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# How does tiger moth (Erebidae, Arctiinae) functional diversity respond to environmental and spatial variables?

Carolina Moreno[1], Jennifer Zaspel[2] and Viviane Ferro[3]

[1]Biota Projetos e Consultoria Ambiental Ltda., CEP 74083-360, Goiânia, GO, Brazil; [2]Milwaukee Public Museum, Milwaukee, WI, USA and [3]Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

**Research Article**

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**Corresponding author:**
Carolina Moreno;
Email: s.moreno.carol@gmail.com

## Abstract

Deterministic and stochastic processes are of great importance in influencing the composition of communities. Here, we tested if deterministic and stochastic processes have the same force of influence on functional traits of tiger moth communities. Specifically, we hypothesised that the functional traits of the tribe Arctiini would be more strongly influenced by stochastic processes (associated with spatial variables), given that these moths are primarily diet and habitat generalists within a highly diverse clade. They also exhibit high morphological trait dissimilarity and are capable of occupying a wide range of vegetation habitats. On the other hand, we hypothesised that the functional traits of the tribe Lithosiini would be more influenced by deterministic processes (associated with environmental variables), given that these moths are primarily diet and habitat specialist moths and tend to occur in more specific vegetation types. In agreement with our hypotheses, the functional traits of Arctiini species were better explained by variables related to stochasticity, while the functional traits of Lithosiini were explained by deterministic processes only. Thus, the processes shaping moth distributions across communities may vary according to species' functional traits and interspecific relationships.

## Introduction

The distribution of species in communities can be influenced by deterministic, stochastic or both processes (Arnan et al. 2015; Leibold et al. 2004; Leonov 2023; Moreno et al. 2016; Sha et al. 2024; Winegardner et al. 2012). Deterministic processes are mainly related to environmental filtering and to species interactions and their relationships to abiotic and biotic factors, corresponding to the niche-based models (Kraft et al. 2008; Leonov 2023; Pavoine and Bonsall 2011). On the other hand, stochastic processes are mainly related to ecological drift, dispersal limitations, random speciation and extinction, and fitness equivalence of all individuals (Hubbell 2001; Leibold et al. 2004; Leonov 2023; Pavoine and Bonsall 2011).

Studies have shed new light on how spatial and environmental processes may shape species diversity at the community scale (Arnan et al. 2015; Carvalho and Tejerina-Garro 2015; Leonov 2023). Both space (related to stochastic forces) and environment (related to deterministic forces) show different results of influence on distinct groups of species, such as habitat generalists and habitat specialists, species that occur in rarity or are common, and groups of species based on their body size and dispersal ability (De Bie et al. 2012; Gonçalves-Souza et al. 2014; Moreno et al. 2016; Padial et al. 2014; Siqueira et al. 2012). Thus, the structure of communities can be influenced by species' functional traits (Arnan et al. 2015; Carvalho and Tejerina-Garro 2015; Siefert et al. 2013; Webb et al. 2002), which are, in large part, dictated by their phylogenetic history (Arnan et al. 2015; Gavilanez and Stevens 2013; Webb et al. 2002).

Characteristics that affect the growth, reproduction and survival of the individual can be considered as a functional trait (Violle et al. 2007), revealing the ecological similarities within communities (Cianciaruso et al. 2009; Pavoine and Bonsall 2011). Thus, using functional traits information for a given species, instead of their taxonomy alone, can help us to better understand the mechanisms of species distributions within communities (McGill et al. 2006). Functional traits can provide critical information that cannot be obtained from scientific nomenclature (Gavilanez and Stevens 2013; McGill et al. 2006), primarily because taxonomic identities offer limited insight into the ecological similarities among species and may not reveal the influence of stochastic and deterministic processes on communities (Pavoine and Bonsall 2011; Siefert et al. 2013).

Within terrestrial arthropods, there is a lack of information about the influence of stochastic and deterministic processes on their communities (reviews by Soininen 2014, 2016), and the few studies addressing this variation partitioning showed a lower percentage of explanation of the pure deterministic factors (i.e., Baldissera et al. 2012; Sattler et al. 2010, but see Gonçalves-Souza

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et al. 2014; Moreno et al. 2016). However, some terrestrial arthropods, such as butterflies and moths, are highly influenced by the environmental conditions of their habitats (Beck et al. 2002; Gonçalves-Souza et al. 2014; Moreno et al. 2014; Moreno et al. 2016; Panzer and Schwartz 1998; Usher and Keiller 1998), as they are often closely associated with plant species, in both the larval (i.e., as herbivores) and adult stages (i.e., as pollinators). Here, we analysed one of the richest clades of Lepidoptera, tiger moths (Brehm 2007; Weller et al. 2009), to answer whether the space or the environment is more important in determining their functional traits structure. About 11,000 species of Arctiinae have been described worldwide (Zahiri et al. 2012), with roughly 6000 occurring in the Neotropics (Watson and Goodger 1986; Weller et al. 2009). Arctiinae is comprised of four tribes: Lithosiini, Amerilini, Syntomini and Arctiini (Zaspel et al. 2014). Species within tribes Arctiini and Lithosiini have different morphological characteristics and highly divergent feeding habits (Hilt and Fiedler 2006; Singer and Bernays 2009; Wagner 2009). The Neotropical region harbours approximately 1170 species of Lithosiini (Heppner 1991). The vast majority of tribe Lithosiini is composed of relatively small moths (Weller et al. 2009) that are primarily lichen feeders (diet specialists, Singer and Bernays 2009; Wagner 2009; Weller et al. 2009) and tend to occur in higher abundances within specialist habitats, such as forested areas (Hilt and Fiedler 2006). Many Lithosiini species are cryptic in the adult phase as an antipredator adaptation (Simmons 2009). Arctiini are the most diverse tribe (around 4758 species occur in the Neotropic region, Heppner 1991), including species variable in their morphology and life histories. They are small- to medium-sized moths that feed on a variety of plants as larvae, including grasses, herbs, shrubs and trees (most of them are diet generalists, Singer and Bernays 2009; Weller et al. 2009). Because Arctiini are mainly diet and habitat generalists, they inhabit a variety of vegetation types (Hilt and Fiedler 2006), making cryptic colouration an unsuitable option (Simmons 2009). The majority of Arctiini moths are aposematic, using this adaptation to display their unpalatability to natural enemies (Simmons 2009). Some Arctiini and Lithosiini species sequester toxic substances from their hosts (mainly pyrrolizidine alkaloids (PAs) and lichen polyphenolics, respectively) that provide them protection against natural enemies (Hartmann 2009; Scott et al. 2014; Zaspel et al. 2014). Many species warn their natural enemies about their unpalatability with bright colouration and mimicry of unpalatable insects like wasps, beetles and butterflies (Bowers 2009; Zaspel et al. 2014).

Differences in morphology, such as body size, wingspan and patterns of colouration of Arctiini and Lithosiini, could be connected to their higher richness and abundance in specific habitat types (Hilt and Fiedler 2006). Body size can also influence the population growth and the distribution of the species in the environment (De Bie et al. 2012; Vogt et al. 2013) and can influence one of the main ecosystem services that is performed by moths in the adult phase (pollination, as described for Sphingidae moths, Agosta and Janzen 2005). Other traits, mainly wing-colour pattern, can influence the probability of moths being predated and parasitised, as many Arctiinae moths signal their unpalatability through warning colouration (Simmons 2009).

Because Arctiini and Lithosiini diverge in several aspects of their ecological niches, it is likely that their functional community structures respond differently to stochastic and deterministic processes. Here, we included other components of biodiversity, the structure of functional traits of moths' communities, to test which processes play a greater role in shaping their community composition. Specifically, we tested if: (1) stochastic processes have a stronger influence on the functional structure of Arctiini, as these moths are primarily diet and habitat generalists and exhibit high morphological diversity (shaped by their phylogenetic relationships), which enables them to occupy a wide range of habitat types. As a result, their functional structure is less constrained by environmental variables (typically associated with deterministic processes); and (2) deterministic processes more strongly influence the functional structure of Lithosiini, as these moths are primarily diet and habitat specialists and tend to occur in higher abundances within specific habitat types. Consequently, environmental variables (associated with deterministic processes) are likely to play a greater role in shaping their functional structure.

## Materials and methods

### Study site

We collected tiger moths in Emas National Park (ENP), located in the Cerrado biome (17°49′–18°28′S, 52°39′–53°10′W), which is one of the 25 documented biodiversity hotspots in the world (Myers et al. 2000). The climate of this tropical region is humid, with three dry months in the winter. The annual rainfall varies from 1200 to 2000 mm, and the average annual temperature is around 25 °C (Ramos-Neto and Pivello 2000). This Brazilian savanna encompasses distinct physiognomies that vary from areas without shrubs or trees, composed of 100% of grasses and herbs (called *campo limpo*), to areas with a very complex structure, with a lot of taller trees and fewer grasses and herbs (forest formations) (Oliveira-Filho and Ratter 2002).

### Community data

We sampled 5632 individuals belonging to 147 tiger moth species across 39 plots (10 x 10 m each) using *Luiz de Queiroz* light traps, with a 15 W black lamp (Silveira-Neto and Silveira 1969). The plots had a minimum distance of 100 m from each other to avoid attracting individuals from other plots (Muirhead-Thompson 1991). We sampled moths over a three-year period during the dry (June 2010, July 2011 and July 2012) and rainy seasons (December 2010, November 2011 and December 2012). We collected only Arctiinae species (tiger moths); all other moths were released alive back into their natural habitat. Specimens were identified to the lowest possible taxonomic level through literature (Hampson 1898, 1900, 1901, 1914; Piñas-Rubio *et al.* 2000; Piñas-Rubio and Manzano 2003; Watson and Goodger 1986). We also compared our specimens with digital images of species deposited in the Becker Collection (Camacan, Bahia, Brazil). Only specimens that were identified to species level were used in the final dataset ($S = 107$ species). All voucher specimens were deposited in the Zoological Collection of the *Universidade Federal de Goiás* (Goiânia, Brazil).

### Functional trait data

We measured the following four functional traits for each species included in our dataset: wingspan, body length, thorax width and forewing colour. Forewing colour was measured categorically, regardless of the surface area occupied by each colour on the wing. As there might be intraspecific differences in body size, we measured three male individuals of different sizes for each species to obtain values for wingspan, body length and thorax width. We then calculated the mean of each variable per species and used

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**Table 1.** Results from partial multiple regressions showing the environmental and spatial variables selected by the forward selection, the percentage of explanation of each component and the *p*-value of the environment and space

| Group | Information | Selected environmental variables | Selected spatial variables | Adjusted $R^2$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | [a] | [b] | [c] | [d] | P[a] | P[c] |
| Arctiinae | Funct. (NTI) | Herbaceous cover, richness of woody plants, leaf mass | 3.8.9.12.18.19 | 0.19 | 0.12 | 0.32 | 0.35 | **0.002** | **0.001** |
| Arctiini | Funct. (NTI) | Herbaceous cover, richness of woody plants, perimeter | 3.8.9.12.18.19 | 0.15 | 0.13 | 0.29 | 0.40 | **0.005** | **0.003** |
| Lithosiini | Funct. (NTI) | Perimeter | 2.3.7.8.9 | 0.15 | 0.07 | 0.03 | 0.72 | **0.010** | 0.271 |

The letters a, b, c and d mean the adjusted $R^2$ values for the environment, shared (between environment and spatial), spatial and error components (respectively). The p (a) and p (c) mean the significance of the environmental and spatial components.

these values in the subsequent analyses. The dataset with the functional traits had 107 species of Arctiinae, in which 91 species belong to tribe Arctiini and 16 to tribe Lithosiini (Table S1).

We performed a Pearson's correlation between the three traits that reflect the body size (wingspan, body length and thorax width). As these three traits were highly correlated with each other (>82%), we performed a principal component analysis (PCA) and used the first axis of the PCA as the body size variable in the subsequent analysis.

### *Environmental variables (one of the features of deterministic factors)*

In all plots that we sampled tiger moths, 10 environmental variables related to the vegetation were obtained. Host plant data were not included in our dataset. Instead, the information on arboreal and herbaceous refers to the plant species occurring within the $10 \times 10$ m plots. Nine of these variables were related to the woody plants (richness, density, and since there was more than one individual of the same plant species in each plot, we also calculated the coefficient of variation for the following traits: height, petiole length, tree perimeter, leaf length, leaf toughness, leaf mass and specific leaf area) (see Zava and Cianciaruso 2014, for more details). The tenth variable was herbaceous cover, measured by the filling of 100 little squares (of 10 x 10 cm) in a square of 1 $m^2$ (mean of two measures in each plot).

We tested for correlations between the environmental variables using the variance inflection factors (VIFs, Satoh 2001) method. The density of woody plants was highly correlated with the richness of woody plants ($r = 0.86$). Thus, we removed the variable density of woody plants in the analyses due to its higher VIF value. Environmental variables specific to each plot, which were used in the calculations, are detailed in the Supplementary Material.

### *Spatial variables (related to stochastic factors)*

We generated the spatial variables using the principal coordinates of neighbour matrices (PCNM) technique (Borcard and Legendre 2002), from the Euclidean distance matrix of the geographical coordinates of each sampled plot. We used all the axes (eigenvectors) with positive eigenvalues resulting from PCNM as the spatial descriptors in the redundancy analyses (Dray et al. 2006).

### *Functional structure (NTI)*

We calculated the nearest taxon index (NTI) for the functional data for each community (each plot). The NTI quantifies the extent of terminal clustering on a functional dendrogram (Webb et al. 2002). This metric is dependent on the species pool of each community, and its values increase when the species of a community are more related (functional grouping) to each other and become negative when the species are not so related to each other (functional overdispersion) (Webb et al. 2002).

The traits variables consisted of quantitative and categorical variables. Thus, we calculated the distances matrices with the Gower's distance (Podani and Schmera 2006) and the NTI as -1 X ses.mntd using the package Picante (Kembel et al. 2010) in the statistical software R (R Core Team 2016; Supplementary Material).

### *Forward selection and variation partitioning*

We performed global multiple regressions for functional structure (NTI) with all the spatial and environmental variables. Then, we selected the most important spatial and environmental variables with forward selection, where the adjusted $R^2$ of the global model and the *p*-values ($\leq 0.05$) of each variable are used as selection criteria (Blanchet et al. 2008). We used the environmental and spatial variables selected in the partial multiple regressions, followed by variation partitioning (Borcard et al. 1992; Peres-Neto et al. 2006) for each dataset separately (functional structure of tribe Arctiini and tribe Lithosiini).

Through variation partitioning, we know the total explained variance (environment, space, shared by environment and space, and residuals); the variance explained exclusively by the environmental variables; the variance explained exclusively by the spatial variables; the variance shared by the environment and space; and the unexplained variance (Peres-Neto et al. 2006). All the analyses were performed in the statistical software package R (R Core Team 2016).

## Results

The environmental variables selected for the multiple regression models were the richness of woody plants, the herbaceous cover and the coefficient of variation of the leaf mass, leaf toughness and perimeter of woody plants (Table 1). The spatial variables selected represent large, intermediate and small-scale patterns, since the first, intermediate and last Moran's eigenvector maps (MEMs) were retained for the multiple regression models (Table 1).

The functional traits of the entire tiger moth dataset were more influenced by space than by the environment (Table 1, Figure 1), even though they were significantly influenced by both (Table 1, Figure 1). The spatial variables (mostly related to stochastic processes) showed a greater importance to the functional structure of the tribe Arctiini (Table 1, Figure 1). Just the environment explained the variance of the functional structure of Lithosiini (Table 1, Figure 1).

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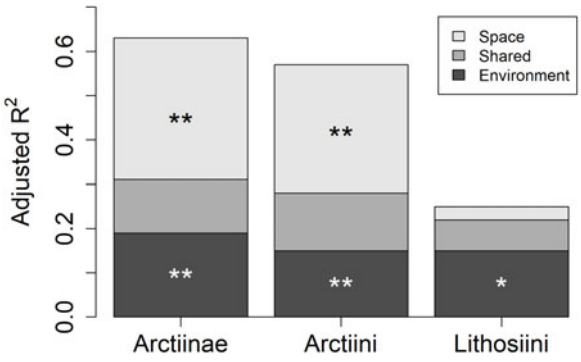



**Figure 1.** Proportion of variation explained by the environment, by space and by the shared variation (space and environment) to the functional structure of tiger moths: subfamily Arctiinae, tribe Arctiini and tribe Lithosiini. The asterisks mean the statistical significance of the variation partitioning. Double asterisks (**) denote $p \leq 0.005$, whereas a single asterisk (*) denotes $p < 0.05$.

## Discussion

Both stochastic and deterministic processes are important in dictating the functional structure of Arctiinae moths. However, as predicted by our hypothesis, tribe Arctiini was more influenced by spatial variables (most of them related to stochasticity) and tribe Lithosiini was influenced by environmental variables only.

Environmental variables are related to deterministic processes, like facilitation, competition and environment filtering, which comprehend the niche-based models (Leibold et al. 2004; Leonov 2023; Pavoine and Bonsall 2011); thus, species interactions and environmental filters influence the distribution of species considering the functional relationships among species in communities. Lithosiini species do not show many differences in their food resources and occupy similar vegetation types (Hilt and Fiedler 2006; Wagner 2009; Weller et al. 2009); thus, this result suggests that the environment might be functioning as a filter to functionally closer species that habit in similar environmental conditions (Keddy 1992; Weiher et al. 1998). This result was just found for the functional structure and not for the taxonomic diversity (Moreno et al. 2016), showing that just the names of species do not show all the ecological patterns along communities. Moreno et al. (2016) showed that Lithosiini species are mainly influenced by space and argued that as they have small size, they might be more stochastically structured mainly due to their limited dispersal capabilities (Hilt and Fiedler 2006; Moreno et al. 2016; Soininen et al. 2013). However, we showed here that Lithosiini can be environmentally structured if we consider their functional traits.

We showed that tribe Arctiini, which comprehends species that occupy several types of habitats and feed in several types of plants (Hilt and Fiedler 2006; Singer and Bernays 2009; Weller et al. 2009), is mainly influenced by spatial variables (most of them related to stochasticity). Our hypothesis was that if they are diet and habitat generalists, then they might occur in several environmental conditions, and the main limiting factor to them would be their dispersal limitations (which are related to stochastic factors, even though we do not know much about their dispersal capabilities). Neutral processes (Hubbel 2001), also related to spatially structured factors, such as random speciation, extinction and ecological drift (Leonov 2023; Pavoine and Bonsall 2011), might be acting on the Arctiini moths as well. Purely stochastic processes can indicate that these species do not present a consistent pattern of evolutionary and ecological similarities (Swenson et al. 2012). Also, stochastic processes can point to intrinsic factors, like biological, ecological and physiological aspects of species that might be more important in response to the functional structure of communities than the environmental variables analysed here (Soininen 2016). But this result can also be due to some spatially structured environmental variables more important to species traits that we did not measure in the field. If this is the case, the functional structure could reveal answers to deterministic processes that are not shown by species diversity alone (Swenson et al. 2011).

The main environmental variables selected for the variation partitioning analyses were the richness of woody plants and the herbaceous cover, as already shown for Arctiinae taxonomic composition (Moreno et al. 2016). These two variables are the main ones that structure the gradient of vegetation occurring in the Cerrado biome (Oliveira-Filho and Ratter 2002), and they are important in dictating the richness and composition of animal species (Almeida and Louzada 2009; Moreno et al. 2014; Ribas et al. 2003; Rodrigues et al. 2002). These variables were selected for the functional structure of the tribe Arctiini, but not to the functional structure of Lithosiini. Two different variables were also selected for the functional structure: the coefficients of variation of leaf mass and of perimeter of woody plants. Leaf mass is related to food resources but also might be related to the concentration of PAs in the plant (Hartmann 1999). PAs are the most studied secondary compounds sequestered by moths of the tribe Arctiini (Zaspel et al. 2014) and are involved in protecting them against predation and parasitism (Bezzerides et al. 2004; Bowers 2009; Singer and Bernays 2009). Lithosiini do not sequester PAs (Weller et al. 1999). The main secondary compounds sequestered by Lithosiini are lichen polyphenolics (Scott et al. 2014). The presence of lichens in the plant might be related to the perimeter (diameter) of trees (which was the only variable related to the functional structure of Lithosiini), as larger-diameter trees present more richness of lichens (Hofmeister et al. 2016).

Our results showed that we can achieve different results and amplify our understanding of community ecology if we consider more components of diversity (i.e., functional diversity), as already suggested by other authors (i.e., Pavoine and Bonsall 2011; Swenson et al. 2011). We also corroborate that deterministic and stochastic processes can affect in a distinct way different groups of species, for example, common, rare, habitat specialists, habitat generalist species (Moreno et al. 2016; Pandit et al. 2009; Siqueira et al. 2012) and related clades like tribes Arctiini and Lithosiini (Moreno et al. 2016). Thus, stochastic and deterministic processes are important, but they also respond differently to the community structure, depending on the functional relationships among species (Arnan et al. 2015; Carvalho and Tejerina-Garro 2015), as shown by our results.

**Supplementary material.** To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467425100412

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