Евразиатский энтомол. журнал 24(2): 90–100
doi 10.15298/euroasentj.24.02.06

Assessment of niche space occupation by soil-litter ants in two types of tropical monsoon forests

Оценка освоения нишевого пространства муравьями почвенно-подстилочного комплекса в двух типах муссонного тропического леса

T.V. Popkova, V.A. Zryanin
Т.В. Попкова, В.А. Зрянин

Lobachevsky State University of Nizhny Novgorod, Prospekt Gagarina 23, Nizhny Novgorod 603950 Russia. E-mail: tatyanapopkovaptv@ya.ru; zryanin@list.ru.

Нижегородский государственный университет имени Н.И. Лобачевского, пр. Гагарина 23, Нижний Новгород 603950 Россия.

Key words: Niche differentiation, ant communities, functional diversity, resource use.

Ключевые слова: нишевая дифференциация, сообщества муравьёв, функциональное разнообразие, использование ресурсов.

Abstract. In our study, we conducted a preliminary assessment of the volume of potentially available resources and their use by soil and leaf litter ants in two types of tropical monsoon forests (the *Lagerstroemia* forest on loamy soil and the dipterocarp forest on sandy soil) using functional diversity analysis. The functional approach enables the assessment of the relationship between available resources in the niche space and their utilization by ants based on analysis of morphological traits. The research was carried out on two tropical forest sites measuring 25×25 m, within which model plots of 100 m^2 were laid. On two model plots, we conducted ant counting using nest mapping, carbohydrate-baited traps, and soil sifting. We measured the morphological traits of 38 ant species from 18 genera and 5 subfamilies (head length, head width, Weber's length, eye length, and hind tibia length). Functional diversity was evaluated using functional diversity indices based on measured morphological traits and species occurrences: functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), functional originality (FOri), and functional evenness (FEve). Our findings revealed that the volume of niche space assessed by functional richness was higher in the dipterocarp forest corresponding to the greater taxonomic richness of soil-litter ants in this forest type. In the *Lagerstroemia* forest, we found higher functional evenness of the soil-litter ant community compared to the dipterocarp forest indicating more efficient resource utilization. Weak differences in functional divergence and originality relative to null models indicated a more stable ant community in the *Lagerstroemia* forest. In the dipterocarp forest, lower values of functional divergence, dispersion, and originality were observed, suggesting a more dynamic ant community with more tightly niche packing of soil-litter ant species. Our findings are preliminary and require further in-depth study and detailed analysis with the inclusion of additional data.

Резюме. Дана предварительная оценка объёма потенциально доступных ресурсов и определена полнота их использования муравьями почвенно-подстилочного комплекса в двух типах муссонного тропического леса (лагерстремиевый лес на суглинистой почве и диптерокарповый лес на песчаной почве) на основе анализа функционального разнообразия. Функциональный подход позволяет оценить взаимосвязь между доступными ресурсами в нишевом пространстве и их использованием муравьями на основе анализа морфологических признаков. Исследования проводились на двух участках тропического леса площадью 25×25 м, внутри которых были выделены модельные полигоны по 100 м^2. На полигонах проведены учёты муравьёв (картирование гнёзд, почвенные углеводные ловушки) и выполнены промеры 5 морфологических признаков (длина и ширина головы, длина груди, максимальный диаметр глаза, длина задней голени) у 38 видов муравьёв из 18 родов 5 подсемейств. Функциональное разнообразие оценивали с помощью индексов функционального богатства (FRic), функциональной дисперсии (FDis), функциональной дивергенции (FDiv), функциональной оригинальности (FOri) и функциональной выравненности (FEve), рассчитанных на основе измеренных признаков и встречаемости видов. Объём нишевого пространства, оценённый индексом функционального богатства, выше в диптерокарповом лесу, что соответствует большему таксономическому богатству почвенно-подстилочных муравьёв в этом типе леса. В лагерстремиевом лесу установлена большая функциональная выравненность почвенно-подстилочного комплекса муравьёв по сравнению с диптерокарповым лесом, что указывает на более эффективное использование доступных ресурсов. В лагерстремиевом лесу выявлены слабые отличия функциональной дивергенции и оригинальности по сравнению с нулевыми моделями, что свидетельствует о более стабильном комплексе почвенно-подстилочных видов. В диптерокарповом лесу ниже значения функциональной дивергенции, дисперсии и оригинальности, что свидетельствует о более динамичном мирмекокомплексе с более плотной упаковкой ниш почвенно-подстилочных видов. Полученные результаты и выявленные особенности являются предварительными и требуют более глубокого изучения и детального анализа с привлечением дополнительного объёма материала.

How to cite this article: Popkova T.V., Zryanin V.A. 2025. Assessment of niche space occupation by soil-litter ants in two types of tropical monsoon forests // Euroasian Entomological Journal. Vol.24. No.1. P.87–100. https://doi.org/10.15298/euroasentj.24.01.06

Introduction

Monsoon tropical forests have a complex vertical structure [Kuznetsov, Kuznetsova, 2013] that provides a significant diversity of nesting sites, foraging opportunities, and refuge from competitors for ants [Mottl et al., 2020]. The highest ant species diversity in tropical forests is observed in the soil and leaf litter [Silva, Brãndao, 2014; Wong, Guenard, 2017]. Traditionally, the concept of the ecological niche has been used to explain the structure and organization of communities [Adler et al., 2007]. Despite numerous studies focusing on individual aspects of ecological niches, such as trophic and size differentiation, spatial distribution, and behavioral differences among ants, there remains a lack of information on the relationship between the volume of resources provided by the environment and the extent to which ants utilize these resources.

In recent years, the concept of functional diversity has been increasingly used in the studies of community structure and organization [Naeem, 2002; Adler et al., 2013]. Unlike classifications based on functional groups or life forms, which overlook interspecific interactions within groups [Petchey et al., 2009], functional diversity accounts for various aspects of species interactions, allowing differentiation based on functional traits [Naeem, 2002; Adler et al., 2013]. In this context, functional diversity is regarded as a component of biodiversity, alongside taxonomic and phylogenetic diversity [Petchey, Gaston, 2002; Flynn et al., 2011]. Its assessment involves data on species composition, species abundance, and their functional traits. Typically, functional traits are morphological characteristics that reflect ecological roles and can be measured in individual specimens [Petchey, Gaston, 2006; Mouillot et al., 2013; Chiu, Chao, 2014]. For instance, morphological features, such as leg length and body size, determine access to microhabitats [Farji-Brener et al., 2004; Gibb, Parr, 2010], whereas eye size and position may indicate specific foraging strategies [Weiser, Kaspari, 2006].

Functional diversity is commonly analyzed using functional indices that illustrate various aspects of species distribution in functional space, including the distribution of their functional traits and abundance [Villéger et al., 2008]. Functional space represents a multidimensional space where the axes are defined by functional traits [Mouillot et al., 2013]. These traits are usually associated with the degree of resource utilization [Bihn et al., 2010] and reflect the size of the ecological niche [Ovadia, Schmitz, 2002; Woodward et al., 2005]. Thus, functional traits can be used to assess the environmental capacity and the degree of niche occupancy [Schleuter et al., 2010; Arnan et al., 2017].

The functional approach is widely applicable to studying different groups of organisms. Specifically, it has been used to investigate the functional characteristics of fish [Mims, Olden, 2012], birds [Meynard et al., 2011], and arthropods [Poff et al., 2006]. In ant communities, this approach allows for the evaluation of diverse aspects of the ecological niche [Gibb, Parr, 2013; Retana et al., 2015; Salas-López, 2017], identification of differences in community structure across different biomes [Schofield et al., 2016], and analysis of the influence of abiotic factors and competition [Fichaux et al., 2019]. This is particularly relevant for studying the structure and functioning of multispecies ant communities in tropical forests.

The aim of this study was to conduct a preliminary assessment of the volume of potentially available niche space and its utilization by soil-litter ants in two types of monsoon tropical forest, based on the analysis of functional diversity. To achieve this aim, we pursued the following objectives: (i) establish the species richness and occurrence of soil-litter ants during their peak activity period (wet season) in two forest types; (ii) assess the morphofunctional diversity of the two soil-litter ant communities based on morphological traits; (iii) evaluate the volume of available niche space and the extent of its utilization by the two soil-litter ant communities using functional traits and null model simulations.

Materials and methods

The study was conducted in 2008 during the wet season within the Cát Tiên National Park (Đồng Nai Province, Southern Vietnam) in the *Lagerstroemia* forest on low basalt ridges and the dipterocarp forest on sandy soil along the Đồng Nai River's floodplain.

General characteristics of the study area

The study area is in the southern sector of Cát Tiên National Park (11°20'50"–11°32'13" N, 107°11'13"–107°28'20" E) within a tropical monsoon climate with distinct seasonality. The average annual precipitation — 2450 mm, and the average air humidity typically exceeds 70 %. The dry season lasts from December to April and the wet season from May to November. The predominant forest type in the study area is tropical monsoon semi-deciduous forest dominated by *Lagerstroemia* spp. in association with Dipterocarpaceae and Fabaceae species [Blanc et al., 2000].

The study was conducted in two 25×25 m plots of tropical forest, within which 100 m^2 model plots were laid: 1) model plot L in the *Lagerstroemia* forest on low basalt ridges; 2) model plot DFL in the dipterocarp forest on sandy soil of the Đồng Nai River floodplain.

In the model plot L, the soil is loamy becoming loess-like in depressions during the wet season. The stand consists of four layers. The first layer is dominated by *Lagerstroemia calyculata* Kurz, 1872 (Lythraceae) with a codominant *Tetrameles nudiflora* R. Br., 1838 (Tetramelaceae). Common species include *Haldina cordifolia* (Roxb.) Ridsdale, 1978 (Rubiaceae), *Hopea odorata* Roxb., 1811 (Dipterocarpaceae), *Sindora siamensis* Teijsm. ex Miq., 1867, and *Afzelia xylocarpa* (Kurz) Craib, 1912 (Fabaceae). The canopy height of the first layer is 40–45 m. The second layer, 16–25 m high, does not form a continuous canopy. The third layer, 5–10 m high, consists of trees with oval and cylindrical crowns. The understory, which is up to 3 m high, is well-developed. Numerous lianas, hemiepiphytes, and epiphytes are abundant. The litter is predominantly composed of *Lagerstroemia calyculata* leaves [Anichkin et al., 2007].

In the model plot DFL, the soil is sandy formed by river deposits (3–5 m). The stand is stratified into four layers. The upper layer at 35–40 m is represented by *Dipterocarpus alatus* Roxb. ex G. Don, 1831 (Dipterocarpaceae) and *Irvingia malayana* Oliv. ex A.W. Benn., 1875 (Irvingiaceae). The second layer, which is 20–25 m high, consists of *Sandoricum koetjape* (Burm.f.) Merr., 1912 (Meliaceae) and *Anthoshorea roxburghii* (G.Don) P.S. Ashton & J. Heck., 2022 (Dipterocarpaceae). The third layer is 10–16 m high, and the fourth is up to 6 m. The model plot DFL contains numerous rattan palms of the genus *Calamus* (Arecaceae). The litter is predominantly composed of leaves of Dipterocarpaceae species [Anichkin et al., 2007]. The leaf litter accumulation by the end of the wet season was greater in this plot than in the model plot L [Zryanin, 2019].

Field study methods

In 2008, the second author conducted counting of soil-litter ants in two 25×25 m forest plots. The primary method of ant sampling was nest mapping carried out during their peak activity in the mid-wet season (August 2008) on model plots of 100 m².

During the mapping, which took approximately one week per plot, soil excavations were conducted, and small woody debris, logs, and fallen fruits were thoroughly inspected. Details on the specifics and results of the mapping have been published previously [Zryanin, 2010, 2011].

As an additional method for more comprehensive counts of soil-litter ants, carbohydrate-baited traps were used. These traps consisted of small plastic containers with lids of 2.5 cm in diameter and 5 cm in height. Each container had holes 1–2 mm in diameter, positioned 0.5 cm from the bottom. Inside, cotton wool soaked in 15 % sugar syrup was placed. Ten containers per plot were buried around the perimeter of the model plots at a depth of 5–10 cm. This method was replicated five times with exposure time ranging from 24 to 72 h depending on weather conditions [Zryanin, 2011].

In October-November 2008, additional ant sampling was conducted on the 25×25 m model plots by hand sampling using soil sifting through a 1-mm mesh. The proposed method successfully collected species that had not been previously recorded on the model plots.

Estimation of species occurrence

The occurrence was calculated based on the results obtained using all the aforementioned methods. In this study, the occurrence of individual species was defined as the total number of records of each species during nest mapping, using carbohydrate bait traps, and hand sampling in 25×25 m forest plots. The number of records for a particular ant species using the applied methods was the sum of three components: the nest number of a species revealed during mapping, the total number of bait traps (out of all those established during 5 counts) in which the species was recorded, and the total number of times the species was found in sieved litter samples during hand sampling. For instance, on the DFL plot, 8 nests of *Lophomyrmex birmanus* were identified. This species was found in 2 bait traps, and it was recorded 4 times during hand sampling. In this case, the occurrence of *L. birmanus* was 14.

Assessment of ant functional diversity

To evaluate the functional diversity of ants, we selected five key morphological traits: head length, head width, Weber's length, hind tibia length, and maximum eye diameter [Weiser, Kaspari, 2006; Bihn et al., 2010; Schofield et al., 2016]. These traits were selected for their functional importance related to food and spatial resources (Table 1). Measurements were taken using a Carl Zeiss Stemi 2000C stereomicroscope fitted with a Jenoptik ProgRes Naos camera at 16–50x magnification. The Gryphax module was used to analyze the microphotographs. Calibration was performed for each magnification using an object micrometer. For each species, six minor workers were measured (in some cases, only 1–3 workers were measured, due to a limited number of sampling specimens). For dimorphic species, measurements were taken from minor workers, which represent the majority of ant colony.

Before functional diversity analysis, the morphological trait values of all species in the dataset were tested for normality. The Shapiro-Wilk, Lilliefors, and Anderson-Darling tests were used for this purpose. Because most

Table 1. The studied morphological traits of ants
Таблица 1. Изученные морфологические признаки муравьёв

Functional trait	Ecological significance
Head length (HL)	An indicator of body size and mass related to the amount of consumed resources [Kaspari, Weiser, 1999; Fichaux et al., 2019].
Head width (HW)	Head width is associated with the volume of the mandibular muscles, which enable efficient prey capture [Kaspari, 1993].
Weber's length (WL)	An indicator of overall body size related to the consumption of food resources [Traniello, 1987], foraging on the soil surface, or in microhabitats [Kaspari, Weiser, 1999; Gibb, Parr, 2013; Seifert, 2017].
Maximum eye diameter (EL)	Eye size reflects the type of diet and is associated with the foraging stratum [Weiser, Kaspari, 2006]. Small eye size among soil-litter ant species is usually characteristic of more predatory species [Yates et al., 2014].
Hind tibia length (HTL)	An indicator reflecting the overall leg length. Short legs allow ant species to use microhabitats and maneuver in the litter [Weiser, Kaspari, 2006].

morphological traits were not normally distributed, except Weber's length, we applied a standardization procedure widely used in functional diversity studies [Bihn et al., 2010; Schofield et al., 2016; Arnan et al., 2018]. We introduced the following indices for standardization: relative head length and width (the ratio of head length/width to Weber's length), relative tibia length (the ratio of tibia length to Weber's length), and relative eye size (the ratio of maximum eye diameter to head width).

Statistical analysis of the data was performed using the vegan and mFD packages in R statistical software [Oksanen, 2011, 2015; Magneville et al., 2021]. The proportion of shared species between two soil-litter ant communities was assessed using the Jaccard similarity index. To evaluate functional diversity, five indices were selected: functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), functional originality (FOri), and functional evenness (FEve).

Functional richness (FRic) represents the range of functional trait values within the functional space and is calculated using the following formula [Mason et al., 2005]:

$$FRic = \frac{\max\limits_{s\in S_c}(X_{ts}) - \min\limits_{s\in S_c}(X_{ts})}{\max\limits_{s\in\cup S_c}(X_{ts}) - \min\limits_{s\in\cup S_c}(X_{ts})},$$

where X_{ts} is the mean trait value of trait t for species s, and S_c is the number of species in community c.

Functional dispersion (FDis) reflects the mean distance of species to the centroid in functional space, considering species occurrence [Laliberté, Legendre, 2010].

$$FDis = \frac{\Sigma a_j z_j}{\Sigma a_j},$$

where a_j is the relative abundance of species j, and z_j is the distance of species j to the weighted centroid c. The centroid is calculated using the following formula:

$$c = \frac{\Sigma a_j x_{ij}}{\Sigma a_j},$$

where a_j is the abundance of species j, and x_{ij} is the value of trait i for species j.

Functional divergence (FDiv) measures the extent to which the distribution of species occurrences is skewed toward the outer edges of the functional space [Villéger et al., 2008]. To calculate this index, the coordinates of the convex hull centroid are determined as follows:

$$g_u = \frac{1}{V}\sum_{i=1}^{V} x_{ui},$$

where x_{ui} is the value of trait u for species i, and the summation is performed over V species that form the vertices of the convex hull. The mean distance to the centroid (G) is calculated as:

$$dG_i = \sqrt{\sum_{u=1}^{K}(x_{ui} - g_u)^2}, \quad \overline{dG} = \frac{1}{S}\sum_{i=1}^{S} dG_i$$

where K represents traits, and S is the number of species.

Next, the weighted sum of deviations is then calculated as follows:

$$\Delta d = \sum_{i=1}^{S} p_i(dG_i - \overline{dG}), \quad \Delta|d| = \sum_{i=1}^{S} p_i|dG_i - \overline{dG}|,$$

where p_i is the abundance of species i.

Thus, functional divergence (FDiv) can be calculated as follows:

$$FDiv = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}.$$

Functional originality (FOri) reflects the contribution of species to the overall diversity of the community and is expressed as follows [Mouillot et al., 2008]:

$$FOri = \frac{1}{n}\sum_{i=1}^{n} FO_i,$$

where n is the total number of species in the community, and FO_i is the functional originality of species i. FOri is determined as:

$$FO_i = \frac{\sum_{j=1, j\neq i}^{n} d_{ij}}{n-1},$$

where d_{ij} is the functional distance between species i and j.

Functional evenness (FEve) reflects the regularity of species distribution in the functional space considering their occurrences. The FEve calculation is based on the minimum spanning tree (MST) that connects all species in the functional trait space such that the sum of branch lengths is minimal. If the MST consists of branches of average length, species are assumed to be uniformly distributed in the functional space; if both long and short branches, the distribution is uneven [Villéger et al., 2008]. Functional evenness (FEve) is calculated using the following formula:

$$FEve = \frac{\sum_{l=1}^{S-1}\min\left(PEW_l \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}},$$

where S is the number of species, PEW_l is the partial weighted evenness calculated according to specific formulas:

$$PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}, \quad EW_l = \frac{dist(i,j)}{w_i + w_j},$$

where EW_l is the weighted evenness, dist(i, j) is the Euclidean distance between species i and j, the included species is branch l, and w_i is the relative abundance of species i.

The applied functional diversity indices and their interpretations are presented in Table 2.

To evaluate the functional diversity of the studied communities, it is crucial to understand the concept of a reference community, known as the null community. Modeling null communities is a standard approach for assessing and analyzing community structure and functioning [Swenson, 2014], including myrmecological studies [Silva et al., 2016; Fichaux et al., 2019].

In the null community, species are distributed in the functional space such that each species can occupy any position in the trait space assuming complete niche separation and full utilization of the niche space by the species. To generate null communities, we used the morphological data of soil-litter ant species and occur-

Table 2. Functional diversity indices and their interpretation
Таблица 2. Индексы функционального разнообразия и их интерпретация

FRic — functional richness	
The volume of functional space occupied by the community [Villéger et al., 2008]. Functional space refers to the distribution of species and their occurrences within the trait functional space [Mouillot et al., 2013].	
$FRic_{Obs} \geq FRic_{Null\ (0.95)}$	High morphological diversity; all available resources are utilized; less unoccupied niche space [Mason et al., 2005].
$FRic_{Obs} < FRic_{Null\ (0.95)}$	Low morphological diversity; only a portion of the potentially available resources are utilized; more unoccupied niche space [Mason et al., 2005].
FDis — functional dispersion	
The mean distance in the multidimensional trait space from individual species to the centroid of functional space of all species [Laliberté, Legendre, 2010].	
$FDis_{Obs} \geq FDis_{Null\ (0.95)}$	Less dense packing of species' ecological niches within the community; community resilience to changes in species composition; absence of unoccupied ecological niches in the community [Fichaux et al., 2019].
$FDis_{Obs} < FDis_{Null\ (0.95)}$	Denser packing of species' ecological niches within the community; lack of resilience to changes in species composition; presence of unoccupied ecological niches in the community [Fichaux et al., 2019].
FDiv — functional divergence	
Distribution of abundance along the functional trait axes within the range occupied by the community [Villéger et al., 2008].	
$FDiv_{Obs} \geq FDiv_{Null\ (0.95)}$	Species are distributed relatively uniformly; niche partitioning occurred in the past; stabilization of species numbers within the community [Mason et al., 2005].
$FDiv_{Obs} < FDiv_{Null\ (0.95)}$	Species are distributed unevenly; lack of complete ecological niche partitioning; absence of species number stabilization within the community [Mason et al., 2005].
FOri — functional originality	
Degree of species isolation within the functional space occupied by the community [Mouillot et al., 2008].	
$FOri_{Obs} \geq FOri_{Null\ (0.95)}$	The presence of a significant number of species with unique morphological traits; morphological differences between species; the stability of size niches [Mouillot et al., 2008].
$FOri_{Obs} < FOri_{Null\ (0.95)}$	Reduced uniqueness in species morphological traits; morphological similarity to other species [Mouillot et al., 2008].
FEve — functional evenness	
This describes the evenness regularity of abundance or occurrence distribution in the functional trait space [Villéger et al., 2008].	
$FEve_{Obs} \geq FEve_{Null\ (0.05)}$	Relatively uniform utilization of resources; all available resources are utilized [Mason et al., 2005].
$FEve_{Obs} < FEve_{Null\ (0.05)}$	Uneven utilization of resources; only a limited amount of resources is utilized [Mason et al., 2005].

Designations. Obs — empirical value, Null — theoretical value. In parentheses are the percentile thresholds calculated based on the null models to which the observed index values are compared.

Обозначения. Obs — эмпирическое значение, Null — теоретическое. В круглых скобках указаны пороговые значения процентилей, рассчитанных на основе нулевых моделей, с которыми сравниваются наблюдаемые значения индексов.

rence data of each species in the community based on counts. Initially, the data were organized into a matrix, where columns represented species and rows indicated their occurrences within the community. The probability (prob) of each species present in the community was calculated using the formula:

$$prob = \frac{1}{S \cdot N} \sum_{i=1}^{S} \sum_{j=1}^{N} I_{ij} ,$$

where S is the number of species, N is the number of communities, and I_{ij} is an indicator function equal to 1 if species i is present in community j, and 0 if it is not.

As a result, we obtained a probability matrix indicating the presence of species in each community, which was then used to generate 999 null communities for each forest type. After modeling the hypothetical community structure, where species were distributed according to their probabilities, we randomly assigned the empirical occurrence values of species to these null communities. Subsequently, for each null community, functional diversity indices were calculated based on the empirical matrix of morphological data and the generated null matrix of species occurrences. These calculations were performed using the alpha.fd.multidim function in mFD package [Magneville et al., 2021], which use principal component analysis results and species occurrence data. Based on the assumption that species in a null community are distributed in functional space without overlapping niches, we used the spatstat package [Baddeley et al., 2021] to model the species distribution. After calculating the principal component values, we modeled the species distribution in functional space to maintain a minimum distance between species, ensuring unique niches for each species and maximizing niche space occupation by the community. Using these principal component values and species occurrence data, functional diversity indices were calculated. The values of each index were standardized by computing the deviations from the mean and dividing by the standard deviation. Subsequently, quantile analysis was performed to determine the range of functional index values in the generated data and compare them with the observed values. To compute the null (theoretical) values of functional diversity indices based on null models, the 5th and 95th percentiles were calculated.

The calculation of functional diversity indices for empirical data was based on the matrix of morphological data and the matrix of species occurrences from the count results. The empirical and theoretical index values were compared. The empirical values of FRic, FDiv, FDis, and FOri were compared with the 95th percentile values of the theoretical indices, while empirical values of FEve were compared with the 5th percentile of the null index values.

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:D7811994-6EC9-4D2E-9464-084DE558872A.

Results

A total of 38 soil-litter ant species from 18 genera and 5 subfamilies were recorded during the study. At the model plot L, 19 species from 11 genera and 4 subfamilies were identified, whereas at the model plot DFL, 27 species from 14 genera and 4 subfamilies were identified. The proportion of shared species according to the Jaccard similarity index between the two soil-litter ant communities was 22 %. The results of the morphometric analysis of the identified species and their occurrences in the model plots are presented in Table 3.

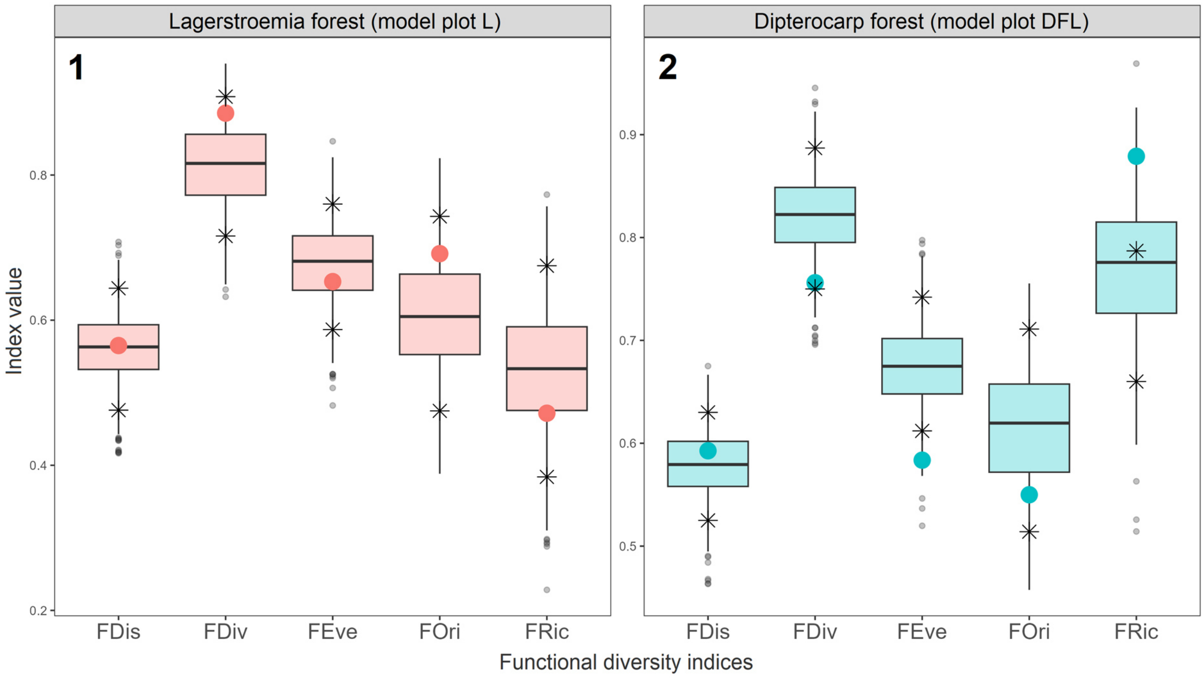
Compared to the average null models, the ant community of the *Lagerstroemia* forest exhibited lower values of functional richness (FRic), functional dispersion (FDis), functional divergence (FDiv), and functional

Table 3. Morphometry and occurrence of soil-litter ant species on the plots studied
Таблица 3. Морфометрия и встречаемость почвенно-подстилочных муравьёв на исследованных полигонах

Species	Mean trait values, mm					Occurrence	
	HL	HW	WL	EL	HTL	L	DFL
Amblyoponinae							
Stigmatomma crenatum (Xu, 2001)	1.307	1.116	1.913	0.086	0.924	1	0
Stigmatomma quadratum Karavaiev, 1935	1.842	1.734	2.434	0.245	1.333	2	0
Dorylinae							
Cerapachys sulcinodis Emery, 1889	1.035	0.859	1.450	0.245	0.741	4	0
Parasyscia dohertyi (Emery, 1902)	1.173	1.029	1.458	0.242	0.921	1	0
Formicinae							
Pseudolasius silvestrii Wheeler, 1927	0.616	0.573	0.754	0.093	0.575	0	13
Pseudolasius sp.1	0.732	0.714	0.907	0.076	0.637	0	2
Myrmicinae							
Calyptomyrmex rectopilosus Dlussky, Radchenko, 1990	0.617	0.602	0.634	0.029	0.321	0	1
Carebara lignata Westwood, 1840	0.455	0.432	0.509	0.000	0.252	0	5
Carebara sp. 1	0.355	0.313	0.370	0.019	0.188	4	1
Carebara sp. B	0.306	0.271	0.288	0.007	0.134	6	3
Lophomyrmex birmanus Emery, 1893	0.626	0.585	0.661	0.113	0.438	43	14
Pheidole aspidata Eguchi & Bui, 2005	0.591	0.554	0.716	0.089	0.455	0	3
Pheidole taipoana Wheeler, 1928	0.432	0.383	0.523	0.099	0.294	12	15
Pheidole tjibodana Forel, 1905	0.563	0.500	0.727	0.135	0.487	0	10
Pheidole sp. E	0.622	0.598	0.615	0.102	0.317	0	1
Proatta butteli Forel, 1912	0.564	0.422	0.785	0.084	0.491	0	3
Solenopsis sp. 1	0.650	0.590	0.807	0.098	0.628	0	2
Strumigenys feae Emery, 1895	0.714	0.417	0.684	0.040	0.419	0	5
Strumigenys sp. 1	0.521	0.416	0.508	0.024	0.326	0	1
Syllophopsis cf. *australica*	0.377	0.322	0.410	0.022	0.255	0	1
Tetramorium aptum Bolton, 1977	0.539	0.505	0.589	0.126	0.310	20	5
Tetramorium inglebyi Forel, 1902	0.566	0.508	0.641	0.051	0.293	2	0
Tetramorium kraepelini Forel, 1905	0.468	0.424	0.515	0.114	0.230	7	11
Ponerinae							
Anochetus graeffei Mayr, 1870	0.956	0.887	1.129	0.073	0.673	12	0
Anochetus sp. 1	1.650	1.523	2.129	0.277	1.448	1	0
Anochetus sp. 2	1.243	1.239	1.630	0.197	1.014	1	0
Ectomomyrmex annamitus (André, 1892)	1.199	1.141	1.752	0.147	0.732	0	12
Ectomomyrmex astutus (Smith, 1858)	1.838	1.773	2.705	0.271	1.252	0	2
Ectomomyrmex leeuwenhoeki (Forel, 1886)	1.620	1.478	2.383	0.245	1.082	14	6
Hypoponera sp. 1	0.489	0.395	0.640	0.026	0.305	13	32
Hypoponera sp. 2	0.632	0.522	0.864	0.039	0.423	0	4
Leptogenys cf. *lucidula*	1.122	0.911	1.710	0.173	0.905	1	0
Leptogenys cf. *punctiventris*	1.171	0.841	1.765	0.247	1.106	0	1
Leptogenys sp. 4	0.760	0.584	1.102	0.114	0.581	4	0
Leptogenys sp. A	1.233	0.912	1.878	0.279	1.215	0	1
Leptogenys sp. D	0.941	0.691	1.474	0.098	0.796	0	2
Ponera sp. 1	0.560	0.517	0.805	0.011	0.321	3	0
Ponera sp. 2	0.423	0.320	0.508	0.014	0.197	0	1

Designations. HL — head length, HW — head width, WL — Weber's length, EL — maximum eye diameter, HTL — hind tibia length.

Обозначения. HL — длина головы, HW — ширина головы, WL — длина груди, EL — максимальный диаметр глаза, HTL — длина задней голени.



Figs 1–2. Distribution of functional diversity index values based on null communities and empirical data for soil-litter ants at the studied plots. 1 — in ant communities of *Lagerstroemia* forest; 2 — in ant communities of dipterocarp forests. Designations: FDis — functional dispersion, FDiv — functional divergence, FEve — functional evenness, FOri — functional originality, FRic — functional richness, null model values: boxplot — from 25 % to 75 %; whiskers — from minimum to maximum model values; horizontal line inside the box — median; gray dots — outliers; stars — 5th and 95th percentile values. Circles show empirical data values.

Рис. 1–2. Распределение значений индексов функционального разнообразия на основе нулевых сообществ и эмпирические данные для комплексов почвенно-подстилочных муравьёв на модельных полигонах. 1 — в лагерстремиевом лесу; 2 — в диптерокарповом лесу. Обозначения: FDis — функциональная дисперсия, FDiv — функциональная дивергенция, FEve — функциональная выравненность, FOri — функциональная оригинальность, FRic — функциональное богатство, значения нулевых моделей: бокспλот — от 25 % до 75 %; усы — от минимального до максимального значений модели; горизонтальная линия внутри бокса — медиана; серые точки — выбросы; звёздочки — значения 5-го и 95-го перцентилей, кружки — значения эмпирических данных.

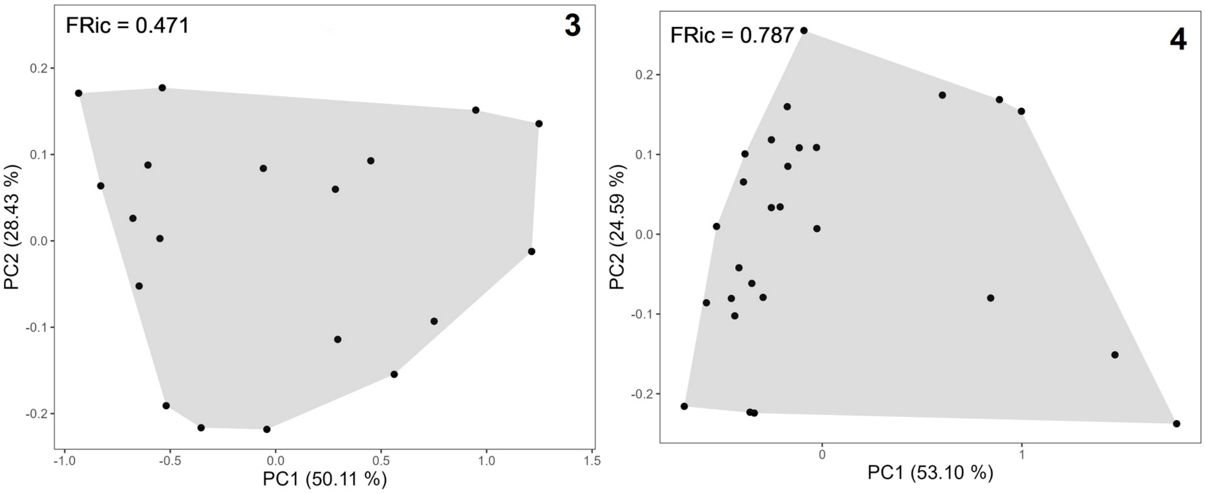
originality (FOri), and a higher value of functional evenness (FEve), whereas the ant community of the dipterocarp forest showed low values of FDis, FDiv, FOri, and FEve, and an increased value of FRic (Figs 1–2).

Figures 3–4 show the morphofunctional trait space of the ant communities in *Lagerstroemia* and dipterocarp forests. The relatively uniform distribution of species in the morphofunctional space for the ant community in the *Lagerstroemia* forest (Fig. 3) seemingly indicates a low representation of species with similar morphological traits. However, a slight clustering of species indicating morphological similarity can be observed in the region of negative PC1 axis values.

This finding is also supported by the differences in the observed and null values of functional originality (FOri) (Fig. 1). According to the null model, a portion of the niche space occupied by the soil-litter ants in the *Lagerstroemia* forest presumably remains unfilled compared with the potentially available space ($\mathrm{FRic}_{\mathrm{Obs}} < \mathrm{FRic}_{\mathrm{Null}}$). The slight differences between the null and observed values of functional divergence may indicate niche partitioning among most species.

The observed value of the functional evenness (FEve) in the ant community of *Lagerstroemia* forest was higher than the 5th percentile value of the null model (Fig. 1). FEve may reflect the degree to which species are distributed in the niche space to ensure efficient use of the available resource spectrum. Assuming resource availability is uniform across the niche space, it is crucial to analyze the entire functional trait space. Figure 5 presents the minimum spanning tree, which mainly consists of medium-length branches, potentially indicating relatively uniform resource utilization.

For the dipterocarp forest ant community, principal component analysis revealed a significant number of species with similar morphological traits in the region of negative values on the PC1 axis (Fig. 4). The low functional originality (FOri) compared to the null model may also indicate the presence of morphologically similar species. The increased value of functional richness (FRic) and the decreased value of the functional divergence (FDiv) suggest that the niche space is filled but with a low degree of ecological niche differentiation (niche overlap). The ant community in the dipterocarp forest exhibited lower functional evenness (FEve) compared to the null model. The minimum spanning tree (Fig. 6) comprises both long and short branches, which may indicate a uniform distribution of species in functional space and uneven utilization of potentially available resources across different parts of the niche space.



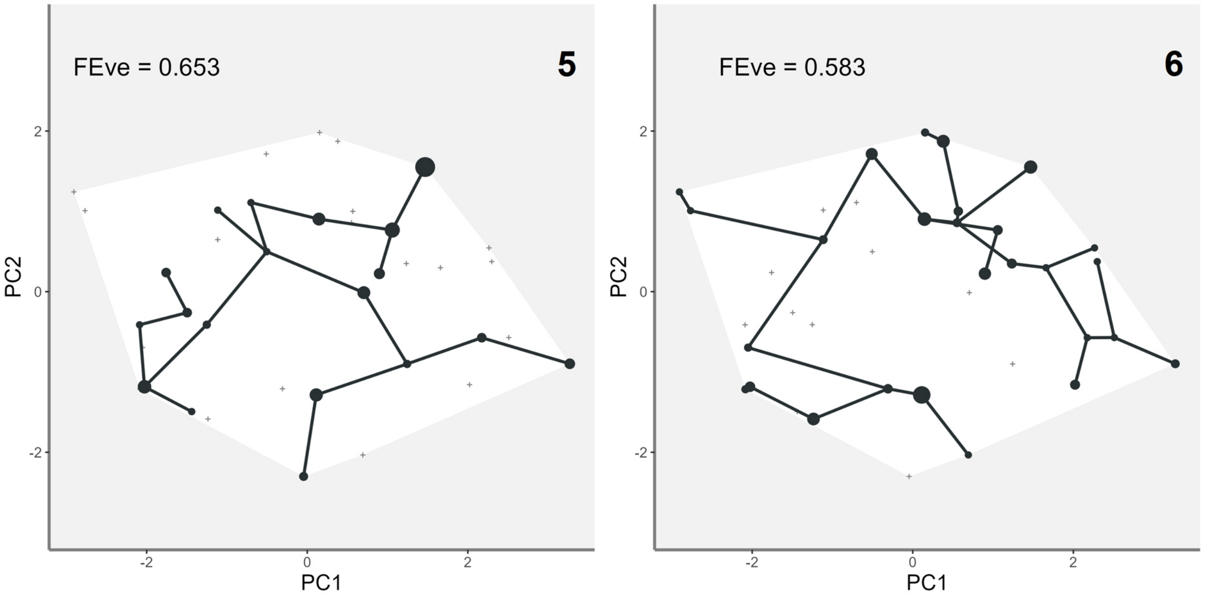
Figs 3–4. Morpho-functional trait space (grey area) at the studied plots in the ant communities of different forests. 3 — *Lagerstroemia* forest; 4 — dipterocarp forest. Dots indicate different ant species.

Рис. 3–4. Морфофункциональное пространство признаков (серая область) на исследованных полигонах в сообществах муравьёв в лесах разного типа. 3 — лагерстремиевый лес; 4 — диптерокарповый лес. Точками обозначены разные виды муравьёв.

The low functional dispersion (FDis) values calculated for soil-litter ants in both the *Lagerstroemia* and dipterocarp forests, in comparison to the null models, may indicate ongoing dynamic processes within these communities (Figs 1–2). However, in the ant community of the *Lagerstroemia* forest, these dynamic processes seem less pronounced due to the relative stabilization of species numbers and niche differentiation. Based on the preliminary data obtained, there is reason to believe that these processes are more expressed in the dipterocarp forest ant community, where significant ecological niche overlap ($FRic_{Obs} > FRic_{Null}$ and $FDiv_{Obs} < FDiv_{Null}$) is evident, suggesting that some parts of the niche space likely remain underutilized ($FEve_{Obs} < FEve_{Null}$).

Discussion

Our study provided preliminary data on soil-litter ant communities in two types of monsoon tropical forests, which differ in both stand composition and structure, as well as in edaphic conditions. In the dipterocarp forest, the azonal character of the soil is clearly pronounced [Kuznetsov, Kuznetsova, 2013], which may significantly impact soil-litter ants. In this study, we used a functional



Figs 5–6. Functional evenness in the ant communities of different forests. 5 — *Lagerstroemia* forest; 6 — the dipterocarp forest. Dots indicate different ant species; dot size is proportional to the number of occurrences; lines indicate branches of the minimum spanning tree.

Рис. 5–6. Функциональная выравненность в сообществе муравьёв в лесах разного типа. 5 — лагерстремиевый лес; 6 — диптерокарповый лес. Круглыми значками обозначены виды муравьёв; размер значков пропорционален числу встреч; линиями обозначены ветви минимального остовного дерева.

approach to assess the volume of potentially available resources and determine the extent to which these resources are used by soil-litter ants.

There is reason to believe that in the ant community of the *Lagerstroemia* forest, competition that may have occurred in the past has led to the niche differentiation of most species. This is supported by the values of functional originality (FOri) and functional divergence (FDiv) based on which it can be concluded that most species in the community have distinct morphological differences. For instance, species such as *Anochetus graeffei* Mayr, 1870 (Ponerinae) and *Stigmatomma crenatum* (Xu, 2001) (Amblyoponinae) possess such traits. These morphological differences among ant species serve as indicators of ecological niche partitioning.

In the ant community of the *Lagerstroemia* forest, part of the niche space apparently remains unoccupied indicating that the volume of resources available to ants is not fully utilized (functional richness: $FRic_{Obs} < FRic_{Null}$). This could suggest that not all available resources in the environment meet the needs of the ants. Additionally, the unoccupied niche space may be available to species with unique morphological traits (functional dispersion index: $FDis_{Obs} < FDis_{Null}$). In the latter case, such species are typically rare and often involved in dynamic community processes [Lyons et al., 2005; Säterberg et al., 2019]. Moreover, the availability of unoccupied niche space for species with unique morphological traits may imply that competition plays a significant role in shaping the soil-litter ant community in the *Lagerstroemia* forest. Consequently, species with morphological traits that allow them to avoid competition with closely related species may appear in the community. If a species with similar morphological characteristics emerges in the community, competitive exclusion is likely to occur. It is probable that reduced interspecies competition in the ant community of the *Lagerstroemia* forest contributes to greater community stability [Yanoviak, Kaspari, 2000; Leibold, McPeek, 2006].

According to our preliminary data, soil-litter ant species in the *Lagerstroemia* forest use only a part of the available niche space (functional richness: $FRic_{Obs} < FRic_{Null}$). This indicates that the available volume of resources is sufficient to maintain the observed number of species in the ant community, apparently contributing to the stabilization of species numbers at an optimal level. Additionally, the relatively uniform distribution of ant species in functional space suggests that all available resources are being used effectively (functional evenness: $FEve_{Obs} > FEve_{Null}$). However, for ants with similar morphological traits that may reflect comparable environmental requirements, resource use efficiency decreases. This can lead to the concentration of ant colonies in certain areas of space, resulting in increased competition for food and spatial resources. In the *Lagerstroemia* forest, the level of heterogeneity is lower [Anichkin et al., 2007] and there are fewer microhabitats for ant colonization compared to the dipterocarp forest [Zryanin, 2010]. Consequently, a lack of nesting substrates for colonization in the *Lagerstroemia* forest likely affects the formation of intraspecific forms of diversity and may lead to a decrease in taxonomic diversity. This mechanism has been observed in ant communities on tropical islands such as Tonga and Western Samoa [Zakharov, 1994]. Furthermore, the developed forms of sociality in ants promote a high level of intraspecific diversity, ensuring functional interchangeability among species and supporting the ecological integrity of the community [Zakharov, Sablin-Yavorsky, 1998].

In the soil-litter ant community of the dipterocarp forest, the increased value of functional richness (FRic) compared to null models indicates the occupancy of available niche space. Unlike the soil-litter ants of the *Lagerstroemia* forest, the ecological niches of many species in the dipterocarp forest significantly overlap (functional divergence: $FDiv_{Obs} < FDiv_{Null}$). This is further confirmed by the presence of morphologically similar species in the community (functional originality: $FOri_{Obs} < FOri_{Null}$), which seemingly experience competition due to limited resources (*Carebara*, *Ectomomyrmex*, *Leptogenys*, *Pheidole*). For example, *Ectomomyrmex leeuwenhoeki* Forel, 1886 actively colonized artificial nests [Zryanin, 2019], suggesting a shortage of natural nesting substrates for this species.

In contrast to the ant community of the *Lagerstroemia* forest, preliminary data indicate that the ant community in the dipterocarp forest exhibits an uneven distribution of species in functional space and low resource utilization efficiency in particular regions of the niche space (functional evenness: $FEve_{Obs} < FEve_{Null}$). This increases the likelihood of competitive interactions between species. Indeed, it has previously been shown that in the middle of the wet season, ant nest distribution tends to be aggregated. This is because ants require suitable microhabitats and substrates [Torres, 1984]. Moreover, the low FEve value and the presence of both short and long branches in the minimum spanning tree for the dipterocarp forest ant community may indicate that gaps remain in the community's niche space. These gaps may facilitate the entry of new ant species from the local species pool. This phenomenon could be attributed to the high diversity of nesting substrates available [Anichkin et al., 2007] and the dynamics of species richness within this forest. Low functional dispersion (FDis) and functional divergence (FDiv), along with the high value of the functional richness (FRic), suggest that niches within the ant community of the dipterocarp forest are more densely packed. Previous studies have demonstrated dense niche packing in soil-litter ant communities in the seasonally flooded forests of French Guiana [Fichaux et al., 2019]. This may indicate that the distinct ecotone effect in the dipterocarp forest [Zryanin, 2011], which contributes to an increase in species diversity, allow species to minimize competition for resources through dense niche packing. Additionally, the diversity of nesting substrates is likely contributing to increased functional richness, enabling species to occupy unique niches and reducing the risk of competitive displacement. However, the degree of niche space occupancy, especially in the dipterocarp forest, may be significantly higher when considering the soldiers of dimorphic (*Pheidole* spp., *Carebara* spp.) and polymorphic (*Pseudolasius* spp.) species. This issue requires further consideration.

Conclusions

Based on our preliminary findings, there is evidence to suggest that the number of soil-litter ant species in the *Lagerstroemia* forest is stabilizing. The availability of resources provided by the environment appears to be constrained by the presence of suitable substrates for ant colonization, which may significantly limit species diversity within the community. In the *Lagerstroemia* forest, the distinct morphological differences among most species indicate the prevailing role of niche mechanisms in the organization of the soil-litter ant community. These morphological differences among ant species in the *Lagerstroemia* forest are likely the result of niche differentiation stemming from interspecific competition that occurred in the past.

Conversely, the dipterocarp forest demonstrates a notably higher environmental capacity than the *Lagerstroemia* forest, facilitating the maintenance of greater species richness. The denser packing of ecological niches within the soil-litter ant community of the dipterocarp forest suggests that competitive interactions among species have a weak influence on the community's structure. The findings regarding niche space utilization by soil-litter ants in these two types of monsoon tropical forests are preliminary and require further in-depth investigation and detailed analysis including additional data.

Acknowledgments

We thank the authorities of the Southern department of Joint Russian-Vietnamese Tropical Research and Technological Center for organizing the research in Cát Tiên National Park, as well as to A.E. Anichkin for providing detailed geobotanical maps of the forest sites, which served as model plots for ant nest mapping.

References

Adler P.B., Fajardo A., Kleinhesselink A.R., Kraft N.J.B. 2013. Trait-based tests of coexistence mechanisms // Ecology Letters. Vol.16. No.10. P.1294–1306. https://doi.org/10.1111/ele.12157

Adler P.B., Hille Ris Lambers J., Levine J.M. 2007. A niche for neutrality // Ecology letter. Vol.10. No.2. P.95–104. http://dx.doi.org/10.1111/j.1461-0248.2006.00996.x

Anichkin A.E., Belyaeva N.V., Dovgobrod I.G., Shveenkova Yu.B., Tiunov A.V. 2007. [Soil microarthropods and macrofauna in monsoon tropical forests of Cat Tien and Bi Dup-Nui Ba National Parks, Southern Vietnam] // Izvestiia Akademii nauk. Seriia biologicheskaia. Rossiiskaia akademiia nauk. Vol.34. No.5. P.498–506. [In Russian]. http://dx.doi.org/10.1134/S1062359007050135

Arnan X., Arcoverde G.B., Pie M.R., Ribeiro-Neto J.D., Leal I.R. 2018. Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest // Science of the Total Environment. Vols 631–632. P.429–438. https://doi.org/10.1016/j.scitotenv.2018.03.037

Arnan X., Cerdá X., Retana J. 2017. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe // Ecography. Vol.40. No.3. P.448–457. http://dx.doi.org/10.1111/ecog.01938

Baddeley A., Turner R., Rubak E. 2021. Package 'spatstat' // Spatstat: Spatial point pattern analysis, model-fitting, simulation, tests. Available from: https://spatstat.org

Bihn J.H., Gebauer G., Brandl R. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests // Ecology. Vol.91. No.3. P.782–792. https://doi.org/10.1890/08-1276.1

Blanc L., Maury-Lechon G., Pascal J.P. 2000. Structure, floristic composition and natural regeneration in the forests of Cat Tien National Park, Vietnam: an analysis of the successional trends // Journal of biogeography. Vol.27. No.1. P.141–157. http://dx.doi.org/10.1046/j.1365-2699.2000.00347.x

Chiu C.-H., Chao A. 2014. Distance-based functional diversity measures and their decomposition: a framework based on hill numbers // PLoS ONE. Vol.9. No.7. P.e100014. P.1–17. http://dx.doi.org/10.1371/journal.pone.0100014

Farji-Brener A.G., Barrantes G., Ruggiero A. 2004. Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants // Oikos. Vol.104. No.1. P.165–171. http://dx.doi.org/10.1111/j.0030-1299.2004.12740.x

Fichaux M., Béchade B., Donald J., Weyna A., Delabie J.H.C., Murienne J., Baraloto C., Orivel, J. 2019. Habitats shape taxonomic and functional composition of Neotropical ant assemblages // Oecologia. Vol.189. No.2. P.501–513. https://link.springer.com/article/10.1007/s00442-019-04341-z

Flynn D.F., Mirotchnick N., Jain M., Palmer M.I., Naeem S. 2011. Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships // Ecology. Vol.92. No.8. P.1573–1581. http://dx.doi.org/10.2307/23034883

Gibb H., Parr C.L. 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents // Oecologia. Vol.164. No.4. P.1061–1073.

Gibb H., Parr C.L. 2013. Does structural complexity determine the morphology of assemblages? An experimental test on three continents // PLoS One. Vol.8. No.5. P.e64005. http://dx.doi.org/10.1371/journal.pone.0064005

Kaspari M. 1993. Body size and microclimate use in Neotropical granivorous ants // Oecologia. Vol.96. No.4. P.500–507. http://dx.doi.org/10.1007/BF00320507

Kaspari M., Weiser M. D. 1999. The size–grain hypothesis and interspecific scaling in ants // Functional ecology. Vol.13. No.4. P.530–538. http://dx.doi.org/10.1046/j.1365-2435.1999.00343.x

Kuznetsov A.N., Kuznetsova S.P. 2013. Tropical monsoon forests of Vietnam (results of 20 years of phytoecological research) // Biology Bulletin. Vol.40. No.2. P.187–196. http://dx.doi.org/10.1134/S1062359013020076

Laliberté E., Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits // Ecology. Vol.91. No.1. P.299–305. http://dx.doi.org/10.1890/08-2244.1

Leibold M.A., McPeek M.A. 2006. Coexistence of the niche and neutral perspectives in community ecology // Ecology. Vol.87. No.6. P.1399–1410. http://dx.doi.org/10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2

Lyons K.G., Brigham C.A., Traut B.H., Schwartz M.W. 2005. Rare species and ecosystem functioning // Conservation biology. Vol.19. No.4. P.1019–1024. http://dx.doi.org/10.1111/j.1523-1739.2005.00106.x

Magneville C., Loiseau N., Albouy C., Casajus N., Claverie T., Escalas A., Leprieur F., Maire E., Mouillot D., Villéger S. 2022. mFD: an R package to compute and illustrate the multiple facets of functional diversity // Ecography. Vol.2022. No.1. Art.e05904. P.1–15. http://dx.doi.org/10.1111/ecog.05904

Mason N.W., Mouillot D., Lee W.G., Wilson J.B. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity // Oikos. Vol.111. No.1. P.112–118. http://dx.doi.org/10.1111/j.0030-1299.2005.13886.x

Meynard C.N., Devictor V., Mouillot D., Thuiller W., Jiguet F., Mouquet N. 2011. Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? //

Global Ecology and Biogeography. Vol.20. No.6. P. 893–903. http://dx.doi.org/10.1111/j.1466-8238.2010.00647.x

Mims M.C., Olden J.D. 2012. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies // Freshwater Biology. Vol.58. No.1. P.50–62. http://dx.doi.org/10.1111/fwb.12037

Mottl O., Yombai J., Fayle T.M., Novotný V., Klimeš P. 2020. Experiments with artificial nests provide evidence for ant community stratification and nest site limitation in a tropical forest // Biotropica. Vol.52. No.2. P.277–287. http://dx.doi.org/10.1111/btp.12684

Mouillot D., Culioli J.M., Pelletier D., Tomasini, J.A. 2008. Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve // Biological Conservation. Vol.141. No.6. P.1569–1580. http://dx.doi.org/10.1016/j.biocon.2008.04.002

Mouillot D., Graham N.A., Villéger S., Mason N.W., Bellwood D.R. 2013. A functional approach reveals community responses to disturbances // Trends in Ecology & Evolution. Vol.28. No.3. P.167–177. https://doi.org/10.1016/j.tree.2012.10.004

Naeem S. 2002. Disentangling the impacts of diversity on ecosystem functioning in combinatorial experiments // Ecology. Vol.83. No.10. P.2925–2935. http://dx.doi.org/10.2307/3072027

Oksanen J. 2011. Multivariate analysis of ecological communities in R: vegan tutorial. Available from: http://cc.oulu.fi/wjarioksa/opetus/metodi/vegantutor.pdf

Oksanen J. 2015. Vegan: an introduction to ordination. Available from: http://cran.r-project.org/web/packages/vegan/vignettes/introvegan.pdf

Ovadia O., Schmitz O.J. 2002. Linking individuals with ecosystems: experimentally identifying the relevant organizational scale for predicting trophic abundances // Proceedings of the National Academy of Sciences of the United States of America. Vol.99. No.20. P.12927–12931. https://doi.org/10.1073/pnas.192245499

Petchey O.L., Gaston K.J. 2002. Functional diversity (FD), species richness and community composition // Ecology Letters. Vol.5. No.3. P.402–411. http://dx.doi.org/10.1046/j.1461-0248.2002.00339.x

Petchey O.L., Gaston K.J. 2006. Functional diversity: back to basics and looking forward // Ecology Letters. Vol.9. No.6. P.741–758. http://dx.doi.org/10.1111/j.1461-0248.2006.00924.x

Petchey O.L., O'Gorman E.J., Flynn D.F. 2009. A functional guide to functional diversity measures // Naeem S., Bunker D.E., Hector A., Loreau M., Perrings C. (Eds): Biodiversity, Ecosystem Functioning and Human Wellbeing: An Ecological and Economic Perspective. Oxford: Oxford University Press. P.49–59. http://dx.doi.org/10.1093/acprof:oso/9780199547951.003.0004

Poff N.L., Olden J.D., Vieira N.K.M., Finn D.S., Simmons M.P., Kondratieff B.C. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships // Journal of the North American Benthological Society. Vol.25. No.4. P.730–755.

Retana J., Arnan X., Cerdá X. 2015. A multidimensional functional trait analysis of resource exploitation in European ants // Ecology. Vol.96. No.10. P.2781–2793. https://doi.org/10.1890/14-2326.1

Salas-López A. 2017. Predicting resource use in ant species and entire communities by studying their morphological traits: Influence of habitat and subfamily // Ecological Indicators. Vol.78. No.10. P.183–191. http://dx.doi.org/10.1016/j.ecolind.2017.02.034

Säterberg T., Jonsson T., Yearsley J., Berg S., Ebenman B. 2019. A potential role for rare species in ecosystem dynamics // Scientific reports. Vol.9. No.1. P.11107. https://www.nature.com/articles/s41598-019-47541-6

Schofield S.F., Bishop T.R., Parr C.L. 2016. Morphological characteristics of ant assemblages (Hymenoptera: Formicidae) differ among contrasting biomes // Myrmecological News. Vol.23. P.129–137.

Schleuter D., Daufresne M., Massol F., Argillier C. 2010. A user's guide to functional diversity indices // Ecological monographs. Vol.80. No.3. P. 469–484.

Seifert B. 2017. The ecology of Central European non-arboreal ants — 37 years of a broad-spectrum analysis under permanent taxonomic control // Soil Organisms. Vol.89. No.1. P.1–69.

Swenson N.G. 2014. Functional and phylogenetic ecology in R. London, New York: Springer New York Heidelberg Dordrecht. 217 p. https://doi.org/10.1007/978-1-4614-9542-0

Silva R.R., Brandão C.R.F. 2014. Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient // PloS One. Vol.9. No.3. Art.e93049. P.1–11. http://dx.doi.org/10.1371/journal.pone.0093049

Silva R.R., Del Toro I., Brandão C.R.F., Ellison A.M. 2016. Morphological structure of ant assemblages in tropical and temperate forests // bioRxiv. Preprint. https://doi.org/10.1101/065417

Torres J A. 1984. Niches and coexistence of ant communities in Puerto Rico: repeated patterns // Biotropica. Vol.16. No.4. P.284–295. https://doi.org/10.2307/2387937

Traniello J.F.A. 1987. Comparative foraging ecology of north temperate ants: the role of worker size and cooperative foraging in prey selection // Insectes Sociaux. Vol.34. No.2. P.118–130.

Villéger S., Mason N.W., Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology // Ecology. Vol.89. No.8. P.2290–2301.

Weiser M.D., Kaspari M. 2006. Ecological morphospace of New World ants // Ecological Entomology. Vol.31. No.2. P.131–142.

Wong M.K.L., Guenard B. 2017. Subterranean ants: summary and perspectives on field sampling methods, with notes on diversity and ecology (Hymenoptera: Formicidae) // Myrmecological News. Vol.25. P.1–16.

Woodward G., Ebenman B., Emmerson M., Montoya J. M., Olesen J. M., Valido A., Warren P.H. 2005. Body size in ecological networks // Trends in Ecology and Evolution. 2005. Vol.20. No.7. P.402–409.

Yanoviak S.P., Kaspari M. 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter // Oikos. Vol.89. No.2. P.259–266.

Yates M.L., Andrew N.R., Binns M., Gibb H. 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale // Peer Journal. Vol.2. Art.e271. P.1–20. https://doi.org/10.7717/peerj.271

Zakharov A.A. 1994. [Ant population structure on the islands of Tonga and Western Samoa] // [Animal population of the islands of Southwestern Oceania (ecogeographic studies)]. Moscow: Nauka. P.94–142. [In Russian].

Zakharov A.A., Sablin-Yavorsky A.D. 1998. [Ants in studying of biological diversity] // [Advances in current biology]. Vol.118. No.3. P.246–264. [In Russian].

Zryanin V.A. 2010. Seasonal peculiarities of ant population (Hymenoptera: Formicidae) in tropical monsoon forest // Proceedings of the Russian Entomological Society. Saint Petersburg. Vol.81. No.2. P.95–102. [In Russian].

Zryanin V.A. 2011. Analysis of the local ant fauna (Hymenoptera, Formicidae) in Southern Vietnam // Entomological Review. Vol.91. No.2. P.198–2011. http://dx.doi.org/10.1134/S0013873811020084

Zryanin V.A. 2019. [Colonization of artificial nests by ants (Hymenoptera: Formicidae) in a tropical monsoon forest during the wet season] // [Thesis of IV Euroasian Symposium on Hymenoptera]. Vladivostok 9–15 September 2019. Vladivostok: FSC Biodiversity FEB RAS. P.91–92. [In Russian].

Поступила в редакцию 17.10.2024