



Original research papers

## Predicting resource use in ant species and entire communities by studying their morphological traits: Influence of habitat and subfamily



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### ABSTRACT

I investigated whether the morphological traits of Neotropical ants can be used to infer food resource use by individual species and by entire communities, and whether these relationships are related to habitat type and/or by morphological differences between ant subfamilies. I attracted ants using food baits that represented different ecological processes (e.g. predation, granivory, detritivory, nectarivory) in five habitat types along a land-use gradient (from forests to gardens). I assessed ant activity at the baits and characterized 64 species from six subfamilies according to their food use and community-level resource exploitation intensity in the different habitats. Next, I performed a Mantel test to reveal the relationships between 13 morphological measures and resource use at the species level. I then used ant clades (i.e. subfamily) and habitat to rank the ants along three axes of variation in relation to their morphology and food resource use. Finally, I tested whether associations existed between the community-level exploitation intensity for such resources and the distribution of morphological trait values using the “4th-corner” analysis. Morphological traits were closely linked to the species' ability to exploit different resources. These relationships were affected by subfamily and, to a lesser extent, by habitat type. The characterization of trait sets for entire communities was not useful, however, in predicting the intensity of the exploitation of different types of resources in varying environmental conditions. I conclude that morphological traits are accurate predictors of the ecology of species, but they should be used with caution when trying to understand community-level patterns.

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### 1. Introduction

How important is the shape of an organism in determining its ecological performance exploiting resources? The relationships between form and function have long fascinated ecologists (Darwin, 1859; Nyhart, 1995; Russell, 1916). Nature provides many examples of morphologically similar organisms living in analogous environments or using the same type of resources despite their different origins and histories (ecological convergence *sensu* McGhee, 2011). In the last decade, the morphological characterization of species from very different taxa (including terrestrial vertebrates and invertebrates, fish and plants) has been progressively applied towards understanding how ecological communities are organized so as to provide and maintain ecosystem functions *via* their use of resources (Frimpong and Angermeier, 2010; Kattge et al., 2011; Pey et al., 2014; Wilman et al., 2014). The premise is that morphological differences between species directly affect their ecological

performance in exploiting different resources, thus mediating their ecological functions (Lavorel and Garnier, 2002; Violle et al., 2007; Wainwright, 1994).

On the other hand, organisms differing in their forms can also display similar ecological functions (e.g. ants, birds and rodents consume seeds; Brown et al., 1979). Moreover, the necessity of species to adapt to their biophysical environment, to limited resources and to competitors simultaneously may result in ecological trade-offs when trait value combinations beneficial in a particular situation result in a poor performance in another (Kneitel and Chase, 2004; Ravel et al., 2012; Schuwirth et al., 2015). Finally, species with a common ancestry (i.e. clades) are frequently phenotypically similar, which is why understanding taxonomic structure provides an alternative to relying on adaptive hypotheses to elucidate ecomorphological patterns (Losos, 2008; Mayfield and Levine, 2010). Therefore, considering the common ancestry of species may be helpful in accounting for the underlying ecological traits essential to the ecological role or the survival of species in a given environment (Barton et al., 2011; Gibb et al., 2015).

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In this study, I investigated the relationships between morphology and the use intensity of different food resources by Neotropical ants in a series of habitats representative of a land use gradient. Ants are ecologically successful organisms consuming a wide variety of food resources in many types of ecosystems (Brandão et al., 2012; Folgarait, 1998). Ant species can be, *inter alia*, predators, granivores, indirect herbivores, fungus-eaters, or detritivores. (Brandão et al., 2012; Fowler and Delabie, 1995; Houadria et al., 2015). Several studies have provided evidence of the relationships between the morphology of ant species and their use of food resources and/or their survival in different habitat conditions (Arnan et al., 2012; Gibb et al., 2015; Gibb and Parr, 2013; Weiser and Kaspari, 2006). Moreover, the morphological and ecological characteristics of species such as food use, habitat preference are frequently conserved at greater taxonomic levels like subfamilies (Andersen, 1995; Brandão et al., 2012; Gibb et al., 2015; Weiser and Kaspari, 2006); but see (Yates et al., 2014). No studies to date have tried to examine, however, how the links between morphology and food resource use vary in different environments or whether these relationships are affected when the species belong to different clades. I hypothesized that morphological traits (considered for both single species and for entire communities) can be used as a surrogate for ecological functions that are related to the use of food resources (e.g. predation, detritivory, nectarivory). Because I wanted to understand the role of morphology in explaining such trophic functions regardless of other major drivers of morphology, I separated the influence of local resource use from that of habitat and clade (*i.e.* subfamily).

The following questions were particularly addressed: i) is the morphology of Neotropical ant species related to their use of food resources?, ii) are these relationships affected by habitat and subfamily?, and iii) can we use sets of traits obtained for entire communities to predict the foraging intensity of ants for different types of food?

## 2. Materials and methods

### 2.1. Study site and sampling

The study took place at La Montagne de Singes and several agricultural areas nearby situated in the coastal part of French Guiana. The area presents a mosaic of habitat types that enabled to examine a gradient of land-use intensity representative of the landscape transformations occurring in much of the tropics (FAO and Jrc, 2012). For this purpose, I selected five habitat types: *terra firme* forests, floodplain forests, forest edges, croplands, and gardens. The *terra firme* and floodplain forests are old-growth forests representative of the rainforests covering a large part of the Amazon Basin. The floodplain forests are seasonally flooded so that they include a greater regime of natural disturbance than do the *terra firme* forests. The forest edges run alongside paths providing access to agricultural areas. The croplands are traditional cropping systems which were 3–5 years old at the time of this study and contained a mixture of crops including, *inter alia*, manioc, pineapple, mango trees, and sugar cane. The gardens are essentially lawns surrounding houses which are frequently mowed for aesthetic reasons, and represent the most disturbed environment. I selected three representative 0.12 ha plots for each type of habitat. The plots consisted of (30 × 40 m) rectangular grids where 20 sampling locations were separated by 10 m in a grid system. In each sampling location, six food types were used to attract ants to the baits. All of the plots were within a radius of 3 km to ensure that the species present belonged to the same pool of species. In addition, to avoid spatial autocorrelation effects, the plots representing different habitat types

were interspersed and a minimal distance of 200 m was respected between plots of the same kind.

The food resources used to attract ants were seeds (a mixture of seeds and peanuts ground to different sizes), dead insects (mashed *Tenebrio molitor* mealworms), sucrose (25% w/w water solution), chicken excrements, live termites (about 20 *Anoplotermes* sp. with fragments of termite mound to induce them into staying in the Petri dish), and large prey (two differently sized, live *Tenebrio molitor*). To avoid attraction biases related to food quantity, all of the baits contained approximately 2.5–3 g of food. The baits were offered in Petri dishes lined with parafilm. For each bait trap, the lid was placed next to the base to enable the Petri dish to be closed at the end of the experiment. All of the baits were presented once in each of the locations in two separate sampling sessions. In the first session, non-prey items were placed in alternative positions, encircling the sampling locations and separated by at least 50 cm from one another. In the second session, only prey items were offered. This was necessary because the prey were allowed to move in order to assess which ants were capable of capturing live insects. When the insects escaped from the baits, they were returned or replaced by another insect. For each sampling session, the ant activity at the baits was monitored for 1 h. Each sampling location was surveyed every 5 min on average to record information on the ant species present and their behaviour (e.g. whether they actively exploited the items). While some ants may have been overlooked, this technique allowed to provide a more thorough general description of the ant activity in the area studied. After the experiments were completed, the ants were taken back to the laboratory and killed by freezing. Then, the specimens were counted and identified to genera using the identification guide developed by Bolton (1994) as well as other guides providing updates on ant classification (Bolton, 2003; Schmidt and Shattuck, 2014). Then genera were split into morphospecies on the basis of their morphological characters.

### 2.2. Morphological measures

Thirteen continuous morphological measurements were chosen to characterize the shape of the ant species studied (Table 1). The traits chosen were selected for their ecological relevance based on previous studies (Gibb et al., 2015; Parr et al., 2016; Silva and Brandão, 2010; Weiser and Kaspari, 2006). Measurements were carried out on six workers from monomorphic species (*i.e.* species with a unimodal type of worker) and ten workers for those species with several types of workers (multimodal; *i.e.* *Camponotus*, *Solenopsis*). In each case, I tried to encompass the variability of the workers. For species belonging to the genus *Pheidole*, the soldier caste was not considered in the measurements since this special type of ant has an ambiguous function depending on the species, and they neither forage nor participate in recruitment (Wilson, 2005). For each ant, standard linear measurements were taken using an ocular micrometer mounted on a dissecting microscope accurate to 0.01 mm.

Weber's length (the distance from the anterodorsal margin of the pronotum to the posteroventral margin of the propodeum; (Weber, 1938) was used as the main descriptor of body size while other traits were used to describe the shape. Allometries were obtained by dividing all of the traits by Weber's length. Average species' trait values were used for all of the analyses.

### 2.3. Species-level foraging intensity for resources

To assess the ecological roles of ant species, I considered that two aspects were of importance: the use frequency of each of the six resources by a species, and the number of workers recruited towards these resources. To provide a balanced weight to exploitation frequency and recruitment, I applied the 4th-root

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