Ecology, Behavior and Bionomics: Functional response of Heterotermes tenuis Hagen (Insecta: Blattaria: Isoptera) in forests of the Colombian Orinoquía

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Abstract

Background

The functional traits of insects and, in particular, those associated with termites have not been widely studied. Some studies present purely taxonomic approaches and overestimate interspecific variation and ignore intraspecific variation. Likewise, it is unknown how the functional morphological traits of termites are modified as a result of disturbances, in this case, the change in land use. Therefore, in order to contribute to the understanding of the response mechanisms of termites against land use change and its implications in intraspecific variation, we carried out morphological medition of 38 functional morphological traits (FMT) of the worker and soldier caste of xylophagous species *Heterotermes tenuis* (Hagen, 1858) in four periods of *Pinus caribaea* plantation (Morelet, 1851) and gallery forest relicts. Comparisons between relict forest and plantations were made using non-metric multidimensional scaling analysis, PERMANOVA and multinomial models.

Results

The intraspecific variation of 16 traits of the 38 studies presented lower values both in plantations and in gallery forests. Traits related to general body size are not considered useful due to their observed variation. Likewise, a more significant effect of the type of land use was observed than the plantation ages in the greater size of the workers, while the results were not conclusive in the military caste.

Conclusions

The results suggested a homogenization of the TMF of the worker caste of *H. tenuis* in the pine plantations, most likely, but not only related to an increase in the softwood food supply of *P. caribaea.*

Background

Epigeal and subterranean arthropods are considered indicators of soil quality due to their great diversity, participation in various ecosystem processes, and sensitivity to changes in land use (Bignell et al., 2008; Doran & Zeiss, 2000). However, most monitoring studies focus on taxonomic diversity indices, but ecosystem processes depend on the relationship of a specific set of species (Levrel, 2007; Vandewalle et al., 2010) and its functional diversity (Moretti et al., 2016). Therefore, including the analysis of morphological and functional traits facilitates the understanding of the response of organisms to land use change and generates reference predictions for ecosystem services (Vandewalle et al., 2010)

In the case of insects, the most studied functional traits are the trophic level, the organism's dispersal capacity, voltinism, and body size (Brousseau et al., 2018). In the particular case of termites, four or five trophic functional groups (Bignell et al., 2008; Donovan et al., 2001, Inward et al., 2007; Jones & Eggleton, 2010), separated according to the type (wood, soil, organic matter, and fungi) and the degree of humification of the food substrate.

The methods to study the functional traits of insects are still under development and change among the different taxonomic groups: carabids (Torma et al., 2019), springtails (Winck et al., 2017), and termites (Liu et al., 2019). There are some databases of functional traits for carabids and arachnids; however, the scope is limited, and they focus on incomparable functional traits between taxa (Simons et al., 2015). The morphological and functional traits of termites have been little studied and include those related to the tasks of food acquisition, digestion, and nesting, among others (Bignell et al., 2008).

Ecological studies focused on the analysis of functional traits use the average values of the traits and generally assume low or dismiss intraspecific variability (IV). Ignorance of this variability can mask or overestimate the interspecific effects and lead to false conclusions about the mechanisms that determine the patterns of diversity, habitat filtration, and habitat differentiation, among others (Gaugard et al., 2019). Recent studies have estimated IV in various species of ants (Gaugard et al., 2019) and coprophagous beetles (Griffiths et al., 2016), organisms widely used as bioindicators. Estimating morphological size and their variation is standard in termites for taxonomic purposes (Ferrigno et al., 1997). Still, few studies refer to the ecological implications of the variation of those traits (Liu et al., 2019).

The functional morphological response of termites to changes in land use is mostly unknown and referred to as the effects of reforestation of previously deforested areas (Liu et al., 2019). In termites, the soldier caste performs defensive and exploratory functions but does not feed itself. Therefore, it is expected that changes related to the quantity and quality of available food will directly impact the functional traits of the termite's worker caste. Likewise, morphological changes are expected in the caste of soldiers who respond to various predators, especially ants. In afforestation of the Colombian East Plains, for example, the increase in the frequency of the xylophagous species *Heterotermes tenuis* (Hagen, 1858) compared to the previous use of the land is reported; in part, attributed to the more significant amount of food available in the forests (Beltrán & Pinzón, 2018). However, the functional morphological responses of this species that allow it to adapt to changing environmental conditions are unknown, as has been observed in other recent studies (Liu et al., 2019). In such a way, responses to changes in the quantity and type of food can express the size of the mouthparts of the workers. In contrast, the characteristics of the soldiers reflect aspects related to defense (for example, in the face of changes in the abundance of predators).

This work aimed to compare the functional traits related to foraging, feeding, and defense in the species *H. tenuis* between different land uses in a forest core of the Colombian Eastern Plains after estimating the intraspecific variation of these traits. To this end, this paper compares the size of various morphological and functional traits of the worker and soldier castes at different ages of *Pinus caribaea* plantation (Morelet, 1851) and gallery forest relicts. We expect to contribute to the functional perspective of the ecology of this species and to understand better the mechanisms of adaptive response to the alteration of the

food source as a basis for predicting changes in ecosystem services derived from the activity of these insects, such as the rate of wood decomposition, nutrient regulation, and soil formation.

Methods

Study area

The research used specimens of *H. tenuis* from *P. caribaea* plantations and relict gallery forests of the San Pedro plateau, Villanueva, Casanare, Colombia (4° 36' 0" N, 72° 55' 1" W) ; collected and reported by Pinzón et al. (2017) and Beltrán & Pinzón (2018). The locality presents a monomodal regime, with an average annual temperature and precipitation of 25.7°C and 2911 mm, respectively. The period of rains occurs between April to November and dry period between December to March. The average relative humidity is 76%, with May to September being the wettest months (up to 85%), while the least humid is between December and March (REFOCOSTA, 2013). The study area comprises landscapes of floodplain savannahs of the eolian plain and undifferentiated intervened rural areas (REFOCOSTA, 2013). In particular, the Meseta de San Pedro corresponds to a high terrace of sandy to sandy loam soils of a quartzous nature and low fertility belonging to the entisol and inceptisol orders (REFOCOSTA, 2013).

Pinus caribaea**plantations**

The *P. caribaea* plantations, where the collections were made, were established at 358 m altitude and occupied an area of 1,500 hectares at the time of the stud. These plantations had several ages: 1 to 2 years, 6 to 7 years, 7 to 8 years, and 19 to 23 years. According to Beltrán & Pinzón (2018), the last two age ranges (7 to 8 years; 19 to 23 years) presented thinning and pruning (Table 1) (REFOCOSTA, 2013). The total height of the trees in the transects was measured with a Haglof Vertx IV hypsometer and the DBH (diameter at breast height) using a diameter tape. In addition, the canopy's opening was estimated by processing photographs taken with a digital reflex camera adapted with a 5.6 mm fisheye lens installed on a tripod with the WinCAM V.2012a program (Regent Instruments Canada Inc. 2012 In addition, the percentage of organic carbon and the pH were analyzed from a single sample of soil. The pH values remained relatively constant between the plantation ages, while the percentage of light decreased with the age of the plantation.

Relicts of gallery forests

The relicts of gallery forests surrounding the plantation stand between 2 and 5 km of distance (Pinzón et al., 2017). These forest relics border the Huerta la Grande, Claro, and Los Micos and streams in the Upía river basin. The diversity of the vegetation and the structure of the sampling sites were characterized by Fernández et al. (2012). In each relict, the pH was measured by the soil suspension method and the organic carbon content by the Walkley Black method (Beltrán & Pinzón, 2018). The height and diameter of the trees were measured using a Vertex (Haglof Vertex IV) and a diameter tape, respectively. In addition, canopy cover was estimated from photographs taken with a fisheye lens adapted to a camera compatible with Winscanopy software. In addition, the pH, moisture, and organic carbon content were obtained from a single soil sample per site (Pinzón et al., 2017).

Table 1
Characterization of the four ages of *Pinus caribaea* and gallery forest relicts, modified from Beltrán & Pinzón (2018) and Pinzón et al. (2017)

Coverage	Silvicultural management	Average DBH (cm)	Average height (m)	pH	Organic carbon (%)	Average brightness (%)
Pinus caribaea 1–2 años	without thinning	7,2 ± 0,9	4,2 ± 0,7	4,4	1,3	74,6 ± 6,2
Pinus caribaea 6–7 años	without thinning, pruning	18,7 ± 2,8	13,5 ± 2,7	4,3	1,1	71,7 ± 3,5
Pinus caribaea 7–8 años	with thinning, pruning	21,7 ± 5,0	14,8 ± 3,3	4,4	1,4	71,0 ± 2,7
Pinus caribaea 19–23 años	with thinning, pruning	24,5 ± 16,5	20,2 ± 10	4,1	1,2	68,4 ± 2,8
		11,7 ± 6,3	11,1 ± 2,5	4.3	4,3	15,8 ± 6,0
Gallery forest	no handling	13,6 ± 3,4	10,2 ± 4,7	4.5	1,2	16,0 ± 5,3
		24,2 ± 8,4	15,3 ± 3,3	4.4	3,0	13,7 ± 5,6

Specimen selection

The samples of the worker and soldier termites of *H. tenuis* were collected following the transect method (Jones et al., 2005) with modifications (Pinzón et al., 2017; Beltrán & Pinzón, 2018; Appendix) at four ages of *P. caribaea* plantation: 1–2 years, 6–7 years, 7–8 years, 19–23 years and in three relicts of gallery forest surrounding the plantations. The identification of the genus and the species was carried out with the keys of Constantino (2000; 2002). The specimens are deposited in the Forest Entomological Collection of the Francisco José de Caldas District University (CEFUD, RNC 045). Workers and soldiers were measured to estimate changes in the size of functional morphological traits associated with foraging for food and colony defense. Seven soldiers and sever workers from three representative colonies of each of the following land soil use: four plantation ages of *P. caribaea* and relicts of forest gallery), as recommended by Gaudard et al. (2019). Each colony was represented by fourteen individuals (seven workers and seven soldiers); a total of 210 individuals were measured (105 workers and 105 soldiers). Considering that the soldier of *H. tenuis* is dimorphic (Constantino, 2000), only the minor soldier was selected due to its greater abundance in the samples. Although the area that an *H. tenuis* nest can occupy is not known, in this work, a maximum of one sample was used from each sampling subtransects to ensure a minimum distance of 10 m between samples, which was considered a different colony. This distance was assumed according to the average feeding distance of other species of this genus (Haverty & Nutting, 1975). Therefore, the analyzed samples maintained a

distance between 10 and 40 m in the field according to the availability of the individuals collected. While samples coming from adjacent subtransects would be separated by 10 m, those coming from the ends would have a 40m distance.

Measurement of functional morphological traits of termites

Functional morphological traits (FMT) related to worker caste foraging and soldier defense activity were selected and measured (Liu et al., 2019). The FMT included parts of each caste's head and the buccal and locomotor apparatus and were measured on the right dorsal side. FMT measurements were made according to standardized termite definitions (Roonwal, 1969).

Functional morphological traits of the worker and soldier

Fourteen morphological features of the thorax and the head of the worker caste were measured. In the thorax, the maximum width and length of the pronotum, the length of the tibia, and the femur of the prothoracic right leg. In the head, the maximum width and length of the head and the following characteristics of the buccal apparatus were included: in the left mandible, the distance between the first apical tooth and the first marginal tooth (La), the distance between the first and second tooth marginal (L1), distance between the second and third marginal teeth (L2), the distance between the third marginal tooth and the molar prominence (MPr). In the right mandible, were measured the distance between the first apical tooth and the first marginal tooth (Ra), the distance between the first and second marginal tooth (R1), the distance between the second marginal tooth and the molar plate (R2), the distance between the second marginal tooth and the molar plate (R2), and molar plate extension (MP; Fig. 1).

The FMT measured for the soldier caste included (Fig. 1): left (LMI) and right (LMD) mandible length, width, and the maximum length of the head (ANC and LCA, respectively), length and maximum width of the pronotum (LPRO and APR, respectively), anterior pronotal notch depth (MAP), posterior pronotal notch depth (MPP), and prothoracic leg tibia and femur length.

Morphological indexes

Additionally, the following morphological indices were calculated according to Roonwal's (1969) wordy estimate proportions between the FMT of both castes.

Worker caste

a. Index 1: Maximum head width/cephalic capsule length: Cephalic capsule shape
b. Índex 2: Maximum length pronotum / maximum width pronotum: Shape of the pronotum
c. Index 3: Maximum pronotum width / maximum head width: Head-pronotum ratio

Caste soldier

a. Index 1: Maximum width of the head/length of the head to the lateral line of the mandibles: Cephalic capsule shape
b. Index 2I: Maximum left mandible length / maximum head width: Proportion of left mandible and head
c. Index 2D: Maximum length of the right mandible / maximum width of the head: Proportion of right mandible and head
d. Index 3: Maximum length of the pronotum / maximum width of the pronotum: Shape of the pronotum

The FMT were measured in millimeters (mm), from high-resolution photographs, magnified and taken with an Axiocam 506 color camera adapted to a Discovery V8 stereomicroscope, Zeiss brand, and the use of the ZEN brand photography and measurement software (version 2.6).

Analysis of data

Selection of functional morphological traits with less intraspecific variation

To explore the clustering patterns of the FMT measured in each caste, a Principal Component Analysis (PCA) was performed using the type of cover as an illustrative variable. For this grouping, the samples were categorized into five subgroups: 1–2 years, 6–7 years, 8–9 years, 19–23 years, and gallery forests.

To select the FMT having less intraspecific variation, the Coefficient of Variation (CV) of each FMT of *H. tenuis* was estimated for each colony of the compared types of land use without transforming the original values. The CV percentage was calculated using the formula: (DS/X) *100. Additionally, a univariate comparison was made between the FMT values of both castes per colony of the plantations and gallery forests, using the non-parametric Kruskal-Wallis (KW) test; because the data did not meet the necessary assumptions of normality (Shapiro-Wilk) to implement an analysis of variance (ANOVA). Subsequently, using both tools (CV and KW), the FMT with the least intraspecific variation for the worker and soldier caste was selected.

Effect of plantation age/coverage on the size of functional morphological traits

To estimate changes in the FMT in the Community-Weighted Mean (CWM) index corresponding to the weighted mean of each trait was estimated and compared (Ricotta & Moretti, 2011). For this analysis, each colony was assumed as a different species with the same abundance. The comparisons between the type of land use and ages were made through a PERMANOVA analysis with 999 permutations and a *p*-value equal to or less than 0.05. Additionally, to complement the results of PERMANOVA, the differences between the individuals of both colonies in the different coverages were evaluated using non-metric multidimensional scales (NMDS) with Manhattan distance. For this purpose, only the FMT with the lowest percentage of CV was taken into account. Then, to estimate the effect of the type of coverage and the colony in the worker and soldier caste, multinomial models were implemented for both cases. For all models, only the lowest %CV FMTs were used for debugging purposes. For each model, the following variables were included: DBH, average height, percentage of organic carbon, pH, and percentage of luminosity. For the first model, the type of coverage was used as a factor, while for the second, the colony was used as a factor. In each model, the Akaike value and three Pseudo R2 values (CoxSnel, Nagelkerke, and McFadden) were estimated to estimate which model

presented better predictive quality and which model better explained the variation found in both castes. These analyzes were calculated using the R-Project V 1.4.1717 packages (R Core Team, 2020; Appendix).

Results

Selection of functional morphological traits with less intraspecific variation

The size of the morphological traits of the workers made it possible to separate the colonies from natural forests and gallery forests (Fig. 2). The FMT of the first two axes of the PCA analysis explained 83.3% of the observed variation. While the first axis differentiated the gallery forest workers from the pine plantation treatments, the second axis suggested grouping between individuals from the intermediate plantations and the younger and more mature plantations (Fig. 2).

The analysis of the size of the traits of the soldier caste does not allow to completely separate the individuals of each cover (Fig. 3). The PCA explained 71.6% of the observed variation, but in this case, the individuals from the gallery forests and the 8 year old plantations concentrated among the largest individuals.

The intraspecific variation of the FMT of *H. tenuis* was within the range of 0.15–50.56%. In the worker caste, the FMT presented a CV between 0.15% and 18.5% at the colony and ground cover level (Table 2), where the trait with the highest CV percentage was the head's length. In contrast, the mandibular trait L1 presented the lowest value. In the case of the soldier caste, the CV% fluctuated between 0.14% and 50.56% (Table 3). The trait with the highest percentage of CV was the posterior notch of the pronotum, and the one with the lowest CV percentage was the length of the tibia.

The FMT with less variation for the worker caste were: L1, L2, MPr, Ra, R1, R2, MP, and Index 2 (*gl*:2, *p*-value: 0.05) (Table 2), and there are related to the feeding activity of the working caste. In the case of the soldier caste, the FMT with the slightest variation were: the width and length of the head, the width of the pronotum, the maximum length of the mandibles, length of the tibia, Index 2 left mandible, and Index 3 (Table 3), which are related to colony defense (gl:2, p-value: 0.05).

Effect of soil cover type and plantation age on the size of functional morphological traits

The individuals of the worker caste and soldiers of *H. tenuis* from the gallery forests presented a larger size compared to those from the pine plantations. In particular, for the worker caste, the specific traits of the left mandible (La, L1, L2, Mpr) and the right mandible (Ra, R1, R2, MP) increased in the mature plantations (19–23 years) and the gallery forest relicts; while index 2 was higher in the younger and more mature plantations (1–2 years, 19–23 years; Table 4). For the soldier caste, traits related to head size, pronotum, length of both mandibles and tibia, and indices 2I and 3, increased in size in gallery forests and plantations aged 7 to 8 years (Table 4).

The workers from the gallery forests presented larger FMT than the pine plantations for most of the CWM values (Table 4). The results of PERMANOVA (gl = 4, p = 0.05) show differences between the average size of the FMT selected from the workers of pine plantations compared to gallery forests. Likewise, there were differences between the average sizes of the individuals of the plantations of intermediate ages (6–8 years) and the mature plantations (19–23 years; Appendix).

Table 2

Coefficient of variation (CV) expressed in % of the functional morphological traits of the worker caste of *Heterotermes tenuis*, in three colonies of each type c cover. Colonies are organized by planting age: 1.1 to 1.3 (1–2 years), 2.1–2.3 (6–7 years), 3.1–3.3 (7–8 years), 4.1–4.3 (19–23 years), 5.1–5.3 (gallery forest (Left Mandible): distance between the first apical tooth and the first marginal tooth (La), distance between the first and second marginal tooth (L1), distance b second and third marginal tooth (L2), distance between the third marginal tooth and the molar prominence (MPr). Ra-MP(Right Mandible): distance betwee apical tooth and the first marginal tooth (Ra), KW distance between the first and second marginal teeth (R1), distance between the marginal second tooth and (R2), and molar plate extension (MP).* KW traits that differ statistically significantly from colonies of the same plantation age/gallery forest with a *p*-value of 0 = 7 individuals measured per colony. Extreme values of percent CV are highlighted

COLONY	L1	La	L2	MPr	Ra	R1	R2	MP	Index 2	Index 3	Index 1	Pronotum length	Femur	Head width	Pronotum width	Tibi
1.1	0,48	0,49*	0,68*	0,63*	0,73*	0,74	1,68*	1,45	2,61	5,14*	4,88*	4,14*	4,41*	5,07*	6,08*	6,70
1.2	0,54	0,64*	0,67*	0,62*	0,95*	0,51	1,18*	1,09	3,14	3,29*	3,28*	3,31*	2,52*	2,79*	3,24*	8,23
1.3	0,44	0,49*	0,76*	0,82*	0,74*	0,29	1,06*	1,62	3,65	3,29*	3,63*	2,83*	4,67*	3,80*	4,01*	4,33
2.1	0,26	0,28	0,22	0,44	0,33	0,28	0,52*	0,72*	1,49	2,22*	4,89	1,67	2,68*	1,25*	2,09*	4,18
2.2	0,24	0,32	0,44	0,17	0,35	0,45	0,69*	1,19*	5,40	2,80*	3,82	2,24	3,21*	3,29*	4,27*	6,27
2.3	0,45	0,51	0,65	0,56	0,49	0,48	1,52*	1,68*	3,14	2,15*	6,71	1,89	3,60*	2,28*	1,34*	2,90
3.1	0,15	0,33	0,26*	0,33*	0,38*	0,40	0,94	0,83	5,64	1,33	2,02	4,18	2,11*	1,89*	1,18*	1,59
3.2	0,51	0,71	0,63*	0,65*	0,64*	0,71	1,60	1,66	3,67	3,05	2,74	4,43	4,33*	4,98*	5,51*	6,57
3.3	0,23	0,27	0,38*	0,32*	0,34*	0,64	1,07	1,52	4,10	2,75	4,38	2,41	5,77*	2,67*	2,29*	5,74
4.1	0,35	0,61	0,48*	0,62	0,70	0,43	1,18*	0,72*	2,97	4,37	6,81	3,39	4,21	2,94	4,32*	3,50
4.2	0,32	0,23	0,32*	0,64	0,29	0,24	0,89*	0,98*	7,55	3,02	2,79	7,43	7,10	5,52	5,28*	5,79
4.3	0,30	0,27	0,49*	0,71	0,44	0,22	0,86*	1,34*	3,10	3,00	3,11	2,56	3,45	2,89	3,32*	3,49
5.1	0,41*	0,55	0,66	0,49	0,50	0,45	1,36	1,03*	1,70	1,68	5,05*	2,47	4,83*	5,15*	3,89*	7,54
5.2	0,47*	0,33	0,51	0,71	0,55	0,32	1,44	0,94*	1,35	5,65	4,63*	3,96	3,13*	2,05*	6,89*	4,09
5.3	0,48*	0,56	0,56	0,55	0,62	0,62	0,49	0,86*	5,80	3,15	3,06*	5,35	3,90*	4,84*	2,69*	5,41

Table 3

Coefficient of variation (CV) expressed in % of the functional morphological traits of the soldier caste of *Heterotermes tenuis*, in three colonies of each type o cover. Colonies are organized by planting age: 1.1 to 1.3 (1–2 years), 2.1–2.3 (6–7 years), 3.1–3.3 (7–8 years), 4.1–4.3 (19–23 years), 5.1–5.3 (gallery forests Index. KW traits this present statistically significant differences between colonies of the same age of plantation/gallery forest with *p*-value of 0.05. GI:2 N = 7 i measured per colony. Extreme values of percent CV are highlighted

COLONY	Tibia length	Ind. 3	Largo mandíbula izq.	Ind. 1	Mandibles length Rig.	Ind. 2 left	Head width	Pronotum width	Head length	Ind. 2 rig.	Femur length	Pronotum length	Anterior notch pronotum	P r p
1.1	5,15	8,71	10,49	6,97	12,7	6,37	8,97	9,91	14,71	8,07	9,36	18,74	17,82	4
1.2	7,49	3,77	4,94	2,71	6,06	1,32	6,27	3,84	3,53	1,24	5,39	6,72	11,82	2
1.3	14,99	7,58	13,15	5,29	13,87	6,21	9,68	11,62	11,91	5,02	15,37	15,19	13,12	2
2.1	13,84	4,52	12,13	6,13	13,94	8,73	5,03	9,86	10,45	9,86	15,52	13,50	36,41	3
2.2	8,92	11,36	6,63	6,64	15,57	11,33	14,42	11,86	19,14	22,45	9,18	22,65	25,21	3
2.3	0,14	5,10	2,39	14,00	1,11	10,68	13,06	9,2	0,95	14,16	9,58	14,27	14,54	2
3.1	9,27	1,47	5,42	4,12	5,13	13,60	9,52	8,71	9,27	13,48	2,80*	9,43	16,62	5
3.2	8,80	6,33	10,02	3,29	11,55	19,47	14,28	12,3	13,27	23,86	10,28*	15,81	18,40	3
3.3	4,41	4,31	3,21	10,05	2,33	3,51	3,4	1,89	8,76	4,63	1,16*	4,04	16,06	3
4.1	12,48*	12,19	11,16	8,38*	11,65	13,46	11,12	13,81	14,62	13,51	11,53*	20,63	32,47	2
4.2	4,57*	2,32	1,88	5,39*	14,55	2,51	0,73	1,06	5,65	14,69	5,71*	2,69	38,92	1
4.3	6,19*	5,64	5,75	44,33*	5,05	14,29	17,4	17,88	20,46	15,36	5,25*	22,07	20,16	4
5.1	2,56	3,67*	4,65	4,05*	2,81	5,83	3,09	3,64	3,93	5,16	4,20*	1,84	8,96	3
5.2	5,01	3,33*	4,78	3,00*	4,72	2,98	4,13	7,64	5,27	2,41	4,47*	5,02	14,46	3
5.3	2,91	3,52*	1,54	3,48*	1,01	4,19	3,85	4,09	4,08	3,11	3,23*	3,08	11,70	3

The ordination analysis showed a strong correlation between the size of the FMT and the habitat type (Table 4). Two subgroups within the worker caste were observed. The first group corresponded to the colonies of the ages of pine plantation, whose FMT were significantly lower than the workers of group two,

which corresponds to the relicts of the gallery forest. (Fig. 4). The prominence and molar plate feature, R2, L2, and the pronotum shape defined group one, while group two was more related to the traits Ra, La, R1, and L1 (Fig. 4).

For the soldier caste, the FMT and the CWM values behaved differently compared to the worker caste, forming two patterns (Table 4). Individuals from 6-8-year-old plantations and gallery forests presented larger FMT than the rest of the plantation ages for most CWM values (Table 4). The PERMANOVA results (*gl* = 4, $p = 0.05$) show that there are differences between the youngest plantations (1–2 years) and the intermediate plantations (7–8 years). Likewise, differences were observed between the plantations of 1–2 years, 6–7 years, and 19–23 years with the gallery forests (Appendix). In addition, the ordination analysis made it possible to show how the size of the FMT of the soldier caste is strongly correlated with the type of habitat (Fig. 5), and the formation of two subgroups was observed. The first group corresponded to the colonies of the youngest pine plantation ages (1–2 years; 6–7 years) and more mature (19 to 23 years), whose FMT were significantly lower than the soldiers of group two, which corresponds to the relicts of the gallery forests. Group one is defined by the length of both mandibles, the length of the tibia, and Index 3; while group two was more related to the width and length of the head and the length of the pronotum (Fig. 5).

The multinomial models of the worker and soldier caste presented a similar trend. Regarding the Akaike predictive quality value, this value was lower when planting age/coverage was a factor, in contrast to the value obtained when the colony was a factor. Likewise, the models obtained for both castes explained a large part of the variation observed due to the type of coverage and the colony, showing values of the three Pseudo R2 equal to or close to 1. The models obtained from the soldier caste were slightly less robust than the worker caste (Table 5).

Table 4
CWM index of the worker and soldier caste of *Heterotermes tenuis* in the different ground covers. La = distance between the first apical tooth and the first marginal tooth, L1 = distance between the first and second second marginal tooth, L2 = distance between the second and third marginal tooth, MPR = Molar Prominence, Ra = distance between the first apical tooth and the first marginal tooth, R1 = distance between the first and second marginal teeth, R2 = distance between the second marginal tooth and the molar plate, MP = Molar plate. Ind.2 = Index 2. ANC = Width of the head, LCA = Length of the head, LMI = Maximum left mandible length, LMD = Maximum right mandible length, APR = Pronotum width

Caste	Types of coverage	Functional morphological features								
		La	L1	L2	MPr	Ra	R1	R2	MP	Ind2
	P. caribaea 1–2 años	0,05	0,04	0,08	0,08	0,06	0,05	0,16	0,14	0,57
	P. caribaea 6–7 años	0,05	0,04	0,08	0,08	0,06	0,05	0,16	0,14	0,54
Workers	*P. caribaea* 7–8 años	0,05	0,04	0,08	0,08	0,06	0,05	0,16	0,14	0,53
	P. caribaea 19–23 años	0,05	0,05	0,09	0,08	0,07	0,05	0,17	0,14	0,58
	Gallery	0,06	0,06	0,1	0,1	0,08	0,06	0,21	0,18	0,52
		ANC	LCA	LMI	LMD	APR	TIBIA	Ind2I	Ind3	
	P. caribaea 1–2 años	0,969	1,5	1,17	1,19	0,7	0,81	1,21	0,63	
	P. caribaea 6–7 años	1,01	1,55	1,25	1,26	0,71	0,89	1,25	0,62	
Soldiers	*P. caribaea* 7–8 años	1,12	1,65	1,33	1,35	0,78	0,92	1,2	0,65	
	P. caribaea 19–23 años	0,994	1,5	1,33	1,35	0,71	0,91	1,36	0,64	
	Gallery	1,17	1,71	1,32	1,33	0,8	0,94	1,12	0,65	

Table 5
Multinomial models of the worker and soldier caste of *Heterotermes tenuis* using colonies and land use type as factors. CV: Coefficient of variation

Caste	Response	AIC	Pseudo R2			Predictor
Work	Coverage	112	0,96	1	0,99	FMT with lower CV, DBH, C organic, average heigth, % brigthness, pH
	Colony	392	0,99	1	0,99	
Soldier	Coverage	112	0,96	0,99	0,99	FMT with lower CV, DBH, C organic, average heigth, % brigthness, pH
	Colony	392	0,95	0,99	0,99	

Discussion

The size of the functional morphological traits of the worker and minor soldier castes of *H. tenuis* was mainly influenced by the type of cover and, to a lesser extent, by the ages of the pine plantations. Likewise, the intraspecific variation of 16 traits out of the 38 studied presented lower CV values, both in plantations and in gallery forests, and allowed their use to compare the effect of the change in cover type, minimizing the effect of intraspecific variability.

Variation of functional morphological traits

The FMT with more significant variability in the worker caste of *H. tenuis*, in the four ages of plantation and gallery forests were related to the general size of the body (head, thorax, and extremities), that is, with the food search. In contrast, the FMT with less variability were the specific characters of the oral apparatus, affecting food foraging. This observation coincides with previous studies in social insects, where intraspecific variation is significantly high in activities related to time and the active search for food between and within populations (Bockoven et al., 2015; Jandt & Gordon, 2016). Highly variable traits can improve colony fitness by extending the range of behavior (for example, foraging) and allowing better and faster responses to changes (Bockoven et al., 2015).

The FMT having the most significant variation in the soldier caste were the general size of the insect body (thorax and extremities), the shape of the head, and the size ratio of the head/right mandible; while the size of the head, the size of the pronotum and the length of both mandibles were the least variable characters. This observation agrees with previous reports in another xylophagous termite species, *Cryptotermes secundus* (Hill, 1925), where the size of the characters related to mechanical defense was more stable than the non-defensive morphological features (Roux et al., 2009). Another explanation relates to the soldier caste of Rhinotermitidae contribution to food exploration as a possible response to predation diminishing (Reinhard et al., 1997), since the foraging time and the time of exposure of the workers to predation is variable (Bockoven et al., 2015). In this study, we selected the minor soldiers, the most common size of the soldier; and this soldier type may be more related to the accompanying activity in the exploration of food by the workers than in the function of defense (Traniello & Leuthold, 2000). Therefore, in this soldier size, there could be a more significant intraspecific variation related to the movement characters for exploration than defensive ones. It is interesting to continue studying this species' functional and behavioral differentiation between older and younger soldiers.

The FMT of the soldier caste of *H. tenuis* were more variable than in the worker caste. In termites, the difference in the CV of the size of morphological traits between castes is attributed to several origins (Eggleton, 2010). First, the soldier caste of termites can be derived from all stages of workers and immature apterans, which can cause differences in final individual size polymorphisms in various species (Roisin et al., 2000). In addition, the size of the workers from which the soldiers are derived is smaller in incipient colonies (Crosland et al., 2006; Noirot, 1985), and therefore their final size is expected to be partially dependent on the development pathway (Pinzón 2007). Therefore, younger plantation workers may produce smaller soldiers. Furthermore, polymorphism in the soldier caste of termites is related to polyethism (the division of labor) and has different patterns in the genus Heterotermes (Noirot & Darlington, 2000).

Therefore, the traits that presented the lowest intraspecific CV were considered the most appropriate to estimate the type of cover's effect on the species' functional response. Traits with lower CV minimize the possible overlapping or oversizing of the functional response due to high variation (Gaudard et al., 2019). The traits considered most appropriate for comparison, including the worker caste, were: the mandibular traits (La, L1, L2, MPr, Ra, R1, R2, MP) and index two and the soldier caste: the width and length of the head, width of pronotum, length of the tibia and both mandibles, and indices 2I and 3.

Relationship of the size of morphological features with the type of land cover

Heterotermes tenuis workers from the gallery forests evaluated were larger than those from the pine plantations, regardless of the age of the plantation. This result coincides with the reduction of FMT reported in *Hevea brasiliensis* monocultures compared to deforested natural forest areas and is attributed to the greater variety of food resources, microhabitats, and microclimates in the latter (Liu et al., 2019). But the quality and quantity of the food resource and the environmental conditions must also be taken into account since, although the frequency of wood-eating termites increases with greater availability of food in deforested areas (Eggleton et al., 2015).

The size of the worker termites is related to physiological factors, such as nutrition and energy expenditure, and mainly to the quantity and quality of food, although the results are contrasting. The larger size of worker termites may affect their ability to absorb nutrients (Dahlsjö et al., 2015), but at the same time may favor a lower rate of energy expenditure than small and medium-sized termites (Dahlsjö et al., 2015). Additionally, large termites may have a longer food retention time by having larger intestines, which is beneficial, considering that wood is a nutritionally poor substrate (Dahlsjö et al., 2015). However, the largest workers of the Rhinotermitidae species, known as the formosan subterranean termite (*Coptotermes formosanus* Shiraki, 1909), consume less wood and therefore suffer higher mortality than small workers, especially in declining colonies, which produce larger and less vigorous termites (Su & Fage, 1984). On the other hand, wood-eating termite workers can benefit from smaller sizes because the smaller mandibles can grind the food into smaller pieces, improving the absorption of nutrients(Eggleton et al., 1998).

In the study area, the frequency of *Heterotermes tenuis* increases as the *P. caribaea* crops is older (Beltrán & Pinzón, 2018) compared to the surrounding natural forests (Pinzón et al., 2017). Additionally, in the study area, a positive response of the frequency of this species to the degree of decomposition and the size of the pieces of pine wood produced by pruning is known (Beltrán and Pinzón, 2017). Previous studies document how the frequency of subterranean xylophagous termites responds positively to the availability of wood resources, which they require both for food and habitat, and is also recorded that Rhinotermitidae termites prefer to feed on soft woods such as *Pinus* (Santos et al., 2010) and can feed on needles of this genus (Pinzón et al., 2006). The FMT of *H. tenuis* that was smaller in the plantations are concentrated in the mouthparts, possibly as a response to the lower resistance of the pine wood. At the same time, in the gallery forests, the food consists of heterogeneity of species having harder woods (Fernández et al., 2012), in such a way that a smaller size of the mouthparts can be adequate and imply energy savings. Alternatively, the smaller size may result of a nutritional supply from pine wood that does not allow optimal body development. Still, this study did not compare individual biomass between land uses (Pinzón et al., 2006).

On the other hand, future studies may consider the influence of intraspecific competition on the individual size of *H. tenuis*. Competition influences the size of offspring because competitive environments encourage the colony to invest in larger individuals in smaller numbers (Cronin et al., 2011). Furthermore, competition is relevant in organisms that tend to saturate their environments (Cronin et al., 2011), such as ants and termites. The workers of H. tenuis of the four plantation ages would have less interspecific competition compared to the workers of the relict gallery forests because the composition of xylophagous species was 24% in the pine plantations (Beltrán & Pinzón, 2018) and 42.7% in gallery forest relicts (Pinzón et al., 2012). Therefore, it is possible that *H. tenuis*

gallery forest workers increased the size of their FMT and decreased their abundance, while plantations present smaller FMT, but a greater number of individuals.

The FMT of soldiers versus workers did not differ between the different types of land use. However, they tend to be smaller in the youngest and most mature plantations than intermediate plantations and gallery forests. The variation in the size of the soldier caste of termites is mainly in response to their predator (Eggleton, 2010) and, as also occurs in other social insects traits associated with nest defense and locomotion increase proportionally to the abundance of insects predators, because a larger size may be a better defense (Hattori et al., 2016). Likewise, ants are the most important predators of invertebrates (Sheppe, 1970) and can reduce termite densities, even if they do not specialize in predation (Lima & Pantoja, 2012). The difference in the size of some characters of the minor soldier of *H. tenuis* may be influenced by the frequency of predators, but this study did not include this variable.

Homogeneity of functional diversity

Intraspecific variation of *H. tenuis* FMT was more significant between colonies than cover types. The multinomial models improved their predictive quality and the adjustment of the Pseudo R^2 when the type of coverage was used as a factor. Therefore, more significant variation is expected between colonies than cover types. This variation between colonies may be due to the range of individual phenotypes in one colony differing from the range in another (Jandt & Gordon, 2016). However, despite the high variation between colonies, its importance is relegated by the effect of the type of cover on the insect's body. Therefore, *P. caribaea* plantations may act as a filter for the functional diversity of *H. tenuis* since no relevant differences between the plantation ages regarding FMT size, especially in the worker caste were detected.

Homogenization consists of an increase in the similarity of the functional composition (Rousseau et al., 2019). This homogenization can alter some ecosystem processes such as waste decomposition and nutrient cycling (Rousseau et al., 2019), alter food webs (Simons et al., 2015), and generate losses in taxonomic diversity (Liu et al., 2016; Salas et al., 2017). Although the pine-planted areas do not correspond to transformed gallery forests, the results observed were similar to those reported for converting primary forests to rubber plantations (Liu et al., 2019; Liu et al., 2016). Rubber plantations were found to reduce the functional diversity of ants and termites, due to a loss of microhabitats, compared to primary forests. Primary forests have greater structural complexity, variety of resources, and microclimates, facilitating the coexistence of more functional features, while plantations limit specific traits. Additionally, functional diversity decreases with higher levels of disturbance (March 2013; Olden & Rooney, 2006); therefore, it is expected that pine plantations present greater disturbance than the relicts of gallery forests, a decrease in the functional diversity of both castes. Therefore, pine plantations may restrict the functional variability of *H. tenuis* to specific traits, with a higher incidence in the worker caste.

Conclusions

The functional morphological response of *H. tenuis* was expressed in a smaller size of the workers in the plantations compared to the gallery forests, less contrasting in the minor soldier caste. The observed size difference suggests an environmental filter effect of the plantations with the effect of homogenizing the functional traits of the *H. tenuis* workers favoring the establishment of smaller functional traits.

Morphological traits of the worker and soldier caste related to the general size of the insect exhibited the highest percentages of coefficient of variation. Therefore, they are less valuable for evaluating the functional response of termites to changes in coverage. To better understand wood decomposition processes in new forested areas, we recommend deepening studies referring to effects on the diversity and functional effects on soil macrofauna.

List Of Abbreviations

FMT: Functional morphological traits

H. tenuis: Heterotermes tenuis

P. caribaea: P. caribaea

IV: Intraspecific variability

DBH: Diameter at breast height

CEFUD: Forest Entomological Collection of the Francisco José de Caldas District University

Worker caste:

La: Distance between the first apical tooth and the first marginal tooth

L1: Distance between the first apical tooth and the first marginal tooth

L2: Distance between the first and second tooth marginal

MPr: Distance between the third marginal tooth and the molar prominence

Ra: Distance between the first apical tooth and the first marginal tooth

R1: Distance between the first and second marginal tooth

R2: Distance between the second marginal tooth and the molar plate

MP: Molar plate extension

Index 1: Maximum head width/cephalic capsule length: Cephalic capsule shape

Índex 2: Maximum length pronotum / maximum width pronotum: Shape of the pronotum

Index 3: Maximum pronotum width / maximum head width: Head-pronotum ratio

Soldier caste:

LMI: Left mandible length

LMD: Right mandible length

ANC: Maximum width of the head

LCA: Maximum length of the head

LPRO: Maximum length of the pronotum

APR: Maximum width of the pronotum

MAP: Anterior pronotal notch

MPP: Posterior pronotal notch depth

Index 1: Maximum width of the head/length of the head to the lateral line of the mandibles:

Index 2I: Maximum left mandible length / maximum head width:

Index 2D: Maximum length of the right mandible / maximum width of the head

Index 3: Maximum length of the pronotum / maximum width of the pronotum

PCA: Principal Component Analysis

CV: Coefficient of Variation

KW: Kruskal-Wallis

ANOVA: Analysis of variance

CWM: Community-Weighted Mean

NMDS: non-metric multidimensional scales

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The R Studio codes and PERMANOVA results are attached as supplementary material. The database used can be requested from the mail of the corresponding author.

Competing interests

All authors read and approved the final manuscript, and declare that they have no competing interests.

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Authors' Contributions

All authors contribute to the sampling, collection of specimens, data processing and presentation of this research.

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Figures

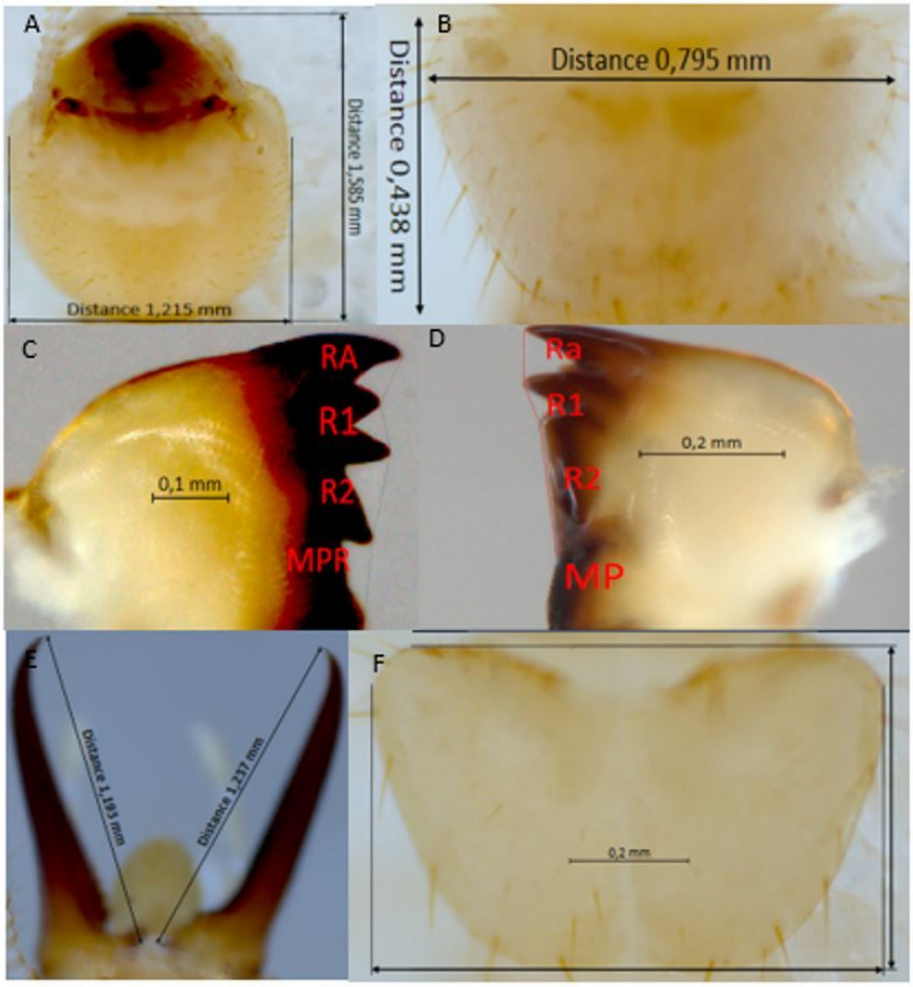

Figure 1

Dorsal view of the head at 50x (1A), thorax (1B), left (1C) and right mandible (1D) at 60x of a *Heterotermes tenuis* worker. Dorsal view mandibles at 20x (1E), notches of the pronotum 60x (1F) of a soldier of *Heterotermes tenuis*. Taken by O.P y Salazar, L.R

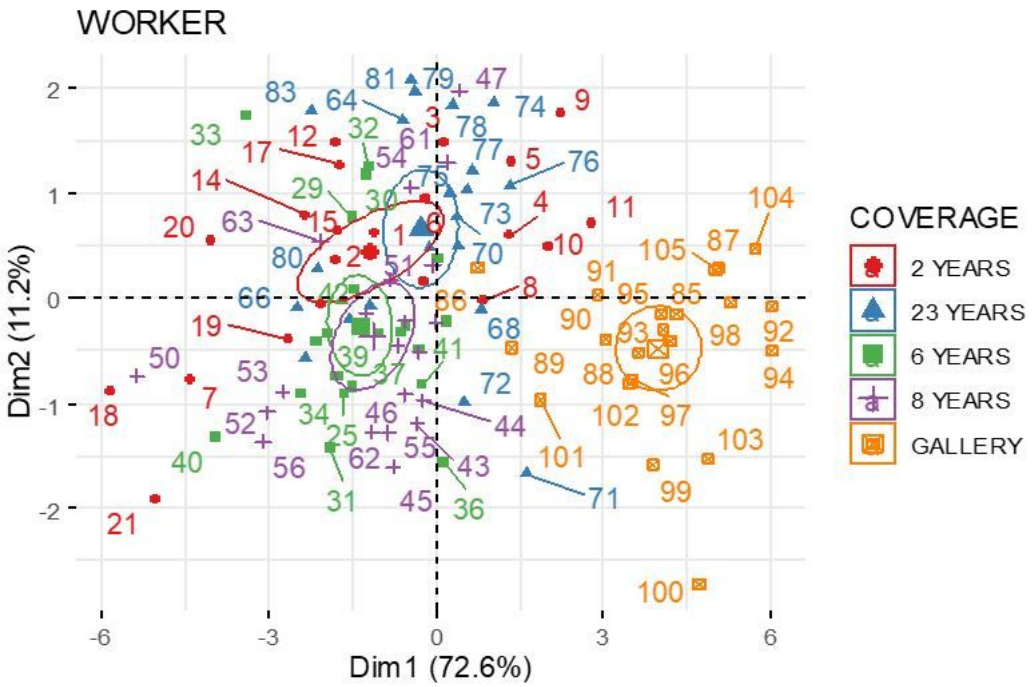

Figure 2

Biplot of the principal components analysis (PCA) of the morphological traits of the worker caste *Heterotermes tenuis* using the type of ground cover as a descriptive variable

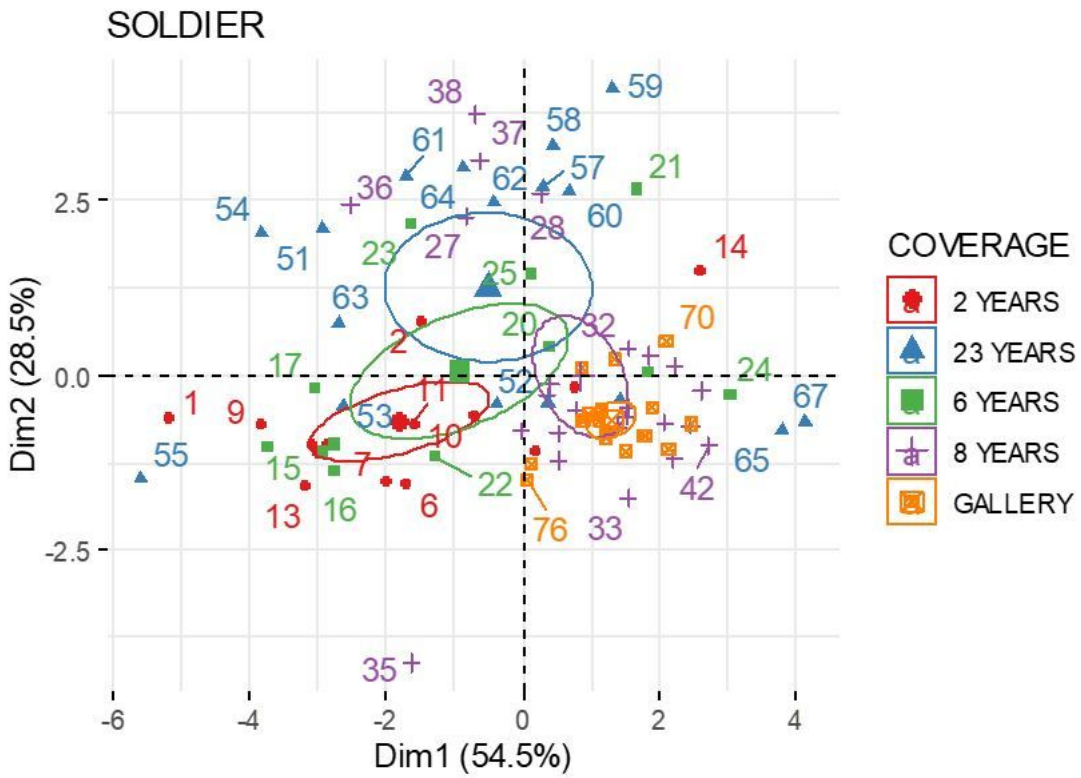

Figure 3

Biplot of the principal components analysis (PCA) of the morphological traits of the soldier caste *Heterotermes tenuis* using the type of ground cover as a descriptive variable

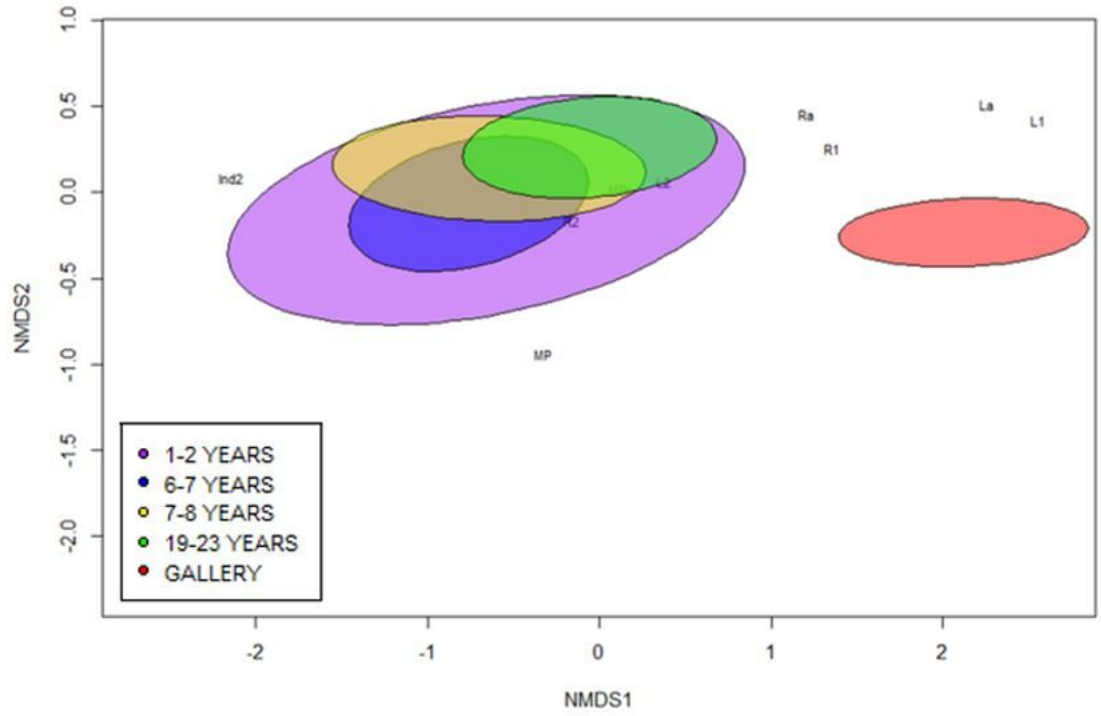

Figure 4

Non-metric multidimensional ordination (NMDS) of the size of the FMT of the worker caste of Heterotermes tenuis in pine plantations of different ages and gallery forests. La= distance between the first apical tooth and the first marginal tooth, L1= distance between the first and second marginal tooth, L2= distance between the second and third marginal tooth, MPR= Molar Prominence, Ra= distance between the first apical tooth and the first marginal tooth, R1= distance between the first and second marginal teeth, R2= distance between the second marginal tooth and the molar plate, MP=Molar plate. Ind.2=Index 2

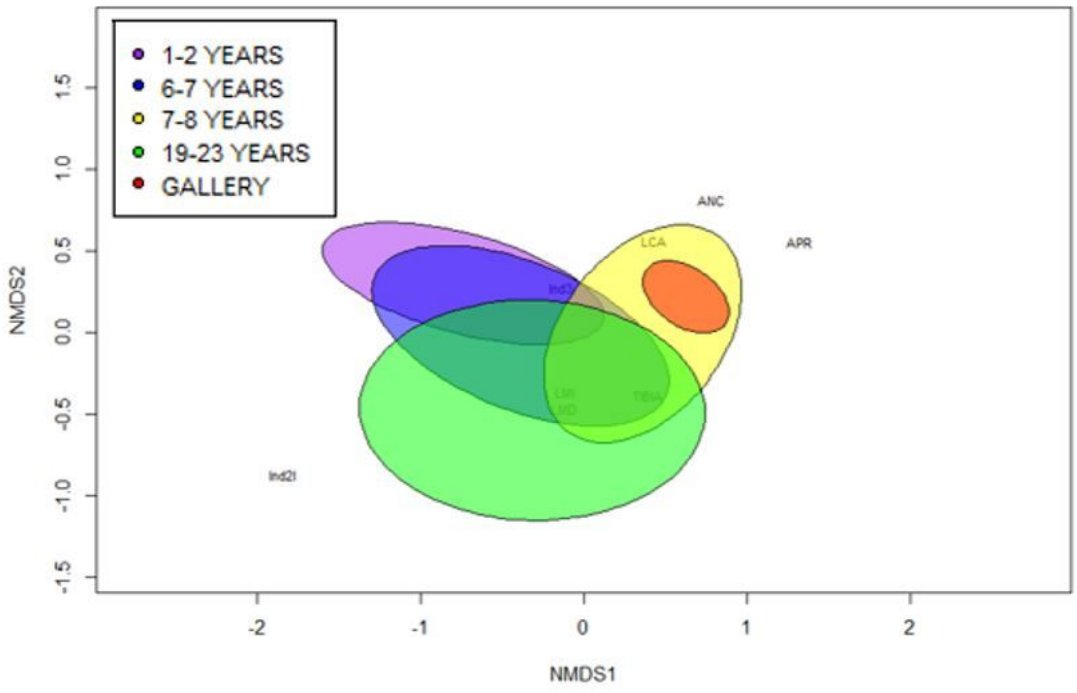

Figure 5

Non-metric multidimensional (NMDS) ordination of the soldier caste of *Heterotermes tenuis* in pine plantations of different ages and gallery forests. ANC=Width of the head, LCA=Length of the head, LMI=Maximum left mandible length, LMD=Maximum right mandible length, APR= Pronotum width, Ind2l=Index 2 left mandible, Ind3=Index 3

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