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Trait-based paleontological niche prediction recovers extinct ecological breadth of the earliest specialized ant predators

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Abstract

Paleoecological estimation is fundamental to the reconstruction of evolutionary and environmental histories. The ant fossil record preserves a range of species in three-dimensional fidelity and chronicles faunal turnover across the Cretaceous and Cenozoic; taxonomically rich and ecologically diverse, ants are an exemplar system to test new methods of paleoecological estimation in evaluating hypotheses. We apply a broad extant ecomorphological dataset to evaluate Random Forest machine learning classification in predicting the total ecological breadth of extinct and enigmatic “hell ants”. In contrast to previous hypotheses of extinction-prone arboreality, we find hell ants were primarily leaf litter or ground-nesting and foraging predators, and by comparing ecospace occupations of hell ants and their extant analogues, we recover a signature of ecomorphological turnover across temporally and phylogenetically distinct lineages on opposing sides of the KPg boundary. This paleoecological predictive framework is applicable across lineages and may provide new avenues for testing hypotheses over deep time.

Introduction

Estimating the ecological niche occupation of extinct taxa is a central component of paleontology. The putative ecologies of extinct organisms are routinely incorporated into analyses of extinction risk, paleoenvironmental reconstruction, and lineage evolutionary history (Palmqvist et al. 2003; Benson et al. 2014; Frederickson et al. 2018). Even as aspects of extinct species' niche occupation may be reliably inferred by the preservation of individual traits in fossil specimens, organismal ecology remains multifaceted. Morphology may often - though not always (Miller et al. 2017) - reflect ecology across entire phenotypes (Williams 1972; Losos 1992) and phenotypes may be linked to multiple aspects of an organism's ecological niche spanning habitat, diet, and interactions. These ecologically-linked body plans – ecomorphs – are found in such disparate taxa as fish, reptiles, arthropods, and mammals (Barton et al. 2011; Gerry et al. 2011; Sanders et al. 2013; Figueirido et al. 2019). The relationship between ecological niche and multi-trait morphology can also be leveraged to estimate paleoecologies. In lineages with surviving relatives, extant taxa may serve as data-rich analogs for ecological niche estimation: however, the partial preservation of many fossil specimens and aberrant phenotypes in some extinct lineages may reduce the utility of extant-to-extinct comparisons.

Across vertebrate species, limb anatomy is a predictor of locomotion, prey items, and substrate behaviour. In particular, the forelimb anatomy of carnivores has been used to predict the likely predatory habits and prey size of extinct carnivorous mammals and mammaliaforms (Dunn et al. 2019; Ercoli et al. 2012; Figueirido et al. 2016; Jenkins et al. 2020; Lungmus and Angielczyk 2021; Meloro and Louys 2014). Other examples of the morphology of extant species being used in the prediction of extinct species' ecology include estimating diet in extinct raptor species from present-day birds of prey (Hertel 1995); predicting prey items and modes of scavenging in extinct crocodyliforms from extant crocodyliform snout morphology (Drumheller and Wilberg 2019); approximating arboreal behaviour in extinct primates (Rector and Vergamini 2018); and predicting habitat preferences in fossil *Anolis* lizards using ear canal shape (Dickson

et al. 2017). In many cases, these methods incorporate isolated body parts rather than full-body morphology, potentially because trait ecomorphology has been more intensely studied in vertebrates than in other animal taxa, and is thus more well-defined. However, morphometric analyses of full mammalian skeletons have been used to predict the locomotion mode of various Mesozoic mammaliaforms (Chen and Wilson 2015; Meng et al. 2017).

Attempts to predict paleoecology from extant morphology frequently use techniques such as canonical correlations analysis or canonical variate analysis, and in particular linear discriminant analysis (Dickson et al. 2017; Dunn et al. 2019; Hertel 1995; Janis and Figueirido 2014; Meloro and Louys 2014; Rector and Vergamini 2018). These methods maximize variation in the measured traits between predetermined classes in morphospace. The fossil specimen's most likely ecology is then determined by proximity to each class mean in this constructed morphospace (Strauss 2010). These approaches are powerful tools for establishing sets of traits most strongly associated with predetermined classes, but are limited to linear relationships only among measured traits, which may restrict accuracy by failing to incorporate non-linear predictive relationships between traits.

While most predictive paleoecology studies have focused on vertebrate paleoecology, minimal attention has been paid to these approaches in invertebrates, particularly insects. Many extant insect lineages reach back to the Mesozoic or Paleozoic, and are highly ecologically diverse. One example are the ants, which arose between ~150 and 100 Ma (Mega-annum) (Moreau et al. 2006; Brady et al. 2006; Borowiec et al. 2019). With over 15,000 species comprising a significant component of terrestrial biomass, ants are globally ubiquitous, speciose, and are present in most post-producer ecological niches (Hölldobler and Wilson 1990; Bolton 2021). Importantly, despite this ecological diversity, ants are also morphologically conserved with respect to broad body plan functionality and possess a rich fossil record extending 100 Ma to the mid-Cretaceous. A majority of ant fossils are known from fossil amber, which often preserves entire specimens with high fidelity. Because of their well-defined

homology and uniquely preserved fossil history, extinct ants are strongly suited for testing paleoecological niche prediction methods.

The earliest known ant fossils date to the Early–Late Cretaceous transition and comprise extinct stem lineages that began to diversify prior to the most recent common ancestor of all living ants. While crown lineages diversified concomitant with these stem lineages, all stem lineages went extinct near the end of the Cretaceous, while crown lineages persisted into the Cenozoic, exemplifying a distinct faunal turnover across the Cretaceous–Paleogene (KPg) boundary. Cretaceous fossils have fueled speculation on the ecological occupation of the earliest ants because these taxa have bearing on the evolution of eusociality more broadly. Early speculation on Cretaceous ant ecology posited that these early species were unlikely to construct nests, but instead used already-present cavities in soil and wood, based on assumptions that these early species were primitively eusocial and thus unlikely to cooperate as well in nest building, or that their mandible morphology was prohibitively specialized to allow for nest construction (Dlussky 1996; Wilson 1967; Wilson 1987a; Wilson 1987b; Grimaldi and Agosti 2000; Engel and Grimaldi 2005). Based on their presumed wasp ancestors, they were additionally argued to be predators (Dlussky 1996; Wilson 1987a; Wilson 1987b). As the taxonomic diversity of extinct ant species increased with the discovery of new fossils, paleoclimate and phylogenetic reconstructions suggested that early ants occupied soil and leaf litter microhabitats in newly emerging angiosperm forests (Wilson and Hölldobler 2005, Perrichot et al. 2008, Moreau et al. 2006, Moreau and Bell 2013). Phylogenetic reconstructions using extant lineages have also recovered ant ancestors as potentially hypogaeic soil-dwellers (Lucky et al. 2013). While there have been secondary inferences regarding the ecology of the earliest ants, no fossil-derived data have yet been included in the reconstruction of ancient ant ecology.

Haidomyrmecines, or hell ants, are an enigmatic and morphologically aberrant extinct subfamily of ants comprising 16 described species and 10 genera (Perrichot et al. 2020). Hell

ants occupy a stem group position relative to modern ants and are frequently recovered as sister to all other extinct and extant ants (Barden et al. 2016; 2020). They persisted throughout the mid-to-late Cretaceous as evidenced by amber fossils ranging from 100 to 78 Ma on three different continents in Canada, Myanmar, and France (Dlussky 1996; Perrichot et al. 2008; McKellar et al. 2013) and are hypothesized to have undergone extinction concomitant with the early radiation and diversification of extant lineages. These ants are morphologically unusual in having vertically-articulating mandibles, unlike the horizontal alignment of modern ants. Remarkably, hell ants possess an array of horn-like cranial appendages that have been directly observed to facilitate solitary predation through fossil remains (Barden et al. 2020): haidomyrmecines captured prey individually by articulating their mandibles against their horns. Hell ants have been hypothesized as arboreal predators, considering the potential difficulty of substrate manipulation with their vertically-aligned mandibles, and frequent preservation in amber, potentially indicating close proximity to tree resin (Dlussky 1996; Barden and Grimaldi 2012; Lattke and Melo 2020). Arboreality may be a risk factor in cataclysmic mass extinction events, given the dependency on habitats that are more exposed to extreme weather fluctuations and other extreme events such as wildfires, etc. (Field et al. 2018). If hell ants were indeed arboreal, it may have been a contributing factor to their extinction towards the end of the Cretaceous.

Were hell ants indeed arboreal, potentially increasing their risk of extinction? How do the ecologies of the earliest ants compare to extant lineages today? Did functional or ecological succession accompany ant faunal turnover from the Cretaceous to the Cenozoic? Here, we use a wide-ranging extant morphometric dataset spanning over 160 species that has previously demonstrated a quantitative link between morphology and ecology to predict the paleoecology of several hell ant species. Using a supervised machine learning classification algorithm, Random Forest, we predict foraging niche, nesting niche, and functional role for hell ants. With these predictions, we reconstruct known ecomorphological space for haidomyrmecines and

compare these ecological occupations to those of extant lineages of specialized solitary predators. Our results demonstrate repeated filling of functional niche space across phylogenetically and temporally distant lineages. This approach provides a generalizable framework for paleoecological estimation beyond either single-trait interpretations or subjective interpretations from taxonomic expertise, opening future directions for the reconstruction of extinct communities and ecosystems.

Methods

Extant morphological data sampling and ecological niche binnings

We sampled extant ant morphological data following the protocol of Sosiak and Barden (2021) (Figure 1). Our extant dataset spans 15 subfamilies, 113 genera, and 167 species, sampling three specimens per species where possible, and measuring as many conspecifics as were present in museum collections otherwise. Polymorphic species are represented by the media caste, or caste representing a morphological “midpoint” between small and large workers, and species with specialized castes are represented by non-specialized “minor” workers. There is currently no evidence for specialized hell ant worker castes, and specialized worker castes are not a synapomorphy of crown ants, informing our choices of caste sampling.

Our morphometric sampling comprised linear measurements of 12 cephalic traits and five post-cephalic traits (Table 1). Most sampled traits have been previously linked to ecology (Weiser and Kaspari 2006; Yates and Andrew 2011; Gibb et al. 2015; Yates et al. 2014). All measurements were conducted on point-mounted specimens under stereo microscopy. Because linear measurements alone may not fully capture important trait variation, and body size in diverse species can drive most variation in a dataset and potentially mask other important contributors, we created three datasets: one comprising raw linear measurements; one comprising shape ratios calculated from the linear measurements; and one size-corrected

dataset comprising log-shape variables and log-body length or Weber's length (Mosimann 1970). A list of all shape ratio traits with associated definitions may be found in Table S1.

All specimens were assigned a binning from each of three ecological niche aspect categories, following the protocol of Sosiak and Barden (2021): functional role (referring to the diet of the species), nesting niche (the type of nest and stratum in the environment), and foraging niche (the stratum in the environment where the species forages for food) (Figure 1, Table 2). Specimen binnings were assigned based on literature surveys. When any particular aspect of a species' ecological niche was uncertain, the species was assigned an "unknown" binning and excluded from further model training. We found 35 total observed combinations of niche binnings across all niche aspects and specimens; we additionally collapsed these 35 combinations into 10 simplified ecomorph syndromes (based on ecological and morphological overlap) to evaluate whole-body ecomorphological correlates. A list of all ecological niche aspect combinations and ecomorph syndromes with associated definitions may be found in Table S2.

Fossil morphological data sampling

We measured fossil hell ant specimens using a combination of stereo microscopy and reconstructions of X-ray micro-computed tomography (micro-CT) scans (Figure 1). All hell ant specimens were from Kachin amber (99 Ma). Twenty specimens from 16 species and morphospecies were measured under stereo microscopy. We submerged the amber specimens in water to reduce light distortion; some measurements were not possible due to specimen positioning. Three specimens were micro-CT scanned and reconstructed for subsequent measurements: two species of hell ant (*Haidomyrmex scimitarus* and *Linguamyrmex vladi*) and a *Pseudomyrmex macrops* specimen from Dominican amber (16 Ma) to assess the reliability of CT-scan based data. Congeners of the Dominican *Pseudomyrmex* fossil are extant today and their ecology is consistent across the genus and well-characterized. The *H. scimitarus*

(specimen AMNH Bu-FB80) and *L. vladi* (specimen AMNH BuPH-1) specimens were scanned at the American Museum of Natural History Microscopy and Imaging Facility using a GE phoenix v|tome|x s240 60kV CT-scanner. Specimen AMNH Bu-FB80 was imaged at 180 μ A for 5 second exposures and a voxel size of \sim 8 μ m; specimen AMNH BuPH-1 at 250 μ A for 1 second exposures and a voxel size of \sim 3 μ m. The *Pseudomyrmex macrops* specimen (AMNH DR-14-1021) was imaged at the New Jersey Institute of Technology York Center using a Bruker SkyScan 1275 at 60kV and 150 μ A for 1 second exposures with a subsequent voxel size of \sim 3.5 μ m. Volume reconstruction of the x-ray images was conducted in 3D Slicer v4.11 (Fedorov et al. 2012) using the Segmentation modules; still images of the reconstructed specimens were subsequently imported into ImageJ (Abràmoff et al. 2004) for linear measurements to retain consistency with measurements taken under stereo microscopy. Post-cranial morphology of hell ants is similar to extant ant species, while cranial morphology is highly aberrant. To ensure that we were assessing morphological variation in terms of both homologous and functional morphology, we partitioned data according to homologous or functional measurements; a full discussion of homologous versus functional morphology may be found in the Supplementary Information.

Due to limitations measuring specimens directly from amber fossils, we produced two fossil morphometric datasets: one 'incomplete' dataset which excluded a subset of traits for all specimens; and one with all measurements included. The incomplete dataset lacked the frontal head length, head width, frontal mandible length, and pronotal width measurements. These measurements are often difficult to accurately capture because amber fossils are typically prepared to expose a clear lateral profile of any specimen, leaving the dorsal and frontal margins of the amber rounded and distorted. Twenty hell ant specimens were included in this incomplete dataset. The complete dataset comprised the proof-of-concept fossil *Pseudomyrmex macrops* specimen and three hell ant specimens: *Dhagnathos autokrator*, *H. scimitarus*, and *L. vladi*. While the majority of specimens included were workers, two of the specimens – the

complete *D. autokrator* and *H. scimitarus* – were represented by alate (winged) and dealate (wings shed) queens, respectively. We included queens for two reasons: one, hell ant queens are hypothesized to have actively foraged and hunted in early colony foundation, and so likely occupied a similar ecological niche to the workers of the species; and two, fossilized worker specimens are not known for many hell ant species and are entirely unknown for the genus *Dhagnathos*. While we have no comparison for *Dhagnathos* workers, we include a *H. scimitarus* worker in the incomplete morphometric dataset, allowing us to compare the accuracy of the model in predicting queen and worker ecology. A full list of all specimens included with information pertaining to their sampling methods and castes can be found in Table S3; all morphometric data for fossil specimens may be found in the Supplementary Data.

To ensure that morphological diversity for traits measured from fossil species are within the bounds of extant morphological diversity, we conducted principal component analyses (PCA) to compare morphospace occupation of hell ants relative to extant lineages. We conducted separate PCAs for all three measurement datasets. All PCAs were implemented in R packages “corrplot” (Wei et al. 2017) and “FactoMineR” (Lê et al. 2008).

Model training and testing

We implemented Random Forest analysis, a supervised machine learning algorithm, to delimit species into ecological niche binnings by morphology. Random Forest algorithms rely on an ensemble of decision trees with each tree providing a ‘vote’ for a majority consensus determining the predicted class (Breiman 2001). Each decision tree is built through iteratively sampling the training dataset with replacement, with each internal node or ‘split’ in the tree being selected from the variable contributing highest accuracy from a randomly subsampled set of predictor variables. As the trees are iteratively built, each tree provides a ‘vote’ on the most likely class for each sample in the training dataset; the algorithm then uses the vote consensus to predict class for each sample. The iterative sampling or bagging of the training dataset to

build the trees and the randomly selected subset of variables at each node ensure that the decision trees are uncorrelated and that the model is not overfitted to the training dataset. Throughout model construction for each tree, Random Forest algorithms iteratively sample two-thirds of the provided training dataset for training the model and one-third of the provided dataset for testing the model; error rate across these iterations is then averaged to provide out-of-bag (OOB) error rate for the model. This removal of testing data during bootstrapping eliminates the need for *a priori* separation of a testing and training dataset, incorporating all collected data. Model parameters include *ntree* (the number of trees in the ensemble model) and *mtry* (the number of variables randomly selected to be tested at each split).

While other supervised machine learning or dimension reduction techniques are more commonly used in morphology-based paleoecological prediction, Random Forest has recently been shown to outperform linear predictive approaches with respect to morphology (Pigot et al. 2020; Sosiak and Barden 2021), hence our use here. We trained our Random Forest models using our extant ant morphometric dataset with known ecological niche binnings (Figure 1). We constructed Random Forest models for the linear measurements, shape ratios, and log-shape variable datasets separately for each ecological niche aspect and overall ecomorph syndrome, allowing for granular classification of ecological niche and more synthesized classification. Model parameters were selected based on initial sensitivity tests: *mtry*=4 and *ntree*=5000. Random Forest analyses were implemented in the R package 'randomForest' (Liaw and Weiner 2018).

Model implementation with extinct specimens

We implemented different sets of Random Forest models; given the missing traits in our incomplete dataset, models needed to be trained once with the missing traits eliminated from the extant ant morphometrics training dataset, and once including all traits measured for the complete fossil dataset (Figure 1). For each dataset (complete or incomplete), we implemented

three models: using the linear measurements, shape ratios, and log-shape variables. Using these three models, we predicted ecological niche aspects of hell ants twice: once using functional morphology, and once using homologous morphology. Thus, each specimen's ecological niche was predicted six times (contingent on whether their measurement set was complete or incomplete): using linear measurements with functional morphology, linear measurements with homologous morphology, shape ratios with functional morphology, shape ratios with homologous morphology, log-shape variables with functional morphology, and log-shape variables with homologous morphology. We compiled all model votes into a heatmap of model predictions for each specimen with the R package 'ggplot2' (Wickham 2016) to better visualize the consensus among models for each predicted ecological niche aspect.

Comparative ecomorphological niche occupation

To assess the specificity and breadth of niche occupations in haidomyrmecines, we generated three-dimensional ecomorphological matrices comprising living and extinct predatory taxa. Our taxonomic sampling included five lineages: hell ants, and four distantly related extant groups with trap-jaw like morphology and behavior, wherein workers act as solitary hunters that capture prey, many doing so through rapid closure of specialized mandibles (Gronenberg and Ehmer 1996, Hölldobler & Wilson 1990). While the speed of prey capture is not known in hell ants, haidomyrmecines are united with some extant trap-jaw taxa by the presence of elongate setae (interpreted as trigger hairs) in the path of mandible closure and dramatic morphological adaptations related to predation (Dlussky 1996; Barden and Grimaldi 2012). Importantly, all species within our sampling are primarily solitary hunters (Larabee et al. 2014; Barden et al. 2020) in contrast to group raiding or collective prey capture that typify many other predatory ant lineages (Dornhaus and Powell 2010). Trap-jaw mechanisms have evolved at least ten times in living ants (Larabee et al. 2014; Booher et al. 2021); these origins are distributed among four monophyletic lineages. Extant trap-jaw predation has evolved once within each of the

subfamilies Ponerinae and Formicinae, thus our sampling included species within relevant genera: *Anochetus* + *Odontomachus* (Ponerinae) and *Myrmoteras* (Formicinae), respectively. There are at least eight trap-jaw origins within the subfamily Myrmicinae and seven of these have occurred within the genus *Strumigenys*. Our myrmicine sampling therefore included *Strumigenys* as well as the five “dacetine” trap-jaw genera: *Acanthognathus*, *Daceton*, *Epopostruma*, *Microdaceton*, and *Orectognathus*. Although it is not yet clear whether all dacetine trap-jaws are the product of a single origin, we grouped these taxa in analyses as they are more closely related to each other than any are to *Strumigenys* (Ward et al. 2015).

To estimate the total number of unique ecomorphological combinations for each specialized predatory lineage, we gathered niche occupation and size data for a total of 982 species, including 15 hell ant species with ecologies estimated under random forest. Our extant sampling represents a minimum of 50% species sampling for each genus. Each species was assigned one of three foraging and three nesting niche aspects according to our modeling results for haidomyrmecines or published natural history observations for extant taxa (Supplementary Data_Trap Jaw Ecomorphospace). Because observational data do not exist for all species, we applied published generalizations in some cases (e.g. *Strumigenys* are noted as almost always leaf litter nesting and foraging, thus we assumed this occupation by default except when otherwise noted in the literature). For the predicted hell ant ecomorphological combinations, considering that there were multiple predictions using different models that did not always converge on the same predicted class, we constructed two matrices: an expansive one incorporating all ecomorphological combinations predicted across all models, and a conservative second matrix incorporating only predictions using the linear measurements dataset with functional morphology. All niche occupation and size data may be found in the Supplementary Data.

To estimate body size, we gathered minimum and maximum Weber's length (a measurement of mesosoma length and traditional metric of ant size) measurements from

taxonomic descriptions and revisions. To include taxa without published morphometric data, we collected Weber's length measurements from publicly available images on AntWeb (AntWeb 2021) using ImageJ version 1.53 (Schneider et al. 2012). We discretized species sizes by delimiting Weber's length ranges for each species into at least one of twelve equal size binnings. Size binning ranges were defined as one half of the standard deviation of Weber's length measurements across all species. In cases where a species Weber's length range exceeded any one size binning, we assigned multiple size binnings for that species.

We generated three-dimensional ecological disparity values for each lineage following a modification of Chen et al. (2019). We assigned each ecological binning a numerical value from 1 to 3 based on inferred ecological proximity (nesting niche: leaf litter = 1, ground = 2, lignicolous = 3; foraging niche: leaf litter = 1, epigaeic = 2, arboreal = 3), while values for the third ecological dimension, body size, were continuous from 1 to 12. We included raw body size as size can act as a constraint on ecological role in the environment. To reduce the impact of species sampling bias between fossil and extant lineages, we calculated ecological disparity only among unique occupations, not between species. We created a matrix of unique niche occupations for each lineage and calculated intra-lineage ecological disparity values by summing the distances between niche aspects for all pairwise combinations of unique occupations using the equation. For example, the ecological disparity between unique occupation 1 (uo_1) and unique occupation 2 (uo_2) would be: $| \text{Nesting Niche}_{uo_1} - \text{Nesting Niche}_{uo_2} | + | \text{Foraging Niche}_{uo_1} - \text{Foraging Niche}_{uo_2} | + | \text{Body Size}_{uo_1} - \text{Body Size}_{uo_2} |$. We summarized mean and standard deviations for each lineage using 'ggplot2' (Wickham 2016). Visual representations of lineage specific ecomorphological occupations (ecospaces) were generated using the R package "rgl" (Adler et al. 2021) and redrawn in Adobe Illustrator.

Results

Model performance and prediction accuracy

Visualization of extant and extinct morphospace through principal component analysis illustrated that extinct morphospace fully overlaps with extant morphospace representing linear trait measurements and log-shape variable measurements, and mostly overlaps with extant morphospace representing shape ratio measurements (Figures S3-5). Although aspects of hell ant morphology are distinct, hell ant morphospace represented by measurements incorporated in our models is primarily within the bounds of extant diversity. Principal component 1 in the shape ratio morphospace is primarily driven by mandible size relative to body size, which is greater in many hell ants compared to extant ants, likely resulting in the small portion of unique hell ant morphospace. Predictions from shape ratio measurements are often not significantly different from predictions using linear measurements or log-shape variable measurements, however, and this along with a great degree of morphospace overlap suggests that extant morphology is an appropriate analog for extinct ecomorphology.

Out-of-bag error rate estimates ranged from 11-22%, reflecting accuracies of 78-89% depending on the training data partition used and the ecological niche aspect being predicted. While models trained on the linear measurement and log-shape variable measurement datasets were typically more accurate than the shape ratio dataset, this was not always the case, and the accuracies were not higher by more than a few percentage points. Consistently, nesting niche and foraging niche were predicted with higher accuracy, while functional role and ecomorph models generally had lower accuracy. Models trained on the complete morphometric dataset were more accurate compared to those trained on the subset morphometric dataset, though the difference was generally only a few percentage points. Additionally, model consensus votes were highest with foraging niche and nesting niche predictions, indicating overall greater confidence in the accuracy of these predictions; while functional role and ecomorph had lower consensus vote totals (Figure 2, Table 3, Tables S4-51). Trait importance to model accuracies

varied somewhat between models, but overall we found eyes, mandibles, legs, antennae, and body size to be essential to model accuracy (Figures S6-8).

The fossil *Pseudomyrmex macrops* specimen used as a proof-of-concept was consistently and accurately predicted as a lignicolous arboreal-foraging phytophagivore (Figure 2). The arboreal foraging niche was predicted with the highest confidence, while the phytophagous functional role was predicted with the lowest confidence (Figure 2, Tables S4-S27).

Hell ants are primarily recovered as epigaeic foragers that nested directly on the ground surface, though several species are predicted as leaf litter nesters and foragers (Figure 2). Additionally, one *Haidomyrmex* morphospecies (*H. sp3*) was partially predicted as a lignicolous nester and arboreal forager, with *Linguamyrmex brevicornis* also partially predicted as an arboreal forager. Hell ants were primarily predicted as predators, both specialist and generalist, though some species were additionally predicted to be omnivorous (Figure 2, Tables S4-51). Supporting the general accuracy of our models, we find broad congruence across species when multiple conspecifics were included, and also do not recover any strong predictions of unlikely ecological niches: hell ants were not predicted as subterranean nesters, column-raiding foragers, or fungivorous, granivorous, or phytophagous functional roles (Figure 2).

Specimen consensus among the six models used was variable. For some specimens, there was very strong agreement, with all six models predicting the same ecological niche aspect binning; however, there were also cases where two models predicted one niche aspect binning and two predicted another (Figure 2, Tables S4-51). There were rarely scenarios where more than two different niche aspect binnings were predicted for a single specimen. More frequently, in cases of split predictions, the shape ratio models or log-shape variable models would predict the same aspect binning while the linear measurement models would predict another, as opposed to scenarios where predictions would split along the lines of functional versus homologous morphology used in the testing dataset.

We found no robust differences in niche predictions between specimens measured directly and specimens measured from microCT reconstructions; specimens measured from microCT reconstructions were also predicted as epigaeic or leaf litter foragers and nesters (Figure 2, Tables S4-51). Additionally, we find that the dealate *Haidomyrmex scimitarus* (measured from a microCT reconstruction) and the worker *H. scimitarus* (measured using light microscopy) were both predicted to be ground-nesting epigaeic predators (Figure 2, Tables S4-51); illustrating consensus between the two types of input testing data.

Niche occupation in extinct and extant specialized predators

Our most conservative estimates of ecological niche occupation suggest that hell ants occupied primarily ground-nesting epigaeic niches with some leaf litter occupation, while across-model results recover hell ants within arboreal, ground, and leaf litter niches across a moderate body size range. In comparing predicted hell ant ecospace to solitary predator ant ecospace, we find that hell ants occupied at least part of the ecomorphological spaces occupied by each extant trap-jaw lineage (Figure 3). The sister ponerine genera *Anochetus* and *Odontomachus* exhibit the greatest extant ecospace diversity and ecological disparity, occupying most potential ecospace, with species ranging from ~3mm to ~1.7cm spanning arboreal, ground, and leaf litter niches (Brown 1978, Hoenle et al. 2020). The most restricted ecospace is occupied by species within the formicine genus *Myrmoteras*, which are minute leaf litter dwellers. The most taxonomically diverse trap-jaw lineage is *Strumigenys* with over 850 species, but the constrained size and primarily leaf litter habits of the genus produce a within-group ecological disparity that is low relative to the ponerine lineages with 188 total species (Bolton 2021). Similarly, while total species diversity of hell ants is unknown, even within our limited fossil sample, haidomyrmecines are found to be relatively ecologically disparate and diverse compared to extant lineages.

Discussion

We present here a pipeline for paleoecological niche estimation using machine learning and broad ecomorphological sampling. Because this class of supervised machine learning incorporates non-linear modeling and has been shown to outperform other discriminant function methods (Pigot et al. 2020; Sosiak and Barden 2021), it represents a powerful tool in the reconstruction of fossil niche occupations. Considerations identified through sensitivity analysis include alternative assumptions of input data, hypotheses of homology, and dataset completeness. Through implementation of this method, we find broad consensus across models for hell ants as leaf litter foraging-and-nesting or epigaeic ground-nesting predators, in contrast to previous assumptions regarding hell ant ecology. Paleoecological niche estimation reveals repeated ecological niche occupation across ant taxa, even across Earth's last major extinction boundary, suggesting functional succession in ant lineages through deep time.

Utility of Random Forest in paleoecological estimation

Our results demonstrate the utility of amber specimens in paleoecological estimation and the capacity for microCT reconstructions to aid in data collection. The congruence between the known ecology of extant *Pseudomyrmex* species and the predicted ecology of our sampled fossil *Pseudomyrmex macrops* specimen highlights both that taphonomic preservation of amber specimens does not prohibitively distort morphology, and that microCT data from fossil specimens is congruent with morphological data collection derived from extant taxa.

Estimates from our Random Forest models emphasize the need for selectivity and caution in assembling training data. We find that accuracy and congruence among our models was influenced more by the input training data, rather than the usage of either functional or homologous morphology in testing data: i.e., models trained on linear measurement data tended to predict the same nesting or foraging class for hell ants regardless of whether functional or homologous morphology was considered, while models trained on other datasets might predict

a different ecology. This trend may reflect variable importance; traits in hell ants that were measured differently based on alternate assumptions of homology were also traits that were not ranked as highly important to model accuracy, therefore homology assumptions may not have made much difference to the ultimate predicted class. However, this trend may not hold true in other taxa where a questionably homologous trait is of much greater importance to its ecological niche, such cases should be evaluated through assessments of trait importance in model construction. Additionally, we found only a minor loss in model accuracy from models trained on the complete morphometric dataset (17 traits) relative to models trained on the subset morphometric dataset (13 traits). Many of the measurements left out in the subset dataset were ranked as of low importance in the accuracy of the model, highlighting again the necessity of identifying important variables to model accuracy. While the problem of extraneous variables in the model itself is one mostly of unnecessary computing power, it is important to identify crucial traits when sampling fossil data to collate the greatest number of sufficiently complete specimens.

Sources of intraspecific and inter-specimen variability in Random Forest model predictions range from model error to actual ecological variability within the taxa sampled. While we found that each of the six models did not always predict the same ecological niche for one specimen, most frequently these differences were between niche aspects that were physically or ecologically proximate, i.e. two models for one specimen might predict generalist predator and specialist predator, or leaf litter foraging and epigeic foraging. This variability might reflect morphological similarity among proximate aspects, resulting in model error, but it may also reflect ecological variability within species; for example predatory ants may supplement their diet with plant material or occasionally forage across strata. While it is difficult to strictly attribute prediction mismatches to model error or ecological variability, we suggest that model error is more readily identifiable when two models predict ecologies with no known affinities.

Additionally, consensus votes can be assessed on a specimen-by-specimen basis: when the

consensus vote is less than 50%, meaning that the prediction is a result of a plurality of votes rather than a majority, confidence in that prediction is lower. This assessment, however, can be influenced by the number of classes; in our datasets, prediction accuracy was higher with niche aspects that had fewer classes. It is important to contextualize the number of possible classes with consensus votes.

The implementation of this pipeline requires a taxonomic group with both fossil and extant representatives with morphological continuity that allows for homologous trait measurements across time series. The application of extant trait data in extinct ecological estimation is best suited among lineages that exhibit a high degree of extant diversity relative to fossil samples: the more ecologies that the extant group occupies, the more likely it is that all potential ecological niches of the extinct group are represented. Predicted ecologies should also be evaluated in the context of other fossil evidence. For example, several extant ant taxa are primarily granivorous seed-eaters (Cole 1968; Plowes et al. 2013), thus the functional role of an extinct species could potentially be predicted as granivorous. However, while grasses first evolved in the early Cretaceous, grassland ecosystems did not develop broadly until later in the Cenozoic, making it unlikely that Mesozoic ants would have been granivorous (Stromberg 2011; Boyce and Lee 2017).

Ecological extinction and succession in the earliest ants

We recover broad consensus across models for hell ant ecological niche occupation: our models consistently predict haidomyrmecine taxa as leaf litter foraging or epigaeic ground-nesting predators, with few outliers (Figure 4). Our results contrast with previous hypotheses suggesting a primarily arboreal lifestyle among hell ants. Initial hypotheses were based on qualitative assessments of morphology (Barden and Grimaldi 2012), expected amber entrapment bias towards arboreal-associated species (Solórzano-Kraemer et al. 2015, 2018), and an assertion that hell ants' vertically aligned mandibles might have precluded the fine

manipulation of soil required to create ground nests (Dlussky 1996). The susceptibility of arboreal-associated species to extinction during cataclysmic events (Field et al. 2018) also provided a plausible explanation of the hell ants' demise. However, in addition to our own quantitative estimations of hell ant ecology, extant and fossilized behavioral evidence provide additional support for predicted ground and leaf litter habits among haidomyrmecines. Many extant trap-jaw ant species are capable of manipulating soil with their highly specialized mandibles, allowing for ground-nesting trap-jaw species (Cerquera and Tschinkel 2010). Soil nesting is also estimated as the ancestral state among all crown ants, though fossils have not yet been included in such reconstructions (Lucky et al. 2013). Additionally, two fossilized examples of hell ant prey reflect leaf litter and surficial habitats: a beetle larva in association with a *Linguamyrmex vladi* worker (Barden et al. 2017), likely reflecting a humid leaf litter habitat; and a cockroach relative *Caputoraptor elegans* in association with *Ceratomyrmex ellenbergeri* (Barden et al. 2020), possibly living in leaf litter or surficial strata, although arboreal habits have been proposed (Bai et al. 2018). This reconstructed nesting ecology of hell ants also aligns with proposed "extrinsic factors" related to the evolution of eusociality (Evans 1977).

While our results do not support the hypothesis of hell ant arboreality as a factor in their extinction, we do find support for specialized predation in several hell ant genera. Species with specialized diets are at higher risk of extinction during cataclysmic events due to the greater likelihood of their food sources' extinction and lack of flexibility in diet (Chichorro et al. 2022; Machado et al. 2022). While it is unclear whether haidomyrmecines went extinct prior to the KPg boundary or were lost during the mass extinction event, a specialized predatory diet may have been a factor in their demise.

Our comparison of ecomorphospace occupation in hell ants and in four monophyletic lineages with independent origins of trap-jaw mechanisms illustrate ecological coherence across deep time and distantly related lineages. Our reconstructions suggest that hell ants were functional analogs to many modern-day trap-jaw lineages in surficial and leaf litter arthropod

communities: solitary-foraging hunters seeking out prey across the forest floor and in interstitial leaf litter spaces. The morphological adaptations of modern-day trap-jaw workers necessitate solo foraging: rapid power-amplified closure of their specialized mandibles following the activation of elongate trigger setae in the path of mandible movement, subsequently stinging their prey. This specialized prey capture typically precludes group predation; workers individually subdue a single prey item before returning to the nest (Becker et al. 1989; Larabee and Suarez 2014). There are some morphological traits that support a trap-jaw mechanism in hell ants, including trigger hairs and a structurally-reinforced clypeal paddle at the point of mandible articulation (Barden & Grimaldi 2012; Barden et al. 2017). Moreover, there is direct paleoethological evidence of solitary foraging among hell ant workers (Barden et al. 2020).

Our paleoecological estimation allows for the recovery of repeated ecological niche occupation across lineages of predators. Hell ants occupied approximately 10% of hypothetical potential sampled ecomorphospace and yet radiated into leaf litter, surficial, and to a lesser degree, arboreal habitats in an ecomorphospace occupation that mirrors living lineages; hell ants entirely or at least partially overlap with each independent origin of extant trap jaw ants. Even as molecular-based divergence estimates place the origin of modern ants during the Cretaceous (Moreau et al. 2006; Borowiec et al. 2019), the earliest extant trap-jaw predators emerged later in the Cenozoic, from ~65 Ma in ponerines to ~35 Ma in *Strumigenys*, and after the last appearance of hell ants in the fossil record (Figure 3) (Ward et al. 2015; Booher et al. 2021; Fernandes et al. 2021). The last known hell ant fossil dates to 78 Ma in Campanian-age Canadian amber (McKellar et al. 2013). It is unclear precisely when hell ants went extinct, but the overlap of ecospace occupation between hell ants and the ponerine and dacetine lineages arising very soon after the KPg extinction may be a signature of faunal turnover in niche occupation. The extinction of hell ant lineages may have provided vacant ecospace that was filled by modern trap-jaw lineages. Additionally, while we included most known trap-jaw species in our extant ecospace reconstructions, fossil sampling remains much more limited; thus the full

ecospace occupation of hell ants was probably more broad than our current reconstruction suggests. The ecological breadth of the more than 1000 modern trap-jaw ant species (Bolton 2021) may represent echoes of their Cretaceous counterparts.

Faunal and ecological turnovers are a frequent feature of evolutionary history on Earth; the fossil record contains a plethora of examples (Sallan et al. 2011; Benson and Druckenmiller 2014; Moon and Stubbs 2020). We provide here a new quantitative framework for testing a variety of paleoecological hypotheses, including evaluations of ecology-based extinction risk, ecological succession in deep time, and competition between temporally and spatially proximate lineages. Our investigation of hell ant ecology generated a new test of ecology-linked extinction, and revealed a detailed ecological turnover in ecomorphospace occupation among temporally disjunct monophyletic lineages. By reconstructing the ecological community of the earliest ants, we find repeated lineage occupation of ecospace that is consistent with functional succession across Earth's last mass extinction event.

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Statement of Authorship

C.S., P.B. conceptualized the study; C.S., P.B. developed methodology and conducted statistical analyses; C.S., T.J., V.P., J.P.T., P.B. all contributed to data compilation and collection, data visualization, writing of the original draft, and reviews and edits of the final draft.

Ethics of the study: The fossil specimens used in this research are preserved primarily within Burmese amber. We affirm that all specimens were acquired prior to June 2017, pursuant to the proposed boycott of Burmese amber by the Society of Vertebrate Paleontologists (Rayfield et al. 2020). Some specimens are located in a private collection, while others are located in institutional museums: specimen repositories are indicated in the Supplementary Information associated with this manuscript, and we have provided photomicrographs of all specimens residing in a private collection. All data associated with this manuscript are available as Supplementary Information, including all morphometric measurements for privately-owned specimens.

Data and materials availability

All data and scripts needed to reproduce the analyses and evaluate the conclusions in the paper are present in the paper, Supplementary Information, and archived on the data repository Zenodo (doi: 10.5281/zenodo.7897553).

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Tables

Table 1. All morphological traits measured, with description of measurements taken, and known ecological significance of traits.

TRAIT	DESCRIPTION OF MEASUREMENT	KNOWN ECOLOGICAL SIGNIFICANCE
Head width (HW)	Taken in frontal view along widest axis of head capsule excluding eyes	Mandibular musculature of workers (Kaspari 1993); size of spaces workers can move through (Sarty et al. 2006)
Head length (HL)	Medially from anterior margin of clypeus to vertex of head capsule in frontal view	Size of spaces workers can move through (Kaspari and Weiser 1999)
Eye length (EL)	Measured along longest axis of eye	Foraging behaviour and foraging period (Weiser and Kaspari 2006)
Mandible length (lateral profile view) (MLP)	From point of insertion to apical-most tooth of mandible	Diet (Fowler et al. 1991)
Anteroposterior eye position (3 measurements taken) (LHL; ELA; ELP)	Taken in lateral view: length from midpoint of eye to anterior clypeal margin (ELA); length of head from midpoint of eye to posterior margin (ELP); total lateral head length (LHL) used to calculate eye position ratios	Foraging and diet (Fowler et al. 1991); habitat stratum (Gibb and Parr 2013)
Dorsoventral eye position (3 measurements taken) (HH; EHD; EHV)	Taken in lateral view: height of head from midpoint of eye to dorsal margin of head (EHD); height of head from midpoint of eye to ventral margin of head (EHV); total head height (HH) used to calculate eye position ratios	Related to foraging and diet (Fowler et al. 1991); habitat stratum occupied (Gibb and Parr 2013)
Mandible length (frontal view) (MLF)	From point of clypeal insertion to apical-most tooth of mandible	Diet (Fowler et al. 1991)
Scape length (SL)	From antennal socket to distal margin of scape	Chemosensory; detection of pheromone trails (Weiser and Kaspari 2006)
Weber's length (WL)	Taken in lateral view from the anterodorsal margin of the pronotum to the posteroventral margin of the mesosoma	Established proxy for worker body size (Weber 1938)

Procoxal length (PL)	From articulation point with propleuron to the distal tip of the procoxa	N/A
Mesosoma height (MH)	Taken at a right angle to Weber's length from the ventral margin of propleuron to dorsal margin of pronotum	N/A
Pronotal width (PW)	Measured at the widest point of the pronotum when viewed dorsally	Body mass of workers (Kaspari and Weiser 1999)
Metafemur length (ML)	Measured from articulation point with trochanter to distal tip of the metafemur	Foraging speed and habitat complexity (Feener et al. 1988)

Table 2. Ecological niche aspect binning abbreviations, definitions, and exemplar taxa.

BINNING DESIGNATOR	DEFINITION	EXEMPLAR TAXA
FUNCTIONAL ROLE		
GP	Generalist predator – broad taxonomic diet	<i>Odontomachus</i> ; <i>Diacamma</i> ; <i>Harpegnathos</i>
SP	Specialist predator – obligate feeding on specific taxon (e.g. termites)	<i>Acanthostichus</i> ; <i>Megaponera</i> ; <i>Simopelta</i>
Om	Omnivorous – prey items, plant matter, etc.	<i>Paraponera</i> ; <i>Camponotus</i> ; <i>Iridomyrmex</i>
Py	Phytophagous – extrafloral nectaries, herbivory, etc.	<i>Pseudomyrmex</i> ; <i>Tetraponera</i> ; <i>Myrmelachista</i>
Fg	Fungus-growing	<i>Cyphomyrmex</i> ; <i>Trachymyrmex</i> ; <i>Atta</i>
Tr	Trophobiotic – symbiotic relationship with other insects (homopteran secretions, etc.)	<i>Acropyga</i> ; <i>Melissotarsus</i> ; <i>Rhopalomastix</i>
Gn	Granivorous – seed-harvesting	<i>Acanthomyrmex</i> ; <i>Pogonomyrmex</i> ; <i>Veromessor</i>
Mh	Mushroom-foraging	<i>Euprenolepis</i>
NESTING NICHE		
Cn	Carton-nesting – structured nests from plant material in trees and shrubs	<i>Oecophylla</i> ; <i>Azteca</i> ; <i>Liometopum</i>

Gr	Ground-nesting – nests in dirt mounds, under stones, rock cracks, etc.	<i>Platythyrea</i> ; <i>Formica</i> ; <i>Pheidole</i>
Lg	Lignicolous – nests in twig and tree cavities	<i>Pseudomyrmex</i> ; <i>Simopone</i> ; <i>Cylindromyrmex</i>
LI	Leaf litter-nesting – nests in leaf litter interstitial space, rotten wood, etc.	<i>Strumigenys</i> ; <i>Discothyrea</i> ; <i>Typhlomyrmex</i>
Sb	Subterranean-nesting	<i>Leptanilloides</i> ; <i>Leptanilla</i>
FORAGING NICHE		
Ab	Arboreal – in and on trees and shrubs	<i>Daceton</i> ; <i>Tetraponera</i> ; <i>Crematogaster</i>
CR	Column-raiding – cooperative, nomadic or raiding predation	<i>Simopelta</i> ; <i>Dorylus</i> ; <i>Eciton</i>
Eg	Epigaeic – active foraging on the ground surface	<i>Leptomyrmex</i> ; <i>Rhytidoponera</i> ; <i>Myrmecocystus</i>
LI	Leaf litter – within interstitial spaces in leaf litter	<i>Discothyrea</i> ; <i>Amblyopone</i> ; <i>Heteroponera</i>
Sb	Subterranean – underground	<i>Acropyga</i>

Table 3. Out-of-bag accuracies (given in percentages) for each Random Forest model constructed.

COMPLETE MORPHOMETRIC DATASET				
	NESTING NICHE	FORAGING NICHE	FUNCTIONAL ROLE	ECOMORPH
Linear trait measurements	85.77	83.63	85.88	81.78
Shape ratio measurements	82.92	85.05	80.92	79.84
Log-shape variable measurements	88.61	88.97	82.06	82.56
SUBSET OF COMPLETE MORPHOMETRIC DATASET				
Linear trait measurements	85.41	82.92	80.53	81.78
Shape ratio measurements	80.07	81.14	82.06	77.91
Log-shape variable measurements	86.83	84.34	83.21	81.78

Figure Legends

Figure 1. Diagrammatic workflow of predictive model development and testing. A comprehensive morphometric dataset of extant ants was compiled; species were binned according to various ecological niche aspects based on surveys of the literature. Random Forest models were then trained on subsets of the original dataset. Homologous traits were measured on fossil ant specimens; when available, traits were measured from CT reconstructions, and otherwise were measured under light microscopy. Finally, the pre-trained Random Forest models were used to predict extinct ecology from fossil morphometric datasets.

Figure 2. Consensus model votes for niche aspect predictions. Each species' niche aspect predictions are represented by six models derived from alternate datasets; from top left, clockwise: linear functional measurements; log-shape variable functional measurements; shape ratio functional measurements; shape ratio homologous measurements; log-shape variable homologous measurements; linear homologous measurements. Taxonomic sampling includes described (named) taxa as well as putative morphospecies. Alternate specimens of the same species are denoted with superscripts, *denotes specimens included through CT-scan reconstruction data. All model votes are available in Tables S4-51; full specimen information is available in Table S3.

Figure 3. Ecospace occupation of haidomyrmecine and extant specialist predator lineages. (Top left) Subfamily-level time-calibrated phylogeny of ants with divergence dates from Borowiec et al. (2019), Haidomyrmecinae and extant lineages denoted with colored bars; haidomyrmecine range derived from oldest and youngest deposit ages, extant ranges based on available crown age estimations for each lineage: Ponerinae – *Anochetus* + *Odontomachus* (Fernandes et al. 2021); Myrmicinae – *Strumigenys* (Booher et al. 2021); Myrmicinae – dacetine trap-jaws (Ward et al. 2015). No divergence date estimates are available for the formicine trap-jaw genus *Myrmoterus*. (Right) Lineage-specific ecomorphological niche occupations. Each colored cube represents a unique occupied niche. Hashed cubes in

haidomyrmecine ecospace indicate “maximum” hypothetical niche occupation based on all unique combinations estimated across all six random forest models while remaining cubes reflect only the majority aspect from the linear functional measurement model. All extant ecospace compiled from literature. (Bottom left) Within-lineage ecological disparity calculated as average pairwise distance between each unique three-dimensional occupation. Maximum and minimum haidomyrmecine values represent alternate niche occupations described in the right panel. Ecological disparity values are listed in Table S52.

Figure 4. Reconstruction of the putative nesting and predatory foraging habits of the hell ant *Linguamyrmex vladi*. Artist: John Paul Timonera.

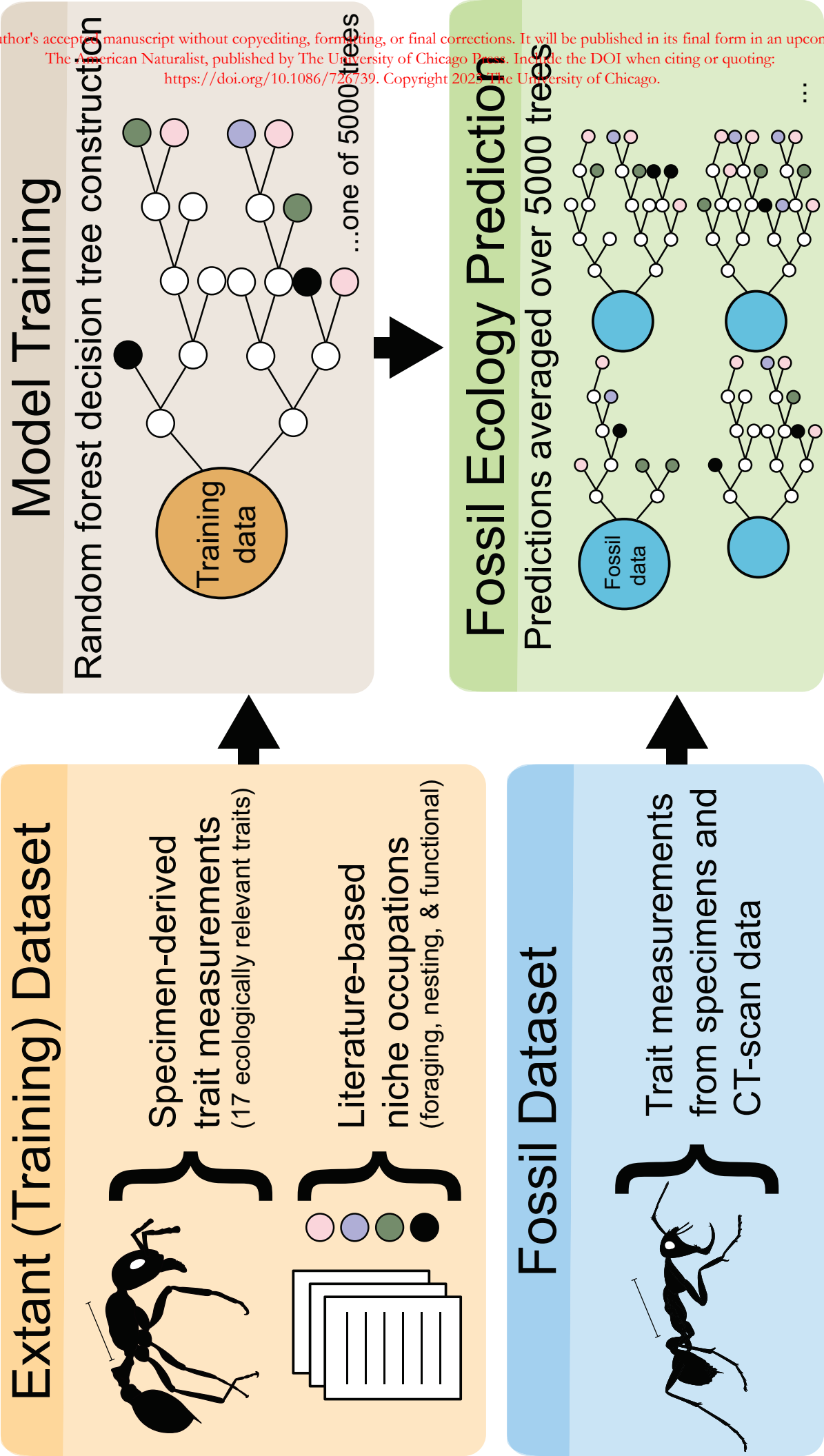
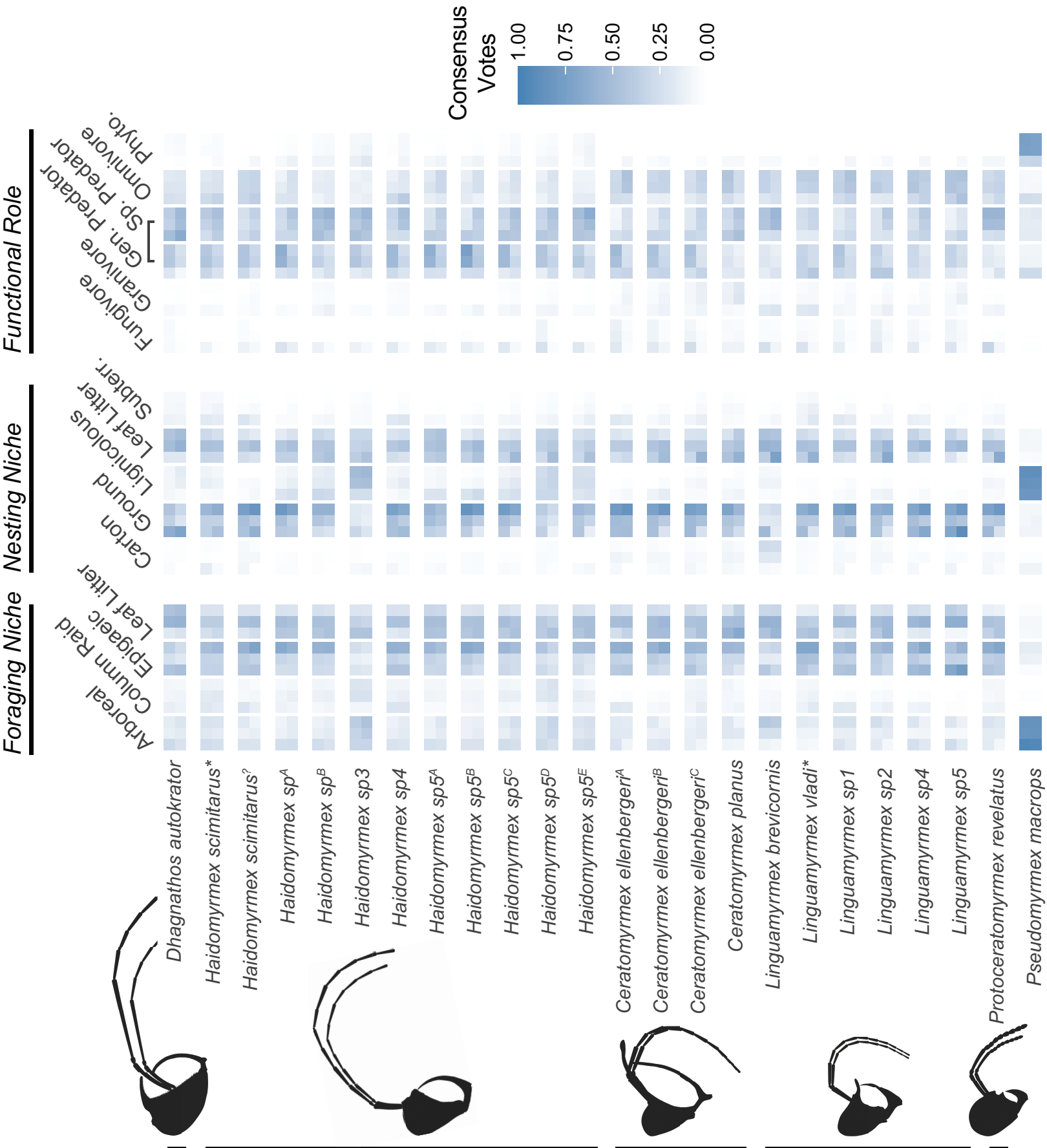


Figure 2

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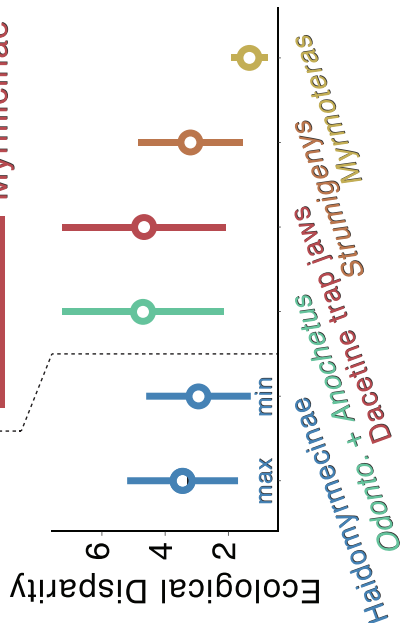


Figure 4

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Supplementary Information for: Trait-based paleontological niche prediction recovers extinct ecological breadth of the earliest specialized ant predators

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Keywords: paleoecology; ants; morphology; machine learning

Methods – Homologous versus functional morphology of hell ants

Most hell ant traits were distinguished as homologous to extant species; however, because haidomyrmecine cranial morphology is highly modified, eye position is difficult to assess in the context of modern ant variation. Extant ants (and most extinct ants, including the Dominican *Pseudomyrmex* fossil) have a prognathous head posture, in which the long axis of the head is held parallel to the ground with the oral opening pointing anteriorly. In many other insect taxa, such as wasps and grasshoppers, the head is held in a hypognathous posture; the long axis of the head is held perpendicular to the ground, with the oral opening positioned ventrally. A hypognathous-like head posture is also present in hell ants, a configuration not seen in any extant ant. This difference in head posture means that, interpreted strictly on the basis of homology, the dorsoventral axis of the extant ant head is the anteroposterior axis of the hell ant head, and vice versa; that eye positioning along each axis is similarly swapped. When interpreted this way, the eye position of the hell ant is more similar to many *Camponotus* species: positioned extremely posteriorly and more dorsally.

Functionally, however, the hell ant would have been moving with its head held hypognathously, as evidenced by fossilized posture as well as preserved predation (Perrichot et al 2008; Barden & Grimaldi 2012; Perrichot et al. 2016; Barden et al. 2020) thus the functional anteroposterior axis of the hell ant head would be from its clypeal protrusion or horn to the occipital foramen, rather than the homologous anteroposterior axis of the head running perpendicular to the ground from vertex to oral opening. Considering that our question is a question of functional ecology - what is the ecological occupation of hell ants? - we measured traits related to eye position both functionally and homologically, to incorporate this possible variation (Figures S1, S2).

Ecological breadth of the earliest ants

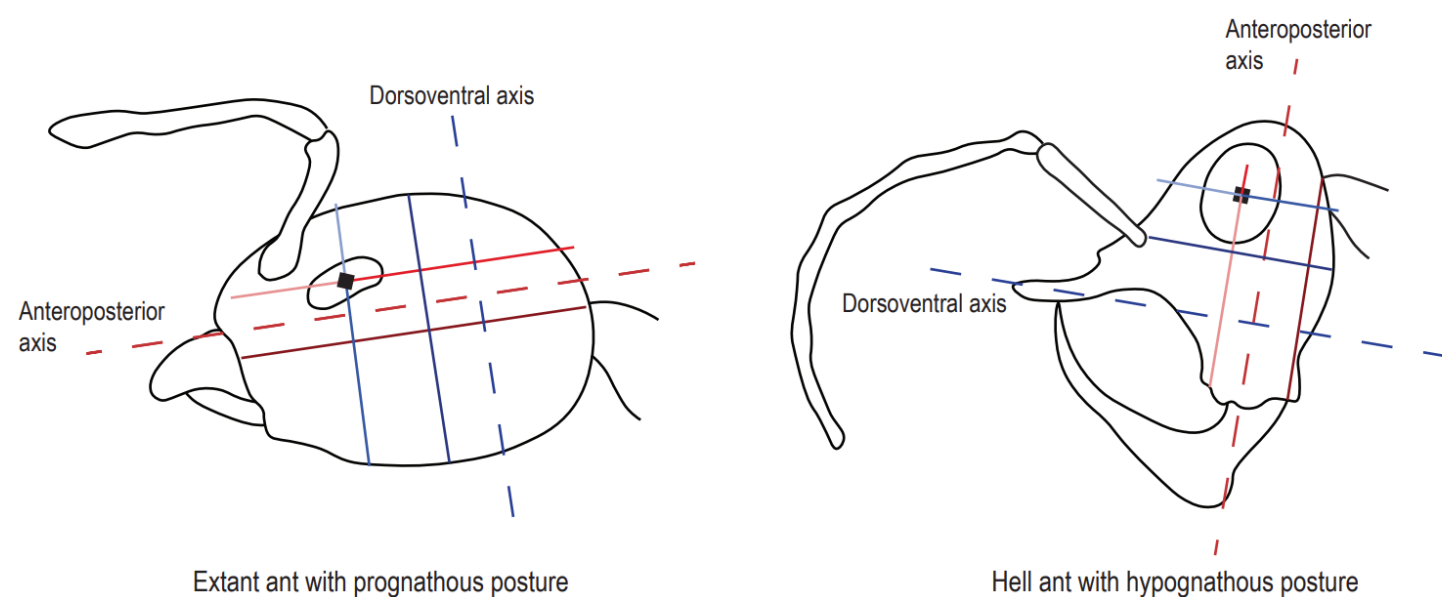


Figure S1.

Eye positioning measurements consistent with homologous morphology.

Ecological breadth of the earliest ants

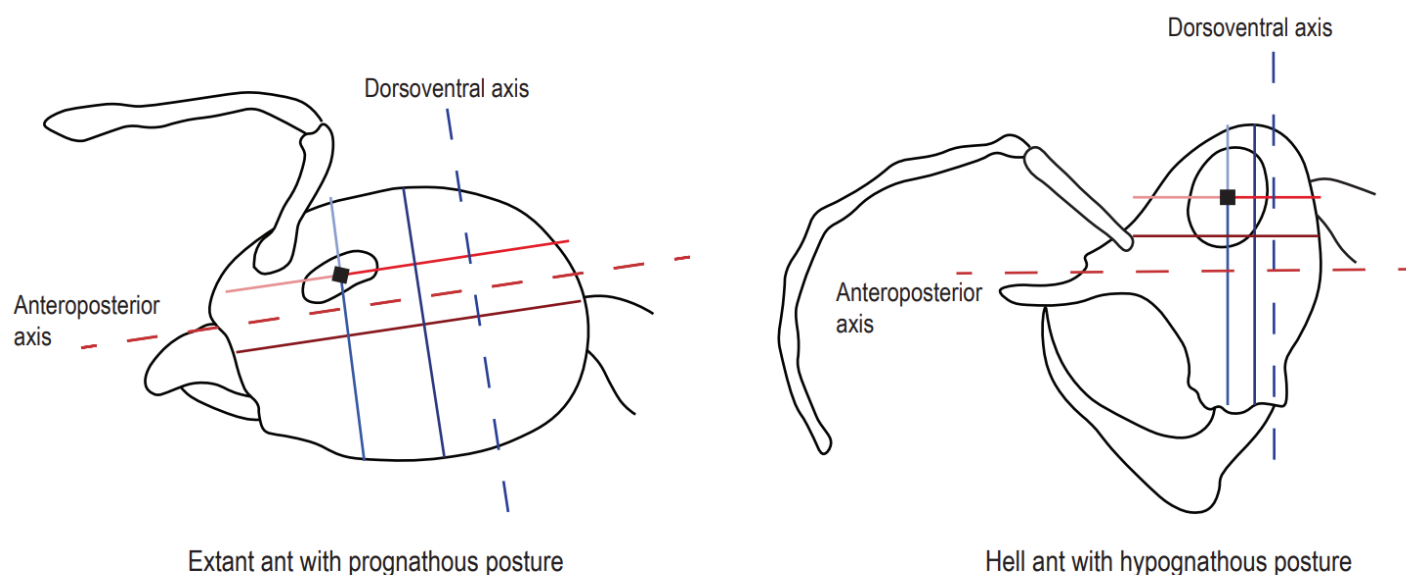


Figure S2.

Eye positioning measurements consistent with functional morphology.

Ecological breadth of the earliest ants

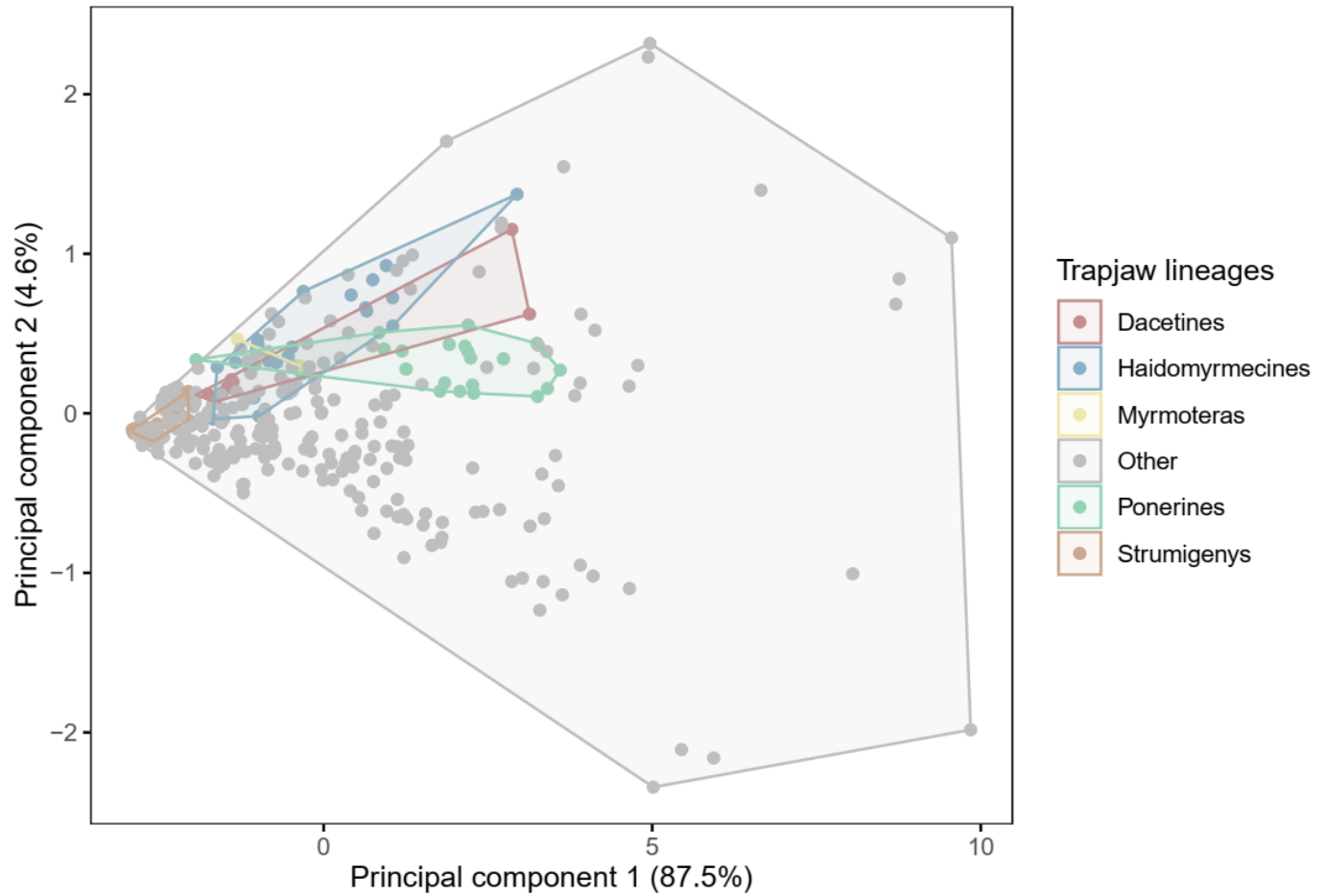


Figure S3.

Principal component analysis of extant and extinct morphospace using raw trait measurements. The morphospace of each lineage with an independent origin of trap-jaw mechanics is delineated.

Ecological breadth of the earliest ants

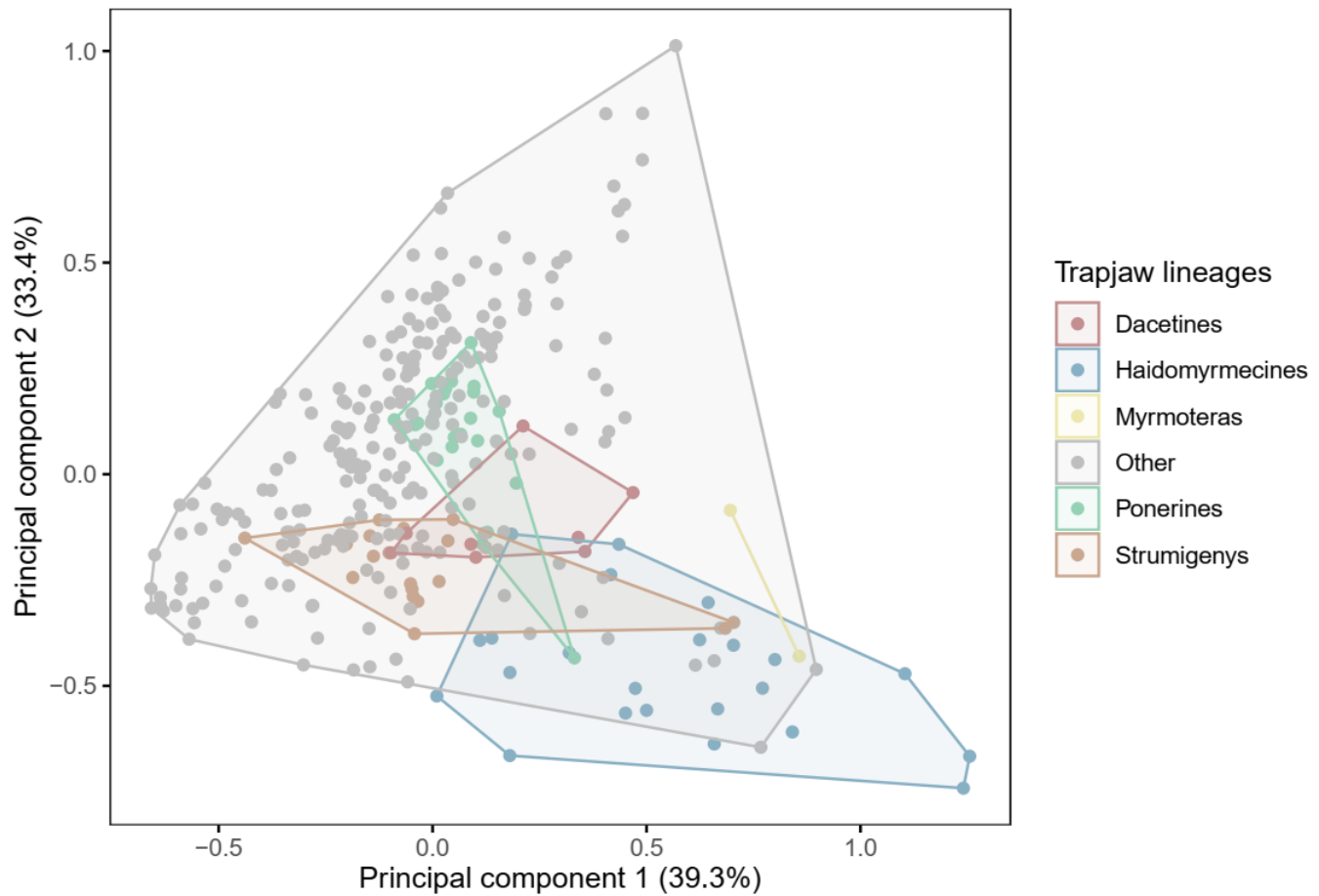


Figure S4.

Principal component analysis of extant and extinct morphospace using shape ratio measurements. The morphospace of each lineage with an independent origin of trap-jaw mechanics is delineated.

Ecological breadth of the earliest ants

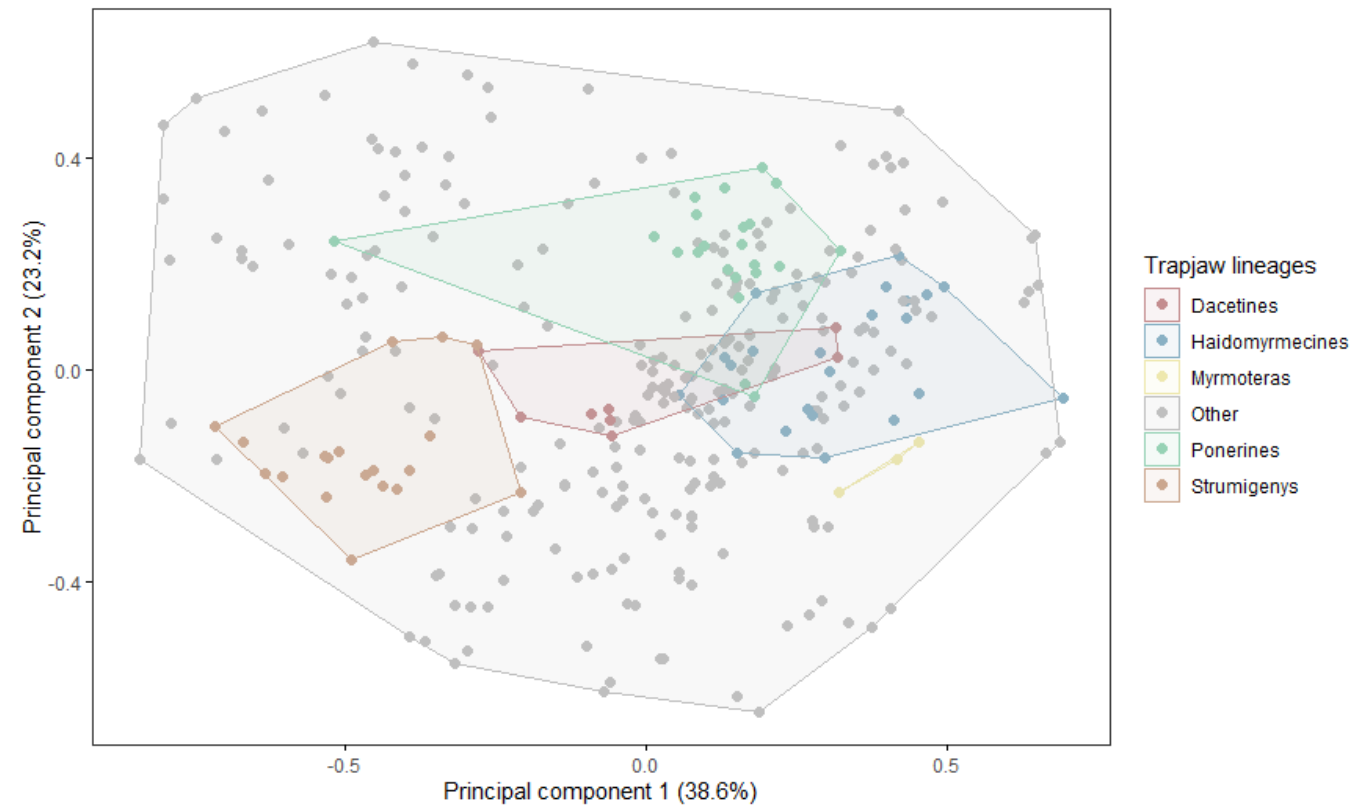


Figure S5.

Principal component analysis of extant and extinct morphospace using log-shape variable measurements. The morphospace of each lineage with an independent origin of trap-jaw mechanics is delineated.

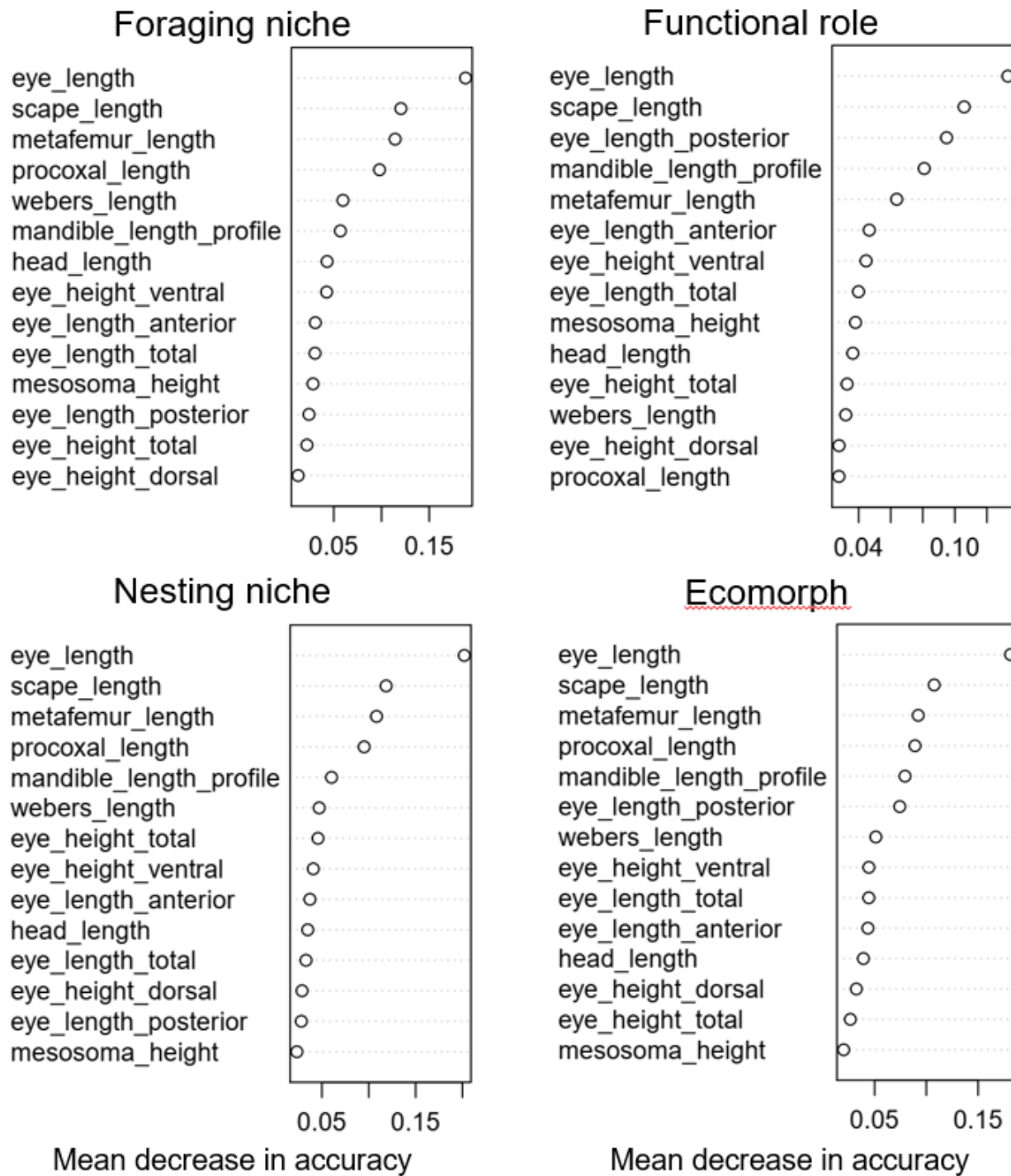


Figure S6.

Variable importance plots for each Random Forest classification model (foraging niche; functional role; nesting niche; ecomorph syndrome) using linear trait measurement data. Variable importance is calculated as the mean decrease in accuracy across splits when the variable was eliminated; a higher decrease in accuracy when that variable was omitted indicates greater importance to the model.

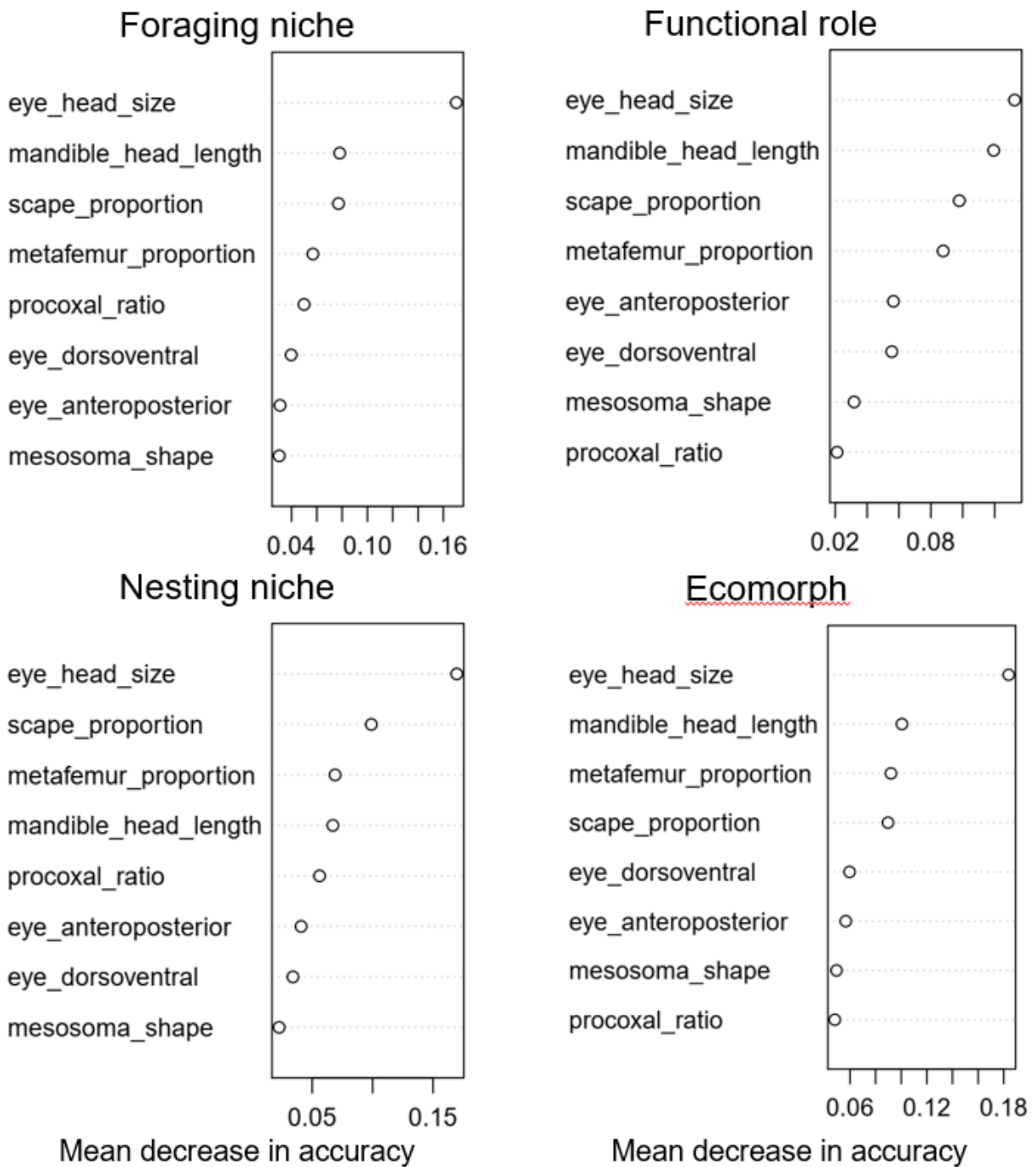


Figure S7. Variable importance plots for each Random Forest classification model (foraging niche; functional role; nesting niche; ecomorph syndrome) using shape ratio measurement data. Variable importance is calculated as the mean decrease in accuracy across splits when the variable was eliminated; a higher decrease in accuracy when that variable was omitted indicates greater importance to the model.

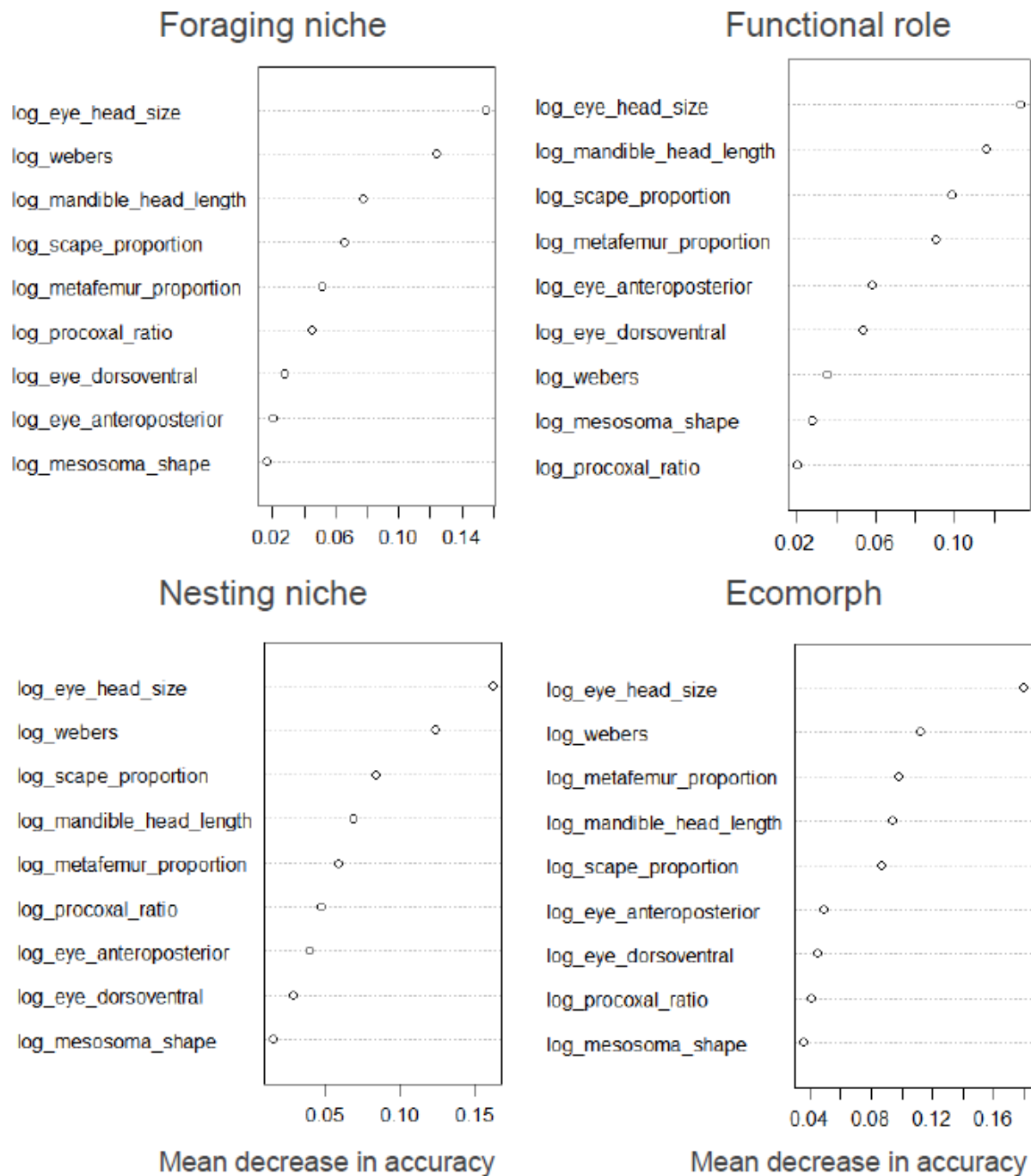


Figure S8.

Variable importance plots for each Random Forest classification model (foraging niche; functional role; nesting niche; ecomorph syndrome) using log-shape variable measurement data. Variable importance is calculated as the mean decrease in accuracy across splits when the variable was eliminated; a higher decrease in accuracy when that variable was omitted indicates greater importance to the model.

Trait	Formula	Interpretation
Head shape (HS)	HW/HL	Larger value = more boxy, square head Smaller value = more elongate along anteroposterior axis
Procoxal proportion (PP)	PL/WL	Larger value = procoxa longer in comparison to body length Smaller value = procoxa shorter in comparison to body length
Eye proportion (EP)	EL/HL	Larger value = eyes large in comparison to head Smaller value = eyes small in comparison to head
Pronotum expansion (PE)	PW/WL	Larger value = pronotum laterally expanded in relation to body size Smaller value = pronotum laterally narrow in relation to body size
Pronotum flattening (PF)	PW/MH	Larger value = pronotum broad and dorsoventrally flattened Smaller value = pronotum narrow and dorsoventrally expanded
Mesosoma shape (MS)	MH/WL	Larger value = overall elongate narrow body Smaller value = overall stocky squarish body
Mandible curvature (MC)	MLP/MLF	Larger value = low degree of mandible curvature Smaller value = high degree of mandible curvature
Mandible proportion (MP)	MLP/HL	Larger value = elongate mandibles in comparison with head size Smaller value = short mandibles in comparison with head size
Dorsoventral eye position (DEP)	EHD/HH	Larger value = eye positioned more ventrally Smaller value = eye positioned more dorsally
Anteroposterior eye position (AEP)	ELA/LHL	Larger value = eye positioned more posteriorly Smaller value = eye positioned more anteriorly
Scape proportion (SP)	SL/HL	Larger value = scape elongate in comparison with head size Smaller value = scape short in comparison with head size
Metafemur proportion (MeP)	ML/WL	Larger value = elongate leg in relation to body size Smaller value = shorter leg in relation to body size

Table S1.

Shape ratios of traits measured, formulae for calculation, and interpretation of ratio value.

Ecomorph designation based on granular binnings	Functional role binnings collapsed	Final ecomorph syndromes
fg_gr_eg	om_gr_eg	Ground or leaf litter-nesting epigaeic omnivore om_grll_eg Exemplars: <i>Camponotus</i> ; <i>Dinoponera</i> ; <i>Aphaenogaster</i>
gn_gr_eg		
mh_gr_ll		
om_gr_eg		
om_gr_ab		
om_gr_ll		
om_ll_eg		
gn_leaf	om_leaf	Leaf litter omnivore om_leaf Exemplars: <i>Aneuretus</i> ; <i>Acanthomyrmex</i> ; <i>Cyphomyrmex</i>
om_leaf		
om_lg_ab	om_lg_ab	Lignicolous arboreal omnivore om_lg_ab Exemplars: <i>Pseudomyrmex</i> ; <i>Cataulacus</i> ; <i>Cephalotes</i>
py_lg_ab		
tr_lg_ab		
om_cn_ab	om_cn_ab	Carton-nesting arboreal omnivore om_cn_ab Exemplars: <i>Crematogaster</i> ; <i>Oceophylla</i> ; <i>Azteca</i>
om_cn_eg	om_cn_eg	
om_sub	om_sub	Subterranean omnivore om_sub Exemplars: <i>Acropyga</i>
gp_gr_eg	pred_gr_eg	Ground-nesting epigaeic or leaf litter predator pred_gr_egll Exemplars: <i>Odontomachus</i> ; <i>Diacamma</i> ; <i>Harpegnathos</i>
sp_gr_eg	pred_gr_ll	
gp_gr_ll		
gp_leaf	pred_leaf	Leaf litter predator pred_leaf Exemplars: <i>Hypoconera</i> ; <i>Mystrium</i> ; <i>Strumigenys</i>
sp_leaf		
sp_lg_ab	pred_lg_ab	Lignicolous arboreal predator pred_lg_ab Exemplars: <i>Simopone</i> ; <i>Cylindromyrmex</i> ; <i>Daceton</i>
gp_lg_ab		
gp_ll_cr	pred_ll_cr	Column-raiding predator pred_cr Exemplars: <i>Simopelta</i> ; <i>Neivamyrmex</i> ; <i>Cheliomyrmex</i>
gp_sb_cr	pred_sb_cr	
sp_sb_cr		

Ecological breadth of the earliest ants

sp_gr_cr	pred_gr_cr	
gp_ll_eg	pred_ll_eg	Leaf litter-nesting epigaeic predator pred_ll_eg Exemplars: <i>Leptogenys</i> ; <i>Platythyrea</i>
sp_ll_eg		
gp_sb_ll	pred_sb_ll	Subterranean predator pred_sub Exemplars: <i>Proceratium</i> ; <i>Stigmatomma</i> ; <i>Leptanilla</i>
sp_sb_ll		

Table S2.

Schematic of ecomorph syndrome collapse: ecomorphs were collapsed based on ecological and morphological overlap between groups, and qualitative assessment of likely ecological overlap (leaf litter foragers may also forage on the surface of the ground, for example). Final column shows ecomorph syndrome abbreviations, definitions, and exemplar taxa (abbreviations used in raw dataset available on Dryad (DOI: <https://doi.org/10.5061/dryad.kh1893243>)).

Species	Specimen accession number	Caste	Sampling method
<i>Ceratomyrmex planus</i>	BALTJ_025	Worker	Measured under light microscopy
<i>Ceratomyrmex ellenbergeri</i>	BALTJ_016	Worker	Measured under light microscopy
<i>Ceratomyrmex ellenbergeri</i>	BALTJ_027	Worker	Measured under light microscopy
<i>Ceratomyrmex ellenbergeri</i>	BALTJ_029	Worker	Measured under light microscopy
<i>Protoceratomyrmex revelatus</i>	BALTJ_043	Worker	Measured under light microscopy
<i>Linguamyrmex sp5</i>	BALTJ_050	Worker	Measured under light microscopy
<i>Linguamyrmex sp4</i>	BALTJ_031	Worker	Measured under light microscopy
<i>Linguamyrmex brevicornis</i>	BALTJ_030	Worker	Measured under light microscopy
<i>Linguamyrmex sp2</i>	BALTJ_059	Worker	Measured under light microscopy
<i>Linguamyrmex sp1</i>	BALTJ_056	Worker	Measured under light microscopy
<i>Haidomyrmex sp3</i>	BALTJ_022	Worker	Measured under light microscopy
<i>Haidomyrmex sp5</i>	BALTJ_017	Worker	Measured under light microscopy
<i>Haidomyrmex sp5</i>	BALTJ_009	Worker	Measured under light microscopy
<i>Haidomyrmex sp5</i>	BALTJ_066	Worker	Measured under light microscopy
<i>Haidomyrmex sp5</i>	BALTJ_007	Worker	Measured under light microscopy
<i>Haidomyrmex scimitarus</i>	BALTJ_004	Worker	Measured under light microscopy
<i>Haidomyrmex sp5</i>	BALTJ_011	Worker	Measured under light microscopy
<i>Haidomyrmex sp4</i>	BALTJ_003	Worker	Measured under light microscopy
<i>Haidomyrmex indet1</i>	BALTJ_010	Worker	Measured under light microscopy
<i>Haidomyrmex indet2</i>	BALTJ_065	Worker	Measured under light microscopy
<i>Linguamyrmex vladi</i>	BuPH-1	Worker	Measured from micro-CT reconstruction
<i>Haidomyrmex scimitarus</i>	Bu-FB80	Dealate queen	Measured from micro-CT reconstruction
<i>Pseudomyrmex c.f. macrops</i>	DR-14-1021	Worker	Measured from micro-CT reconstruction
<i>Dhagnathos autokrator</i>	IGR.BU-003	Alate queen	Measured under light microscopy

Table S3.

List of all fossil specimens included in the study, with caste and measurement type information included. All specimens with accession numbers beginning in BALTJ are from a private collection, while specimens with alternate accession numbers are housed at the American Museum of Natural History (*Linguamyrmex vladi* and *Haidomyrmex scimitarus*); the New Jersey Institute of Technology (*Pseudomyrmex macrops*); and at the University of Rennes (*Dhagnathos autokrator*).

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Linguamyrme vlad</i>	0.0322	0.502	0.0182	0.35	0.0976	Gr
<i>Haidomyrmex scimitarus</i>	0.136	0.3546	0.0466	0.3012	0.1616	Gr
<i>Pseudomyrmex macrops</i>	0.0892	0.0846	0.7778	0.0416	0.0068	Lg
<i>Dhagnathos autokrator</i>	0.0424	0.6124	0.0658	0.1712	0.1082	Gr

Table S4.

Nesting niche prediction votes when using model trained on full morphometric dataset, linear trait measurements; functional morphology.

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Linguamyrmech vladi</i>	0.075	0.1058	0.4062	0.413	Ll
<i>Haidomyrmex scimitarus</i>	0.2614	0.1728	0.3334	0.2324	Eg
<i>Pseudomyrmex macrops</i>	0.9048	0.0074	0.0322	0.0556	Ab
<i>Dhagnathos autokrator</i>	0.2752	0.1276	0.43	0.1672	Eg

Table S5.

Foraging niche prediction votes when using model trained on full morphometric dataset, linear trait measurements; functional morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Linguamyrme vladii</i>	0.2072	0.1658	0.3222	0.1426	0.0072	0.155	GP
<i>Haidomyrmex scimitarus</i>	0.0994	0.0576	0.304	0.277	0.0062	0.2558	GP
<i>Pseudomyrmex macrops</i>	0.018	0	0.2766	0.2616	0.3034	0.1404	Py
<i>Dhagnathos autokrator</i>	0.043	0.0496	0.1808	0.232	0.0114	0.4832	SP

Table S6.

Functional role prediction votes when using model trained on full morphometric dataset, linear trait measurements; functional morphology.

Ecological breadth of the earliest ants

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Species	om_cn_ ab	om_grll_ eg	om_le af	om_lg_ ab	pred_ cr	pred_gr_e gll	pred_le af	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Linguamyrmer vladi</i>	0.0416	0.4052	0.085	0.0102	0.0718	0.0836	0.2484	0.0122	0.0352	0.0068	om_grll_eg
<i>Haidomyrmex scimitarus</i>	0.096	0.338	0.015	0.01	0.0656	0.1426	0.1952	0.013	0.1214	0.0032	om_grll_eg
<i>Pseudomyrmex macrops</i>	0.159	0.054	0.0154	0.4104	0.0104	0.0078	0.048	0.287	6.00E- 04	0.0074	om_lg_ab
<i>Dhagnathos autokrator</i>	0.0144	0.248	0	0.0102	0.0178	0.4646	0.1218	0.1052	0.0174	0	pred_gr_egll

Table S7.

Ecomorph prediction votes when using model trained on full morphometric dataset, linear trait measurements; functional morphology.

Ecological breadth of the earliest ants

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Linguamyrme vladii</i>	0.0232	0.1886	0.03	0.5856	0.1726	Ll
<i>Haidomyrmex scimitarus</i>	0.039	0.4696	0.0574	0.2966	0.1374	Gr
<i>Pseudomyrmex macrops</i>	0.0924	0.084	0.7782	0.04	0.0054	Lg
<i>Dhagnathos autokrator</i>	0.0088	0.68	0.0474	0.1728	0.091	Gr

Table S8.

Nesting niche prediction votes when using model trained on full morphometric dataset, linear trait measurements, homologous morphology.

Ecological breadth of the earliest ants

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Linguamyrme vladii</i>	0.0528	0.158	0.3324	0.4568	Ll
<i>Haidomyrmex scimitarus</i>	0.2258	0.1488	0.334	0.2914	Eg
<i>Pseudomyrmex macrops</i>	0.9014	0.0084	0.0304	0.0598	Ab
<i>Dhagnathos autokrator</i>	0.2124	0.1082	0.4696	0.2098	Eg

Table S9.

Foraging niche prediction votes when using model trained on full morphometric dataset, linear trait measurements, homologous morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Linguamyrme vlad</i>	0.055	0.1854	0.3942	0.1782	0.0268	0.1604	GP
<i>Haidomyrmex scimitarus</i>	0.019	0.0436	0.2066	0.3202	0.0476	0.363	SP
<i>Pseudomyrmex macrops</i>	0.0188	2.00E-04	0.2766	0.2478	0.313	0.1436	Py
<i>Dhagnathos autokrator</i>	0.0248	0.0418	0.0614	0.2192	0.0254	0.6274	SP

Table S10.

Functional role prediction votes when using model trained on full morphometric dataset, linear trait measurements, homologous morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_e gll	pred_le_ af	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Linguamyrmer vladi</i>	0.0308	0.3514	0.0834	0.0508	0.116	0.0496	0.283	0.0048	0.0244	0.0058	om_grll_eg
<i>Haidomyrmex scimitarus</i>	0.0216	0.3756	0.0134	0.0598	0.0558	0.112	0.2732	0.0128	0.0708	0.005	om_grll_eg
<i>Pseudomyrmex macrops</i>	0.1624	0.0568	0.0116	0.4136	0.0142	0.0092	0.0456	0.279	2.00E- 04	0.0074	om_lg_ab
<i>Dhagnathos autokrator</i>	0.0048	0.2558	0	0.0328	0.0202	0.475	0.1918	0.0134	0.0052	0	pred_gr_egll

Table S11.

Ecomorph prediction votes when using model trained on full morphometric dataset, linear trait measurements, homologous morphology.

Ecological breadth of the earliest ants

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Linguamyrme vladii</i>	0.049	0.6252	0.0074	0.2694	0.049	Gr
<i>Haidomyrmex scimitarus</i>	0.0266	0.5414	0.0972	0.2838	0.051	Gr
<i>Pseudomyrmex macrops</i>	0.0086	0.0686	0.843	0.0678	0.012	Lg
<i>Dhagnathos autokrator</i>	0.0184	0.4248	0.0814	0.42	0.0554	Gr

Table S12.

Nesting niche prediction votes when using model trained on full morphometric dataset; shape ratio trait measurements; functional morphology.

Ecological breadth of the earliest ants

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Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Linguamyrme vlad</i>	0.1572	0.062	0.6564	0.1244	Eg
<i>Haidomyrmex scimitarus</i>	0.2086	0.108	0.4724	0.211	Eg
<i>Pseudomyrmex macrops</i>	0.8186	0.0142	0.1376	0.0296	Ab
<i>Dhagnathos autokrator</i>	0.1462	0.067	0.3526	0.4342	Ll

Table S13.

Foraging niche prediction votes when using model trained on full morphometric dataset; shape ratio trait measurements; functional morphology.

Ecological breadth of the earliest ants

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Linguamyrmech vladi</i>	0.037	0.0328	0.3172	0.362	8.00E-04	0.2502	Om
<i>Haidomyrmex scimitarus</i>	0.0074	0.02	0.4008	0.1708	0.0202	0.3808	GP
<i>Pseudomyrmex macrops</i>	8.00E-04	0.0044	0.0866	0.051	0.7116	0.1456	Py
<i>Dhagnathos autokrator</i>	0.0458	0.0158	0.383	0.1612	0.0322	0.362	GP

Table S14.

Functional role prediction votes when using model trained on full morphometric dataset; shape ratio trait measurements; functional morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_e gll	pred_le_ af	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Linguamyrme vladi</i>	0.0684	0.2738	0.0552	6.00E- 04	0.0558	0.4122	0.1088	0.0058	0.0192	2.00E- 04	pred_gr_egll
<i>Haidomyrmex scimitarus</i>	0.0114	0.1738	0.0102	0.0146	0.0308	0.4666	0.1072	0.0624	0.1136	0.0094	pred_gr_egll
<i>Pseudomyrmex macrops</i>	0.0066	0.0354	0.0048	0.6404	0.0072	0.0222	0.0098	0.231	0.0406	0.002	om_lg_ab
<i>Dhagnathos autokrator</i>	0.0136	0.1948	0.025	0.0136	0.0216	0.2822	0.3438	0.0352	0.059	0.0112	pred_leaf

Table S15.

Ecomorph prediction votes when using model trained on full morphometric dataset; shape ratio trait measurements; functional morphology.

Ecological breadth of the earliest ants

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Linguamyrme vlad</i>	0.0366	0.674	0.0064	0.2228	0.0602	Gr
<i>Haidomyrmex scimitarus</i>	0.0206	0.6094	0.0786	0.234	0.0574	Gr
<i>Pseudomyrmex macrops</i>	0.0138	0.0708	0.8422	0.0638	0.0094	Lg
<i>Dhagnathos autokrator</i>	0.0202	0.2926	0.1466	0.485	0.0556	Ll

Table S16.

Nesting niche prediction votes when using model trained on full morphometric dataset, shape ratio trait measurements; homologous morphology.

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Linguamyrme vladii</i>	0.1468	0.0678	0.6546	0.1308	Eg
<i>Haidomyrmex scimitarus</i>	0.1956	0.1006	0.509	0.1948	Eg
<i>Pseudomyrmex macrops</i>	0.8224	0.0124	0.1394	0.0258	Ab
<i>Dhagnathos autokrator</i>	0.1982	0.062	0.261	0.4788	Ll

Table S17.

Foraging niche prediction votes when using model trained on full morphometric dataset, shape ratio trait measurements; homologous morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Linguamyrmech vladi</i>	0.0276	0.0546	0.2514	0.3588	0.001	0.3066	Om
<i>Haidomyrmex scimitarus</i>	0.003	0.0196	0.2828	0.1952	0.037	0.4624	SP
<i>Pseudomyrmex macrops</i>	0	0.005	0.0872	0.0454	0.6976	0.1648	Py
<i>Dhagnathos autokrator</i>	0.0114	0.017	0.2314	0.1764	0.046	0.5178	SP

Table S18.

Functional role prediction votes when using model trained on full morphometric dataset, shape ratio trait measurements; homologous morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_e gll	pred_le_ af	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Linguamyrme vladi</i>	0.05	0.303	0.0564	2.00E- 04	0.0574	0.4042	0.1094	0.0082	0.011	2.00E- 04	pred_gr_egll
<i>Haidomyrmex scimitarus</i>	0.0058	0.2034	0.0114	0.0124	0.0298	0.5468	0.091	0.0528	0.0294	0.0172	pred_gr_egll
<i>Pseudomyrmex macrops</i>	0.0062	0.04	0.003	0.6426	0.0074	0.0238	0.0102	0.2282	0.0372	0.0014	om_lg_ab
<i>Dhagnathos autokrator</i>	0.0156	0.1462	0.0214	0.0344	0.0212	0.1492	0.4522	0.1158	0.0172	0.0268	pred_leaf

Table S19.

Ecomorph prediction votes when using model trained on full morphometric dataset, shape ratio trait measurements; homologous morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Linguamyrme vladii</i>	0.033	0.3944	0.0242	0.4636	0.0848	Ll
<i>Haidomyrmex scimitarus</i>	0.0164	0.3428	0.1238	0.4516	0.0654	Ll
<i>Pseudomyrmex macrops</i>	0.0214	0.0716	0.8258	0.0712	0.01	Lg
<i>Dhagnathos autokrator</i>	0.0202	0.3486	0.0812	0.488	0.062	Ll

Table S20.

Nesting niche prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; functional morphology.

Ecological breadth of the earliest ants

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Linguamyrme vlad</i>	0.0954	0.0816	0.4652	0.3578	Eg
<i>Haidomyrmex scimitarus</i>	0.1636	0.1528	0.3204	0.3632	Ll
<i>Pseudomyrmex macrops</i>	0.8032	0.024	0.112	0.0608	Ab
<i>Dhagnathos autokrator</i>	0.1284	0.0824	0.2326	0.5566	Ll

Table S21.

Foraging niche prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; functional morphology.

Ecological breadth of the earliest ants

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Linguamyrmech vladi</i>	0.0526	0.0516	0.3292	0.3226	0.0034	0.2406	GP
<i>Haidomyrmex scimitarus</i>	0.011	0.0138	0.4252	0.1884	0.0314	0.3302	SP
<i>Pseudomyrmex macrops</i>	4.00E-04	0.0042	0.0998	0.0572	0.7034	0.135	Py
<i>Dhagnathos autokrator</i>	0.041	0.0124	0.3924	0.1872	0.031	0.336	GP

Table S22.

Functional role prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; functional morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_e gll	pred_le_ af	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Linguamyrme vladi</i>	0.0692	0.2434	0.1376	0.0034	0.0574	0.247	0.2016	0.0224	0.0174	6.00E-04	om_grll_eg
<i>Haidomyrmex scimitarus</i>	0.0158	0.184	0.0396	0.0274	0.0394	0.22	0.2782	0.096	0.0882	0.0114	pred_leaf
<i>Pseudomyrmex macrops</i>	0.0138	0.0518	0.0072	0.6466	0.0082	0.0104	0.025	0.2114	0.0238	0.0018	om_lg_ab
<i>Dhagnathos autokrator</i>	0.0198	0.1836	0.0484	0.0204	0.0262	0.157	0.4384	0.055	0.0412	0.01	pred_leaf

Table S23.

Ecomorph prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; functional morphology.

Ecological breadth of the earliest ants

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Linguamyrme vlad</i>	0.0302	0.3864	0.0254	0.4378	0.1202	Ll
<i>Haidomyrmex scimitarus</i>	0.0142	0.3404	0.1008	0.4436	0.101	Ll
<i>Pseudomyrmex macrops</i>	0.021	0.089	0.8096	0.069	0.0114	Lg
<i>Dhagnathos autokrator</i>	0.0194	0.1982	0.1256	0.5806	0.0762	Ll

Table S24.

Nesting niche prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; homologous morphology.

Ecological breadth of the earliest ants

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Linguamyrmech vladi</i>	0.0966	0.1034	0.4488	0.3512	Eg
<i>Haidomyrmex scimitarus</i>	0.151	0.1666	0.3178	0.3646	Ll
<i>Pseudomyrmex macrops</i>	0.8098	0.022	0.1072	0.061	Ab
<i>Dhagnathos autokrator</i>	0.1552	0.0962	0.1778	0.5708	Ll

Table S25.

Foraging niche prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; homologous morphology.

Ecological breadth of the earliest ants

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Linguamyrme vlad</i>	0.0416	0.0556	0.2538	0.346	0.0014	0.3016	Om
<i>Haidomyrmex scimitarus</i>	0.0058	0.018	0.3232	0.2082	0.0364	0.4084	SP
<i>Pseudomyrmex macrops</i>	6.00E-04	0.007	0.0938	0.0638	0.6954	0.1394	Py
<i>Dhagnathos autokrator</i>	0.0144	0.0166	0.2528	0.1814	0.0472	0.4876	SP

Table S26.

Functional role prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; homologous morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_e gll	pred_le_ af	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Linguamyrme x vladi</i>	0.0486	0.2668	0.1392	0.0044	0.0634	0.2518	0.1924	0.0168	0.0126	0.004	om_grll_eg
<i>Haidomyrmex scimitarus</i>	0.0104	0.2208	0.0362	0.0306	0.0522	0.2444	0.268	0.0764	0.0426	0.0184	pred_gr_egll
<i>Pseudomyrmex macrops</i>	0.0114	0.0492	0.0068	0.6548	0.0106	0.0108	0.0258	0.2054	0.024	0.0012	om_lg_ab
<i>Dhagnathos autokrator</i>	0.0236	0.1238	0.033	0.0284	0.025	0.0812	0.5186	0.1332	0.0132	0.02	pred_leaf

Table S27.

Ecomorph prediction votes when using model trained on full morphometric dataset, log-shape variable measurements; homologous morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0598	0.3838	0.0762	0.4338	0.0464	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.057	0.485	0.0416	0.2394	0.177	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0382	0.4644	0.1014	0.3522	0.0438	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0736	0.519	0.0402	0.2826	0.0846	Gr
<i>Protoceratomyrmex revelatus</i>	0.0762	0.5304	0.0466	0.2896	0.0572	Gr
<i>Linguamyrmex sp5</i>	0.0912	0.6572	0.0166	0.202	0.033	Gr
<i>Linguamyrmex sp4</i>	0.0646	0.5374	0.0234	0.2556	0.119	Gr
<i>Linguamyrmex brevicornis</i>	0.0552	0.5154	0.0342	0.36	0.0352	Gr
<i>Linguamyrmex sp2</i>	0.0572	0.4372	0.0872	0.3666	0.0518	Gr
<i>Linguamyrmex sp1</i>	0.0662	0.4752	0.0368	0.2536	0.1682	Gr
<i>Haidomyrmex sp3</i>	0.0508	0.3036	0.2456	0.3598	0.0402	Ll
<i>Haidomyrmex sp5</i>	0.0426	0.355	0.1906	0.361	0.0508	Ll
<i>Haidomyrmex sp5</i>	0.0352	0.3664	0.2152	0.3422	0.041	Gr
<i>Haidomyrmex sp5</i>	0.0468	0.3816	0.1986	0.3056	0.0674	Gr
<i>Haidomyrmex sp5</i>	0.0376	0.3426	0.2926	0.2666	0.0606	Cn
<i>Haidomyrmex scimitarus</i>	0.0806	0.442	0.0288	0.249	0.1996	Gr
<i>Haidomyrmex sp5</i>	0.0412	0.4184	0.1834	0.2888	0.0682	Gr
<i>Haidomyrmex sp4</i>	0.0752	0.4584	0.0474	0.2482	0.1708	Gr
<i>Haidomyrmex indet1</i>	0.0294	0.3846	0.1996	0.3448	0.0416	Gr
<i>Haidomyrmex indet2</i>	0.0192	0.2474	0.2866	0.3914	0.0554	Ll

Table S28.

Nesting niche prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; functional morphology.

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0986	0.0744	0.2564	0.5706	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.1966	0.1784	0.384	0.241	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.172	0.0578	0.2922	0.478	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.13	0.0842	0.4284	0.3574	Eg
<i>Protoceratomyrmex revelatus</i>	0.1536	0.089	0.4234	0.334	Eg
<i>Linguamyrmex sp5</i>	0.252	0.019	0.653	0.076	Eg
<i>Linguamyrmex sp4</i>	0.238	0.0954	0.512	0.1546	Eg
<i>Linguamyrmex brevicornis</i>	0.1	0.0648	0.3994	0.4358	Ll
<i>Linguamyrmex sp2</i>	0.1608	0.0972	0.3546	0.3874	Ll
<i>Linguamyrmex sp1</i>	0.2018	0.1692	0.425	0.204	Eg
<i>Haidomyrmex sp3</i>	0.3014	0.0798	0.1928	0.426	Ll
<i>Haidomyrmex sp5</i>	0.2274	0.0466	0.2878	0.4382	Ll
<i>Haidomyrmex sp5</i>	0.2136	0.076	0.3052	0.4052	Ll
<i>Haidomyrmex sp5</i>	0.2506	0.0792	0.2868	0.3834	Ll
<i>Haidomyrmex sp5</i>	0.2774	0.0734	0.2738	0.3754	Ll
<i>Haidomyrmex scimitarus</i>	0.2156	0.1968	0.3992	0.1884	Eg
<i>Haidomyrmex sp5</i>	0.2306	0.1016	0.2492	0.4186	Ll
<i>Haidomyrmex sp4</i>	0.216	0.2006	0.4204	0.163	Eg
<i>Haidomyrmex indet1</i>	0.2432	0.1048	0.2476	0.4044	Ll
<i>Haidomyrmex indet2</i>	0.2582	0.0602	0.2704	0.4112	Ll

Table S29.

Foraging niche prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; functional morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Ceratomyrmex planus</i>	0.1016	0.0506	0.1618	0.253	0.0566	0.3764	SP
<i>Ceratomyrmex ellenbergeri</i>	0.1676	0.0496	0.2944	0.2472	0.014	0.2272	GP
<i>Ceratomyrmex ellenbergeri</i>	0.1592	0.0742	0.3004	0.1192	0.0364	0.3106	SP
<i>Ceratomyrmex ellenbergeri</i>	0.2452	0.0546	0.2304	0.152	0.0104	0.3074	SP
<i>Protoceratomyrmex revelatus</i>	0.3096	0.08	0.0948	0.2104	0.0666	0.2386	Fg
<i>Linguamyrmex sp5</i>	0.1842	0.055	0.1616	0.3338	0.0028	0.2626	Om
<i>Linguamyrmex sp4</i>	0.1486	0.0734	0.2288	0.268	0.0068	0.2744	SP
<i>Linguamyrmex brevicornis</i>	0.229	0.1706	0.135	0.1818	0.0452	0.2384	SP
<i>Linguamyrmex sp2</i>	0.1612	0.0706	0.3864	0.161	0.0234	0.1974	GP
<i>Linguamyrmex sp1</i>	0.1314	0.0716	0.2904	0.2572	0.0114	0.238	GP
<i>Haidomyrmex sp3</i>	0.11	0.042	0.151	0.1024	0.1224	0.4722	SP
<i>Haidomyrmex sp5</i>	0.1528	0.047	0.2392	0.1324	0.0618	0.3668	SP
<i>Haidomyrmex sp5</i>	0.1302	0.0378	0.2434	0.1506	0.0624	0.3756	SP
<i>Haidomyrmex sp5</i>	0.1756	0.06	0.1452	0.1302	0.0696	0.4194	SP
<i>Haidomyrmex sp5</i>	0.2224	0.0808	0.1288	0.101	0.0666	0.4004	SP
<i>Haidomyrmex scimitarus</i>	0.108	0.0286	0.2866	0.3028	0.0176	0.2564	Om
<i>Haidomyrmex sp5</i>	0.1756	0.0372	0.187	0.1384	0.0416	0.4202	SP
<i>Haidomyrmex sp4</i>	0.1548	0.0384	0.275	0.278	0.0132	0.2406	Om
<i>Haidomyrmex indet1</i>	0.208	0.0376	0.2088	0.1938	0.0544	0.2974	SP
<i>Haidomyrmex indet2</i>	0.113	0.075	0.1456	0.0944	0.0948	0.4772	SP

Table S30.

Functional role prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; functional morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_ egll	pred_l_ eaf	pred_lg_ ab	pred_ll_ eg	pred_s_ ub	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0578	0.2526	0.158	0.0544	0.075 4	0.064	0.2268	0.0848	0.0038	0.0224	om_grll_eg
<i>Ceratomyrmex ellenbergeri</i>	0.0656	0.3268	0.010 8	0.0118	0.056 4	0.1744	0.2716	0.017	0.0654	0	om_grll_eg
<i>Ceratomyrmex ellenbergeri</i>	0.0436	0.2244	0.076 2	0.0712	0.044 4	0.0384	0.4158	0.0436	0.0324	0.01	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.0506	0.2992	0.026 4	0.026	0.046 2	0.0866	0.3874	0.012	0.0626	0.003	pred_leaf
<i>Protoceratomyrmex revelatus</i>	0.1194	0.405	0.108	0.0892	0.071 8	0.028	0.111	0.0174	0.0446	0.0056	om_grll_eg
<i>Linguamyrmex sp5</i>	0.0838	0.396	0.002 8	0.0014	0.012	0.2324	0.1946	0.017	0.0598	0	om_grll_eg
<i>Linguamyrmex sp4</i>	0.0814	0.3842	0.003 4	0.0026	0.023 6	0.1794	0.2432	0.0106	0.0714	0	om_grll_eg
<i>Linguamyrmex brevicornis</i>	0.0716	0.4046	0.201 2	0.065	0.037 8	0.0432	0.138	0.0076	0.0254	0.0056	om_grll_eg
<i>Linguamyrmex sp2</i>	0.0468	0.2786	0.031 2	0.0276	0.064	0.0502	0.4588	0.0112	0.0298	0.0018	pred_leaf
<i>Linguamyrmex sp1</i>	0.079	0.3368	0.008	0.0062	0.043	0.2066	0.234	0.0132	0.073	0	om_grll_eg
<i>Haidomyrmex sp3</i>	0.1102	0.1584	0.075 8	0.1518	0.039 4	0.0286	0.2254	0.189	0.0086	0.0128	pred_leaf
<i>Haidomyrmex sp5</i>	0.0472	0.1746	0.056 2	0.1264	0.041 6	0.0444	0.3034	0.1356	0.0572	0.0134	pred_leaf
<i>Haidomyrmex sp5</i>	0.0438	0.207	0.044	0.1276	0.071	0.0358	0.2872	0.1122	0.0628	0.0086	pred_leaf
<i>Haidomyrmex sp5</i>	0.06	0.1958	0.053 8	0.1508	0.064 6	0.0372	0.2004	0.147	0.0746	0.0158	pred_leaf
<i>Haidomyrmex sp5</i>	0.0418	0.2396	0.042 6	0.1212	0.054 2	0.0428	0.209	0.1694	0.0548	0.0246	om_grll_eg

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<i>Haidomyrmex scimitarus</i>	0.082	0.3636	0.0036	0.0108	0.0596	0.2104	0.1606	0.0096	0.0998	0	om_grll_eg
<i>Haidomyrmex sp5</i>	0.0688	0.2302	0.091	0.0952	0.0628	0.0496	0.176	0.1854	0.0224	0.0186	om_grll_eg
<i>Haidomyrmex sp4</i>	0.0898	0.3548	0.0016	0.0156	0.0662	0.2046	0.1214	0.011	0.1344	0	om_grll_eg
<i>Haidomyrmex indet1</i>	0.0544	0.2744	0.106	0.109	0.053	0.0436	0.1388	0.1768	0.0294	0.0146	om_grll_eg
<i>Haidomyrmex indet2</i>	0.0358	0.2108	0.0304	0.162	0.0486	0.0794	0.1852	0.1034	0.125	0.0194	om_grll_eg

Table S31.

Ecomorph prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; functional morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0384	0.2442	0.0898	0.5854	0.0422	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.0074	0.4942	0.0608	0.2844	0.1532	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0574	0.1966	0.1402	0.507	0.0988	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.034	0.2198	0.0466	0.5722	0.1274	Ll
<i>Protoceratomyrmex revelatus</i>	0.033	0.2098	0.0432	0.6314	0.0826	Ll
<i>Linguatomyrmex sp5</i>	0.0084	0.8596	0.0304	0.0828	0.0188	Gr
<i>Linguatomyrmex sp4</i>	0.0058	0.6526	0.046	0.1858	0.1098	Gr
<i>Linguatomyrmex brevicornis</i>	0.0482	0.1406	0.0376	0.708	0.0656	Ll
<i>Linguatomyrmex sp2</i>	0.019	0.184	0.1028	0.6352	0.059	Ll
<i>Linguatomyrmex sp1</i>	0.0088	0.577	0.0556	0.2204	0.1382	Gr
<i>Haidomyrmex sp3</i>	0.0662	0.2	0.2552	0.4328	0.0458	Ll
<i>Haidomyrmex sp5</i>	0.043	0.3078	0.2038	0.401	0.0444	Ll
<i>Haidomyrmex sp5</i>	0.0374	0.1636	0.2776	0.4484	0.073	Ll
<i>Haidomyrmex sp5</i>	0.0424	0.1274	0.234	0.5152	0.081	Ll
<i>Haidomyrmex sp5</i>	0.0202	0.1118	0.2906	0.4878	0.0896	Ll
<i>Haidomyrmex scimitarus</i>	0.0134	0.5824	0.0606	0.214	0.1296	Gr
<i>Haidomyrmex sp5</i>	0.062	0.1338	0.223	0.4516	0.1296	Ll
<i>Haidomyrmex sp4</i>	0.0292	0.5052	0.079	0.2054	0.1812	Gr
<i>Haidomyrmex indet1</i>	0.0266	0.3602	0.2272	0.3438	0.0422	Gr
<i>Haidomyrmex indet2</i>	0.0136	0.2024	0.2682	0.446	0.0698	Ll

Table S32.

Ecological breadth of the earliest ants

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Nesting niche prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; homologous morphology.

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0864	0.0914	0.1778	0.6444	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.0928	0.1676	0.4108	0.3288	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.1808	0.075	0.2518	0.4924	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.0866	0.1364	0.3178	0.4592	Ll
<i>Protoceratomyrmex revelatus</i>	0.0776	0.102	0.3904	0.43	Ll
<i>Linguamyrmex sp5</i>	0.1526	0.0194	0.7488	0.0792	Eg
<i>Linguamyrmex sp4</i>	0.1634	0.1106	0.5472	0.1788	Eg
<i>Linguamyrmex brevicornis</i>	0.0778	0.0826	0.2944	0.5452	Ll
<i>Linguamyrmex sp2</i>	0.065	0.1212	0.2836	0.5302	Ll
<i>Linguamyrmex sp1</i>	0.1474	0.1606	0.4448	0.2472	Eg
<i>Haidomyrmex sp3</i>	0.3078	0.0824	0.1786	0.4312	Ll
<i>Haidomyrmex sp5</i>	0.217	0.0488	0.3048	0.4294	Ll
<i>Haidomyrmex sp5</i>	0.2186	0.0836	0.2414	0.4564	Ll
<i>Haidomyrmex sp5</i>	0.232	0.059	0.263	0.446	Ll
<i>Haidomyrmex sp5</i>	0.232	0.1114	0.2186	0.438	Ll
<i>Haidomyrmex scimitarus</i>	0.2052	0.13	0.414	0.2508	Eg
<i>Haidomyrmex sp5</i>	0.2532	0.0988	0.171	0.477	Ll
<i>Haidomyrmex sp4</i>	0.1976	0.1906	0.4222	0.1896	Eg
<i>Haidomyrmex indet1</i>	0.2514	0.085	0.2622	0.4014	Ll
<i>Haidomyrmex indet2</i>	0.208	0.0832	0.258	0.4508	Ll

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Table S33.

Foraging niche prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; homologous morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0998	0.0466	0.1796	0.1574	0.0518	0.4648	SP
<i>Ceratomyrmex ellenbergeri</i>	0.0318	0.061	0.3106	0.2362	0.08	0.2804	GP
<i>Ceratomyrmex ellenbergeri</i>	0.0848	0.1064	0.322	0.1258	0.0582	0.3028	GP
<i>Ceratomyrmex ellenbergeri</i>	0.046	0.0978	0.3204	0.2192	0.037	0.2796	GP
<i>Protoceratomyrmex revelatus</i>	0.0794	0.0954	0.216	0.289	0.067	0.2532	Om
<i>Linguamyrmex sp5</i>	0.0396	0.0306	0.1186	0.4328	0.0542	0.3242	Om
<i>Linguamyrmex sp4</i>	0.0216	0.0636	0.1878	0.3358	0.0732	0.318	Om
<i>Linguamyrmex brevicornis</i>	0.0844	0.1938	0.194	0.2334	0.0452	0.2492	SP
<i>Linguamyrmex sp2</i>	0.0386	0.1178	0.3982	0.1722	0.0582	0.215	GP
<i>Linguamyrmex sp1</i>	0.0234	0.055	0.2526	0.3058	0.081	0.2822	Om
<i>Haidomyrmex sp3</i>	0.057	0.0388	0.1812	0.1338	0.1736	0.4156	SP
<i>Haidomyrmex sp5</i>	0.1042	0.0644	0.2236	0.1662	0.0912	0.3504	SP
<i>Haidomyrmex sp5</i>	0.0878	0.0904	0.2576	0.1102	0.1004	0.3536	SP
<i>Haidomyrmex sp5</i>	0.0544	0.0852	0.195	0.1636	0.0974	0.4044	SP
<i>Haidomyrmex sp5</i>	0.0322	0.0854	0.2618	0.1664	0.085	0.3692	SP
<i>Haidomyrmex scimitarus</i>	0.0564	0.0386	0.1404	0.3496	0.0724	0.3426	SP
<i>Haidomyrmex sp5</i>	0.0554	0.0408	0.2708	0.1428	0.0882	0.402	SP
<i>Haidomyrmex sp4</i>	0.044	0.0378	0.1976	0.3738	0.0844	0.2624	Om
<i>Haidomyrmex indet1</i>	0.1206	0.0274	0.2576	0.1944	0.1068	0.2932	SP

<i>Haidomyrmex indet2</i>	0.0356	0.113	0.2284	0.1366	0.0994	0.387	SP
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Table S34.

Functional role prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; homologous morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_ egll	pred_l_ eaf	pred_lg_ ab	pred_ll_ eg	pred_s_ ub	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0424	0.135	0.219	0.0462	0.071 8	0.1054	0.2652	0.093	0.0024	0.0196	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.0082	0.2986	0.014 4	0.0644	0.050 8	0.1856	0.3356	0.0094	0.0322	0	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.0492	0.1868	0.091 8	0.0972	0.058 6	0.0274	0.4056	0.0386	0.0272	0.0176	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.0366	0.2668	0.039 2	0.052	0.084 8	0.0512	0.409	0.0092	0.0462	0.005	pred_leaf
<i>Protoceratomyrmex revelatus</i>	0.0812	0.4286	0.073 8	0.0708	0.105	0.0378	0.1346	0.0224	0.0384	0.0074	om_grll_eg
<i>Linguamyrmex sp5</i>	0.0114	0.4306	0.003 6	0.0464	0.016	0.2274	0.224	0.0142	0.026	0	om_grll_eg
<i>Linguamyrmex sp4</i>	0.0122	0.3858	0.006 2	0.051	0.041 4	0.1664	0.2982	0.0082	0.0302	0	om_grll_eg
<i>Linguamyrmex brevicornis</i>	0.0688	0.373	0.195 4	0.0668	0.067 2	0.0338	0.1634	0.0052	0.0162	0.0102	om_grll_eg
<i>Linguamyrmex sp2</i>	0.019	0.1966	0.056 8	0.065	0.089	0.0274	0.517	0.0056	0.0182	0.0054	pred_leaf
<i>Linguamyrmex sp1</i>	0.0102	0.3314	0.009 4	0.0618	0.048 4	0.199	0.295	0.011	0.0332	0	om_grll_eg
<i>Haidomyrmex sp3</i>	0.1096	0.167	0.065 8	0.1542	0.040 6	0.0172	0.2366	0.1888	0.0072	0.013	pred_leaf
<i>Haidomyrmex sp5</i>	0.0464	0.212	0.073 8	0.1242	0.037 8	0.0362	0.2596	0.1398	0.0498	0.0204	pred_leaf

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<i>Haidomyrmex sp5</i>	0.0406	0.163	0.083 6	0.1436	0.083 2	0.0212	0.2748	0.1196	0.0544	0.016	pred_leaf
<i>Haidomyrmex sp5</i>	0.057	0.2198	0.048 6	0.1436	0.068 2	0.0162	0.2008	0.1536	0.067	0.0252	om_grll_eg
<i>Haidomyrmex sp5</i>	0.0332	0.19	0.044	0.1394	0.113 2	0.014	0.2506	0.1464	0.0426	0.0266	pred_leaf
<i>Haidomyrmex scimitarus</i>	0.0154	0.3938	0.008	0.0652	0.040 6	0.2328	0.1854	0.009	0.0492	0	om_grll_eg
<i>Haidomyrmex sp5</i>	0.0706	0.1688	0.065 2	0.1158	0.092 8	0.0496	0.198	0.1944	0.0238	0.021	pred_leaf
<i>Haidomyrmex sp4</i>	0.0254	0.4188	0.004 2	0.0784	0.072 8	0.1626	0.163	0.011	0.0628	0.001	om_grll_eg
<i>Haidomyrmex indet1</i>	0.043	0.2726	0.074 4	0.1262	0.042 2	0.0516	0.1436	0.213	0.022	0.0114	om_grll_eg
<i>Haidomyrmex indet2</i>	0.0324	0.1804	0.048 8	0.1762	0.103 8	0.0574	0.1936	0.0774	0.1062	0.0238	pred_leaf

Table S35.

Ecomorph prediction votes when using model trained on subset of complete morphometrics dataset; linear trait measurements; homologous morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0684	0.6814	0.0074	0.2158	0.027	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0424	0.7562	6.00E-04	0.1998	0.001	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0482	0.704	0.0018	0.2322	0.0138	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0326	0.7176	0.023	0.2146	0.0122	Gr
<i>Protoceratomyrmex revelatus</i>	0.0256	0.6942	0.0226	0.242	0.0156	Gr
<i>Linguamyrmex sp5</i>	0.0252	0.6544	0.002	0.3162	0.0022	Gr
<i>Linguamyrmex sp4</i>	0.0212	0.6548	0.0044	0.3188	0	Gr
<i>Linguamyrmex brevicornis</i>	0.2636	0.2216	0.0608	0.4474	0.0066	Ll
<i>Linguamyrmex sp2</i>	0.0634	0.6044	0.0108	0.3094	0.012	Gr
<i>Linguamyrmex sp1</i>	0.0434	0.7008	0.0024	0.239	0.0144	Gr
<i>Haidomyrmex sp3</i>	0.0206	0.1626	0.5006	0.2918	0.0244	Lg
<i>Haidomyrmex sp5</i>	0.004	0.548	0.0458	0.4	0.0022	Gr
<i>Haidomyrmex sp5</i>	0.0116	0.8092	0.0194	0.1556	0.0042	Gr
<i>Haidomyrmex sp5</i>	0.0022	0.743	0.0856	0.1658	0.0034	Gr
<i>Haidomyrmex sp5</i>	0.0304	0.3702	0.258	0.32	0.0214	Gr
<i>Haidomyrmex scimitarus</i>	0.055	0.7134	0.0088	0.2052	0.0176	Gr
<i>Haidomyrmex sp5</i>	0.0026	0.5238	0.2264	0.2288	0.0184	Gr
<i>Haidomyrmex sp4</i>	0.0066	0.707	0.0744	0.2032	0.0088	Gr

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<i>Haidomyrmex indet1</i>	0.0022	0.7738	0.0692	0.1506	0.0042	Gr
<i>Haidomyrmex indet2</i>	0.003	0.5718	0.1326	0.2886	0.004	Gr

Table S36.

Nesting niche prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; functional morphology.

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Ceratomyrmex planus</i>	0.1752	0.0844	0.5354	0.205	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.1584	0.0032	0.59	0.2484	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.1658	0.0132	0.5646	0.2564	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.11	0.0826	0.5422	0.2652	Eg
<i>Protoceratomyrmex revelatus</i>	0.2024	0.0676	0.6052	0.1248	Eg
<i>Linguamyrmex sp5</i>	0.1838	0.0022	0.4504	0.3636	Eg
<i>Linguamyrmex sp4</i>	0.1978	0.002	0.5542	0.246	Eg
<i>Linguamyrmex brevicornis</i>	0.403	0.0424	0.2646	0.29	Ab
<i>Linguamyrmex sp2</i>	0.2446	0.0182	0.502	0.2352	Eg
<i>Linguamyrmex sp1</i>	0.2264	0.0142	0.4928	0.2666	Eg
<i>Haidomyrmex sp3</i>	0.3572	0.2008	0.2432	0.1988	Ab
<i>Haidomyrmex sp5</i>	0.1086	0.0674	0.5246	0.2994	Eg
<i>Haidomyrmex sp5</i>	0.1166	0.0642	0.6328	0.1864	Eg
<i>Haidomyrmex sp5</i>	0.1594	0.0844	0.5338	0.2224	Eg
<i>Haidomyrmex sp5</i>	0.2292	0.162	0.4284	0.1804	Eg
<i>Haidomyrmex scimitarus</i>	0.165	0.0598	0.5762	0.199	Eg
<i>Haidomyrmex sp5</i>	0.1918	0.0992	0.4758	0.2332	Eg

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<i>Haidomyrmex sp4</i>	0.1104	0.0872	0.584	0.2184	Eg
<i>Haidomyrmex indet1</i>	0.0934	0.057	0.6406	0.209	Eg
<i>Haidomyrmex indet2</i>	0.1078	0.0872	0.5662	0.2388	Eg

Table S37.

Foraging niche prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; functional morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0434	0.1026	0.1652	0.4172	2.00E-04	0.2714	Om
<i>Ceratomyrmex ellenbergeri</i>	0.1128	0.0178	0.5196	0.2742	0	0.075	GP
<i>Ceratomyrmex ellenbergeri</i>	0.0924	0.0332	0.4498	0.283	0.001	0.1406	GP
<i>Ceratomyrmex ellenbergeri</i>	0.066	0.0764	0.4536	0.2248	0.0022	0.177	GP
<i>Protoceratomyrmex revelatus</i>	0.0106	0.0128	0.1504	0.2706	0.001	0.5546	SP
<i>Linguamyrmex sp5</i>	0.0942	0.0364	0.3288	0.4298	0	0.1106	Om
<i>Linguamyrmex sp4</i>	0.0596	0.0104	0.2864	0.4004	0	0.243	Om
<i>Linguamyrmex brevicornis</i>	0.0314	0.024	0.1766	0.3368	0.0014	0.4298	SP
<i>Linguamyrmex sp2</i>	0.1124	0.0122	0.336	0.34	0	0.1994	Om
<i>Linguamyrmex sp1</i>	0.0606	0.0218	0.4288	0.331	0	0.1578	GP
<i>Haidomyrmex sp3</i>	0.009	8.00E-04	0.3848	0.101	0.0618	0.4426	SP
<i>Haidomyrmex sp5</i>	0.0032	0.0014	0.6024	0.1608	0.0156	0.2166	GP
<i>Haidomyrmex sp5</i>	0.0036	2.00E-04	0.7118	0.1194	0.0092	0.1558	GP
<i>Haidomyrmex sp5</i>	0.0038	0.0296	0.5182	0.1168	0.0202	0.3114	GP
<i>Haidomyrmex sp5</i>	0.0934	0.0184	0.4184	0.1162	0.0288	0.3248	GP
<i>Haidomyrmex scimitarus</i>	0.0352	0.0128	0.428	0.2884	0.0012	0.2344	GP

<i>Haidomyrmex sp5</i>	0.0064	0.0106	0.3556	0.094	0.0446	0.4888	SP
<i>Haidomyrmex sp4</i>	0.003	0.035	0.522	0.1148	0.0182	0.307	GP
<i>Haidomyrmex indet1</i>	0.002	0.0092	0.6058	0.0974	0.0182	0.2674	GP
<i>Haidomyrmex indet2</i>	0.0038	0.0374	0.2948	0.1204	0.0324	0.5112	SP

Table S38.

Functional role prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; functional morphology.

Species	om_cn_ ab	om_grll_ eg	om_le af	om_lg_ ab	pred_ cr	pred_gr_ egll	pred_l eaf	pred_lg_ ab	pred_ll_ eg	pred_s ub	Predicted aspect
<i>Ceratomyrmex planus</i>	0.055	0.328	0.110 2	0	0.029 2	0.3218	0.1372	0.0062	0.0116	0	om_grll_eg
<i>Ceratomyrmex ellenbergeri</i>	0.063	0.2064	0.046 6	0	0.002 8	0.5138	0.1148	0	0.0522	0	pred_gr_egll
<i>Ceratomyrmex ellenbergeri</i>	0.059	0.216	0.060 6	0	0.014 2	0.3868	0.2192	0.001	0.0428	0	pred_gr_egll
<i>Ceratomyrmex ellenbergeri</i>	0.02	0.2284	0.027 2	0.0028	0.02	0.549	0.1062	0.009	0.0364	0.001	pred_gr_egll
<i>Protoceratomyrmex revelatus</i>	0.0142	0.2096	0.004	0.0026	0.014 6	0.5278	0.0854	0.0326	0.1084	0	pred_gr_egll
<i>Linguamyrmex sp5</i>	0.0452	0.3486	0.061	0	0.001 2	0.238	0.272	0.0036	0.0304	0	om_grll_eg
<i>Linguamyrmex sp4</i>	0.0426	0.2928	0.030 6	0	0.001	0.32	0.2546	0.0018	0.0566	0	pred_gr_egll
<i>Linguamyrmex brevicornis</i>	0.1488	0.1564	0.017 2	0.0018	0.019 6	0.2324	0.3284	0.0674	0.0274	0	pred_leaf
<i>Linguamyrmex sp2</i>	0.0688	0.2716	0.032	0	0.013 6	0.3018	0.2594	0.0064	0.0456	0	pred_gr_egll
<i>Linguamyrmex sp1</i>	0.0508	0.2064	0.032 6	0	0.011	0.3674	0.283	0.001	0.0472	0	pred_gr_egll
<i>Haidomyrmex sp3</i>	0.0154	0.0296	0.001	0.088	0.024	0.147	0.1572	0.4262	0.1048	0.0068	pred_lg_ab

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<i>Haidomyrmex sp5</i>	0.0038	0.1488	0.003 4	0.0074	0.004 6	0.5314	0.1946	0.0162	0.0892	0	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.0078	0.0982	0.001 2	0.003	0.006	0.6876	0.0702	0.0122	0.1134	0	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.0016	0.1446	0.002	0.0246	0.007 6	0.5886	0.1084	0.044	0.0768	0.0018	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.0298	0.111	0.022 2	0.0962	0.043 4	0.2588	0.1262	0.1654	0.141	0.006	pred_gr_egll
<i>Haidomyrmex scimitarus</i>	0.0334	0.1938	0.017 2	0.0014	0.02	0.4756	0.208	0.0042	0.046	0	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.002	0.0712	0	0.1434	0.008 6	0.3544	0.1126	0.1754	0.1244	0.008	pred_gr_egll
<i>Haidomyrmex sp4</i>	0.0062	0.1108	0.001	0.0096	0.022	0.6138	0.0988	0.0278	0.109	0.001	pred_gr_egll
<i>Haidomyrmex indet1</i>	0.0014	0.084	0	0.0096	0.011 8	0.7518	0.084	0.0246	0.0304	0.0022	pred_gr_egll
<i>Haidomyrmex indet2</i>	0.002	0.095	0.003 6	0.0882	0.015 6	0.431	0.1304	0.1152	0.1168	0.0022	pred_gr_egll

Table S39.

Ecomorph prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; functional morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0392	0.5364	0.0298	0.3762	0.0184	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0236	0.8092	0.0024	0.1628	0.002	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.024	0.7864	0.0026	0.176	0.011	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0238	0.6812	0.0424	0.2208	0.0318	Gr
<i>Protoceratomyrmex revelatus</i>	0.0202	0.7678	0.0176	0.1806	0.0138	Gr
<i>Linguamyrmex sp5</i>	0.0102	0.7622	0.002	0.2246	0.001	Gr
<i>Linguamyrmex sp4</i>	0.0062	0.7626	0.0038	0.2252	0.0022	Gr
<i>Linguamyrmex brevicornis</i>	0.2566	0.2498	0.0588	0.4286	0.0062	Ll
<i>Linguamyrmex sp2</i>	0.048	0.6416	0.0176	0.2768	0.016	Gr
<i>Linguamyrmex sp1</i>	0.0272	0.7662	0.0028	0.187	0.0168	Gr
<i>Haidomyrmex sp3</i>	0.013	0.1366	0.5272	0.2864	0.0368	Lg
<i>Haidomyrmex sp5</i>	0.0052	0.4744	0.0716	0.4432	0.0056	Gr
<i>Haidomyrmex sp5</i>	0.0084	0.7316	0.0324	0.2228	0.0048	Gr
<i>Haidomyrmex sp5</i>	0.004	0.655	0.1158	0.202	0.0232	Gr
<i>Haidomyrmex sp5</i>	0.0328	0.2728	0.3176	0.341	0.0358	Ll
<i>Haidomyrmex scimitarus</i>	0.0308	0.7934	0.01	0.1502	0.0156	Gr
<i>Haidomyrmex sp5</i>	0.0024	0.4766	0.2318	0.2524	0.0368	Gr

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<i>Haidomyrmex sp4</i>	0.008	0.6384	0.094	0.2388	0.0208	Gr
<i>Haidomyrmex indet1</i>	0.0034	0.6742	0.0928	0.2118	0.0178	Gr
<i>Haidomyrmex indet2</i>	0.0022	0.5782	0.149	0.2532	0.0174	Gr

Table S40.

Nesting niche prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; homologous morphology.

Species	Ab	CR	Eg	LI	Predicted aspect
<i>Ceratomyrmex planus</i>	0.099	0.0394	0.5154	0.3462	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.151	0.004	0.6054	0.2396	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.0936	0.01	0.6584	0.238	Eg
<i>Ceratomyrmex ellenbergeri</i>	0.1374	0.0996	0.5312	0.2318	Eg
<i>Protoceratomyrmex revelatus</i>	0.1694	0.0638	0.6568	0.11	Eg
<i>Linguamyrmex sp5</i>	0.1136	0.0012	0.5652	0.32	Eg
<i>Linguamyrmex sp4</i>	0.1068	0.0036	0.6584	0.2312	Eg
<i>Linguamyrmex brevicornis</i>	0.3652	0.0286	0.3038	0.3024	Ab
<i>Linguamyrmex sp2</i>	0.177	0.0234	0.5522	0.2474	Eg
<i>Linguamyrmex sp1</i>	0.2352	0.014	0.5354	0.2154	Eg
<i>Haidomyrmex sp3</i>	0.4392	0.183	0.1976	0.1802	Ab
<i>Haidomyrmex sp5</i>	0.1836	0.0676	0.4668	0.282	Eg
<i>Haidomyrmex sp5</i>	0.1196	0.0638	0.611	0.2056	Eg
<i>Haidomyrmex sp5</i>	0.2378	0.079	0.4984	0.1848	Eg
<i>Haidomyrmex sp5</i>	0.31	0.2054	0.3108	0.1738	Eg
<i>Haidomyrmex scimitarus</i>	0.0926	0.0464	0.6744	0.1866	Eg

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<i>Haidomyrmex sp5</i>	0.2252	0.0598	0.4966	0.2184	Eg
<i>Haidomyrmex sp4</i>	0.1356	0.0852	0.5698	0.2094	Eg
<i>Haidomyrmex indet1</i>	0.1418	0.0776	0.5776	0.203	Eg
<i>Haidomyrmex indet2</i>	0.1302	0.0806	0.5828	0.2064	Eg

Table S41.

Foraging niche prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; homologous morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0398	0.1744	0.1106	0.2534	0.0066	0.4152	SP
<i>Ceratomyrmex ellenbergeri</i>	0.036	0.0692	0.2244	0.432	0.0066	0.2318	Om
<i>Ceratomyrmex ellenbergeri</i>	0.035	0.0788	0.2684	0.32	0	0.2976	Om
<i>Ceratomyrmex ellenbergeri</i>	0.0192	0.1224	0.1888	0.3344	0.0098	0.3254	Om
<i>Protoceratomyrmex revelatus</i>	0.0102	0.0098	0.1038	0.3094	0.0104	0.5564	SP
<i>Linguamyrmex sp5</i>	0.0436	0.0836	0.2366	0.4418	0.0068	0.1876	Om
<i>Linguamyrmex sp4</i>	0.0288	0.0316	0.1772	0.3616	0.0072	0.3936	SP
<i>Linguamyrmex brevicornis</i>	0.0306	0.0304	0.1222	0.2642	0.0108	0.5418	SP
<i>Linguamyrmex sp2</i>	0.0474	0.0388	0.194	0.322	0.0074	0.3904	SP
<i>Linguamyrmex sp1</i>	0.0226	0.0386	0.236	0.4348	0.0076	0.2604	Om
<i>Haidomyrmex sp3</i>	0.0024	0.001	0.2646	0.1186	0.0788	0.5346	SP
<i>Haidomyrmex sp5</i>	0.0018	0.0062	0.3228	0.295	0.0144	0.3598	SP
<i>Haidomyrmex sp5</i>	0.0026	0.0036	0.3648	0.233	0.0166	0.3794	SP
<i>Haidomyrmex sp5</i>	0	0.0362	0.2278	0.2348	0.0382	0.4622	SP
<i>Haidomyrmex sp5</i>	0.0178	0.0274	0.2834	0.1914	0.0402	0.4398	SP

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<i>Haidomyrmex scimitarus</i>	0.0136	0.0302	0.2974	0.316	0.0084	0.3344	SP
<i>Haidomyrmex sp5</i>	0	0.0166	0.1994	0.091	0.075	0.618	SP
<i>Haidomyrmex sp4</i>	0.0024	0.0464	0.2456	0.1742	0.054	0.4774	SP
<i>Haidomyrmex indet1</i>	0	0.0136	0.3086	0.2266	0.0214	0.4292	SP
<i>Haidomyrmex indet2</i>	0.003	0.044	0.195	0.139	0.0464	0.5726	SP

Table S42.

Functional role prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; homologous morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_ egll	pred_l_ eaf	pred_lg_ ab	pred_ll_ eg	pred_s_ ub	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0384	0.2122	0.167	0.0048	0.015 6	0.3348	0.1734	0.037	0.0086	0.0082	pred_gr_egll
<i>Ceratomyrmex ellenbergeri</i>	0.065	0.33	0.092 8	0	0.011 8	0.3258	0.159	0.0016	0.013	0	om_grll_eg
<i>Ceratomyrmex ellenbergeri</i>	0.042	0.275	0.091 8	0	0.018 8	0.4	0.1646	0.0022	0.005	0	pred_gr_egll
<i>Ceratomyrmex ellenbergeri</i>	0.0268	0.3134	0.068 2	0.005	0.043 6	0.3316	0.1656	0.018	0.0242	0.0036	pred_gr_egll
<i>Protoceratomyrmex revelatus</i>	0.0134	0.2224	0.003	0.003	0.012	0.5712	0.053	0.0196	0.102	0	pred_gr_egll
<i>Linguamyrmex sp5</i>	0.0264	0.3414	0.082 4	0	0.004	0.2906	0.2442	0.0048	0.0058	0	om_grll_eg
<i>Linguamyrmex sp4</i>	0.021	0.3078	0.036 2	0	0.007 4	0.387	0.2282	0.0038	0.0078	0	pred_gr_egll
<i>Linguamyrmex brevicornis</i>	0.1364	0.1412	0.02	0.0016	0.015 4	0.2688	0.3134	0.0702	0.0324	0	pred_leaf
<i>Linguamyrmex sp2</i>	0.0464	0.2742	0.039 6	0.0012	0.026 2	0.344	0.2514	0.01	0.0064	0	pred_gr_egll
<i>Linguamyrmex sp1</i>	0.0456	0.312	0.050 2	0.0016	0.021	0.338	0.2114	0.0028	0.0172	0	pred_gr_egll

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<i>Haidomyrmex sp3</i>	0.0076	0.0364	0	0.0766	0.0324	0.1066	0.1654	0.5032	0.0552	0.0158	pred_lg_ab
<i>Haidomyrmex sp5</i>	0.0122	0.2678	0.0028	0.0114	0.0102	0.3234	0.2796	0.0332	0.0586	0	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.0046	0.209	0.0018	0.0068	0.013	0.5734	0.1688	0.0108	0.0102	0.0016	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.008	0.2518	0	0.0352	0.02	0.3826	0.1464	0.0668	0.082	0.0068	pred_gr_egll
<i>Haidomyrmex sp5</i>	0.0284	0.1194	0.0216	0.0964	0.0712	0.1498	0.1526	0.2766	0.072	0.012	pred_lg_ab
<i>Haidomyrmex scimitarus</i>	0.0258	0.2276	0.0248	0.002	0.0206	0.5198	0.1688	0.0052	0.005	0	pred_gr_egll
<i>Haidomyrmex sp5</i>	0	0.0894	0	0.122	0.0102	0.3502	0.104	0.1666	0.1328	0.0236	pred_gr_egll
<i>Haidomyrmex sp4</i>	0.0102	0.1858	0.0022	0.016	0.0342	0.4946	0.1404	0.0396	0.0736	0.0034	pred_gr_egll
<i>Haidomyrmex indet1</i>	0.0036	0.2082	0	0.018	0.0268	0.5342	0.1424	0.0396	0.0224	0.0044	pred_gr_egll
<i>Haidomyrmex indet2</i>	0	0.1146	0.0048	0.0846	0.0274	0.426	0.1068	0.148	0.081	0.006	pred_gr_egll

Table S43.

Ecomorph prediction votes when using model trained on subset of complete morphometrics dataset; shape ratio trait measurements; homologous morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0934	0.4272	0.0378	0.3904	0.0512	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.099	0.506	0.0084	0.3752	0.0114	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0666	0.4758	0.0116	0.428	0.018	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.058	0.5162	0.0504	0.3572	0.0182	Gr
<i>Protoceratomyrmex revelatus</i>	0.0644	0.3684	0.0812	0.4566	0.0294	Ll
<i>Linguamyrmex sp5</i>	0.0324	0.4826	0.006	0.4702	0.0088	Gr
<i>Linguamyrmex sp4</i>	0.0366	0.4748	0.0128	0.4688	0.007	Gr
<i>Linguamyrmex brevicornis</i>	0.1668	0.1614	0.0912	0.5662	0.0144	Ll
<i>Linguamyrmex sp2</i>	0.0764	0.466	0.0174	0.4264	0.0138	Gr
<i>Linguamyrmex sp1</i>	0.0572	0.4728	0.0146	0.438	0.0174	Gr
<i>Haidomyrmex sp3</i>	0.019	0.17	0.4544	0.323	0.0336	Lg
<i>Haidomyrmex sp5</i>	0.024	0.4822	0.0516	0.4348	0.0074	Gr
<i>Haidomyrmex sp5</i>	0.0362	0.4968	0.0372	0.4196	0.0102	Gr
<i>Haidomyrmex sp5</i>	0.0224	0.4752	0.1224	0.3714	0.0086	Gr
<i>Haidomyrmex sp5</i>	0.0388	0.2972	0.2782	0.3556	0.0302	Ll
<i>Haidomyrmex scimitarus</i>	0.063	0.4644	0.0406	0.4016	0.0304	Gr
<i>Haidomyrmex sp5</i>	0.0114	0.4092	0.2424	0.3072	0.0298	Gr

<i>Haidomyrmex sp4</i>	0.0294	0.462	0.1	0.397	0.0116	Gr
<i>Haidomyrmex indet1</i>	0.0254	0.4692	0.0872	0.4104	0.0078	Gr
<i>Haidomyrmex indet2</i>	0.0196	0.414	0.1536	0.4066	0.0062	Gr

Table S44.

Nesting niche prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; functional morphology.

Species	Ab	CR	Eg	Ll	Predicted aspect
<i>Ceratomyrmex planus</i>	0.1734	0.0744	0.2814	0.4708	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.1654	0.018	0.3412	0.4754	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.1154	0.0274	0.371	0.4862	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.1242	0.0908	0.3442	0.4408	Ll
<i>Protoceratomyrmex revelatus</i>	0.1476	0.0512	0.3506	0.4506	Ll
<i>Linguamyrmex sp5</i>	0.055	0.012	0.33	0.603	Ll
<i>Linguamyrmex sp4</i>	0.08	0.0168	0.3772	0.526	Ll
<i>Linguamyrmex brevicornis</i>	0.2284	0.0568	0.1408	0.574	Ll
<i>Linguamyrmex sp2</i>	0.1228	0.038	0.3622	0.477	Ll
<i>Linguamyrmex sp1</i>	0.1184	0.0254	0.3564	0.4998	Ll
<i>Haidomyrmex sp3</i>	0.3172	0.2226	0.1234	0.3368	Ll
<i>Haidomyrmex sp5</i>	0.1	0.0884	0.3318	0.4798	Ll
<i>Haidomyrmex sp5</i>	0.1158	0.0856	0.366	0.4326	Ll
<i>Haidomyrmex sp5</i>	0.1338	0.1186	0.2666	0.481	Ll
<i>Haidomyrmex sp5</i>	0.2274	0.1792	0.2126	0.3808	Ll
<i>Haidomyrmex scimitarus</i>	0.1154	0.0564	0.3712	0.457	Ll
<i>Haidomyrmex sp5</i>	0.1728	0.1386	0.2284	0.4602	Ll

Ecological breadth of the earliest ants

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<i>Haidomyrmex sp4</i>	0.1216	0.1048	0.33	0.4436	Ll
<i>Haidomyrmex indet1</i>	0.1166	0.0936	0.3088	0.481	Ll
<i>Haidomyrmex indet2</i>	0.1326	0.1128	0.3008	0.4538	Ll

Table S45.

Foraging niche prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; functional morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Ceratomyrmex planus</i>	0.048	0.1128	0.1886	0.3946	0	0.256	Om
<i>Ceratomyrmex ellenbergeri</i>	0.132	0.0242	0.4678	0.2874	0.001	0.0876	GP
<i>Ceratomyrmex ellenbergeri</i>	0.089	0.0388	0.4276	0.3064	0.001	0.1372	GP
<i>Ceratomyrmex ellenbergeri</i>	0.09	0.0678	0.4188	0.2426	0.0026	0.1782	GP
<i>Protoceratomyrmex revelatus</i>	0.0176	0.017	0.1616	0.3042	0.0022	0.4974	SP
<i>Linguamyrmex sp5</i>	0.0878	0.0592	0.318	0.423	2.00E-04	0.1118	Om
<i>Linguamyrmex sp4</i>	0.0688	0.0196	0.2792	0.4124	8.00E-04	0.2192	Om
<i>Linguamyrmex brevicornis</i>	0.037	0.0358	0.1808	0.3312	0.002	0.4132	SP
<i>Linguamyrmex sp2</i>	0.1198	0.0192	0.3082	0.3652	0.001	0.1866	Om
<i>Linguamyrmex sp1</i>	0.0666	0.0274	0.3956	0.3476	0.0014	0.1614	GP
<i>Haidomyrmex sp3</i>	0.012	0.0012	0.4136	0.1192	0.0708	0.3832	GP
<i>Haidomyrmex sp5</i>	0.0158	0.0018	0.5512	0.2036	0.0124	0.2152	GP
<i>Haidomyrmex sp5</i>	0.02	0.001	0.6432	0.1574	0.0078	0.1706	GP
<i>Haidomyrmex sp5</i>	0.0088	0.0244	0.5178	0.1464	0.029	0.2736	GP
<i>Haidomyrmex sp5</i>	0.0942	0.0186	0.4072	0.1458	0.0346	0.2996	GP
<i>Haidomyrmex scimitarus</i>	0.0326	0.0216	0.428	0.2988	0.0028	0.2162	GP

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<i>Haidomyrmex sp5</i>	0.009	0.0102	0.409	0.1138	0.0532	0.4048	GP
<i>Haidomyrmex sp4</i>	0.0114	0.0294	0.5126	0.148	0.0192	0.2794	GP
<i>Haidomyrmex indet1</i>	0.0094	0.0112	0.5726	0.1398	0.0168	0.2502	GP
<i>Haidomyrmex indet2</i>	0.0046	0.0336	0.342	0.1354	0.0408	0.4436	SP

Table S46.

Functional role prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; functional morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_ egll	pred_l_ eaf	pred_lg_ ab	pred_ll_ eg	pred_s_ ub	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0888	0.321	0.150 6	6.00E- 04	0.029 6	0.1382	0.2322	0.03	0.0088	2.00E- 04	om_grll_eg
<i>Ceratomyrmex ellenbergeri</i>	0.0802	0.261	0.101	0.0032	0.012 4	0.2796	0.198	0.0098	0.0548	0	pred_gr_egll
<i>Ceratomyrmex ellenbergeri</i>	0.0906	0.2436	0.126 2	6.00E- 04	0.017	0.1904	0.2918	0.0128	0.027	0	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.048	0.2664	0.070 8	0.0114	0.026 8	0.2836	0.2234	0.032	0.0376	0	pred_gr_egll
<i>Protoceratomyrmex revelatus</i>	0.049	0.2998	0.029 6	0.0046	0.018 2	0.1426	0.3026	0.0886	0.0646	4.00E- 04	pred_leaf
<i>Linguamyrmex sp5</i>	0.068	0.2888	0.153	0	0.004 4	0.131	0.3354	0.0064	0.013	0	pred_leaf
<i>Linguamyrmex sp4</i>	0.0674	0.2842	0.118 4	4.00E- 04	0.006	0.1452	0.3466	0.0118	0.0198	2.00E- 04	pred_leaf
<i>Linguamyrmex brevicornis</i>	0.1492	0.1262	0.045 2	0.0024	0.016 4	0.065	0.483	0.0832	0.0292	2.00E- 04	pred_leaf
<i>Linguamyrmex sp2</i>	0.0918	0.2704	0.105 2	8.00E- 04	0.019 8	0.1434	0.3318	0.0182	0.0184	2.00E- 04	pred_leaf
<i>Linguamyrmex sp1</i>	0.0832	0.2314	0.097	0.001	0.016 2	0.1732	0.3564	0.0144	0.0272	0	pred_leaf
<i>Haidomyrmex sp3</i>	0.0166	0.0496	0.004 2	0.1486	0.017 8	0.0474	0.2848	0.383	0.0428	0.0052	pred_lg_ab

<i>Haidomyrmex sp5</i>	0.02	0.222	0.024 8	0.015	0.014	0.2062	0.3946	0.0338	0.0694	2.00E- 04	pred_leaf
<i>Haidomyrmex sp5</i>	0.0218	0.2072	0.023 4	0.0104	0.016 8	0.2662	0.3408	0.0362	0.0772	0	pred_leaf
<i>Haidomyrmex sp5</i>	0.0152	0.1692	0.019 2	0.0602	0.015 4	0.2122	0.3526	0.0756	0.0794	0.001	pred_leaf
<i>Haidomyrmex sp5</i>	0.0362	0.1434	0.047 4	0.1438	0.033 6	0.0942	0.2466	0.1788	0.0718	0.0042	pred_leaf
<i>Haidomyrmex scimitarus</i>	0.0664	0.223	0.080 4	0.0032	0.024	0.216	0.3364	0.0248	0.0256	2.00E- 04	pred_leaf
<i>Haidomyrmex sp5</i>	0.0062	0.0916	0.004 2	0.219	0.009 4	0.114	0.2782	0.1802	0.0864	0.0108	pred_leaf
<i>Haidomyrmex sp4</i>	0.0192	0.1936	0.02	0.0242	0.026 2	0.2316	0.3518	0.055	0.0784	0	pred_leaf
<i>Haidomyrmex indet1</i>	0.0156	0.1758	0.016 2	0.0238	0.020 6	0.267	0.3672	0.0548	0.058	0.001	pred_leaf
<i>Haidomyrmex indet2</i>	0.0134	0.1458	0.011 6	0.1266	0.015 8	0.119	0.3458	0.1424	0.0794	2.00E- 04	pred_leaf

Table S47.

Ecomorph prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; functional morphology.

Species	Cn	Gr	Lg	Ll	Sb	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0826	0.3726	0.049	0.4512	0.0446	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.0784	0.4816	0.0228	0.3806	0.0366	Gr
<i>Ceratomyrmex ellenbergeri</i>	0.0618	0.3738	0.0342	0.488	0.0422	Ll
<i>Ceratomyrmex ellenbergeri</i>	0.0442	0.4592	0.0816	0.3652	0.0498	Gr
<i>Protoceratomyrmex revelatus</i>	0.058	0.4034	0.0646	0.4356	0.0384	Ll
<i>Linguatomyrmex sp5</i>	0.0356	0.4168	0.0062	0.5208	0.0206	Ll
<i>Linguatomyrmex sp4</i>	0.0402	0.378	0.017	0.538	0.0268	Ll
<i>Linguatomyrmex brevicornis</i>	0.1576	0.1788	0.094	0.546	0.0236	Ll
<i>Linguatomyrmex sp2</i>	0.07	0.3254	0.0278	0.5388	0.038	Ll
<i>Linguatomyrmex sp1</i>	0.0532	0.4182	0.0364	0.4416	0.0506	Ll
<i>Haidomyrmex sp3</i>	0.0136	0.1222	0.4748	0.3456	0.0438	Lg
<i>Haidomyrmex sp5</i>	0.0236	0.408	0.08	0.4736	0.0148	Ll
<i>Haidomyrmex sp5</i>	0.0402	0.3582	0.0678	0.5082	0.0256	Ll
<i>Haidomyrmex sp5</i>	0.0212	0.3798	0.1676	0.396	0.0354	Ll
<i>Haidomyrmex sp5</i>	0.037	0.1992	0.317	0.3978	0.049	Ll
<i>Haidomyrmex scimitarus</i>	0.0628	0.375	0.045	0.4716	0.0456	Ll
<i>Haidomyrmex sp5</i>	0.0142	0.3124	0.2436	0.365	0.0648	Ll
<i>Haidomyrmex sp4</i>	0.0262	0.3586	0.142	0.4406	0.0326	Ll

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<i>Haidomyrmex indet1</i>	0.0268	0.3394	0.13	0.4684	0.0354	L1
<i>Haidomyrmex indet2</i>	0.0186	0.3626	0.162	0.4262	0.0306	L1

Table S48.

Nesting niche prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; homologous morphology.

Species	Ab	CR	Eg	L1	Predicted aspect
<i>Ceratomyrmex planus</i>	0.1662	0.0568	0.2846	0.4924	L1
<i>Ceratomyrmex ellenbergeri</i>	0.1582	0.031	0.3118	0.499	L1
<i>Ceratomyrmex ellenbergeri</i>	0.1248	0.0416	0.3102	0.5234	L1
<i>Ceratomyrmex ellenbergeri</i>	0.1452	0.1064	0.29	0.4584	L1
<i>Protoceratomyrmex revelatus</i>	0.135	0.069	0.3774	0.4186	L1
<i>Linguamyrmex sp5</i>	0.0552	0.0238	0.317	0.604	L1
<i>Linguamyrmex sp4</i>	0.0862	0.0284	0.3164	0.569	L1
<i>Linguamyrmex brevicornis</i>	0.2326	0.0652	0.1356	0.5666	L1
<i>Linguamyrmex sp2</i>	0.1406	0.0558	0.2954	0.5082	L1
<i>Linguamyrmex sp1</i>	0.1288	0.0486	0.3258	0.4968	L1
<i>Haidomyrmex sp3</i>	0.3742	0.218	0.1058	0.302	Ab
<i>Haidomyrmex sp5</i>	0.1432	0.086	0.297	0.4738	L1
<i>Haidomyrmex sp5</i>	0.1374	0.0982	0.3052	0.4592	L1
<i>Haidomyrmex sp5</i>	0.1838	0.125	0.2616	0.4296	L1
<i>Haidomyrmex sp5</i>	0.294	0.199	0.1668	0.3402	L1
<i>Haidomyrmex scimitarus</i>	0.1294	0.0678	0.326	0.4768	L1
<i>Haidomyrmex sp5</i>	0.207	0.118	0.2002	0.4748	L1
<i>Haidomyrmex sp4</i>	0.155	0.1198	0.2902	0.435	L1

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<i>Haidomyrmex indet1</i>	0.1522	0.1192	0.2776	0.451	L1
<i>Haidomyrmex indet2</i>	0.1544	0.1236	0.2832	0.4388	L1

Table S49.

Foraging niche prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; homologous morphology.

Species	Fg	Gn	GP	Om	Py	SP	Predicted aspect
<i>Ceratomyrmex planus</i>	0.0526	0.1876	0.1334	0.2536	0.0062	0.3666	SP
<i>Ceratomyrmex ellenbergeri</i>	0.0434	0.0884	0.237	0.4156	0.0074	0.2082	Om
<i>Ceratomyrmex ellenbergeri</i>	0.0424	0.0982	0.2884	0.3152	0.0014	0.2544	Om
<i>Ceratomyrmex ellenbergeri</i>	0.033	0.1188	0.2166	0.317	0.009	0.3056	Om
<i>Protoceratomyrmex revelatus</i>	0.022	0.0202	0.1314	0.3288	0.0114	0.4862	SP
<i>Linguamyrmex sp5</i>	0.0532	0.1232	0.247	0.387	0.007	0.1826	Om
<i>Linguamyrmex sp4</i>	0.0408	0.0478	0.2056	0.3484	0.0066	0.3508	SP
<i>Linguamyrmex brevicornis</i>	0.032	0.049	0.1414	0.2564	0.0112	0.51	SP
<i>Linguamyrmex sp2</i>	0.0582	0.0512	0.2278	0.324	0.0072	0.3316	SP
<i>Linguamyrmex sp1</i>	0.0362	0.0588	0.2594	0.405	0.0076	0.233	Om
<i>Haidomyrmex sp3</i>	0.0036	0.0042	0.324	0.1058	0.101	0.4614	SP
<i>Haidomyrmex sp5</i>	0.003	0.0082	0.3546	0.2944	0.0206	0.3192	GP
<i>Haidomyrmex sp5</i>	0.0056	0.0062	0.4012	0.2294	0.0212	0.3364	GP
<i>Haidomyrmex sp5</i>	0.0026	0.0298	0.2894	0.219	0.0462	0.413	SP
<i>Haidomyrmex sp5</i>	0.0186	0.0334	0.3224	0.1716	0.0522	0.4018	SP
<i>Haidomyrmex scimitarus</i>	0.0236	0.0414	0.32	0.313	0.0082	0.2938	GP
<i>Haidomyrmex sp5</i>	0.0016	0.016	0.2758	0.1076	0.0928	0.5062	SP
<i>Haidomyrmex sp4</i>	0.0052	0.0418	0.3006	0.164	0.0578	0.4306	SP

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<i>Haidomyrmex indet1</i>	0.0016	0.013	0.3696	0.2216	0.03	0.3642	GP
<i>Haidomyrmex indet2</i>	0.0036	0.0402	0.255	0.1484	0.0568	0.496	SP

Table S50.

Functional role prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; homologous morphology.

Species	om_cn_ ab	om_grll_ eg	om_le_ af	om_lg_ ab	pred_ cr	pred_gr_ egll	pred_l_ eaf	pred_lg_ ab	pred_ll_ eg	pred_s_ ub	Predicted aspect
<i>Ceratomyrmex planus</i>	0.062	0.2386	0.182 2	0.0032	0.019 4	0.1806	0.2468	0.0564	0.0058	0.005	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.0832	0.3168	0.150 6	0.0024	0.018 2	0.159	0.2412	0.0138	0.013	0.0018	om_grll_eg
<i>Ceratomyrmex ellenbergeri</i>	0.075	0.256	0.169 4	0.0016	0.025 8	0.1868	0.2578	0.0156	0.0102	0.0018	pred_leaf
<i>Ceratomyrmex ellenbergeri</i>	0.0556	0.2986	0.112	0.0048	0.038 2	0.1558	0.2606	0.0502	0.0188	0.0054	om_grll_eg
<i>Protoceratomyrmex revelatus</i>	0.052	0.3228	0.030 6	0.005	0.020 4	0.1462	0.2766	0.0724	0.0696	0.0044	om_grll_eg
<i>Linguamyrmex sp5</i>	0.0506	0.2688	0.176 2	4.00E- 04	0.005 2	0.1628	0.324	0.0078	0.0026	0.0016	pred_leaf
<i>Linguamyrmex sp4</i>	0.0538	0.2644	0.128 2	0.001	0.008 6	0.1702	0.3502	0.0148	0.0072	0.0016	pred_leaf
<i>Linguamyrmex brevicornis</i>	0.1362	0.13	0.05	0.0046	0.019 8	0.066	0.469	0.0882	0.033	0.0032	pred_leaf
<i>Linguamyrmex sp2</i>	0.0838	0.2446	0.113 2	0.0014	0.027 8	0.154	0.3418	0.0254	0.0058	0.0022	pred_leaf
<i>Linguamyrmex sp1</i>	0.0702	0.2666	0.118 8	0.0016	0.027 2	0.1674	0.3092	0.0194	0.0174	0.0022	pred_leaf
<i>Haidomyrmex sp3</i>	0.0118	0.0388	0.002 8	0.1434	0.033 4	0.0326	0.2692	0.4268	0.028	0.0132	pred_lg_ab

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<i>Haidomyrmex sp5</i>	0.0244	0.2566	0.014	0.0154	0.013 8	0.108	0.485	0.0508	0.0304	0.0016	pred_leaf
<i>Haidomyrmex sp5</i>	0.03	0.247	0.013	0.011	0.018 6	0.1454	0.4418	0.0518	0.0362	0.0052	pred_leaf
<i>Haidomyrmex sp5</i>	0.0214	0.2156	0.008 6	0.0574	0.025 4	0.1154	0.3776	0.111	0.0582	0.0094	pred_leaf
<i>Haidomyrmex sp5</i>	0.0432	0.1142	0.036 2	0.1226	0.057 8	0.0582	0.2544	0.2642	0.0384	0.0108	pred_lg_ab
<i>Haidomyrmex scimitarus</i>	0.0598	0.2394	0.092 2	0.0032	0.022 8	0.2304	0.3066	0.027	0.0156	0.003	pred_leaf
<i>Haidomyrmex sp5</i>	0.0064	0.095	0.007 4	0.2178	0.013 6	0.1068	0.2562	0.1764	0.0956	0.0248	pred_leaf
<i>Haidomyrmex sp4</i>	0.0276	0.2278	0.012 8	0.0218	0.035	0.1298	0.4024	0.0826	0.0536	0.0066	pred_leaf
<i>Haidomyrmex indet1</i>	0.023	0.2272	0.011	0.026	0.031 8	0.127	0.4248	0.0804	0.0408	0.008	pred_leaf
<i>Haidomyrmex indet2</i>	0.0148	0.1566	0.011	0.1254	0.027 4	0.1138	0.3098	0.1684	0.0654	0.0074	pred_leaf

Table S51.

Ecomorph prediction votes when using model trained on subset of complete morphometrics dataset, log-shape variable measurements; homologous morphology.

Lineage	Average ecological disparity	Standard deviation of ecological disparity
Ponerines (<i>Anochetus</i> and <i>Odontomachus</i>)	4.701	2.553
Dacetines (<i>Acanthognathus</i> , <i>Daceton</i> , <i>Epopostruma</i> , <i>Microdaceton</i> , and <i>Orectognathus</i>)	4.667	2.570
<i>Strumigenys</i>	3.200	1.600
<i>Myrmoteras</i>	1.333	0.471
Haidomyrmecines (conservative estimate)	2.944	1.632
Haidomyrmecines (comprehensive estimate)	3.448	1.746

Table S52.

Average and standard deviation of ecological disparity calculated as pairwise distances between each unique three-dimensional occupation. Haidomyrmecine conservative estimates are derived from only the majority aspect predicted by the raw functional measurement model, while comprehensive estimates are derived from majority aspects predicted from all four RF models.

