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Effect of Structural Variation of Dead Trunks on Passalid (Coleoptera: Passalidae) Assemblages in Central Amazonian Campinaranas

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Saproxylic beetles, rotten trunks, substrate

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Abstract

The present study investigated the occurrence of passalids in dead trunks with structural variations. Trunks were found in areas of white sand forests, locally known as Campinarana, in the state of Amazonas, Brazil. The collections were extended from May to December 2009. The mean diameter of the trunks and their stage of decomposition were classified, and the species of Passalidae were classified according to the location of their galleries. We used multiple generalized models to investigate the relationship between abundance and permutational multivariate analysis of variance (PERMANOVA) to investigate the relationships between predictors and passalid composition. A total of 361 passalids belonging to 13 species were collected from 11 tree species, of which Aldina heterophylla represented the highest proportion of logs (55%). Only the diameter of the trunk was related to the abundance of species, with trunks of larger diameters presented more individuals. The passalid composition was correlated with the diameter and decomposition of the trunks of all species of trees and only with the diameter of the trunks of A. heterophylla. Most of the species collected in Campinaranas construct their galleries in two or more regions of the trunk. The region that supported a greater number of colonies was the sapwood, followed by the inner bark and the soil-stem interface. The general habit of passalids found may be advantageous, probably to compensate for the low dispersion and isolation in areas with low availability of resources, such as Campinaranas forests in the Amazon.

Introduction

Substrates resulting from tree mortality are medium-to long-term resource for the various organisms that mediate their decomposition. Dead trunks represent important habitats for arthropods and fungi, shelter and nesting sites for vertebrates, safe sites for germinating seeds, plus a source of carbon and other elements whose gradual return to the soil contributes to forest productivity (Grove & Meggs 2003). For deadwood-dependent (saproxylic) beetles (Speight 1989), trunks with larger diameter can also act as buffers against variations in external moisture and

temperature, as well as offering greater abundance of resources and protection against predators (Grove 2002, Yee et al 2006). Wood in the initial stages of decomposition offers resistance to gallery excavation; then, as decomposition advances, the substrate becomes softer and more nutritionally assimilable (Magoulick 1998), which may lead to a continuous turnover of saproxylic species. The part of the trunk in which galleries are constructed may reflect the degree of ecological specialization of these insects and has been correlated to some functional traits in Passalidae beetles (Schuster 1978, Reyes-Castillo & Halffter 1984, Moreno-Fonseca & Amat-García 2016).



The passalids are saproxylic beetles that live and feed in dead tree trunks, accelerating the physical and biological decay of dead wood, and consequently, contributing to the reintegration of organic matter into the soil (Castillo & Moron 1992). These beetles construct their galleries in dead fallen trees (Ohaus 1909, Luederwaldt 1931, Reyes-Castillo 2000). Like other saproxylic insects, the gut of passalid beetles hosts several microorganisms that assist in the decomposition of wood (Ceja-Navarro et al 2014). It is a group with relatively well-resolved taxonomy, of which there are around 930 known species, of which 101 are known from Brazil (Fonseca & Reyes-Castillo 2004, Boucher 2005, Mattos & Mermudes 2014).

There is no doubt that the dead tree trunks are important to passalids; however, how dead tree trunk characteristics affect passalid occurrence is little known for tropical forests (Seibold *et al* 2015). This is curious, considering that passalids are among the most relevant saproxylic insects related with wood decomposition in tropical forests, only behind termites (Ulyshen 2018). For instance, there is virtually no information about occurrence, diversity, and colonization in white forests and many other forest types in the Amazon. The white sand forests, locally known as Campinaranas, are particularly interesting because they grow on sandy soils, which provide little adhesion and hamper deep root penetration into the soil (Ter Steege *et al* 2000, Ferry *et al* 2010, Toledo *et al* 2011), favoring the fall of trees and therefore providing substrates for saproxylic species, such as passalids.

In the current study, we investigated the occurrence of passalids in relation to the structural variations of dead tree trunks found in Campinarana forests. Specifically, we studied the relationships between abundance and species composition and (I) trunk diameter, (II) trunk decomposition classes, and (III) provided a simple species classification based on their galleries' location (bark, sapwood, heartwood, or soil-trunk interface).

Materials and Methods

Study area

This study was conducted in fallen dead trunks found in white sand forests (Campinarana) sensu stricto close to two protected areas in the state of Amazonas, Brazil (Fig 1). The first is located 8 km from the Campina Biological Reserve of the National Research Institute of Amazonia (2°34′S, 60°02′W) (Fig 1, Area 1). In this area, the reserve encloses areas of open *Campina*, the adjacent Campinarana vegetation, surrounded by the dense *Terra-Firme-Forest* (Luizão 2007). The other study area is located within the limits of the Uatumã Sustainable Development Reserve (RDS Uatumã), (2°0′–2°40′S; 58°0′–59°20′W), which is divided NE-SW by the Uatumã River, tributary of the Amazon River (Fig 1, Area 2). The area contains three main vegetation types: terra

firme forests, dominated by dense ombrophylous forest; flood plains, covered by igapó forests; and natural fragments of Campinarana vegetation. The climate types in both areas are similar, tropical humid with average annual temperature of 28°C and annual average precipitation of 2376 mm, with distinct seasonality between rainy (February to April) and dry (July to October) seasons (IDESAM 2009).

Data collection

Sampling took place between May to December 2009. A total of 175 fallen dead trunks were sampled, 43 dead trunks at area 1 and 132 dead trunks at area 2. The higher proportion of dead logs in area 2 is unknown but may be related to common windstorms in the region (Marra et al 2014, Negrón-Juárez et al 2017, Alencar et al unpubl. data). The dead tree trunks with active galleries, with diameters ≥ 5 cm, length ≥ 1 m, were considered a sampling unit because they represent an ecological unit for passalid diversity and for other saproxylic organisms (Graham 1925, Grove & Meggs 2003). Standing trunks and dead branches in the canopy were disregarded for the low amount of passalids found under these conditions (Castillo & Reyes-Castillo 2003, Jackson et al 2012). Trunks were identified and subsequently sliced finely (15 cm) with a chain saw and/or machete. The predictor variables measured were as follows: trunk diameter, decomposition class, and the location where galleries were constructed.

To obtain the mean diameter of the trunk section, we used the mean (cm) of its initial, middle, and final portions using diametric tape. Trunks were classified as small (5–15 cm), intermediate (16–30 cm), and large (>30 cm). For decomposition class classification, a simplified version was used of the four-class system proposed by Castillo & Reyes-Castillo (2003) and based on visual characteristics (Table 1). In cases where multiple classes were found in the same trunk, the decomposition class considered was the one most prevalent in the sliced sections where gallery was found. The first decomposition class (CD1) was removed from the analyses, as no passalids were found using it.

All passalids found on or in the study logs were collected and stored in 60-ml-capacity plastic bottles of containing PAMPEL fixative solution (42% distilled water, 44% alcohol 96°GL, 8% formalin, and 5 to 6% glacial acetic acid), in which adults and immature were left for 12 h. Subsequently they were transferred to vials containing alcohol 96°GL and labeled. Passalids were identified to species using identification keys (Luederwaldt 1931, Vulcano & Pereira 1967, Jiménez-Ferbans et al 2015), comparisons with vouchers in the INPA collection and with the help of experts. All individuals were deposited in the Entomological collection of the National Research Institute of the Amazon (INPA), Manaus, Brazil.



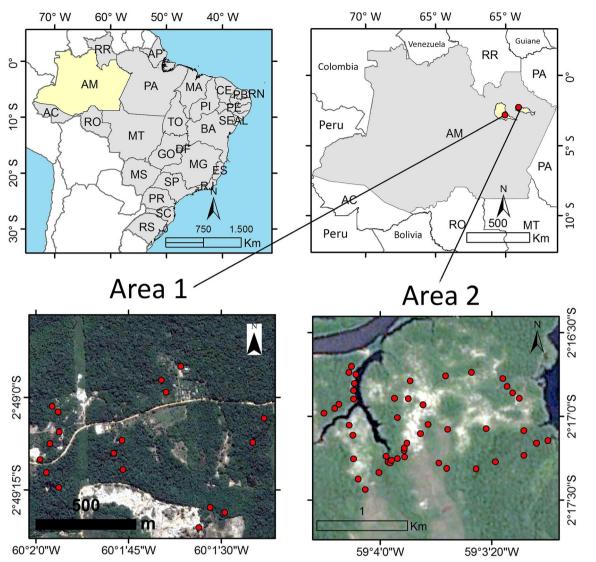


Fig 1 Areas where dead logs were sampled (red dots): area 1—located 8 km from the Campina Biological Reserve of the National Research Institute of Amazonia; area 2—Uatumã Sustainable Development Reserve (RDS Uatumã), both in northeastern Amazonas State, Brazil.

To examine ecological correlates of passalid-distribution patterns, we also grouped species into guilds, based on the location of their galleries following Moreno-Fonseca & Amat-Garcia (2016): cortical species (within bark), albuminic (sapwood), cernicle (heartwood), soil-trunk (soil-trunk interace), or generalists (those found in two or more of the above-listed locations).

Data analysis

We found only one species in each trunk investigated and, in consequence, evaluated the relationships between passalid abundance and composition with the characteristics of individual trunks. We used generalized linear mixed models (GLMMs) to investigate the relationship between passalid

Table 1 Decomposition classes for fallen trunks.

Class	Description
CD1	Bark firmly attached to the trunk; solid wood.
CD2	Bark partially dropping; can be easily separated from the trunk.
CD3	Bark when present found only at trunk/soil interface; outer layers easily disintegrate; the heartwood is still solid.
CD4	Bark totally absent; the trunk can be completely fragmented manually, much moisture present, partially covered with vegetation and mixed with the forest soil.



abundance and trunk diameter and decomposition class for all species of trees together, as well as those only found in the trunks of *Aldina heterophylla* Spruce ex Benth, the most common tree species found and frequently cited as dominant in Campinarana (Vicentini 2004, Guimarães & Bueno 2015, Targhetta *et al* 2015). We used models with negative binomial distribution to accommodate data over-dispersion (Zuur *et al* 2009). We then compared the complete models (with the two predictor variables) with the respective null models (intercept only) using analysis of variance. We estimate pseudo- r^2 proposed by McFadden as a measure of model goodness-of-fit (Long 1997). Subsequently, we used partial graphs to represent the relations between each predictor variable, statistically controlled for the effect of the other variable involved (Breheny & Burchett 2017).

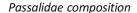
We used permutational analysis of variance PERMANOVA (Anderson 2001), based on the Sorensen Index, to investigate the relationships between trunk diameter and decomposition class and Passalidae composition. We performed analyses for the passalids found in all species of trees and, separately, for individuals only found in *A. heterophylla* trunks. For both models we ran 999 permutations. All analyses and graphs were made with R Program (R Core Team 2019).

Results

Of the total dead trunks (175) investigated, 66 (37.71%) had active galleries (tunnels of live adults and larvae). A total of 361 passalids belonging to 13 species were collected from 66 dead tree trunks of 11 tree species, of which *A. heterophylla* represented the highest proportion of trunks (36 trunks, 55% of the trunks investigated) and 14 trunks unidentified (advanced decomposition). Passalid species with the highest number of individuals were as follows: *Veturius paraensis* Luederwaldt (79 individuals, 21.9%), *Passalus epiphanoides* (Kuwert) (74, 20.5%), *Veturius transversus* (Dalman) (59, 16.3%), and *Passalus rhodocanthopoides* (Kuwert) (54, 15%) (Table 2).

Passalidae abundance

In both models (all species and of only *A. heterophylla*) only trunk diameter was related to abundance of species. The model using data from all tree species explained 12.03% of data variance (p = 0.014) (Fig 2a), while pseudo- r^2 using *A. heterophylla* trunks explained 25.67% of the original data variance (p = 0.005) (Fig 2b). In both cases, trunks with larger diameters contained more individuals (all species, p = 0.002; *A. heterophylla*, p = 0.002). Passalid abundance was not correlated with decomposition classes in any of the models (all species, p = 0.767; *A. heterophylla*, p = 0.979).



The composition of the passalid species was correlated with trunk diameter ($r^2 = 0.056$, p = 0.002) and decomposition class ($r^2 = 0.05$; p = 0.003) in the model of all tree species, so that some species were collected exclusively in specific diameter classes (Fig 3).

The species collected in a wide range of diameters and in all decomposition classes of dead trunk were *P. rhodocanthopoides*, *P. epiphanoides*, *V. paraensis*, and *Passalus abortivus* Percheron. *Passalus bucki* Luederwaldt was found in small and intermediate diameter trunks in CD2 and CD3, and *Passalus coniferus* Eschscholtz were present in intermediate and large diameter trunks in CD2 and CD4 stages. Some species were collected in only one class: *Spasalus elianae* Fonseca, *Passalus elfriedae* Luederwaldt, and *Veturius transversus* all in CD2 and CD3 in small diameter trunks; *Passalus interruptus* Linnaeus in CD2 and *Popilius tetraphyllus* (Eschcholtz) in CD4 in intermediate diameter trunks; and *Paxillus leachi* MacLeay and *Passalus interstitialis* Eschscholtz in large diameter trunks in CD3.

When only *A. heterophylla* trunks were considered, passalid species composition was also correlated with the diameter ($r^2 = 0.125$; p = 0.002), but was not correlated with decomposition class ($r^2 = 0.017$; p = 0.740) (Fig 4).

Passalus epiphanoides and V. paraenses were the species found exploring the largest diameter range and decomposition classes in A. heterophylla. Passalus rhodocanthopoides and P. abortivus were collected in all classes of decomposition, but only in specific diameters, the first in trunks of intermediate diameters and the second in large diameter trunks. All other species were collected in only one diameter and decomposition class (see Fig 4).

Guild classification

Classifying passalid species according to the location of their galleries indicated that most of the species collected in Campinaranas explore two or more regions of the trunk. The region with a greatest number of colonies was the sapwood (35 colonies), followed by the bark (15) and the soilstem interface (14); in contrast only two colonies were found in heartwood. Passaus epiphanoides and V. paraensis were classified as generalists (sapwood preference), found in three or more sectors; P. rhodocanthopoides, P. abortivus, P. coniferus, P. bucki, and V. transversus in two sectors; P. leachi and P. interstitialis as cortical; S. elianae as alburnicolous; and P. elfriedae and P. tetraphyllus as soil-trunkspecies (Table 3).

No species was classified as exclusively cernicolous, with only two colonies of *P. epiphanoides* exploring the heartwood region. The sum of species collected in more than one stratum represented 89% of the total number of individuals.



Table 2 Passalid richness and abundance per plant species.

Passalid species	Abundance	Plant species	No. of trunks
Passalus epiphanoides	43	Aldina heterophylla	6
	25	Minquartia guianensis	2
	3	Vatairea paraensis	1
	3	Annona foetida	1
Veturius paraensis	70	Aldina heterophylla	13
	2	Pradosia praealta	1
	2	Couepia longipendula	1
	5	Unidentified (advanced decomposition)	4
Passalus rhodocanthopoides	47	Aldina heterophylla	3
	5	Simarouba amara	1
	1	Swartzia ingaefolia	1
	1	Unidentified (advanced decomposition)	1
Passalus abortivus	23	Aldina heterophylla	4
	2	Manilkara surinamensis	1
	3	Pradosia praealta	2
	6	Unidentified (Advanced decomposition)	2
Veturius transversus	13	Duroia sp.	1
	2	Swartzia ingaefolia	1
	44	Unidentified (advanced decomposition)	4
Passalus bucki	16	Scleronema praecox	1
	5	Simarouba amara	1
Passalus coniferus	3	Aldina heterophylla	1
	3	Simarouba amara	1
Passalus interruptus	9	Unidentified (advanced decomposition)	2
Spasalus elianae	4	Aldina heterophylla	5
Passalus interstitialis 5		Aldina heterophylla	1
Paxillus leachi	6	Aldina heterophylla	1
Passalus elfriedae	5	Aldina heterophylla	2
Popilius tetraphyllus	5	Unidentified (advanced decomposition)	1

Discussion

Overall 37.71% of the tree trunk investigated had active galleries (tunnels of live adults and larvae), a proportion equivalent to that found by Mouzinho & Fonseca (1998) in terra firme forest area in the Amazon. Our study suggests that the passalid low dispersal habilities (Galindo-Cardona *et al* 2007, Jackson 2010) associated with their general habit of exploring dead trunks (Luederwaldt 1931, Castillo & Reyes-Castillo 2003, Ulyshen *et al* 2018) may favor their colonization in nutrient-poor areas, such as Campinaranas. Also the sophisticated intraspecific communication and gregarious behavior (Ohaus 1909, Luederwaldt 1931, Reyes-Castillo 2000) may cause interspecific competition and result in spatial segregation in dead trunks. This may explain why we consistently found only one passalid species per dead tree trunk.

The commonest species were collected in trunks with the greatest variation in diameter, from logs with diameter (5–15 cm), intermediate (16–30 cm), and large (>30 cm). It is likely that the success of many of these species is correlated to their generalist habit (Luederwaldt 1931, Ulyshen 2018). Castillo & Reyes-Castillo (2003) compiled data about tree trunk use by passalids in various biogeographical regions and recorded 299 tree species belonging to 61 of dicotyledous families being exploited. Adding the 11 species recorded in this study, the total number of tree species used as substrate is 310. This broad range of exploited resources reinforces the idea that passalids are a generalist group of dead trunk exploiters, a condition that enables them to inhabit areas of Campinarana which has a lower abundance of resources than other Amazonian forest types (Anderson 1981, Aragão *et al* 2009).

Differences in the assemblage composition of other saproxylic beetle groups between large and small diameter logs have been documented in Boreal Forest in Scandinavia (Siitonen 2001), Canada (Hammond *et al* 2004), Coniferous



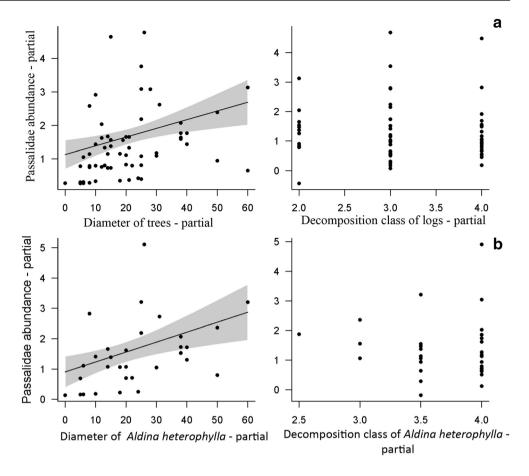


Fig 2 Passalid abundance by diameter and classes of decomposition of fallen dead logs; a dead trunks of all species, and **b** dead trunks of *A. heterophylla* only.

forests in North America (Maser & Trappe 1984, Edmonds & Marra 1999), and in Tazmanian Eucaliptus forests (Yee 2005). Such specificity correlates with tolerance for specific ranges of humidity, temperature, and other indirect attributes linked to trunk diameter (Graham 1925, Grove 2002). Campinaranas are naturally very open environments with vegetation adapted to high solar irradiation (Rodrigues &

Gonçalves 2014); in consequence, fallen logs are often highly exposed to sun, high temperatures, and desiccation (Graham 1925). Thus, species that exploit small diameter trunks such as *S. elianae* and *P. elfriedae* are probably more tolerant to climatic variations than those using larger diameter trunks. Similar patterns were found for *Spasalus balachowskyi* Reyes-Castillo in 5–6 cm tree branches in the city of Leticia

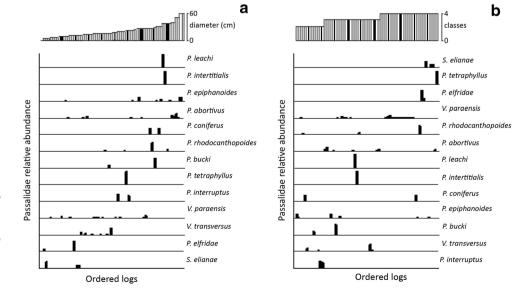


Fig 3 Passalid species ordered by trunk diameter and decomposition for all plant species: a trunk diameters, and b trunk decomposition classes (see Table 1).



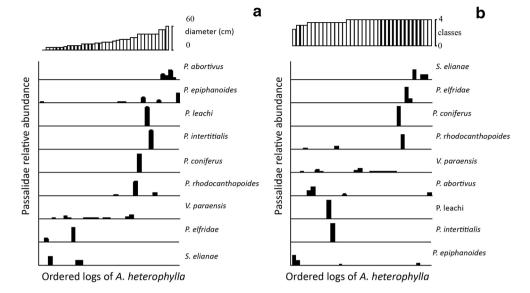


Fig 4 Passalid species ordered by trunk diameter and decomposition of *Aldina heterophylla*: a trunk diameters, and b trunk decomposition classes (see Table 1).

in Colombia (Amat-García & Reyes-Castillo 2007) and in Saül, French Guiana (Boucher 1986). However, the composition of passalid species assemblages in Campinarana cannot be explained by the diameter of the trunks, suggesting that the majority are tolerant to such microclimatic variations.

Tree trunk diameter correlates with several important ecological attributes for saproxylic beetles. Trunks with larger diameter are considered more microclimatic stable habitats compared with smaller trunks (Southwood 1977, Grove & Meggs 2003). This stability did little effect on the composition of the passalid species. However, larger diameter trunks may be an excellent substrate in Campinaranas, as they tend to take longer to decompose (Stone *et al* 1998, Chambers *et al* 2000, Mackensen *et al* 2003). Relative abundance of *P. epiphanoides* and *P. abortivus* was highest in trunks with diameters > 30 cm. Such trunks last longer, allowing overlap

of generations and accumulation of individuals, important conditions for the subsocial behavior, besides maintaining more stable levels of humidity than external environment (Bunnell & Houde 2010). Minimizing the effects of desiccation and temperature fluctuation probably is more important for the larvae and less so for the adults. In addition, they may provide potential refuge during such disturbances as forest fires (Meggs & Taylor 1999, Michaels & Bornemissza 1999) and predator attacks.

Decomposition class explained little of the species composition variation in both Campinarana forests. Again it seems that the generalist habit of passalids may be the explanation, since most were collected between intermediate and final stages of decomposition, exploiting two or more classes. Seven of the 13 species seem to begin colonization on CD2, though only *P. interruptus* was collected exclusively in this

Table 3 Passalidae guild classification based on location of galleries (stratification) in fallen dead trunks. Numbers given represent the number of colonies found in each stratification.

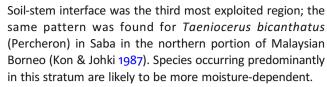
Passalid species	Within-bark	Sapwood	Heartwood	Soil/trunk interface	Guild
Passalus epiphanoides	1	7	2	1	Generalist
Veturius paraensis	1	10	0	9	Generalist
Passalus rhodocanthopoides	3	3	0	0	Cambium/sapwood
Passalus abortivus	4	5	0	0	Bark/Sapwood
Paxillus leachi	1	0	0	0	Cambium
Passalus interstitialis	1	0	0	0	Cambium
Passalus coniferus	1	1	0	0	Bark/sapwood
Passalus elfriedae	0	0	0	2	Trunk/soil
Spasalus elianae	0	3	0	0	Sapwood
Passalus bucki	1	1	0	0	Cambium/sapwood
Veturius transversus	1	5	0	0	Cambium/sapwood
Passalus interruptus	1	0	0	1	Cambium/trunk/soil
Popilius tetraphyllus	0	О	0	1	Trunk/soil



class. Other species were also found in these stages, exploring the region of the interbreeding of fallen tree trunks in French Guiana (Boucher 1986) and Mexico (Castillo 1987). These results are in agreement with the findings of Castillo & Reyes-Castillo (2003) who report that most adult passalids prefer to colonize trunks in the intermediate stages of decomposition. The occurrence of some species may be related to changes in dead wood promoted by other organisms. In Campinarana, passalids begin to colonize after stage CD2 and, as decomposition advances, other species appear.

In the Central Amazonian rainforest, Fonseca (1988) found that Passalus latifrons Percheron and Passalus convexus Dalman began to colonize at the second phase of decomposition and suggests that the occurrence of these species may be correlated with detoxification of dead wood promoted by microorganisms during the decomposition process. Studies carried out in other regions describe the colonization process as a unidirectional modifications over time (Mackensen et al. 2003), and it is possible that these modifications facilitate species segregation by microhabitats and specific microorganismal associations (Haack & Slansky 1987, Lawrence 1989, Speight 1989, Cline & Leschen 2005, Schigel 2012). Consequently, logs in different stages of decomposition appear to represent different ecological niches for different species (Maser et al 1979). However, the passalids collected in Campinaranas seem to depart from this pattern, as the majority of species appeared to be able to explore trunks at various stages of decomposition from the intermediate stage onwards, and only 5% of the variation in species composition was explained by trunk decomposition class.

The generalist nature of passalid species is also revealed in the use of several regions of the trunk for gallery construction. Consequently, attempts to ecologically classify passalids based on the location of their galleries were not effective, since most of the collected species constructed their galleries in two or more sectors of the trunk, indicating an ability to explore different microhabitats for food and shelter. However, the regions where the highest density of colonies and species were observed in the sapwood, the cambium (zone between the inner bark and the sapwood), and the trunk/soil interface. This spatial concentration may be a result of higher nutritional value and the microclimatic conditions (Taylor et al 2002, Jia et al 2017). Sapwood and cambium are physiologically more active regions during secondary tree growth. The inner bark (zone between the vascular and outer shell) and the sapwood are more susceptible to decomposition because they concentrate more moisture and energy reserves and have greater permeability (USDA-FS Forest Products Laboratory 1999, Taylor et al 2002, Jia et al 2017). The inner bark and sapwood also have lower amounts of toxic compounds (phenolics and resins) and lignins than the superficial parts of the trunk wood (USDA-FS Forest Products Laboratory 1999, Taylor et al 2002, Jia et al 2017).



The general habit of passalids may be especially relevant in Campinaranas. Most passalid species can colonize a structurally varied set of trunks (in terms of diameter, decomposition status, and gallery location) from different species. This probably compensate their generally low dispersal and poor flight hability (Galindo-Cardona et al 2007, Jackson 2010) in nutrient-poor areas, such as Campinaras (Anderson 1981, Aragão et al 2009, Fine et al 2010). Our results provide valuable information about how to effectively sample these insects and broaden the understanding of the correlation between dead wood and passalids in Amazonian Campinarana.

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Author Contribution CRV FONSECA: contributed to conducting a research and investigation process, specifically conducting experiments and data collection. The conceptualization of ideas was performed jointly by JBR ALENCAR, CRV FONSECA and FB BACCARO: formulation of research objectives, methodology and model creation. FB BACCARO: application of statistical, mathematical and computational techniques for analysis of study data. MMF BENTO and JM RIBEIRO: Verification, reproducibility of results. JBR ALENCAR wrote the first draft, with the contribution of all authors.

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