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The influence of environmental complexity on the worker morphometry of ant assemblages

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Abstract

The objective of the present study was to test whether environmental complexity influences the morphology of leaf litter worker ants, as predicted by the size-grain hypothesis. We collected data from three types of vegetation (shrubby, shrubby-arboreal, and arboreal) in Restinga da Marambaia, southeastern Brazil. The shrubby vegetation had a very superficial leaf litter compared to the other two vegetation types. We measured head width, body length, and femur length of the ants collected in each vegetation type. We used average head width (HW) as a proxy for body size. The shrubby-arboreal and arboreal vegetation types were assumed to represent more rugose environments than the shrubby vegetation. Leg length allometry was observed in each and all vegetation types. We did not find significant differences in body size and allometry of ant assemblage among vegetation types. Hence, the size-grain hypothesis was corroborated only for leg allometry, but it did not predict a general environmental influence on ant morphometry.

Introduction

Body size is the main phenotypic characteristic of organisms, because it strongly affects the way they interact with the environment. Ants are organisms with wide intra- and interspecific variability in body size (Kaspari & Weiser, 1999; Geraghty et al., 2007, Hurlbert et al., 2008). The size-grain hypothesis predicts that small animals perceive the terrestrial surface more rugose than large animals (Kaspari & Weiser, 1999). A benefit of being small would be exploiting food and shelter available in the interstices of the environment (Kaspari & Weiser, 1999; Espadaler & Gómez, 2001; Hurlbert et al., 2008). Furthermore, large ant species tend to have proportionally longer legs (Kaspari & Weiser, 1999), which allows them to move faster in planar environments, and, hence, makes it easier for them to find resources (Hurlbert et al., 2008; Gibb & Parr, 2013).

Small ant species forage more efficiently in rugose environments than in planar environments (Farji-Brener et al., 2004; Sarty et al., 2006). If small ants have more advantages in rugose environments, we could expect the ant community to have a larger proportion of small-bodied species in more rugose environments. A study carried out in African savannas did not corroborate this prediction (Parr et al., 2003). However, Farji-Brener (2004) suggested that this may have occurred due to the use of environments whose rugosity gradient has been created by recent factors and that new tests should be restricted to natural gradients of environmental rugosity.

In Brazil, Restinga environments are very heterogeneous in terms of vegetation: it is possible to find from forest sites to sites with sparsely distributed herbs on sand banks (Menezes

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& Araújo, 2005). Different vegetation types have different soil cover, which creates environments with different degrees of leaf litter cover (Vargas et al., 2007). The amount of leaf litter affects ant species richness (Vargas et al., 2007; Bastos & Harada, 2011) and sites with differences in leaf litter can be used to carry out natural experiments aimed at testing the size-grain hypothesis. Hence, the objective of the present study was to test whether the Restinga ant communities with different types of vegetation differ in terms of worker ant morphometry. We aimed at testing three predictions: (1) the larger the body size of an ant species, the higher the ratio between leg length and body size; (2) rugose environments should have ant species with smaller body size than planar environments; (3) environmental rugosity influences the relationship between leg size and body size.

Material and methods

Study area

We collected the data in two sampling events: one in the dry season (August, 2004) and the other in the rainy season (March, 2005), in three vegetation types in Restinga da Marambaia (23°03' S 44°03' W), state of Rio de Janeiro, southeastern Brazil. The first vegetation (shrubby) is homogeneous with predominance of *Allagoptera arenaria* (Gomes) O. Kuntze (Arecaceae) and has no or superficial leaf litter, composed mainly of leaves of this palm. The second vegetation (shrubby-arboreal) is more heterogeneous, denser, and has higher plant richness than the first; its soil is covered by leaf litter. The third vegetation (arboreal) is a forest with a plant cover less dense than that of the second vegetation. It is the most heterogeneous vegetation, with the highest plant richness, and tallest trees. It has high density of bromeliads in the understory and deep leaf litter cover (Menezes & Araújo, 2005). The shrubby vegetation was considered a planar or less rugose environment, because its leaf litter cover is thinner and more superficial than that of the other vegetation types. The shrubby-arboreal and arboreal vegetation types had more and deeper leaf litter cover; hence, they were considered rugose environments (Vargas et al., 2007).

Sampling procedures

In each vegetation type, we marked three 1,200-m^2 plots (40 x 30 m), 100 m to 200 m apart from each other. The plots in the shrubby vegetation were ca. 500 m apart from the plots of the shrubby-arboreal vegetation, and the plots of both of these vegetation types were 1,000 m apart from the arboreal vegetation. In each plot, we set up 20 pitfall traps, at 10 m from each other, which remained open for 48 h in the field (see Vargas et al., 2007).

Morphometry data

We measured head width and femur length, in millimeters, of three specimens of each ant species, whenever possible. Head width is considered a precise standard measurement of body size (Hölldobler & Wilson, 1990; Kaspari & Weiser, 1999) and femur length is a good proxy for total leg length.

Data analysis

In total, we analyzed 84 out of the 92 species collected by Vargas et al. (2007). To test the prediction that body size influences the ratio between leg length and body size, we used average head width (HW) as an independent variable and the ratio between femur length (FL) and HW as a dependent variable in a linear regression. To test whether environmental rugosity influenced the morphometry of worker ants, we compared HW and the relationship between HW and FL among the three vegetation types with a non-parametric analysis of variance. All analyses were performed in SYSTAT 8.0.

Results

Head width (HW) explained a significant part of the variation observed in the femur length/head width ratio for both the total set of species ($R^2 = 0.1027$; $p = 0.003$; Figure 1) and for each of vegetation type separately (shrubby, $R^2 = 0.102$; $p = 0.005$; shrubby-arboreal, $R^2 = 0.115$; $p = 0.007$; arboreal, $R^2 = 0.137$; $p = 0.002$; Figure 2).

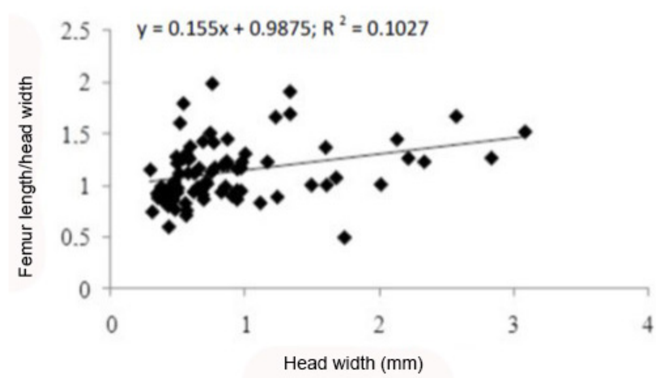

Fig 1. Relationship between head width and femur length/head width ratio (p = 0.003) for the ant fauna of Restinga da Marambaia, state of Rio de Janeiro, southeastern Brazil.

The average ant head width for the total dataset was 0.873 mm (standard error = 0.064). The average head width was 0.944 mm (standard error = 0.119) for the shrubby vegetation, 0.911 mm (standard error = 0.079) for the shrubby-arboreal, and 0.820 mm (standard error = 0.065) for the arboreal vegetation. Average body size did not differ significantly among vegetation types (Kruskal-Wallis, U = 0.418; p = 0.811; Figure 3). In addition, environmental rugosity did not

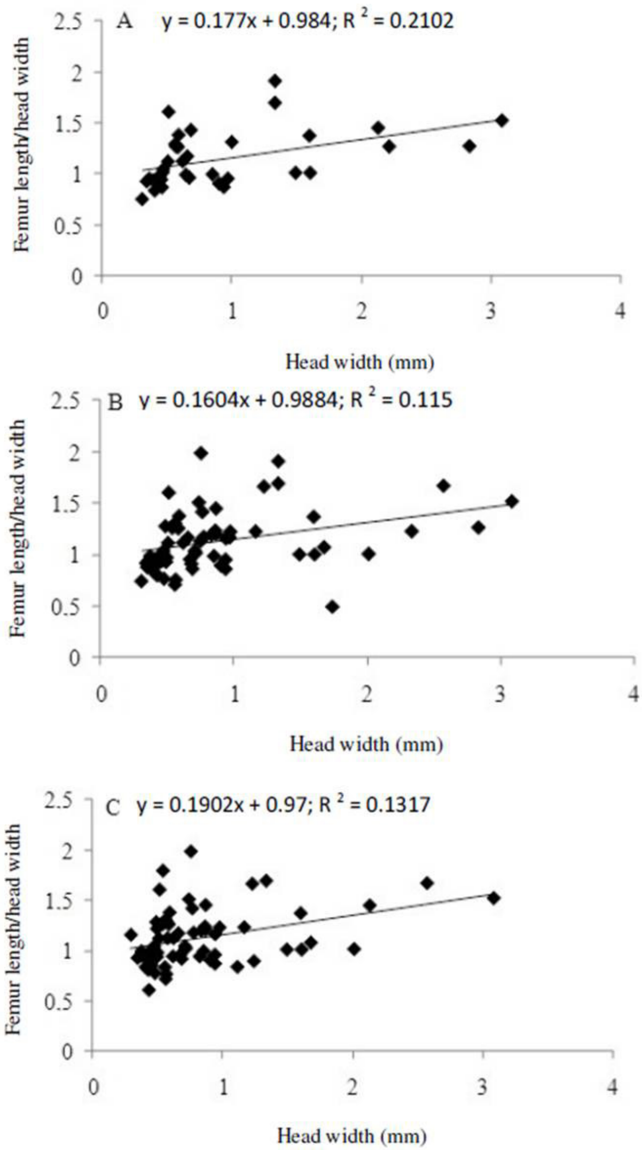

Fig 2. Relationship between ant head width and femur length/head width ratio in each vegetation type in Restinga da Marambaia, state of Rio de Janeiro, southeastern Brazil: (A) shrubby vegetation ($p = 0.005$), (B) shrubby-arboreal vegetation ($p = 0.007$), and (C) arboreal vegetation ($p = 0.002$).

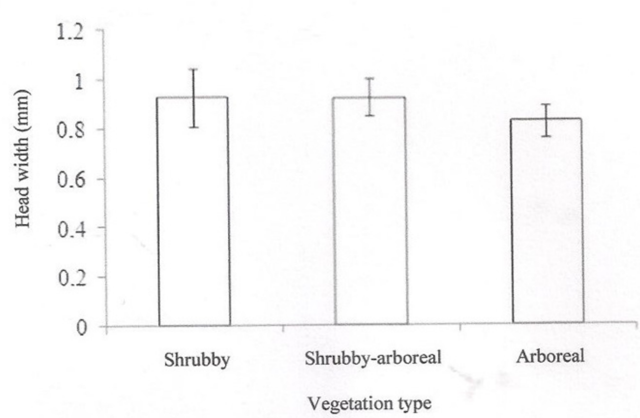

Fig 3. Head width (HW) of ants in different plant vegetation types in Restinga da Marambaia, state of Rio de Janeiro, southeastern Brazil.

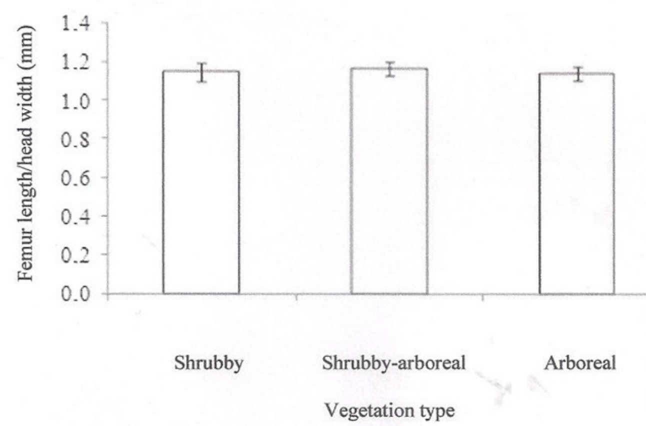

Fig 4. Femur length/head width ratio (FL/HW) of ants in different vegetation types in Restinga da Marambaia, state of Rio de Janeiro, southeastern Brazil.

influence the FL/HW ratio (Kruskal-Wallis, $U = 0.210$; $p = 0.900$; Figure 4).

Discussion

The three vegetation types analyzed in the present study differed from each other in ant species richness. The most complex vegetation type with highest plant diversity has also the richest ant fauna (Vargas et al., 2007). Our results confirmed allometry in leg size (first prediction) for the entire ant fauna and each vegetation separately. Larger ants had disproportionally longer legs than smaller ants, which corroborates previous studies (Kaspari & Weiser, 1999; Espadaler & Gómez, 2001; Parr et al., 2003).

Farji-Brener (2004) suggested that size comparisons of ant species should be done between environments with natural differences in rugosity. This is the case of the vegetation types studied by us, which, due to variations in the amount of leaf litter, formed a rugosity gradient (Vargas et al., 2007). According to the predictions of the size-grain hypothesis, we expected that the most complex environment, which corresponded to the vegetation type with highest plant diversity and highest amount of leaf litter, would have an ant fauna with smaller average body size than the vegetation type with lower amount of leaf litter. In addition, environmental rugosity would also affect the relationship between leg length and body size; more rugose environments would tend to be occupied by species with proportionally shorter legs (Kaspari & Weisser, 1999).

However, we did not find a relationship between workers morphometry and environmental rugosity, because no significant difference in average body size among vegetation types was detected: environmental rugosity did not affect leg allometry either. Parr et al. (2003) carried out similar tests in African savannas and found the highest abundance of small ants in the more planar environment, with the lowest amount of leaf litter, contrary to their expectations. Conversely, Gibb and Parr (2013) found a relationship between environment rugosity and body size, as expected, but not in all situations tested.

Parr et al. (2003) rejected the hypothesis that the ant sampling method (pitfall traps) might have influenced the results. However, pitfall traps tend to capture larger species than other sampling methods (Vargas et al., 2009). Very small species, which do not move much, may not be captured in pitfalls; hence, there might be a bias in the result of size comparisons between faunas (Vargas et al., 2009). It would be important to test this hypothesis with the same morphometric analyses used in the present study, but with samples obtained with different methods.

The lack of significant differences in ant size observed in the studied communities in different Restinga vegetation types may have resulted from large species with relatively short legs that can succeed in rugose environments and from small species with long legs that can succeed in planar environments (Gibb & Parr, 2013). In addition, it is important to consider a potential influence of intraspecific variations on those tests. For example, in the same colony of *Atta robusta* or *Camponotus crassus*, which are species found in the Restinga, worker ants with different body sizes could explore resources of different sizes and forage in environments with different rugosity, and, therefore, increase the total success of the colony (Farji-Brener et al., 2004; Longino, 2005). Besides *A. robusta* and *C. crassus*, other species such as *Odontomachus chelifer* and *Trachymyrmex atlanticus* have intraspecific variations in body measurements.

The lack of consensus about the influence of the environment on the morphometry of leaf litter worker ants suggests that other factors may influence the results (Chow & Parr, 2004). Other morphometric data could also be added to comparative analyses on environmental influence (Silva & Brandão, 2011). However, ants with different body sizes use the habitat in different ways and can explore different resources (Kaspari & Weisser, 1999). The lack of differences in ant morphometry among environments can simply mean that the species in the richest community shares the resources in the rugose environment, which has the highest amount of leaf litter, according to its characteristics; larger ants can forage on the leaf litter, whereas smaller ants walk in the space within the leaf litter. In spite of interpreting these differences as potential spatial segregation among species, we should consider that they might explain the higher species diversity observed in more complex environments.

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