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# Common ant species dominate morphospace: unraveling the morphological diversity in the Brazilian Amazon Basin

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Rare plant and vertebrate species have been documented to contribute disproportionately to the total morphological structure of species assemblages. These species often possess morphologically extreme traits and occupy the boundaries of morphological space. As rare species are at greater risk of extinction than more widely distributed species, human-induced disturbances can strongly affect ecosystem functions related to assemblage morphology. Here, we assess to what extent the distributions of ant morphological traits are supported by morphologically extreme species and how they are distributed among habitats in a global biodiversity hotspot, the Brazilian Amazon. We used a morphological database comprising 15 continuous morphological traits and 977 expert-validated ant species distributed across the Brazilian Amazon. We produced species range estimates using species distribution models or alpha hulls (when few records were available). Next, we conducted a principal components analysis to combine traits into a space with reduced dimensionality (morphospace). Then, we identified morphologically extreme species in this space and quantified their contributions to morphological diversity across different habitat types in the Brazilian Amazon Basin. We identified 114 morphologically extreme ant species across the Amazon ant morphospace. These species also accounted for a large percentage of morphospace filling, exceeding 99% representation in the most disturbed habitats in the Amazon. Our results suggest that a few morphologically extreme species capture most of the variation in ant morphology and, therefore, the spectrum of ecosystem functions performed by ants in the Brazilian Amazon Basin. Further, unlike in many other groups, these extreme morphologies were represented by the set of most common species.

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These results suggest greater functional redundancy and resilience in Brazilian Amazon ants, but more broadly, they contribute to our understanding of ecological processes that sustain ecosystem functions.

Keywords: cluster, conservation, functional diversity, overdispersion, resilience, vegetation

## Introduction

The Amazon Forest is a biodiversity hotspot providing essential ecosystem functions and services such as seed dispersal, nutrient cycling, carbon sequestration, pollination, and pest predation (Constanza et al. 1997, Edwards et al. 2014, Sullivan et al. 2020). Further, this region is often used as a model in discussing the origin and maintenance of Neotropical biodiversity (Antonelli et al. 2018, Oliveira et al. 2019) and community structuring processes (Rull and Carnaval 2020). However, the majority of this knowledge stems from taxonomic-based approaches describing species richness and composition and thus does not incorporate functional measurements based on species traits (ter Steege et al. 2015, Oberdorff et al. 2019). As recent studies have demonstrated a mismatch between taxonomic and morphological diversity of species around the globe (Kuczynski et al. 2018, McWilliam et al. 2018, Koch et al. 2019, Castro et al. 2020), including the Amazon (Rodrigues-Filho et al. 2018, Su et al. 2019, Siqueira and Silva 2021), morphological information has great potential to elucidate unknown aspects of ecosystem functioning within biodiversity hotspots.

Complex habitats with high ecological stability can enhance morphological diversity by supporting rare species with unique traits (Mouillot et al. 2013a), while assemblages subject to severe or repeated disturbances tend to contain more stress-tolerant species and thus lower morphological diversity (Zimov et al. 1995, Rodrigues et al. 2013, Liang et al. 2019, Leong et al. 2023). Further, both rare and common species are expected to make unique contributions to functional diversity in ecosystems unaffected by human activities (Chapman et al. 2018). Ultimately, trait distributions can be good indicators of ecological strategies. Distributions of quantitative traits in multivariate space (i.e. ‘morphospace’) tend to show a core space for generalist species and peripheral regions occupied by specialized or rare species in vertebrates (Ricklefs 2012, Mouillot et al. 2013a) and plants (Umaña et al. 2015). Importantly, such morphologically extreme species (MES) at the boundaries of morphospace may represent functionally irreplaceable organisms that play unique functions in ecosystems (Leitão et al. 2018) and can thus be employed to measure functional vulnerability (Mouillot et al. 2014). Hence, determining the proportion of morphospace filled by MES can help elucidate how vulnerable ecosystems may be to functional collapse, and this approach should thus be fundamental in guiding efficient conservation strategies targeting the maintenance of ecosystems.

MES are expected to perform specialized functions within species assemblages. There is evidence that the loss of MES can result in the disappearance of distinct functional roles within such assemblages (Mouillot et al. 2008, Clavel et al. 2011). For instance, birds with extreme morphologies have been observed to play specialized functional roles within species assemblages, with MES consuming plants that are rarely eaten by other species (Dehling et al. 2016). In freshwater fish, MES constitute a significant portion of the overall morphological diversity (Su et al. 2019), while most amphibians with combinations of extreme morphologies also exhibit the highest levels of functional uniqueness (Zhao et al. 2023). Finally, functional diversity has been significantly influenced by functionally extreme amphibians, despite MES representing a small proportion of the total amphibian species pool (Zhao et al. 2023). These findings support the hypothesis that MES can exhibit functional specialization and can provide valuable insights for identifying key species for ecosystem functioning.

Insects represent approximately 66% of extant animal species (Zhang 2011, Stork 2018) and play critical roles in ecosystems (Wilson 1987, Chapman 2013). The Amazon itself is expected to be home to a significant proportion of the global insect diversity currently described, but despite recent efforts to better understand large-scale patterns of insect trait diversity in the Amazon (Gardner et al. 2013), there remain wide gaps in our knowledge of how habitat characteristics influence this diversity. Most studies in the Amazon have focused on relationships between vertebrates and plants, such as the influence of habitat on fish morphology (Leitão et al. 2018) and the importance of morphologies of rare species for the maintenance of ecosystem services for plants and some vertebrate groups (Mouillot et al. 2013a, Leitão et al. 2016). However, these patterns may not be broadly generalizable. Different responses among taxa can be expected, since environmental differences can affect each species or their evolutionary histories in specific ways (Barton et al. 2014).

Ants (Hymenoptera: Formicidae) perform many ecological functions (e.g. predation, decomposition, seed dispersal, soil nutrient cycling), and the wide range of ecological strategies employed mainly by ant workers can be described using morphological approaches (Silva and Brandão 2010, Gibb and Parr 2013, Parr et al. 2017). For example, mandible size provides information on the size of preferred food resources (Fowler et al. 1991, Weiser and Kaspari 2006), while eye size is an important trait indicating diet type (Weiser and Kaspari 2006) and foraging stratum (Wong and Guénard 2017). Further, ants with proportionally longer legs may have advantages in escaping predators and finding food, but their ability to cross complex soil interstices is constrained (Gibb and Parr 2013). Therefore, trait evolution and diversity in ant assemblages vary according to the environment, allowing the maintenance and emergence of specific functions.

Here, taking an unprecedented approach for a highly diverse group, numerically and ecologically dominant in tropical forests, we delineate the morphospace of ant communities across different habitat types in the Amazon Basin and measure representation of unique trait combinations by MES. We do this by employing new range estimates for ant species in the Brazilian Amazon using species distribution models (SDMs) to generate estimates of ant community composition. These models can make predictions for undersampled or unexplored areas, thus covering more representative areas for the species that may be left out due to sampling bias, which is widely recognized in tropical environments (Barlow et al. 2018, Andrade-Silva et al. 2022). To delineate habitats, we use vegetation types in the Amazon Basin as templates of boundary morphology because plants provide a myriad of habitats for different species, driving both the taxonomic and functional composition of ant communities (Fichaux et al. 2019, Guilherme et al. 2019). Specifically, we 1) calculated the proportion of morphospace filled by MES and more typical morphologies (TYP), evaluating the functional vulnerability across different habitat types in the Amazon, and 2) measured if the contributions of MES to morphological diversity change over space across different habitat types in the Amazon Basin. Given that finer niche subdivision can explain the high species diversity in tropical forests (Hutchinson 1959, MacArthur and MacArthur 1961) and therefore drive changes in the morphological diversity of assemblages, we expect that 1) MES will represent a constant proportion of the ant morphological space across habitats if extreme morphologies are determined by common species (widely distributed in the Amazon (Vasconcelos et al. 2010)), and 2) the contribution of MES to the structure of the morphological space will be greater in more heterogeneous habitats than in anthropized areas.

## Material and methods

### Occurrence and morphological datasets

The primary occurrence database comprises historical and current ant records for the Brazilian Amazon (from 1817 to 2020). Data were obtained from the Global Ant Biodiversity Informatics project (GABI: Guénard et al. 2017; but also see database treatment in Andrade-Silva et al. 2022). We updated this dataset by incorporating new literature published in 2021 and 2022. Valid species names were based on the Online Catalog of the Ants of the World (AntCat: Bolton 2022, last checked in November 2022). We only considered nominal ant taxa (valid species and subspecies); informal taxa (morphospecies) were not included.

We developed the morphological database from a set of 977 ant species (approximately 91% of the species recorded for the Brazilian Amazon Basin) and measured 15 continuous morphological traits (Supporting information) widely recognized in the ant literature (Silva and Brandão 2010, 2014, Del Toro et al. 2015). Because of studies on intraspecific trait variation in ant assemblages suggesting that intraspecific variation accounts for only 1–4% of total trait variation (Gaudard et al. 2019), we measured one specimen for each species present in the Brazilian Amazon, and always prioritized type specimens over non-type specimens. Whenever possible, we used the minor workers to standardize the measurements, as is routinely done in studies of the morphological diversity of ants (Silva and Brandão 2010, Schofield et al. 2016). However, when these were not available, we used major workers to obtain morphological measurements (< 4% of total). We made our trait database based on more than 3000 high-definition images available on Antweb (87.3% of total) or taken during visits to collections (3.2%), including lateral, frontal, and dorsal views. We used ImageJ (Schneider et al. 2012) to record measurements from images, or obtained morphological traits from the taxonomic literature (9.5%) when possible for those species without available high-definition images. Further methodological details for the occurrence and morphological database compilation can be found in Andrade-Silva et al. (2022).

Measurements were not carried out when appropriate images were not available (i.e. such as those for damaged specimens or those lacking the required morphological structures). Thus, we applied data imputation to fill 12.65% of the morphological matrix using multivariate imputation by chained equations (MICE) (Van Buuren and Groothuis-Oudshoorn 2011). The MICE approach preserves the observed data but explicitly provides a set of imputed values for missing data (see 'Data preparation and morphological traits' section in Andrade-Silva et al. (2022) for more details). Measurements performed on different specimens were never combined to fill in species data.

### Vegetation type dataset

We used a vegetation-type shapefile for the Brazilian Amazon provided by the Instituto Brasileiro de Geografia e Estatística (IBGE 2012) to describe the regional morphological structure of ants from different habitats. The complex vegetation structure in the Amazon Basin is one of the main drivers of animal diversity, hosting varied microhabitats that enable interspecific coexistence (Laurance and Vasconcelos 2009, Fichaux et al. 2019). For example, forest biomass (Saatchi et al. 2007) is correlated with the production of leaf litter (Aragão et al. 2009), a key factor determining taxonomic (Queiroz et al. 2013, Souza-Campana et al. 2017, Fernandes et al. 2019) and morphological diversity of ants (Weiser and Kaspari 2006, Schofield et al. 2016). Moreover, ant morphological traits respond to habitat variation in vegetation structure at both small and large scales (Arnan et al. 2014, 2017, Silva and Brandão 2014, Lee et al. 2021), including increased body size and relative mandible length, as well as decreased eye-size of ant species with increasing vegetation complexity (Guilherme et al. 2019).

We defined nine main vegetation types (hereafter, 'habitats') in the Brazilian Amazon: 1) anthropic, 2) white sand forests *Campinaranas*, 3) dense ombrophilous forests, 4)

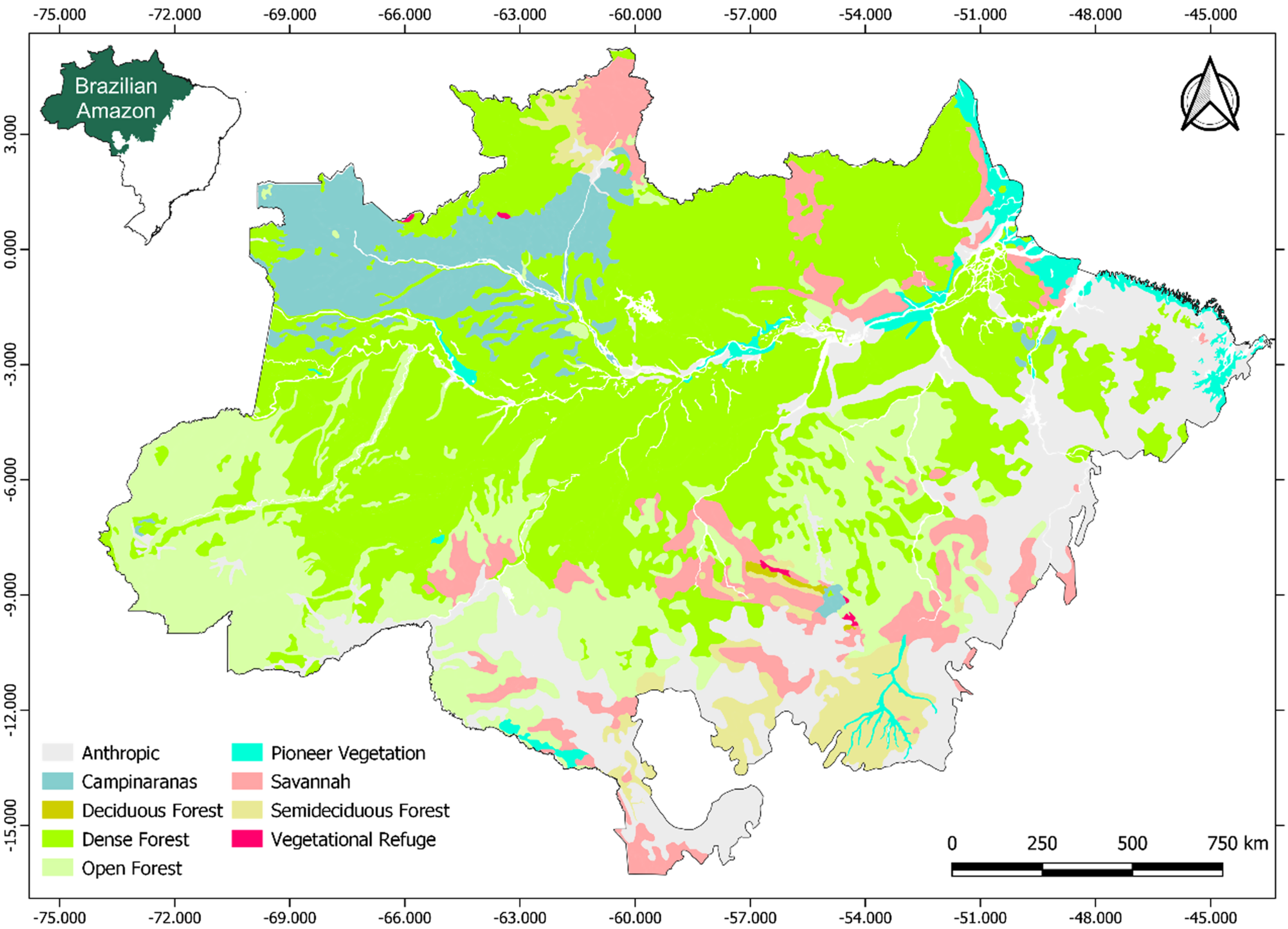

Figure 1. Vegetation types across the Brazilian Amazon according to the Instituto Brasileiro de Geografia e Estatística (IBGE 2012). The complex vegetation structure of the Amazon Basin is recognized as one of the main drivers of terrestrial diversity, creating a rich variety of microhabitats and opportunities for interspecific coexistence.

open ombrophilous forests, 5) pioneer vegetation (i.e. sand bars, mangroves), 6) savannah, 7) seasonal deciduous forest, 8) seasonal semideciduous forest, and 9) vegetational refuge (i.e. high-altitude fields, peat areas) (Fig. 1). The main characteristics of each vegetation type are summarized in Table 1. We reclassified the IBGE vegetation shapefile by grouping vegetation classes within their immediately superior vegetation types. For example, we reclassified the classes 'alluvial dense ombrophilous forest' and 'lowland dense ombrophilous forest' into 'dense ombrophilous forest'. We reclassified vegetation types using shapefile dissolve operations in QGIS, ver. 2.18.2 (QGIS Development Team 2019).

## Ant species classification

We designated the relative rarity of ant species based on examinations of general patterns in their distributions from occurrence data available on www.Antmaps.org (Janicki et al. 2016, Guénard et al. 2017). This web application displays ant species occurrence data from GABI as aggregate diversity patterns by regional polygon for the globe (Janicki et al. 2016). Additionally, we consulted the taxonomic history of the species, which included expert consultations, collection curators, and taxonomic literature available in Bolton (2024). We also checked available taxonomic publications for Amazonian ant species to verify if possible misidentifications had been reported. Finally, we considered information from the literature on the biology of the species, especially related to factors that directly influence dispersal, such as reproductive strategies (e.g. winged or wingless queens). Based on this information, combining data from taxonomic history, biology, and considerations of taxonomic and sample gaps, as well as biases present in the Amazon (Albuquerque et al. 2021, Andrade-Silva et al. 2022), we classified the species qualitatively as 'common' or 'rare'. Species were classified as common if they 1) were widely distributed in the Amazon and other biomes, or 2) were species with sparse distribution but with known gaps, including recently described species or those with challenging taxonomy, lacking available identification tools, and in need of taxonomic revisions in recent decades. Alternatively, species were classified as rare if their occurrence data were aggregated and their distributions were restricted. We also took into consideration the year of description, availability of identification tools, and

Table 1. Primary characteristics of each vegetation type and their contributions to forest cover in the Brazilian Amazon. The vegetation classification was adapted from Instituto Brasileiro de Geografia e Estatística (IBGE 2012) and used in ant morphological diversity analyses across the Brazilian Amazon Basin.

| Vegetation type ($km^2$) | Abbreviation | Main characteristics |
|---|---|---|
| Anthropic (234 772) | AN | Areas impacted by land use (mining, agricultural or livestock purposes), removing the primary vegetation; also including areas occupied by reforestation |
| Campinarana (46 976) | CA | Unique environments in the Amazon. Include many endemic species of both flora and fauna. The vegetation structure varies from open grassland to forest formations, with fine and poorly developed (short-statured) trees. Occupies flat and flooded areas and has sandy soils |
| Dense ombrophilous forest (2 068 057) | DO | Associated with tropical climatic factors: high temperature (average is 25°C), high precipitation (average is 2300 mm $year^{-1}$) and well-distributed throughout the year (from 0 to 60 dry days), without a dry period. Characterized by phanerophytes (autotrophic, perennial, woody, and erect plants with heights that can reach 50 m), woody lianas, and abundant epiphytes |
| Open ombrophilous forest (1 186 150) | OO | Defined as transition areas between the Amazon Forest and extra-Amazonian areas; floristic physiognomy that impose clearings in the dense forest; predominantly forest communities composed of palms, bamboo, sororoca, *Phenakospermum guyannense*, and climbing plants |
| Pioneer vegetation (89 905) | PV | Unique and specialized vegetation, adapted to cyclical variations in water levels. Plants adapted to survive for long periods under conditions of total or partial submersion. Vegetation includes herbaceous plant communities and assemblages dominated by shrubs or trees, with widely varying canopy coverage |
| Savannah (249 228) | SA | Occurs as isolated patches within the Amazon Basin. Floristically similar to the cerrado vegetation of central Brazil; always includes some cover of grasses and sedges, but varies greatly in density of trees and cover of shrubs |
| Seasonal deciduous forest (18 057) | SD | More than 50% of individuals that defoliate during stressful periods. Occurrence is disjointed; very dry vegetation resembling the savannah landscape but with its own unique floral profile. Trees have moderate height (approximately 20–30 m) |
| Seasonal semideciduous forest (222 121) | SS | Associated with regions marked by severe winter drought and intense summer rains. Most taller trees not exceeding 30 m; many emergent trees and palm species. Soil is sandy and small ponds form within this habitat |
| Vegetational refuge (1649) | VR | Defined as all vegetational areas differentiated in terms of floristic and physiognomic–ecological aspects of the dominant flora in Amazonia; relic vegetation, with endemic species, which persists in very special situations, as the case of plant communities at altitudes above 1800 m |

uncertainty in application of species names ('dark taxa'). The species known to be present only in ecotonal zones of the Amazon were classified as 'rare', although they occur in other Neotropical biomes.

## Species' range estimates

To address known geographic sampling biases of ant collections in the Amazon present in our morphological database, we compiled species lists per vegetation type in the Brazilian Amazon using range estimates based on species distribution models (SDMs). Specifically, we made binary (presence/absence) range estimates from SDMs built with climatic variables for a previous study on global ant diversity (Kass et al. 2022). The original data were continuous predictions of environmental suitability for a set of species (Maxent 3.4.1 cloglog estimates of probability of presence; Phillips et al. 2017) restricted to alpha hulls delineated around the species' occurrence records. To threshold these predictions, we employed the 10-percentile suitability value, which was used to select optimal model complexity per species via omission rates by Kass et al. (2022). Range estimates for low-data species were represented by univalue rasterized alpha hulls or circular buffers when sample size was below five or three records, respectively (for more details see Kass et al. 2022). Binary range estimates were necessary for this study in order to estimate community composition per grid cell. For each species, we identified which vegetation classes overlap with its binary range estimate. Due to the substantial bias in ant sampling in the Amazon (Andrade-Silva et al. 2022), we refrained from comparing the composition and richness of various modeled vegetation types against real community data, as these would be widely derived from the biased samples. We conducted all the analyses for range estimates and those following in R (www.r-project.org).

## Morphological diversity

We quantified ant morphological diversity using a hypervolume approach (Blonder et al. 2017). This approach uses high-dimensional kernel density estimates to delineate the shape and volume of the multidimensional distribution of morphologies, and it can also accommodate empty spaces within values of traits, thus increasing the accuracy of our estimates (Blonder 2016, Blonder et al. 2017). Further, the hypervolume approach shows higher performance on large and high-dimensional datasets, which could be generalizable to a broad range of ecological scenarios (Blonder et al. 2017, Jarvis et al. 2019).

For each vegetation type, we calculated the hypervolume area delimited by the first four axes of a principal component analysis (PCA) based on a correlation matrix. We used ordination to reduce the number of input variables, improving analysis time and axis orthogonality (Blonder et al. 2017). We first accounted for correlation with body size by applying a centered log-ratio (CLR, $x + 1$) transformation on the morphological measurements (Peres-Neto and Magnan 2004). This method applies a general measure of size based on the composite of all variables being considered, scaling each individual independently. Additionally, it does not eliminate the variable that is used as the surrogate of size (e.g. Weber's length) from the dataset (Aitchinson 1986). The first four principal component (PC) axes accounted for 75% of the total variance and were selected based on component loadings (> 1.0) (Supporting information). For the hypervolume analysis, we used the *hypervolume_gaussian* function from the R package 'hypervolume' (Blonder et al. 2017).

Morphological diversity measures are often related to species richness because a larger volume is more likely to be estimated with more species in the community (Villéger et al. 2008, Swenson 2014). Therefore, we used standardized effect size (SES; Gotelli and McCabe 2002) to account for the potential influences of species richness on the morphological axes of the hypervolume. We calculated SES values as follows:

$$\frac{x_{obs} - x_{exp}}{SD(x_{sim})}$$

where $x_{obs}$ represents the observed values, $x_{exp}$ the expected values for a null model (the mean of the simulated values; Supporting information), and $SD(x_{sim})$ the standard deviation of the simulated values (Gotelli and McCabe 2002). Negative SES values indicate a lower diversity than expected from the null model (morphological similarity), while positive values indicate a higher morphological diversity than expected (morphological divergence). The expected values for each habitat were determined by calculating the mean of hypervolumes for 999 random null communities. Null communities were generated by randomization of species but restricted to the regional species pool present in each habitat, giving geographically plausible null communities with observed species richness held constant. We evaluated support for the null hypothesis by comparing empirical observations to the 95% confidence interval of the distribution of null values based on 999 randomizations. These randomizations demonstrate how the ant morphospace changes when new MES species are added to or removed from each Amazonian habitat. The corresponding SES values determine, on average, whether morphological diversity is greater or less than what would be expected by chance. Hypervolume averages for these randomizations were used for all further analyses.

We then evaluated whether morphological boundaries characterized by the most extreme morphologies (MES) differ among vegetation types of the Amazon Basin. Given the limitations of the hypervolume algorithm to extract which species delimit the hypervolume area (Benjamin Blonder pers. comm.), we identified MES by 1) selecting species within the 95th percentile density contour of the morphospace (assuming a multivariate normal distribution), and 2) selecting those species representing the vertices of convex hulls in the reduced morphospace (PC1 × PC2 × PC3 × PC4) to characterize the space occupied by ants in each vegetation type. As the results were similar, we present here the results for the simpler convex hull approach (but see results for the MVN approach in the Supporting information). We used the *convhulln* function from the R package 'geometry' (Habel et al. 2022) to identify morphospace boundaries and derived the identities of the species representing the vertices of the convex hulls – these species were labeled as MES. The remaining species were considered to be part of the morphological core and were named as species with more typical morphologies (TYP). We then evaluated the contribution of MES to morphospace volume per vegetation type using two methods. The first involved removing all MES identified by convex hulls in each vegetation type. We did this by nominally identifying MES for each vegetation type and excluding them from the hypervolume calculation (observed and simulated). The second involved removing randomly (999 times) the same number of MES in each habitat. To do this, we quantified the number of species identified as MES through the convex hull in each vegetation type, and then the same number of morphologically extreme species were removed by chance. This method allowed us to construct comparable datasets for hypervolume calculation.

In addition, we calculated the functional originality (FOri) and functional specialization (FSpe) values for ant assemblages in each habitat. FOri represents the isolation of a given species in the morphological space occupied by a given assemblage. It is measured by the average pairwise distance between a species and its nearest neighbor in a multidimensional space; lower FOri values indicate higher functional redundancy Mouillot et al. (2013b). FSpe measures the dominance of specialist species (characterized by extreme trait combinations) in a given assemblage. It is defined in the multidimensional trait space of the regional pool of species and quantifies how distant on average species are from the centroid of the morphological space; higher FSpe values indicate higher proportions of specialist species (Mouillot et al. 2013b, Rodrigues-Filho et al. 2018, Su et al. 2019). We calculated FOri and FSpe values based on the methodologies described in Mouillot et al. (2013b).

Further, we estimated morphological similarity based on the overlap in kernel density estimations to describe the morphological patterns found in ants of the Amazon Basin. The coefficient of overlap was calculated using the *overlapTrue* function in the R package 'overlap' (Ridout and Linkie 2009); the observed values were scaled in radians (0 to 2π) before calculating overlaps as required by this estimator (i.e. vectors of densities between 0 and 2π (Schmid and Schmidt 2006)).

## Results

Of the 977 ant species considered in this study, 114 species (approximately 11% of the total) were identified as morphologically extreme species (MES) in the ant morphospace across Amazonian habitats (Table 2). MES represented a wide variation in morphology (size, shape, and life histories),

Table 2. Morphologically extreme species (MES) in ant assemblages aggregated by nine habitats (vegetation types) across the Brazilian Amazon Basin. Species were classified as common (C) or rare (R) based on examinations of general patterns in their distributions in the Amazon and other regions. The fourth column represents the occurrence of each ant species as a MES in each habitat. MES were defined as those species representing the vertices of a convex hull using the first four PCA axes. AN = anthropic; CA = Campinaranas; DO = dense ombrophilous forests; OO = open ombrophilous forests; PV = pioneer vegetation; SA = savannah; SD = seasonal deciduous forest; SS = seasonal semideciduous forest; VR = vegetational refuge.

| Ant subfamily/species | Category | Classification criterion | MES |
|---|---|---|---|
| **Agroecomyrmecinae** | | | |
| *Tatuidris tatusia* | C | widely distributed | VR |
| **Dolichoderinae** | | | |
| *Dolichoderus attelaboides* | C | widely distributed | SS, VR |
| *Dolichoderus decollatus* | C | widely distributed | All |
| *Dolichoderus imitator* | C | widely distributed | CA, DO, OO, PV, SA, SD, SS, VR |
| *Dolichoderus laminatus* | C | widely distributed | CA, DO, PV, SD, VR |
| *Dolichoderus rugosus* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS |
| *Dolichoderus varians* | C | widely distributed | CA, DO, PV, SD, VR |
| **Dorylinae** | | | |
| *Cheliomyrmex megalonyx* | C | widely distributed | SS, VR |
| *Eciton burchellii* | C | widely distributed | SD |
| *Eciton drepanophorum* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS, VR |
| *Labidus coecus* | C | widely distributed | All |
| **Formicinae** | | | |
| *Acropyga romeo* | C | sparsely distributed | DO |
| *Brachymyrmex aphidicola* | C | widely distributed | All |
| *Brachymyrmex australis* | C | widely distributed | AN, CA, DO, OO, PV, SA, SD, VR |
| *Brachymyrmex heeri* | C | widely distributed | AN, CA, DO, OO, PV, SA, VR |
| *Camponotus ager* | C | widely distributed | All |
| *Camponotus apicalis* | C | widely distributed | CA, DO, OO, PV, SA, SD, SS, VR |
| *Camponotus branneri* | C | widely distributed | OO |
| *Camponotus cacicus* | C | widely distributed | AN, CA, DO, OO, SA, SD, SS, VR |
| *Camponotus diversipalpus* | C | sparsely distributed | AN, SA, SS |
| *Camponotus lespesii* | C | sparsely distributed | AN, CA, DO, OO, SA, PV |
| *Camponotus leydigi* | C | widely distributed | CA, SD, VR |
| *Camponotus macrochaeta* | C | sparsely distributed | PV |
| *Camponotus melanoticus* | C | widely distributed | CA, SD |
| *Camponotus sanctaefidei* | C | widely distributed | CA, DO, OO, PV, SA, SS, VR |
| *Camponotus sericeiventris* | C | widely distributed | CA, DO, OO, PV, SA, SS, VR |
| *Camponotus tonduzi* | C | sparsely distributed | DO |
| *Camponotus traili* | C | widely distributed | CA, VR |
| *Camponotus vittatus* | C | widely distributed | OO, SA, SS |
| **Martialinae** | | | |
| *Martialis heureka* | R | restricted distribution | AN, DO |
| **Myrmicinae** | | | |
| *Acanthognathus brevicornis* | C | sparsely distributed | AN, CA, OO, PV, SA, SS, VR |
| *Acanthognathus teledectus* | C | sparsely distributed | DO |
| *Atta capiguara* | R | ecotonal distribution | AN, PV, SA |
| *Atta cephalotes* | C | widely distributed | All |
| *Atta laevigata* | C | widely distributed | SD, VR |
| *Atta sexdens* | C | widely distributed | All |
| *Carebara arabara* | C | sparsely distributed | All |
| *Carebara brevipilosa* | C | widely distributed | SD |
| *Carebara inca* | C | sparsely distributed | AN, CA, DO, OO, PV, SA |
| *Carebara minuta* | C | sparsely distributed | SS |
| *Cephalotes atratus* | C | widely distributed | All |
| *Cephalotes bruchi* | C | sparsely distributed | AN, DO, SA |
| *Cephalotes christopherseni* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS |
| *Cephalotes clypeatus* | C | widely distributed | All |
| *Cephalotes columbicus* | C | sparsely distributed | AN, SA, SS |
| *Cephalotes conspersus* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS, VR |
| *Cephalotes cordatus* | C | widely distributed | All |
| *Cephalotes cordiventris* | C | sparsely distributed | AN |
| *Cephalotes depressus* | C | widely distributed | CA, DO, OO, PV, SA, SD, SS, VR |
| *Cephalotes laminatus* | C | widely distributed | CA, DO, OO, PV, SD, VR |
| *Cephalotes maculatus* | C | widely distributed | All |
| *Cephalotes minutus* | C | widely distributed | All |
| *Cephalotes oculatus* | C | widely distributed | CA, DO, OO, PV, SD, VR |

*(Continued)*

Table 2. Continued.

| Ant subfamily/species | Category | Classification criterion | MES |
|---|---|---|---|
| *Cephalotes pallidoides* | C | widely distributed | SD |
| *Cephalotes pallidus* | C | widely distributed | All |
| *Cephalotes pellans* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS, VR |
| *Cephalotes persimilis* | C | widely distributed | SD |
| *Cephalotes ramiphilus* | C | widely distributed | PV |
| *Cephalotes serraticeps* | C | widely distributed | AN, CA, DO, OO, PV, SA, SD, SS |
| *Cephalotes solidus* | R | restricted distribution | CA, DO, OO |
| *Cephalotes spinosus* | C | widely distributed | All |
| *Cephalotes targionii* | C | widely distributed | CA, DO, OO, PV, SA, SS, VR |
| *Cyphomyrmex costatus* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS, VR |
| *Daceton boltoni* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS |
| *Lachnomyrmex amazonicus* | C | widely distributed | SD |
| *Ochetomyrmex semipolitus* | C | widely distributed | All |
| *Pheidole ademonia* | C | sparsely distributed | AN, CA, DO, OO, SA, SS |
| *Pheidole astur* | C | sparsely distributed | CA, OO, VR |
| *Pheidole jaculifera* | C | widely distributed | CA, PV |
| *Pheidole leonina* | C | sparsely distributed | DO, OO |
| *Pheidole lovejoyi* | C | widely distributed | AN, DO |
| *Pheidole mendicula* | C | sparsely distributed | PV, VR |
| *Pheidole paraensis* | C | sparsely distributed | PV, SA |
| *Pheidole perpusilla* | C | sparsely distributed | PV, VR |
| *Pheidole puttemansi* | C | widely distributed | AN, CA, DO, OO, PV |
| *Pheidole scimitara* | C | widely distributed | CA |
| *Pheidole triconstricta* | C | sparsely distributed | DO |
| *Pheidole wallacei* | C | sparsely distributed | AN |
| *Sericomyrmex maravalhas* | R | ecotonal distribution | AN, OO, SA |
| *Solenopsis subtilis* | C | widely distributed | AN, DO |
| *Strumigenys alberti* | C | widely distributed | CA, DO, OO, PV, SA, SD, VR |
| *Strumigenys denticulata* | C | widely distributed | CA, PV, SD, SS, VR |
| *Strumigenys diabola* | C | widely distributed | AN, DO, OO, PV, SA |
| *Strumigenys dolichognatha* | C | widely distributed | CA, SS, VR |
| *Strumigenys eggersi* | C | widely distributed | VR |
| *Strumigenys grytava* | C | sparsely distributed | AN, CA, DO, OO, PV |
| *Strumigenys hyphata* | C | widely distributed | SD, SS, VR |
| *Strumigenys marginiventris* | C | sparsely distributed | CA |
| *Strumigenys metopia* | C | widely distributed | All |
| *Strumigenys perparva* | C | widely distributed | CA, VR |
| *Strumigenys trudifera* | C | widely distributed | AN, CA, OO, PV, SA, SD, SS, VR |
| *Wasmannia scrobifera* | C | widely distributed | AN, CA, OO, PV, SA, SD, VR |
| **Ponerinae** | | | |
| *Anochetus horridus* | C | widely distributed | All |
| *Centromyrmex alfaroi* | C | widely distributed | AN, CA, DO, PV, SA, SS, VR |
| *Centromyrmex brachycola* | C | widely distributed | All |
| *Centromyrmex gigas* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS |
| *Dinoponera gigantea* | C | widely distributed | All |
| *Dinoponera hispida* | R | restricted distribution | AN, DO, PV |
| *Dinoponera longipes* | C | widely distributed | AN, CA, DO, OO, PV, SA |
| *Dinoponera mutica* | C | widely distributed | All |
| *Dinoponera quadriceps* | C | widely distributed | SD, SS, VR |
| *Leptogenys famelica* | C | widely distributed | All |
| *Neocerapachys splendens* | C | widely distributed | CA, DO, PV, SS |
| *Neoponera agilis* | C | sparsely distributed | AN, PV, SA, SS |
| *Neoponera globularia* | C | widely distributed | CA, DO, OO, SD, VR |
| *Odontomachus chelifer* | C | widely distributed | All |
| *Odontomachus hastatus* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS, VR |
| *Pachycondyla crassinoda* | C | widely distributed | All |
| *Pachycondyla impressa* | C | widely distributed | SD, VR |
| *Thaumatomyrmex atrox* | C | widely distributed | AN, CA, DO, OO, PV, SA, SS |
| *Thaumatomyrmex ferox* | C | widely distributed | VR |
| *Wadeura guianensis* | C | sparsely distributed | PV, SD, VR |
| **Proceratiinae** | | | |
| *Probolomyrmex boliviensis* | C | sparsely distributed | AN, CA, DO, OO, PV |
| **Pseudomyrmecinae** | | | |
| *Pseudomyrmex sericeus* | C | widely distributed | SD |

including common species with very distinct morphologies, rare species, and specialized morphologies (Table 2). Further, comparatively, MES and TYP of ants across the main habitats in the Brazilian Amazon had a few strong morphological differences. For example, in anthropic areas, MES had wider petioles than TYP species. Overall, the major axes of variance in morphology of MES and TYP ant species across habitats were traits related to leg size, antenna size, eye position, and petiole size (width and length) (Fig. 2).

Proportionally, most species with extreme trait combinations were found in deciduous forests (18% of the local fauna; 51 species) and vegetational refuge (15%, 65 species). In contrast, anthropic habitats had 7% ants (61) with extreme trait combinations (Table 3). Twenty-three MES were associated with all habitats, while 50 MES were associated with fewer than four habitats (Table 2). Of the 114 ants identified as MES, only five (approximately 4% of the total) were classified as rare (Table 2).

The morphological diversity of the ant fauna also varied among habitats. Deciduous forest and vegetation refuge habitats had the highest morphological diversity, while savannah, open forests, and dense forests had the lowest diversity (Table 3). Despite these differences, only deciduous forests (morphological clustering structured), *Campinaranas*, and semideciduous forests (morphological divergence structured) changed morphological patterns after MES removal. Conversely, only three (anthropic, pioneer vegetation, and deciduous forests) of the nine habitats maintained their morphological structure (morphological divergence) when the same number of MES were randomly removed from the morphospace (MD SES – Table 3).

Overall, regardless of how MES were removed from the morphospace, the observed morphological structure of ants in the Amazon did not differ significantly from what would be expected by chance (Table 3), but we detected morphological clustering in dense forests.

On average, the morphologically extreme species filled 65% of the morphological volume for each habitat; in the anthropic habitats, the morphospace filled by MES exceeded 99% (Fig. 3). On the other hand, values of FOri and FSpe for the ant faunas in the nine main Amazon habitats remained low (approximately 6 and 24%, respectively; Table 4). As

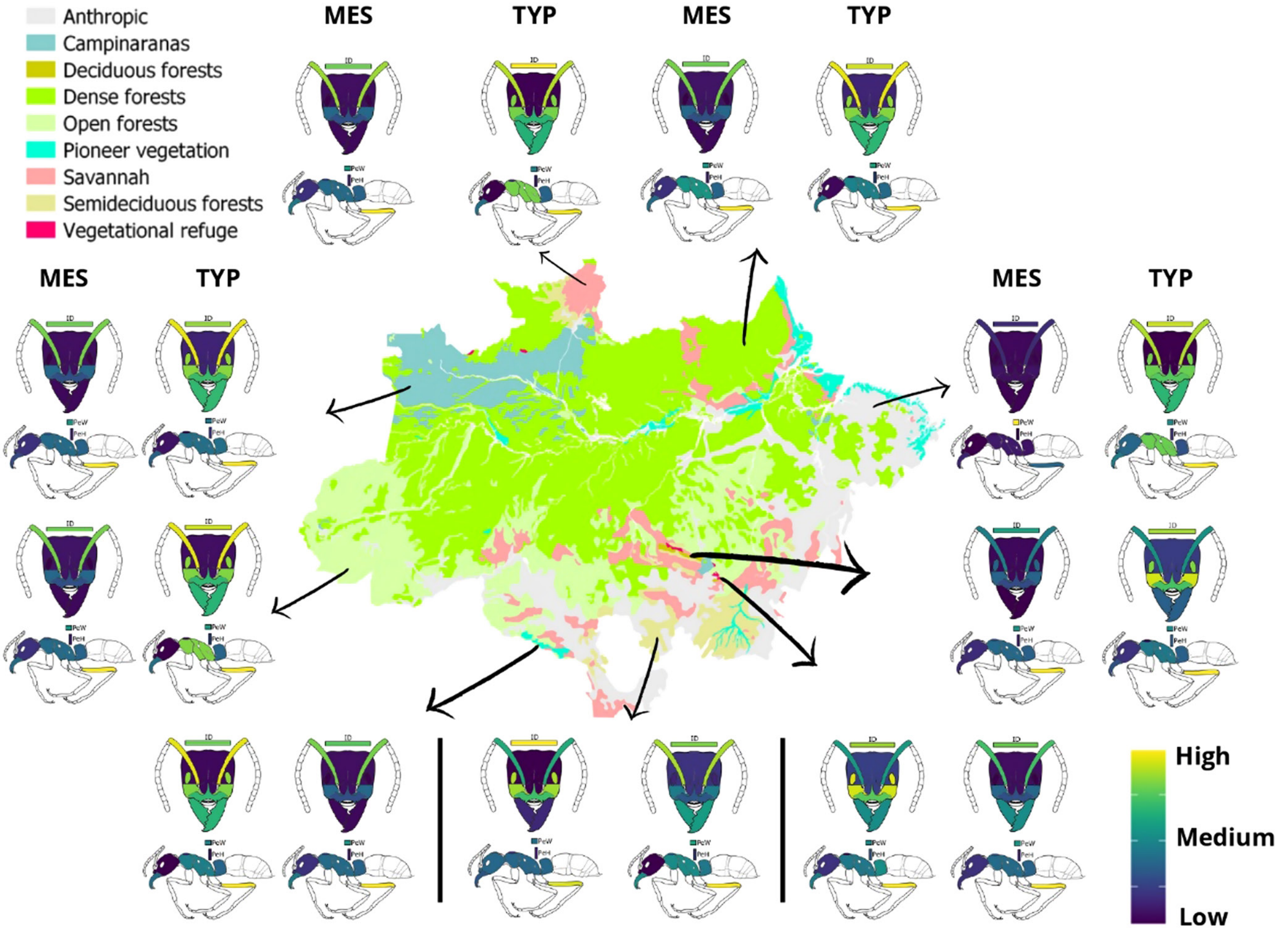

Figure 2. Morphological features for the head and body in lateral view for different vegetation habitats in the Brazilian Amazon. Colors represent the range of variation (low [blue] to high [yellow]) of ant traits by morphologically extreme species (MES, left) and those with more typical morphologies (TYP, right).

Table 3. Main habitats in the Brazilian Amazon and taxonomic diversity (TD), observed (MD obs), and expected (MD SES) morphological diversity for ant assemblages with and without morphologically extreme species (MES). Morphologically extreme species were identified by convex hull analyses using the first four principal components as the morphological matrix. 'With MES' represent the morphological volume of the ant fauna for the species pool in each habitat. More typical morphologies (TYP) represent assemblages with the same number of species as in 'random MES', but morphologically extreme species were excluded. In 'random MES' assemblages have the same taxonomic diversity as in TYP, but the same number of morphologically extreme species were removed by chance. Values in parentheses represent the number of MES in each habitat. The MES contribution to morphological diversity is a proxy for the functional vulnerability of ant faunas in the Brazilian Amazon Basin, given that MES can be considered as functionally irreplaceable organisms that play unique roles in ecosystems. P-values were computed based on 999 randomizations in all models; those in bold are significant (two-tailed test), indicating morphological clustering ($p \leq 0.025$) or morphological divergence ($p \geq 0.975$).

| | Anthropic | Campinaranas | Dense forest | Open forest | Pioneer vegetation | Savannah | Deciduous forest | Semideciduous forest | Vegetational refuge |
|---|---|---|---|---|---|---|---|---|---|
| **With MES** | | | | | | | | | |
| TD | 895 | 624 | 834 | 738 | 615 | 679 | 278 | 545 | 433 |
| MD (obs) | 1899 | 1876 | 1684 | 1725 | 1931 | 1844 | 2796 | 2019 | 2091 |
| MD (SES) | 0.176 | −0.149 | −3.094 | −1.577 | 0.439 | −0.354 | 1.147 | −0.041 | −0.946 |
| p-value | 0.574 | 0.493 | **0.012** | 0.040 | 0.715 | 0.464 | 0.866 | 0.494 | 0.181 |
| **TYP** | | | | | | | | | |
| TD | 834 (61) | 552 (72) | 764 (70) | 673 (65) | 546 (69) | 618 (61) | 227 (51) | 488 (57) | 368 (65) |
| MD (obs) | 1201 | 1084 | 1036 | 1036 | 1110 | 1067 | 1021 | 1109 | 934 |
| MD (SES) | 1.058 | 0.461 | −2.302 | −1.014 | 1.056 | −0.001 | −0.538 | 1.547 | −1.737 |
| p-value | 0.863 | 0.670 | **0.022** | 0.149 | 0.858 | 0.531 | 0.319 | 0.934 | 0.040 |
| Contribution (%) | 36.75 | 42.21 | 38.47 | 39.94 | 42.51 | 42.13 | 63.48 | 45.07 | 55.33 |
| **Random MES** | | | | | | | | | |
| TD | 834 (61) | 552 (72) | 764 (70) | 673 (65) | 546 (69) | 618 (61) | 227 (51) | 488 (57) | 368 (65) |
| MD (obs) | 1918 | 1888 | 1703 | 1728 | 1884 | 1750 | 3031 | 1977 | 2205 |
| MD (SES) | 2.011 | 0.971 | 0.481 | 0.369 | 0.837 | 0.364 | 1.924 | 1.000 | 1.215 |
| p-value | 0.970 | 0.845 | 0.700 | 0.678 | 0.798 | 0.645 | 0.963 | 0.844 | 0.889 |
| Contribution (%) | – | – | – | – | 2.43 | 5.09 | – | 2.08 | – |

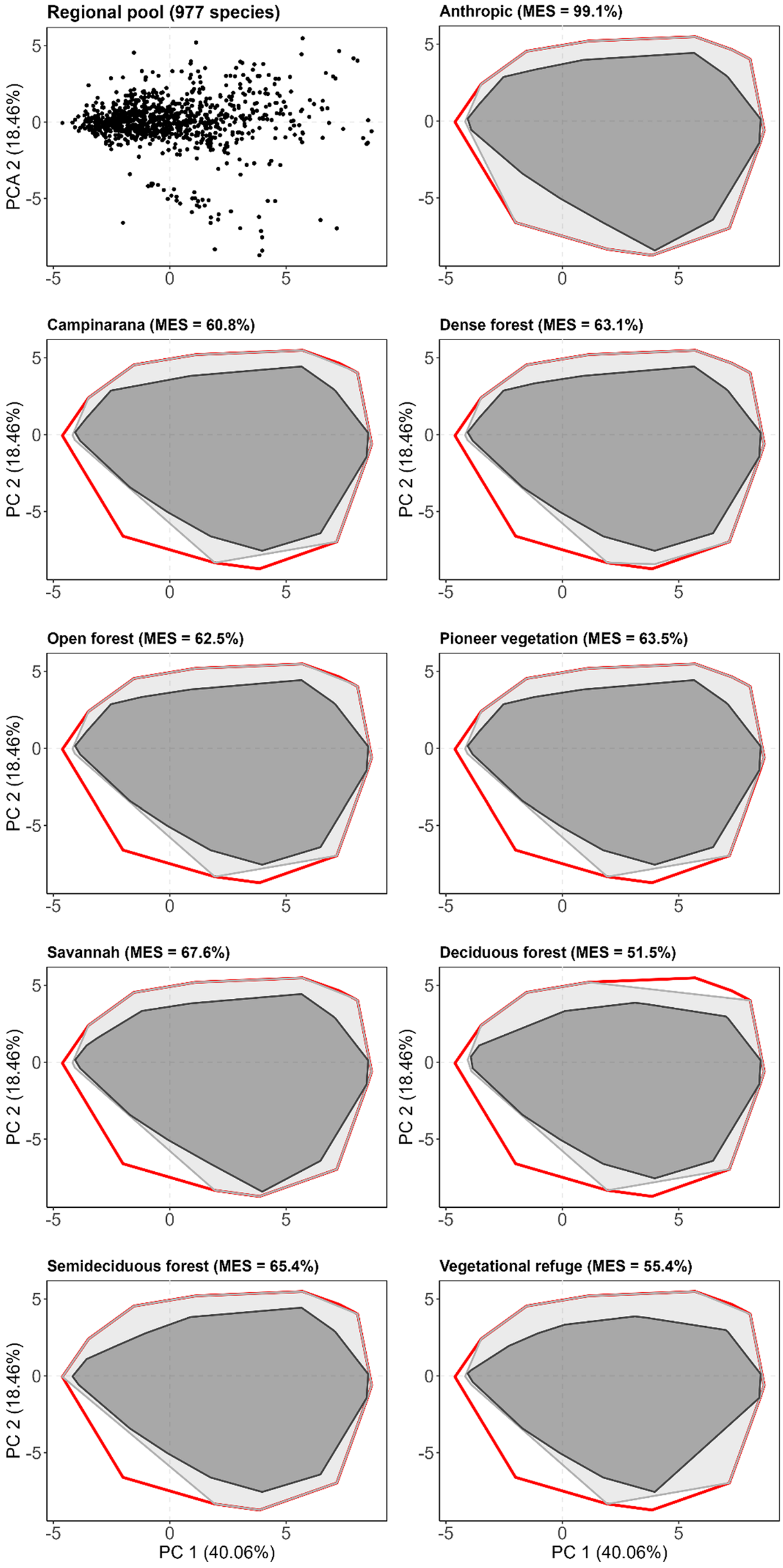

Figure 3. Regional pool and contribution of morphologically extreme species (MES) to the morphological diversity of ant faunas in the nine vegetation types across the Brazilian Amazon Basin. The Amazon-wide convex hull for the regional pool (977 species) is shown in red. Light-gray areas show the morphological volume filled by MES and dark-gray areas the same volume after MES have been excluded (i.e. more typical morphologies). Black dots represent each of the 977 ant species measured in our study.

Table 4. Amazon representativeness, functional originality (FOri), and functional specialization (FSpe) of ants for nine habitats across the Brazilian Amazon Basin. Lower FOri values indicate higher functional redundancy, while higher FSpe values indicate higher proportion of specialized morphologies.

| | Amazon representativeness (%) | FOri (%) | FSpe (%) |
|---|---|---|---|
| Anthropic | 5.59 | 5.96 | 23.39 |
| Campinaranas | 1.11 | 6.12 | 23.48 |
| Dense forest | 49.27 | 5.88 | 23.10 |
| Open forest | 28.26 | 5.96 | 22.90 |
| Pioneer vegetation | 2.14 | 6.10 | 23.86 |
| Savannah | 5.93 | 6.03 | 23.54 |
| Deciduous forest | 0.43 | 6.94 | 25.56 |
| Semideciduous forest | 5.29 | 6.22 | 23.67 |
| Vegetational refuge | 0.03 | 6.36 | 23.84 |

expected, for all habitats, MES always showed a higher density of morphological traits falling in the tails of the distributions than TYP ants (Supporting information).

## Discussion

Our results show that the most extreme ant morphologies across the Amazon Basin are mainly represented by a small proportion of the total resident ant species (114 species, or 11% of the Basin pool). On average, among different habitats, these species filled approximately 65% of the overall morphospace in the Amazon. In contrast to patterns observed in other organisms, we showed that the morphological variation of ants in the Amazon is mainly supported by common species, suggesting high functional resilience for the boundaries of the ant morphospace. Further, the fact that the multidimensional distributions of ant traits by habitat peak around median values indicates that ants have similar morphologies among Amazon Forest types. These results add to existing evidence for high functional redundancy in tropical forests based on a widely diverse group that is often underrepresented in large-scale analyses (Stein et al. 2014).

The boundaries of morphospaces were dominated by common ant species (predators or omnivores), revealing an opposite relationship to those found in fishes, birds, and plants, where the most distinct combinations of traits are mainly supported by rare species (Mouillot et al. 2013a, Leitão et al. 2016). Rare species are more vulnerable to extinction than common species (Rabinowitz 1981, Flather and Sieg 2007) and can contribute significantly less to morphological diversity than common species (Smith and Knapp 2003, Jain et al. 2014), playing a role in temporal complementarity (Naeem 1998). On the other hand, common species have particular trait compositions and unique contributions to functional diversity (Chapman et al. 2018) that give them the ability to successfully outcompete other species for space and resources. These characteristics allow them to achieve high abundances, maintain broad geographic ranges, and occupy many different habitats (Tilman 1999, Gaston 2010, 2011), thus sustaining ecosystem functioning in marine (Connolly et al. 2014) and terrestrial (Winfree et al. 2015) systems. Therefore, as the boundaries of the ant morphospace include many common species among habitats, this indicates greater functional resilience for ants compared to vertebrates and plants in the Brazilian Amazon Basin.

All ecosystems depend on common species to maintain biodiversity by creating and sustaining niches for more specialized species (Ellison et al. 2005, Gaston and Fuller 2008, Ellison and Degrassi 2017). The foundation species concept claims that common species (locally abundant and regionally common) shape the structure of ecological assemblages and modulate ecosystem processes (Dayton 1972, Ellison et al. 2005). Foundation species have unique and functionally irreplaceable combinations of traits (Ellison et al. 2005), making the occupancy of these species critical to maintain community stability (Ellison and Degrassi 2017). Although this relationship (morphological diversity versus functional diversity) is not well elucidated in ants or insects in general, we argue that common ant species may represent a fundamental group of foundation species, as they maintain most of the morphological – and possibly functional – diversity in the Brazilian Amazon Basin.

The diversities of life history, shape, and size in MES suggest that ecological processes are related to species with different traits because they are more likely to play complementary roles (Hooper et al. 2005, Mouillot et al. 2011). In particular, two ant genera, *Cephalotes* and *Camponotus*, drove morphological changes in the boundary of the ant morphospace. *Camponotus* is a hyperdiverse genus with over 1000 species, exhibiting remarkable complexity within its global distribution (Bolton 2024). Species range from moderately small to large, and from highly abundant and conspicuous to rare and cryptic, but also display significant intraspecific and geographic variations (Shattuck 2005). These ants thrive across diverse habitats and microhabitats, including nesting in the ground, twigs, dead wood, or tree canopy (Baccaro et al. 2015, Mackay and Mackay 2019). Most species demonstrate a highly adaptable and generalist diet (Baccaro et al. 2015). In contrast, *Cephalotes* have a diet based largely on pollen and a polymorphic worker caste (for most species), with some individuals presenting elaborate heads used to defend the nest entrance (i.e. phragmotic defense morphology) (De Andrade and Baroni Urbani 1999, Powell et al. 2020). Morphological specialization in *Cephalotes* can lead to greater performance of behaviors and also has been linked to higher diversification rates (Ferry-Graham et al. 2002). The large contribution of these genera to the ant morphospace implies that different life-history strategies (dietary, behavioral, and reproductive) are related to morphology and morphospace occupation in an abundant and diverse group in the Neotropical region.

Traits related to leg size, antenna size, eye position, and petiole size drive variance in the morphology of ant species across habitats, but further studies are still needed to better understand the relationship between ant traits and ecosystem functions. Overall, previous studies have shown that larger ants move more rapidly (Hurlbert et al. 2008) and can carry larger loads (Gravish et al. 2012), which can increase their effectiveness in seed dispersal (Gómez and Espadaler 2013) or efficiency in carrion decomposition and other resources' removal processes (Nooten et al. 2022, Bogar et al. 2024). Ocular characteristics may affect predation rates and foraging efficiency, ultimately influencing the flow of energy within ecosystems. Finally, although petiole measurements have yet to be accurately tested in ant trait-based ecology, the petiole is recognized as a fundamental evolutionary novelty underpinning the success of apocritan hymenopterans (Grimaldi and Engel 2005, Siqueira and Silva 2021). Within this framework, the petiole emerges as a critical trait influencing ant interactions and predation, given its role in connecting the mesosoma and gaster.

We found a smaller contribution of MES to morphological diversity in the anthropic and dense forest habitats. Although they are markedly distinct habitats in their characteristics (Table 1), we hypothesized that disturbed habitats would be more related to this pattern. Common ant species make up most of the MES in the Amazon Basin, and these were mainly recorded in impacted environments. Although dense forests are described as undisturbed (Matricardi et al. 2020), ant surveys in the Brazilian Amazon were conducted mainly close to roads and urban areas (Andrade-Silva et al. 2022). Ultimately, as new species are added to the morphospace, they tend to fall within the area delimited by MES, allowing a more uniform filling of the morphospace and proportionally explaining the high taxonomic diversity found in impacted habitats.

Another factor explaining the contribution of MES in our study could be related to the high heterogeneity of the Amazon Basin, influencing the structure and composition of vegetation within each habitat (Ab'Saber 2002). Differences in vegetation structure have contributed to greater morphological differentiation (Vollstädt et al. 2017, Ng et al. 2018), including ants in the Amazon (Fichaux et al. 2019, Siqueira and Silva 2021). Furthermore, functional diversity has shown different responses when higher or lower grain resolutions are employed (Remeš et al. 2021). Therefore, although we did not control for the effect of vegetation complexity within different Amazonian habitats, it is possible that studies focusing on more refined Amazonian habitats may reveal further detailed patterns.

Functional specialization and functional originality are related to evolutionary mechanisms that promote the use of different niches (Micheli and Halpern 2005, Mouillot et al. 2007). Despite many different habitats, low functional specialization and functional originality values can be explained by shared combinations of traits associated with species distributed in the Amazon. Omnivorous ant species, widely distributed in the Amazon Basin (Vasconcelos et al. 2010, Andrade-Silva et al. 2022), provide the greatest morphological diversity, and thus can also sustain high functional redundancy among habitats. The lower proportion of specialist morphologies, represented by FSpe values, may be related to the absence of surveys in protected areas and those far from main access routes in the Amazon (Andrade-Silva et al. 2022), which are places where rare and unique morphological species are more likely to be recorded (Leitão et al. 2016). Conversely, possible explanations for these results may thus include environmental disturbances. Human-induced disturbances are now widely common in the Brazilian Amazon (Matricardi et al. 2020), and several studies have shown functional impoverishment of assemblages under habitat degradation (Villéger et al. 2010, Reich et al. 2012, Mouillot et al. 2013b, Martello et al. 2018).

Our results suggest that a few morphologically extreme species (approximately 11%) capture most of the morphological variation of ant fauna in the Brazilian Amazon habitats. Although additional studies are needed to understand the interplay between morphological variation and functional responses or ecosystem services, our results suggest high functional redundancy in ants among forest habitats across the Amazon. Simultaneously, our results corroborate previous studies (Mouillot et al. 2014, Su et al. 2019) that have reported that substantial proportions of morphological diversity are supported by a few species, suggesting that similar events may have shaped processes of morphological diversification in highly diverse taxa and ecosystems. Most importantly, species that contributed disproportionally to the morphological space were common, not rare. Taken together, these results shed light on one of the hallmark characteristics of ants, their relative resilience in the face of disturbance, and they also reinforce calls made by others (Ellison et al. 2005, Gaston and Fuller 2008, Gaston 2010) about the need to consider the roles that common species and their morphologies play in maintaining biodiversity and ecosystem processes.

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**Joudellys Andrade-Silva**: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Investigation (lead); Methodology (lead); Validation (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Fabrício B. Baccaro**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Lívia P. Prado**: Data curation

(equal); Methodology (equal); Validation (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Benoit Guénard**: Data curation (lead); Writing – original draft (supporting); Writing – review and editing (equal). **Jamie M. Kass**: Formal analysis (lead); Writing – original draft (supporting); Writing – review and editing (equal). **Dan L. Warren**: Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Evan P. Economo**: Data curation (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Rogério R. Silva**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07121X.

### Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pg4f4qrzf (Andrade-Silva et al. 2024).

### Supporting information

The Supporting information associated with this article is available with the online version.

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