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Worker morphology of the ant *Gnamptogenys striatula* Mayr (Formicidae, Ectatomminae) in different landscapes from the Atlantic Forest domain

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ABSTRACT

Morphological traits, such as size and shape, may reflect a combination of ecological and evolutionary responses by organisms. Ants have been used to evaluate the relationship between the environment and species coexistence and morphology. In the present study, we analyzed the morphology of workers of *Gnamptogenys striatula* Mayr in different landscapes from the Atlantic Domain in southeastern Brazil, focusing on the variation in the morphological attributes of these populations compared to those from a dense ombrophilous forest. Eighteen morphological traits of functional importance for interactions between workers and the environment were measured to characterize the size and shape of the workers. In general, the results show that ants of urban areas possess some morphological attributes of smaller size, with highly overlapped morphological space between the populations in forested ecosystems. Further, some of the traits related to predation were relatively smaller in modified land areas than in the populations from preserved areas of dense ombrophilous forest. These results help broaden the knowledge regarding morphological diversity in *G. striatula*, suggesting that the characterization of the morphology may be important to quantify the effects of land use on morphological diversity, and presumably, to facilitate the use of ants as biological indicators.

Introduction

During evolution, organisms undergo selection based on their morphological traits (Irschick et al., 2013), such as body size (Peters, 1983). These quantitative measurements are influenced by the species' evolutionary history and ecology (Wainwright, 1994; Yates and Andrew, 2011), making them a basic tool for analyzing the relationships between taxa and environment. Body size is related to fertility (Kovacs et al., 2008), survival (Schorr et al., 2009), and dispersal ability (Pearce-Duvet et al., 2011), and can be shaped by direct genetic effects, maternal effects or the social environment (Meunier and Chapuisat, 2009).

Arthropod populations are influenced by climatic factors, different soil-management strategies, and the quality and availability of resources (Andow, 1991; Lomônaco and Germanos, 2001; Silva et al., 2009). Overtime, these factors can lead to morphological and physiological changes and behavioral traits in individuals from each population (Silva et al., 2009). In beetles (Ribera et al., 2001), termites (Scharf et al., 2007), shredders (Larrañaga et al., 2009), and ants (Yates and Andrew, 2011) alterations have been described in the external morphology in response to environmental modifications.

Ants are particularly interesting for the study of the causes and consequences of variations in body size (Oster and Wilson, 1978; Pie and Tschá, 2013) due to their complex social organization, combined with the fact that the morphology of an individual ant colony is a distribution of its workers' size and shape (Weiser and Kaspari, 2006). In these insects, body size can indicate significant interactions among genetic factors, the resource availability in the habitat, the energetic cost of producing individuals of different sizes, abiotic factors such as temperature (Kaspari, 1993; Kaspari et al., 2000a, b), and possibly the environment heterogeneity (Kaspari and Weiser, 1999, 2007; Costa et al., 2010; Gibb and Parr, 2013).

Gnamptogenys striatula Mayr, 1884 is a polygynous ant species and their colonies contain either differentiated queen or gamergates (Giraud et al., 2000). This species can be classified as a medium-sized generalist predator (Silva and Brandão, 2010) and it feeds on small arthropods, among several species of insects (Lattke, 1990). The colonies of this ant consist of 150 to 200 individuals (Lattke, 1990). The ants do not monopolize large amounts of resources, and trails of pheromones are more commonly used for

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shifting the nest than for foraging (Blatrix et al., 2002). This species occurs throughout Central and South America (Kempf, 1972; Giraud et al., 2000) and across biomes, including disturbed areas (Souza et al., 2010; Mentone et al., 2011). *Gnamptogenys striatula* can form nests in trunks (Lattke, 1990) and twigs (Fernandes et al., 2012; Souza et al., 2012) at different stages of decomposition in the litterfall; however, nests can also be built under rocks and in rock crevices (Lattke, 1990), and workers can be observed foraging in the litterfall (Morini et al., 2012; Suguituru et al., 2011, 2013). More data about the biology of *G. striatula* have been reported by Giraud et al. (2000) and Blatrix and Jaisson (2000).

The present study investigates populations of *G. striatula* from different locations in southeastern Brazil using morphological traits. Because this species has been reported in various ecosystems with distinct land uses (Lattke, 1990; Morini et al., 2007; Pacheco et al., 2009), we analyzed the morphology of workers of *G. striatula* compared to those from a dense ombrophilous forest, which represents a preserved environment. The main aim of this study is to characterize continuous morphological traits of *G. striatula* in various landscapes from the Atlantic Forest Domain.

Material and methods

Gnamptogenys striatula workers were obtained during different collection expeditions in southeastern Brazil using Winkler extractors, Berlese funnels, pitfall traps, and sardine baits. A distance of 20m between the sampling points was used for all of the collection methods to avoid pseudoreplication (Baccaro et al., 2011). Four ecosystem types with distinct phytophysiognomies were selected (Table 1). Regardless of their actual floristic composition, all of the ecosystems belonged to the Atlantic Forest Domain (Fiaschi and Pirani, 2009) (Fig. 1). The number of collection areas in each ecosystem ranged from two to four (Table 1).

The morphological parameters were measured using a micrometer ruler coupled to a stereoscopic microscope. Eighteen traits (Table 2) with functional significance were measured in each *G. striatula* worker following Silva and Brandão (2010). According to available nests, eleven to 80 workers were measured in each of the selected ecosystems.

We analyzed trait variability according to the different levels of variation using both single-trait (linear mixed models) and multi-trait analyses (principal component analyses). We used linear mixed effects models, which are appropriate to represent hierarchical data structures. Models were used for each morphological trait using the forest type as a fixed effect and a random-intercept site effect. Variances were estimated by maximizing the log-likelihood using Restricted Maximum Likelihood (REML). The residual of the regression for each trait on a measure of body size (Weber's length) was used in the analysis because ant traits were significantly and positively correlated to body size. We used principal component analysis based on covariance matrix of the original measures at the individual level to describe the morphological space's general structure. Further, we determined the probability of correctly attributing a given individual to a forest based on the individual's morphological traits. This matching was conducted by performing a linear discriminant analysis (LDA), which identifies the linear combination of continuous explanatory variables that best separates two or more classes of a categorical variable. LDA maximizes the ratio of the between-groups variance to the total variance and can be projected onto new observations. All the statistical analyses were performed with R. 3.0.2 (R Core Team, 2014) using the packages nlme, ade4 and MASS.

Results

The variation in morphological traits among *G. striatula* workers in each area of the Atlantic Domain in southeastern Brazil was quantified (Table 2). PCA on the data at the individual level showed that the first axis explains 41% of the variance, which was mainly related to petiole height (0.59), femur length (0.49) and Weber's length (0.45). Principal component 1 reflected size variance, but as the coefficients are not equal and mandible length had a negative coefficient of the eigenvectors, it retained some size allometry. The second principal component explains 22% of the variance, which was related to petiole height (0.58), mandible length (–0.31), tibia length (–0.24) and Weber's length (–0.23) (Table 3; values in bold). The PCA suggested a size gradient from ants from urban areas to exotic and rainforest individuals. The upper left part of the biplot shows individuals with lower size on both PC1 and PC2 axes; the lower right part shows individuals associated with larger size (but smaller petiole height relative to their body size); some individuals from exotic forest and from dense ombrophilous forest showing a large petiole height relative to their size were associated with high positive values along axes 1 and 2, determining a cluster of points in the morphospace (Fig. 2).

The probabilities of attributing individuals to the correct forest based on the individuals' trait values were overall moderate; in total, 58% of specimens were predicted accurately. The specimens of commercial crops were well predicted (100%), while the specimens from other sites were moderately successfully predicted (52%, 58%, and 57%) for exotic forest, dense ombrophilous forest and urban areas, respectively.

Table 1.
Characterization of the *Gnamptogenys striatula* worker-collection areas in the Brazilian Atlantic Domain.

Types of ecosystems	Litterfall	Number of workers			
Dense ombrophilous forest; > 80 years of regeneration.	Abundant litterfall	Rainforest (RF1) N = 20	Rainforest (RF2) N = 20	Rainforest (RF3) N = 20	Rainforest (RF4) N = 20
Exotic vegetation; *Pinus elliotti* and *Eucalyptus saligna*; crops abandoned > 30 years (developed understory).	Litterfall consisting of acicular (*Pinus*) and eucalyptus leaves.	Exotic Forest (EF1) N = 20	Exotic Forest (EF2) N = 20	Exotic Forest (EF3) N = 20	Exotic Forest (EF4) N = 20
Underbrush from squares and urban parks	Not very abundant litterfall	Urban area (UA1) N = 20	Urban area (UA2) N = 20		
Commercial *Eucalyptus saligna;* crop (without understory; managed for 7 years)	Not very abundant litterfall; consists of eucalyptus leaves when present	Commercial crop (CC1) N = 5	Commercial crop (CC2) N = 6		