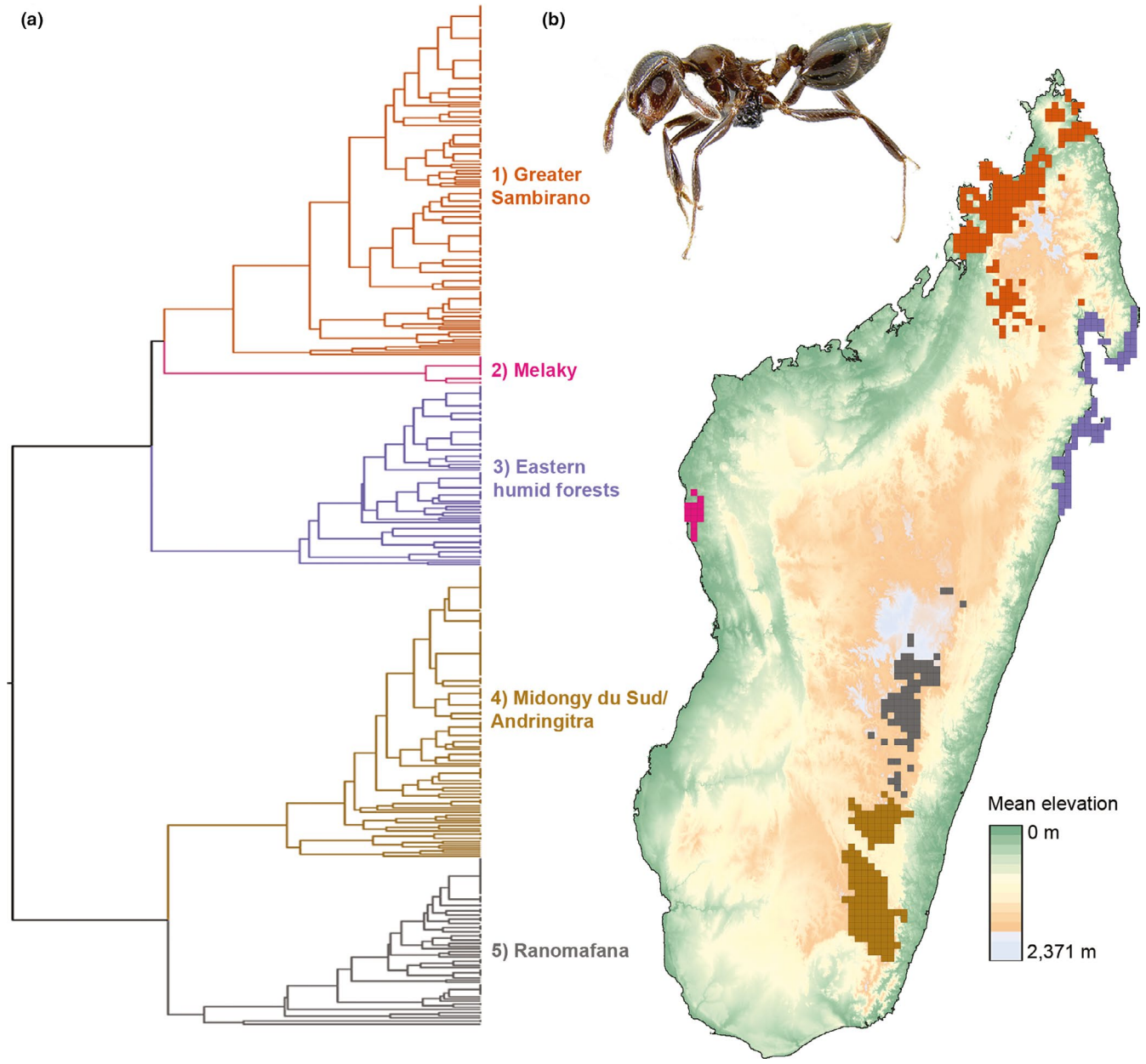

FIGURE 5 Phylo-jaccard phylogenetic turnover analysis among cells that showed significant PE in CANAPE for 33 species of *Crematogaster* ants in Madagascar. a) Dendrogram based on similarities in shared branches among significant cells identified by CANAPE. The colors indicate the corresponding clusters in the dendrogram and show five major groupings (i.e., centers of endemism—COEs); clustered cells share similar branches in the phylogeny; b) Map showing the PD-similarity relationships among grid cells found to be significant in the CANAPE test. Closely clustered cells share many branches of their phylogenetic subtrees and are shown in the same color. Background colors in the map show the mean elevation across the island, in meters. Photo of *Crematogaster malala* (CASENT0140925) by Bonnie Blaimer available from www.antweb.org

4.1 | Overview of spatial patterns of acrobat ant diversity in Madagascar

In our spatial analyses, wetter northern and north central-eastern parts of Madagascar emerged as phylogenetic diversity hotspots for *Crematogaster*. The highest phylogenetic diversity (PD) occurs throughout eastern humid forests, although interestingly, this biome has only moderate estimated species richness. Humid and western dry forests of the Greater Sambirano region are almost equally phylogenetically diverse, as is to a lesser extent the western dry forest in the Melaky region. Taxonomic species richness, in contrast, is estimated generally to be highest in the humid forests and wooded grassland–bushlands of the Central Plateau in the Antananarivo province and Ranomafana, and in the Greater Sambirano region around the Ampasindava peninsula and the Tsaratanana massif. Phylogenetic diversity in lemurs very closely mirrors our findings of high PD in northern and north central-eastern Madagascar (Herrera, 2017); a similar pattern was found for Malagasy lizards, including

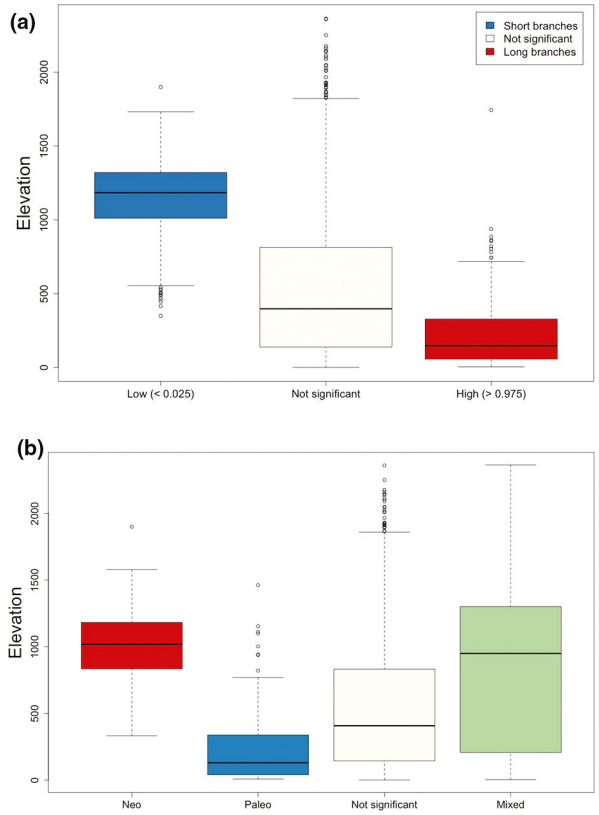

FIGURE 6 Boxplot of the distribution for elevation among the 10 × 10 km grid cells depending on their a) relative phylogenetic diversity (RPD) significance class; and b) categorical analysis of neo- and paleo-endemism (CANAPE) category. Distributions of the mean elevation of grid cells are significantly different (Kruskal–Wallis test, $p < 0.05$). Different letters indicate significant differences ($p < 0.05$; pairwise comparison using Wilcoxon test with Holm's correction; see Table S5.5 and S5.9). For each box, the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to the highest value of the distribution, but no further than the 1.5× interquartile range (IQR, or the distance between the first and third quartiles); the lower vertical line extends from the lower bound of the box to the lowest value of the distribution, but no further than 1.5× IQR; dots are values beyond IQR ("outlier" values)

geckos and chameleons, and snakes for species richness (SR) (Brown et al., 2016). This region is also a center of taxonomic species diversity for cophyline frogs (Wollenberg et al., 2008). However, the highest levels of diversity for other groups of amphibians are found on the Central Plateau in the Antananarivo province and Ranomafana (Brown et al., 2016), similar to our findings for SR in *Crematogaster*.

4.2 | Mountains are centers for phylogenetic diversity, but with recent diversification

Phylogenetic diversity (PD) and relative phylogenetic diversity (RPD) randomizations showed clustering (significantly low PD-sig) and short branch concentrations in the Greater Antananarivo region, Ranomafana, and Midongy du Sud/Andringitra, which indicates predominant occupation by many closely related *Crematogaster* species. This result agrees with the high taxonomic species richness estimated for this region, in contrast to its seemingly moderate PD. Significantly high values for PD and RPD randomizations are associated with the eastern humid forests and the north-western dry forests of the Mahajanga region (for RPD only), as well as the Greater Sambirano region (PD only), indicating an accumulation of more distantly related species, that is, overdispersion, and longer branches. Interestingly, the hotspot for PD in northern Madagascar shows almost no significance in RPD randomizations, indicating no significant representation of either long or short branches. Since PD-sig is significantly high in that region, this combination would indicate a representation of distantly related species with a balanced representation of branch lengths.

Analyzing relative phylogenetic diversity (RPD) and significant phylogenetic diversity (PD-sig) by elevation, we found long branch over-representation (i.e., high RPD) and overdispersion (i.e., high PD-sig) to be most prevalent at lower elevations, while altitudes above 1,000 m harbor an over-representation of short branches (i.e., low RPD) and significantly low PD-sig, indicating clustering of species. A substantial proportion (40%) of grid cells with low RPD are further considered montane habitat (sensu Körner et al. (2016)). In regions with a concentration of low RPD and short branches, recent diversification usually is assumed to play a more important role in species assembly (Mishler et al., 2014). Contrary to expectations, our results indicate mountains or high-elevation habitats have functioned as hubs for recent species diversification. Quaternary paleoclimatic variations leading to habitat contractions and subsequent geographic isolation are assumed to have played a role in the distribution of species in Madagascar (Wilmé et al., 2006), and also could have influenced ant species diversification. Within Malagasy *Crematogaster*, however, even the most recent species divergences may be too old to agree with a quaternary paleoclimatic explanation (Blaimer, 2012a) and one must go deeper in time for an explanation. Intriguingly, many of the shorter branches in the phylogeny originate from one clade of acrobat ants in which the majority of species prefer open-wooded grassland–bushland habitats. This habitat covers vast areas of the Central Highlands of Madagascar (where RPD is low) and is, albeit still contentiously, discussed to be of Late Miocene to Pliocene age (Bond et al., 2008; Hackel et al., 2018). The diversification of this clade, also estimated as Late Miocene to Pliocene age in this study and by Blaimer (2012a), could be linked to the arrival of a grassy biome in Madagascar. Fisher and Robertson (2002) found high levels of endemism among ants in grasslands in Madagascar, supporting a distinct community associated with this habitat.

In contrast, we found significantly high relative phylogenetic diversity (RPD) to be most prevalent at low elevations, in eastern humid forests of the Masoala peninsula and Analanjirofo region, and at low elevations in western dry forests in the Melaky region and the Betsiboka watershed (sensu Wilmé et al., 2006, 2012)). These regions, with concentrations of long branches, may be acting as refugia for older, relict lineages (González-Orozco et al., 2016; Mishler et al.,

2014). Lowland humid forests have long been regarded as centers for ant diversity in Madagascar, a result also recovered in our analyses. Yet this habitat has never been considered a refugium (or museum) for relict lineages. Watersheds of this region may have served as refugia for ant diversity, similar to findings for lemur diversity (Wilmé et al., 2006). The observed pattern of a concentration of long branches could indicate recent species extinctions in this habitat, as lowland humid forests in Madagascar have shrunk drastically within the last few centuries due to exploitation and the expansion of agriculture.

4.3 | Delineating centers of significant phylogenetic endemism and their origin

Another goal of this study was to discern centers of endemism (COEs) for Malagasy ants using *Crematogaster* as a surrogate, and to investigate whether these showed signatures of paleo- or neo-endemism. Categorical analysis of neo- and paleo-endemism (CANAPE) analysis and phylogenetic endemism dissimilarity modeling identified five major centers of ant endemism in Madagascar based on our dataset. Centers of endemism (COEs) in this context are defined as geographic clusters of grid cells that showed significantly high endemism as measured by relative phylogenetic endemism (RPE) in the numerator, denominator, or both, as well as significant turnover to the next cluster.

We predicted that if mountains functioned as museums for acrobat ant diversity, they would be recovered as COEs for paleo-endemism. Paleo-endemism, or the aggregation of many endemic species with long branches, was indicated in our analysis for much of the Greater Sambirano region (COE 1). But while the Tsaratanana massif presents a rugged, high-elevation mountain range in the Greater Sambirano region conforming with our hypothesis for paleo-endemism, much of the Ampasindava peninsula is actually low elevation terrain (albeit still fairly inaccessible). Also contrary to our prediction, the mountain range of Montagne d'Ambre was identified as a significant center for neo-endemism within COE 1, indicating an aggregation of endemic short branches and recent diversification and speciation instead of paleo-endemism. Montagne d'Ambre is an isolated mountain with a distinct microclimate in northernmost Madagascar harboring a humid forest patch surrounded by western dry forest. This area has high herpetofauna and mammalian endemism (Brown et al., 2016; Raxworthy & Nussbaum, 1994), but we are unaware of any *Crematogaster* species endemic to this area. Most endemism identified in acrobat ants in Madagascar in the remaining COEs (COEs 2–5) is classified as mixed endemism or composed of both long and short endemic branches. In these centers of mixed endemism, both "old" species with relict distribution ranges and "new" species of recent origin are suggested to co-occur (Mishler et al., 2014).

Elevation was a significant indicator for areas of significant phylogenetic endemism as defined by categorical analysis of neo- and paleo-endemism (CANAPE) analysis. Neo-endemism was most commonly found at higher elevations, with the proportion of montane grid cells highest among neo-endemic grids (70%). This corroborates our results based on significant phylogenetic diversity (PD-sig) and relative phylogenetic diversity (RPD), and further highlights mountainous or montane regions as hubs for recent species diversification. Mixed endemism also showed a high proportion of montane areas (60%) but is unsurprisingly also associated with the largest spread in elevations. About 50% of the paleo-endemic regions were still categorized as montane, presumably due to their level of steepness; based on elevation alone, paleo-endemism is mostly associated with lower elevations below 500 m. Overall, these results refute our prediction that mountains were centers of ancient diversification or paleo-endemism. Rather, our findings suggest that the latter is most prevalent at lower elevations.

4.4 | Predictions for ant diversity and endemism in Madagascar

Our results indicate that longstanding hypotheses and descriptive analyses must be revisited in light of the increasing availability of data on the distributions of species and their phylogenetic relationships. Here, we build on the most up-to-date spatial phylogenetic data for insects and analyze the relationships between phylogenetic diversity and endemism and environmental characteristics. We derive the following hypotheses regarding the distribution and origin of ant diversity in Madagascar to be tested with other groups in the future:

(a) Mountains are cradles for ant diversification, whereas lowland regions function as museums. (b) Centers of ant endemism are concentrated in northwestern dry and humid forests, eastern humid forests, and humid forests and grassland–bushland habitats of the Central Highland region, and are mainly composed of a mix of neo- and paleo-endemic species. (c) The timing of species diversification in ants in the Central Highlands aligns with arrival of grassland–bushland habitat in the Miocene to Pliocene.

We aim to test these predictions with a comprehensive dataset for all ants of Madagascar to gain a holistic understanding of the origin and history of ant diversity in this region. We believe these predictions are of general interest and importance for investigations based on other insect taxa in Madagascar, and could be expanded to other regions to improve knowledge of insect diversification patterns worldwide.

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DATA AVAILABILITY STATEMENT

All phylogenetic and distribution datasets, as well as code used to generate results within this study are available in the Dryad data repository (https://doi.org/10.5061/dryad.hqbzkh1fj). Raw sequence data files have further been submitted to NCBI's Sequencing Read Archive (BioProject accession number: PRJNA669395).

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Gabriela P. Camacho is broadly interested in the phylogenomics, systematics, and biogeography of ants. This work represents a component of the Madagascar Ant Microendemism (MAMI) project, which studies patterns of diversity and endemism of ants in the Malagasy region. She and the other authors collaborate on questions of ant biodiversity at the California Academy of Sciences, San Francisco, CA, and the Museum für Naturkunde, Berlin, Germany.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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