



# Windthrows promote higher diversity of saproxylic beetles (Coleoptera: Passalidae) in a Central Amazon forest

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**Abstract.** 1. Natural disturbances change environmental conditions that play an important role in controlling biodiversity. Large-scale windthrows (i.e. snapped and uprooted trees) promoted by convective systems cause severe tree mortality and can alter the dynamics of several insect taxons in forests.

2. We assessed the effect of large-scale windthrows resulting from a squall line event in January 2005 on strictly saproxylic beetle assemblages in Central Amazonia. Using a paired sampling design comparing windthrown and old-growth forest, we investigated the responses of different metrics of Passalidae diversity (richness, abundance and composition).

3. We found a higher richness and abundance of species in windthrown areas compared with old-growth forest, and a correlation between species composition and the tree mortality gradient.

4. Differences in the richness and composition of the Passalidae assemblage between disturbed and old-growth forest suggest that the tree mortality gradient created by windthrows promotes the diversity of saproxylic beetles in Central Amazonia.

**Key words.** Deadwood, forest blowdowns, Passalidae, species succession, tree mortality.

## Introduction

Natural disturbances can affect communities by changing the availability of resources or by altering the physical environment (Pickett & White, 1985). The windthrows (i.e. snapped and uprooted trees) in the Amazon are created by down and forward wind associated with convective systems (Fujita, 1981; Nelson, 1994; Garstang *et al.*, 1998). They can vary in size and intensity (amount of energy – rain and wind) resulting in the

mortality of up to 90% of the trees in a given area (Rifai *et al.*, 2016; Marra *et al.*, 2018).

Large-scale windthrows are an important natural disturbance in Central and Western Amazonia, between the Amazonas and Pará States, extending to the far west of Peru, Ecuador, Colombia and Venezuela (Nelson *et al.*, 1994; Espírito-Santo *et al.*, 2014; Negrón-Juárez *et al.*, 2018). This disturbance enhances stocks of deadwood on the forest floor (Bouget & Duelli, 2004) and consequently the concentration of soil organic carbon (Santos *et al.*, 2016). Large windthrows also provide great opportunity to study deadwood-dependent insects because they increase habitat availability in different spatial scales and with a reasonable estimate of the time elapsed (Bouget, 2005a).

While the causes and scale of windthrows are different from simple treefalls, the biological succession of regular treefall recovery dynamics may operate like those observed in low-disturbance plots.

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Higher and lower diversity patterns caused by treefall have been demonstrated for vertebrates (Blake & Hoppes, 1986; Greenberg, 2001, 2002) and invertebrates (Alvarez & Willig, 1993; Kaila *et al.*, 1997; Arpin *et al.*, 1998; Duelli *et al.*, 2002; Nachtergale *et al.*, 2002; Patrick *et al.*, 2012) in several ecosystems. In most cases, the disturbance caused by treefall foster the diversity of some taxa (Wermelinger *et al.*, 2002; Bouget, 2005a) and initiate turnover in community structure along the wood-decaying gradient (Bouget & Duelli, 2004). These changes may cause greater selective pressure and favour other organisms.

In this study, we evaluated the influence of disturbance caused by windthrows on passalid assemblages. Most species of passalid beetles are saproxylic and spend their entire life cycle within or beneath decomposing wood. Passalid dispersion capacity is poorly known for tropical species, with few reports in the literature suggesting around 20 m, but some North American species can fly up to 30 m (MacGown & MacGown, 1996; Galindo-Cardona *et al.*, 2007; Jackson, 2012), and their colonies do not occupy more than one trunk simultaneously (Reyes-Castillo & Halfpiter, 1984; da Fonseca, 1988; Mouzinho & da Fonseca, 1998). Passalids are generalists in the exploitation of deadwood and the higher density of dead trunks seems to favour higher rates of colonisation (Castillo & Moron, 1992; Galindo-Cardona *et al.*, 2007; Ulyshen, 2018; Alencar *et al.*, 2020).

We tested whether windthrow can promote saproxylic insect diversity in Central Amazon by increasing resource availability. To do so, we assessed differences in species richness, abundance and composition of passalids (i) between windthrown areas and adjacent old-growth forest and (ii) the relationship between these diversity metrics and the windthrow severity estimated as the percentage of trees directly killed by the studied event (Negrón-Juárez *et al.*, 2010; Marra *et al.*, 2014).

## Materials and methods

### Study area

The research was conducted at the *Estação Experimental de Silvicultura Tropical* (EEST) (2° 61'S, 60° 20'W) of the *Instituto Nacional de Pesquisas da Amazônia* (INPA), Central Amazonia (Fig. 1a). The average monthly temperature is 26°C (Ranzani, 1980; Sombroek, 2001), and annual precipitation is 2600 mm, with a drought period between July and September (Higuchi *et al.*, 2011). The vegetation is typical of terra-firme forest, while the dominant tree height at the EEST is ~28 m, with some trees reaching up to 55 m (Rankin-de-Mérona *et al.*, 1992). In January 2005, the EEST and adjacent areas were heavily hit by squall line storms that produced several forest windthrows (~2500 ha) in the Manaus region (Negrón-Juárez *et al.*, 2010). The gaps (>2000 m<sup>2</sup>) investigated created a complex mosaic of forest patches with varying disturbance intensity, that is, the amount of deadwood available on the forest floor. The passalid beetles were sampled across this tree-mortality gradient (Fig. 1b).

### Data sampling

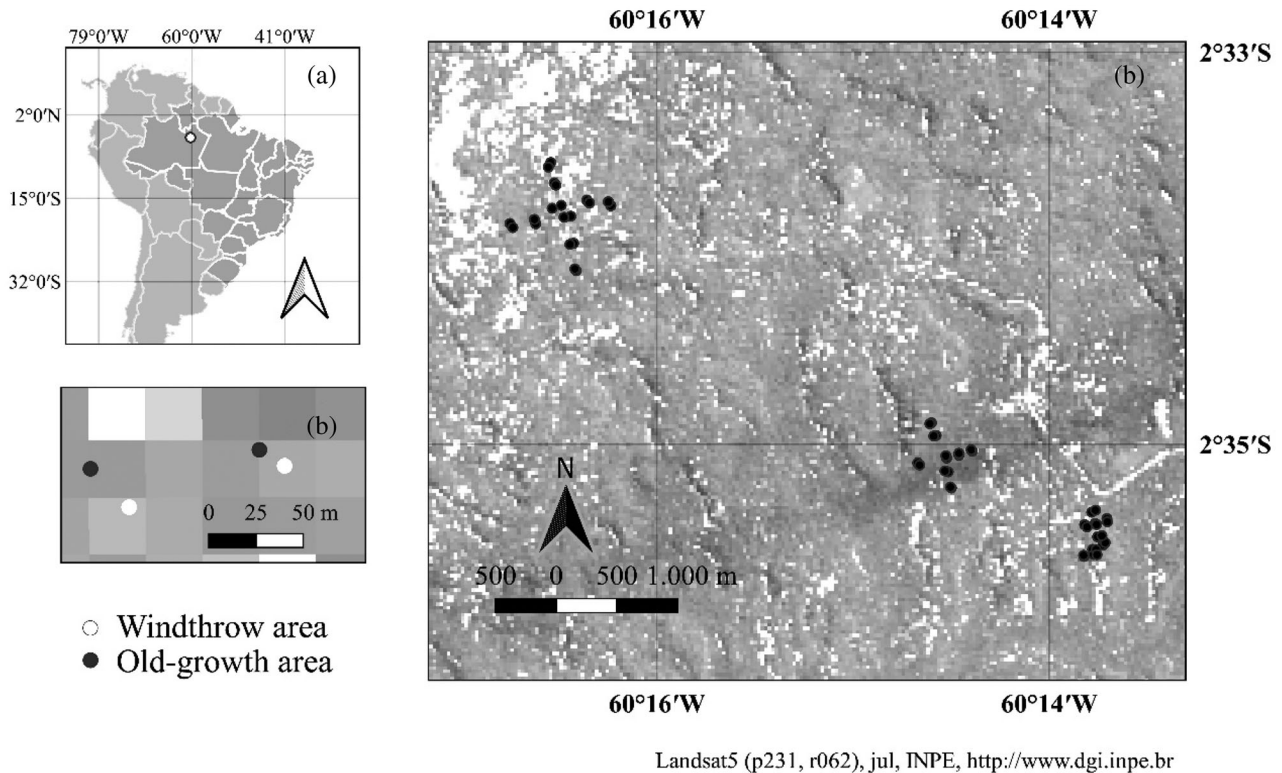
We sampled passalid beetles in a systematic paired-design to compare disturbed (windthrow area) and control (old-growth area) plots. To assess the entire variation in the amount of deadwood, we used three pairs of transects, measuring 200, 600 and 1000 m length by 10 m width, respectively (Fig. 1b). The transect length varied according with the size of the windthrow event. We sampled 27 disturbed plots and 27 old-growth plots (Fig. 1c). The distance within sample pairs (windthrow and old-growth areas) was <50 m, and between different pairs >100 m (Fig. 1c). The minimal 100 m distance between pairs provided independence (Moran's I for richness = 0.059,  $P = 0.258$ ; and Moran's I for abundance = 0.005,  $P = 0.719$ ) given the very low dispersal abilities of the passalids, around 20 m (Galindo-Cardona *et al.*, 2007; Jackson, 2012). Moreover, each trunk represents a distinct ecological unit (Graham, 1925), since passalid colonies do not occupy more than one trunk simultaneously (Reyes-Castillo & Halfpiter, 1984; da Fonseca, 1988; Mouzinho & da Fonseca, 1998).

The field work was undertaken during the dry season of 2017, 12 years after the occurrence of the studied windthrows (January 2005). We standardised the samples by wood volume and decomposition state. Each sample consisted of a volume of 1.205 m<sup>3</sup> of deadwood taken from two to five fallen trunks and at the same decomposition state. We used a simplified version of the four-class system proposed by Castillo and Reyes-Castillo (2003) for decomposition classification (DC). This system, adapted by Alencar *et al.* (2020) (see Table 1), is based on visual characteristics. The exact cubic volume of 1.205 m<sup>3</sup> of deadwood was calculated using the Smalian formula (Loetsch *et al.*, 1973):  $(Asi + Asf)/2 \times h$ , where  $Asi$  = area of the cross section at breast height,  $Asf$  = area of the cross section at the top of the bole and  $h$  = the total bole length. We assume that the trunks used were in the form of a paraboloid and used these measures to standardise the volume of deadwood stipulated in the samples (Gevorkiantz *et al.*, 2016). For non-intact trunks, the volume was calculated from the diameters of the base and top of the dead trees.

First, the deadwood was inspected by removing its bark and searching for beetles. Next, the deadwood was sliced into manageable pieces using a chainsaw. All pieces were carefully inspected for saproxylic beetles. The specimens collected were stored in 60-ml-capacity plastic bottles containing PAMPEL fixative solution (42% distilled water, 44% alcohol 96° GL, 8% formalin, and 5% to 6% glacial acetic acid), for 12 h. Subsequently adult and immature passalids were transferred to vials containing alcohol 96° GL and labelled. The collected passalids were identified using identification keys (Luederwaldt, 1931; Jiménez-Ferbans *et al.*, 2015; Bevilaqua & da Fonseca, 2019). This identification was later refined by comparisons with vouchers from the entomological collection of INPA and with the support of specialists. The material was deposited in the entomological collection of INPA.

### Estimates of windthrow severity

Windthrown areas show an increase in non-photosynthetic vegetation (NPV) due to varying severities of tree mortality



**Fig 1.** Location of the study area (a). Sampled areas – short-wave infrared reflectance (red channel) indicates the 2005 windthrow tree mortality, which was estimated by quantifying the differences in the non-photosynthetic vegetation ( $\Delta$ NPV) (b). Paired sampling points as described in the section data sampling (c).

and consequent accumulation of deadwood and litter on the forest floor. We computed changes in NPV (i.e.  $\Delta$ NPV) from the year before (2004) to the year of the studied windthrow (2005) using spectral mixture analyses (Shimabukuro & Smith, 1991; Adams, 1995) on Landsat-5 Thematic Mapper images (Path 231, Row 062) obtained from the United States Geological Survey (USGS; <http://glovis.usgs.gov>). These analyses were carried out at the pixel level (i.e. 30 m  $\times$  30 m spatial resolution) following the procedures described in previous research conducted in the same study area (Marra *et al.*, 2014, 2018; Santos *et al.*, 2016). Windthrown tree mortality for disturbed plots was estimated using a

locally calibrated equation ( $Y = 103.22 \times \Delta$ NPV-3.32;  $R^2 = 0.8$  and  $P < 0.001$ ), which has  $\Delta$ NPV and tree-mortality (%) as independent and dependent variables, respectively (Negrón-Juárez *et al.*, 2010). This metric was used in previous research developed in the same study area (Marra *et al.*, 2014, 2018; Santos *et al.*, 2016). Our tree mortality estimation model accounts for abrupt changes in NPV and thus, was only applied for windthrown plots. The old-growth forests studied here have background tree mortality typical of the region – ca. 1%  $\text{yr}^{-1}$  (Chambers *et al.*, 2004; de Toledo *et al.*, 2012). The number of dead trees in windthrow plots was based on the average of live trees in old-growth plots per hectare (Marra *et al.*, 2014) multiplied by the tree-mortality at the respective sampling points.

**Table 1.** System used for the decomposition classes of the dead trunks, proposed by Alencar *et al.* (2020).

Class	Description	Sample
DC1	Bark firmly attached to the trunk; solid wood.	2
DC2	Bark partially dropping; it can be easily separated from the trunk.	16
DC3	Bark when present found only at trunk/soil interface; the outer layers easily disintegrate; the heartwood is still solid.	20
DC4	Bark totally absent; the trunk can be completely fragmented manually, much moisture present, it is partially covered with vegetation and mixed with the forest soil.	16

#### Data analysis

We used species accumulation curves to compare the overall number of Passalidae species sampled in windthrow and old-growth areas (Chao *et al.*, 2014). To give a more comprehensive view, we built abundance and incidence (number of logs) accumulation curves. Species accumulation curves in both cases, were computed using Hill's number  $q = 0$ . Confidence intervals (95%) and extrapolated species richness were calculated following Chao *et al.* (2014) and were based on 999 bootstrap permutations.

We used generalised linear mixed models (GLMMs) to compare the number of species and abundance at plot scale. The richness and abundance of passalids in each sample were the dependent variables, and treatment (windthrows or old-growth areas) and number of logs were the fixed predictor variables. The sample pair (windthrow and old-growth areas) was declared as a random variable in the models. We used models with Gaussian distribution for richness and quasipoisson to accommodate over-dispersion in the abundance data (Zuur *et al.*, 2009). Given the number of logs per plot was largely invariant (23 pairs out of 27 were based on samples from 3 logs at each sample), both models did not converge after several attempts using different optimisers. Therefore, we opted to present models based on plots with three logs per samples ( $N = 23$  pairs) only. We calculated the marginal and conditional  $R^2$  for each GLMM to measure the importance of the random variable (sampling pair) in our results. The marginal  $R^2$  provides the variation explained by fixed variables only, while conditional  $R^2$  shows the variation explained by fixed and random variables in the model (Nakagawa & Schielzeth, 2013).

To further understand the role of tree mortality in promoting diversity of saproxylic beetles, we built GLMMs of passalid species richness and abundance against windthrow severity ( $\Delta$ NPV). We used models with Gaussian distribution for richness and Poisson distribution for the abundance data (Zuur *et al.*, 2009). These analyses were also carried out for disturbed plots with three logs per samples ( $N = 23$ ). For GLMM and GLM models, we used residual diagnostic plots to check if the model assumptions were addressed.

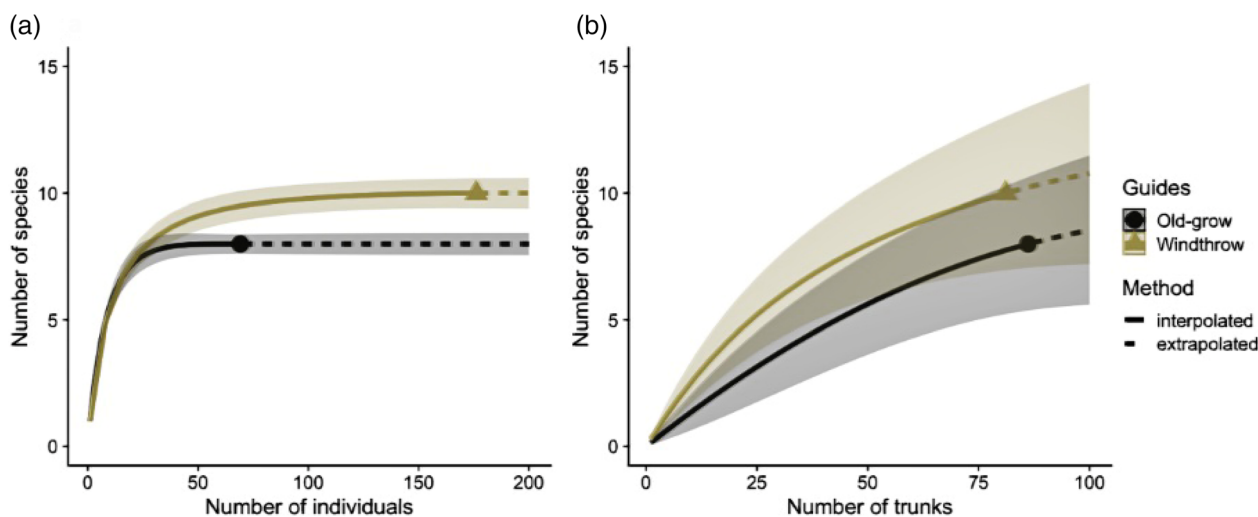
We used a multivariate approach based on a combination of generalised linear models (GLMs) to evaluate habitat–community relationships across our study area. The *manyglm* function from the R package *mvabund* fits individual GLMs to each species and combines the results in an *assemblage* response (Wang *et al.*, 2012). In this function, the hypothesis test is based on bootstrapping procedures. This model framework is

appropriate for data sets with strong mean–variance relationships, typical of community ecology data (Wang *et al.*, 2012). A species composition matrix using abundance data was used as dependent variable and treatment (windthrow or old-growth) as fixed factor. The *manyglm* model was fitted with negative binomial error distribution, and  $P$ -values were estimated from 999 bootstrap resamples. We also fitted a *manyglm* model using the species composition along the gradient of windthrow severity. This procedure was only carried out for disturbed plots for which the  $\Delta$ NPV metric is suitable. All the analyses and graphs were made in the R software (R Core Team, 2020).

## Results

A total of 167 dead trunks were sampled: 81 trunks in the windthrown areas (70.37% of the samples with active galleries) and 86 trunks in the old-growth forest (31.39% with active galleries). All decomposition classes were covered in the sampling pairs. DC1 (lowest decomposition level) represents ~4% of the pairs, DC2 (lowest-middle decomposition) 30%, DC3 (middle-highest decomposition) 37% and DC4 (highest decomposition) accounted for 30% (Table 1). Mean windthrow tree mortality on disturbed plots was 22.03%, with some plots reaching up to 63%. Overall in the windthrow areas sampled, the mean number of dead trunks per hectare was  $130.69 \pm 125.75$ , with a maximum of up to 377.17 dead trees per hectare in more severely affected areas.

The accumulation curves for old-growth and windthrown forests tended to stabilise around 40 and 100 individuals, respectively (Fig. 2a). Ten passalid species and 176 individuals were collected in the windthrown forest and eight species and 69 individuals in the old-growth (Fig 2a). The difference between windthrow and old-growth forests was much less evident, based on incidence data (number of logs). The accumulation of species was steeper rather in windthrow plots, but the confidence



**Fig 2.** Passalidae species accumulation curves for the windthrow area and old-growth forest, based on abundance (a) and incidence (b) data. The shaded area around the continuous lines represents 95% confidence intervals.

**Table 2.** Species abundance collected in areas disturbed by windthrow and old-growth forest areas.

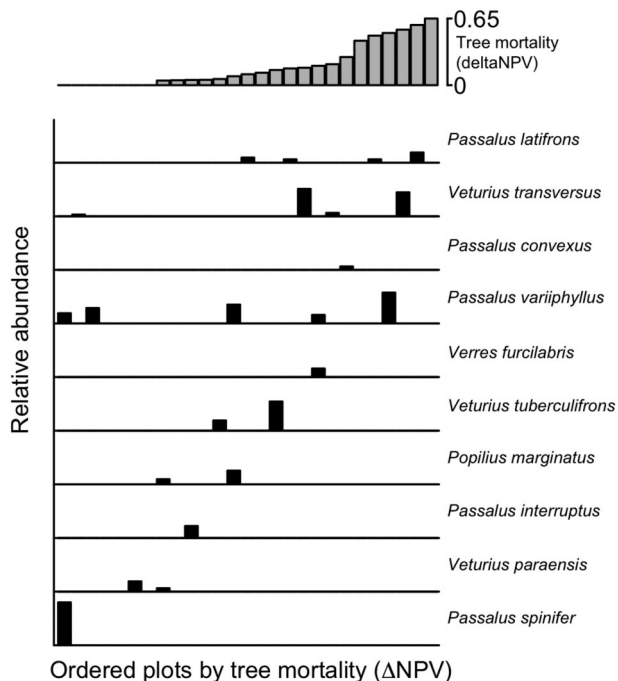
Specie	Windthrown forest	Old-growth forest	Abundance total
<i>Passalus (Passalus) abortivus</i> (Percheron, 1835)	0	13	13
<i>Passalus (Passalus) interruptus</i> (Linnaeus, 1758)	7	0	7
<i>Passalus (Passalus) variiphyllus</i> (Kuwert, 1891)	49	4	53
<i>Passalus latifrons</i> (Percheron, 1841)	13	5	18
<i>Passalus spinifer</i> (Percheron, 1841)	25	0	25
<i>Passalus convexus</i> (Dalman, 1817)	2	0	2
<i>Popilius tetrachyllus</i> (Eschscholtz, 1829)	0	4	4
<i>Popilius marginatus</i> (Percheron, 1835)	11	8	19
<i>Vetres furcillabris</i> (Eschscholtz, 1829)	5	18	23
<i>Veturius transversus</i> (Dalman, 1817)	33	0	33
<i>Veturius tuberculifrons</i> (Kuwert, 1891)	23	9	32
<i>Veturius paraensis</i> (Luederwaldt, 1927)	8	8	16

intervals overlap with old-growth accumulation curve (Fig. 2b). The number of passalid species was higher in windthrow areas, even with a slight larger sample (86 vs. 81 logs).

A congruent pattern was found for species richness and abundance of passalids. In both cases, there was higher species richness (GLMM;  $P = 0.029$ ) and abundance (GLMM;  $P < 0.001$ ) in the windthrown compared to the old-growth forest. The fixed factors (windthrows or old-growth areas) in the GLMM explained  $\sim 9\%$  and  $\sim 11\%$  of the total variance in the richness and abundance data, respectively. Most of the variance was explained by the sampling pair (random effect): both fixed and random effects explained  $\sim 16\%$  of species richness and  $\sim 88\%$

of species abundances in our models. The studied gradient of windthrow severity was not related with richness (GLM;  $b = -0.033$ ;  $P = 0.955$ ) or abundance (GLM;  $b = 0.808$ ;  $P = 0.457$ ) of passalid species sampled on windthrow plots.

The Passalidae assemblage composition showed a different pattern. The old-growth and windthrown forest shared 50% of the recorded species. Four and two species were exclusive to the windthrown and old-growth forests, respectively (Table 2). Although *Passalus variiphyllus* (Kuwert, 1891) and *Veturius transversus* (Dalman, 1817) occurred all along the windthrow tree-mortality gradient, the other species were more restricted (Fig. 3). The species composition was similar between windthrow and old-growth areas (MANYGLM; Wald = 7.338,  $P = 0.128$ ). However, there was a correlation between the species composition and the tree-mortality gradient promoted by the studied windthrows (MANYGLM; Wald = 7.338,  $P = 0.026$ ).

**Fig 3.** Distribution of Passalidae species along tree mortality gradient ( $\Delta$ NPV) in windthrow areas, at the Experimental Tropical Forestry Station (EEST), Central Amazonia.

## Discussion

Our results suggest that large-scale windthrow may promote saproxylic insect diversity in Central Amazon terra-firme forests. Although this study took place 12 years after the event, the number of individuals and species were still higher in the windthrow areas compared to the old-growth areas. However, this pattern was not related to the windthrow severity, which is correlated with deadwood availability. On the other hand, the variation in the amount of deadwood was associated with species composition. Taken together, these results suggest that for passalid assemblages, the occurrence of windthrows is more relevant than associated gradients of tree mortality. The increased amount of deadwood in windthrows may decrease competition, favouring the co-occurrence of species at larger scales.

In general, passalids are generalists (Luederwaldt, 1931; Castillo & Reyes-Castillo, 2003; Ulyshen, 2018), but some species shows preferences for specific deadwood characteristics (Alencar *et al.*, 2020). Windthrows can promote changes in the amount and composition of the substrate available for passalids over larger areas (Chambers *et al.*, 2009; Marra *et al.*, 2014). This heterogeneity of the substrate associated with the higher amount of deadwood can benefit specialised or less competitive

species, explaining why more individuals and species were found in windthrows compared to old-growth forests. Similar results were found for cerambycids and buprestids in temperate forests, where richness and abundance of insects were greater in an area disturbed by windstorm (Wermelinger *et al.*, 2002; Bouget, 2005b). Like other saproxylic insects, aggregation of tree logs is a predictive surrogate for species diversity (Økland *et al.*, 1996; Martikainen *et al.*, 2000; Seibold *et al.*, 2015) and reinforces the hypothesis that the passalids' distribution correlates to the windthrows areas.

The variation in the amount of deadwood produced by windthrows seems to be a key factor to understand patterns of species composition in Central Amazon. This variation in deadwood amount may work as new opportunities for species with low competitive ability and may explain the species composition patterns found along the disturbed areas gradient. It is important to note that deadwood amount sampled in windthrow/old-growth forests was the same. Therefore the patterns reported here for species richness, abundance and composition are more related with landscape features, such as overall deadwood amount, rather local factors, such as specific log characteristics.

For passalids, the windthrows areas may also result in lower isolation of populations and represent potential territories for future reproductive seasons. In an experimental study in Costa Rica, Galindo-Cardona *et al.* (2007) found that the availability and spatial distribution of fallen trunks strongly affected the colonisation of *Spasalus crenatus* (MacLeay, 1819) (Passalidae). This species colonises new resources at noticeably short distances (2–6 m). Studies with *Odontotaenius disjunctus* (Illiger, 1800) (Passalidae) also found low dispersion rates, between 5 and 10 m (Jackson, 2012). These studies indicate that the passalids' colonisation is favoured by shorter distances between substrates. Therefore, windthrows areas may favour dispersion and reduce the search time for a new substrate, due to the better connectivity between already established colonies and new dead trunks.

Windthrows cause high tree mortality in Amazon forests (Marra *et al.*, 2014; Rifai *et al.*, 2016; Negrón-Juárez *et al.*, 2018), but their frequency and intensity vary across different regions and weather regimes. Large-scale windthrows are more frequent in the rainy season and in northwest and Central Amazon (Peru, Colombia, Venezuela and Brazil) (Nelson *et al.*, 1994; Espírito-Santo *et al.*, 2014; Negrón-Juárez *et al.*, 2017, 2018). Under the changing climate, there is a prediction of increased frequency of extreme rainfall for the Amazon (Marengo *et al.*, 2009; sections 2.6.2 and 14.8.5 in IPCC, 2013), which may result in more frequent and severe windthrows. The correlation found between the composition of passalid beetles and the tree mortality gradient may be related with the wider amplitude of niches in windthrow areas, such as greater heterogeneity of substrates for passalid beetles, different levels of decomposition, diameter of the dead trunks and tree species (Thorn *et al.*, 2014; Alencar *et al.*, 2020). This pattern may scale up, and taken together with abundance data, suggesting that windthrows may change demographic rates of the passalid assemblages.

The return-frequency of windthrows in Central Amazon is negatively correlated with the size of the events (Chambers *et al.*, 2013). Relatively small events resulting in the mortality of few trees (1–8 in one hectare) are potentially the most frequent but still not traceable from existing remote sensing data covering

large regions. The event studied here sits in the middle-extreme of this size distribution (~250 ha), and disturbances of this magnitude are often regarded as rare events (Chambers *et al.*, 2013; Negrón-Juárez *et al.*, 2018). Although our data indicate that higher amounts of deadwood associated with large-scale windthrow increase passalid diversity locally, the effects of small windthrows were still not assessed. Small and more recurrent windthrows may act as suitable forest-patches that favour passalid species at the regional scale.

Considering the logistic limitations to accessing and studying windthrows, and the lack of knowledge about saproxylic insects in tropical forests (Seibold *et al.*, 2015), our research contributes novel information on how natural disturbances affect the diversity and demography of passalids in the Central Amazon. Incorporating data from other insect groups will expand current knowledge on the effects of disturbances on tropical saproxylic insect communities.

## Acknowledgements

We thank J. M. Ribeiro, M. M. F. Bento for their assistance in field data collection and M.V. Bevilacqua for granting the use of his photography. We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior CAPES/Brazil (Finance Code 001), FAPEAM-Programa POSGRAD and the Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq/Brazil (grant 2016-2018). We thank the Forest Management Laboratory of the National Institute for Amazonian Research (LMF/INPA) for logistic support. The study site is supported by the INCT *Madeiras da Amazônia* and the ATTO Project, which is funded by the German Federal Ministry of Education and Research (BMBF contracts 01LB1001A and 01LK1602A), the Brazilian Ministry of Science, Technology and Innovation (MCTI/FINEP contract 01.11.01248.00) and the Max Planck Society (MPG). FBB is continuously supported by a CNPq productivity grant (3096002017-0). We sincerely thank anonymous reviewers for their valuable comments and constructive criticisms which have greatly improved the manuscript.

## Conflict of interest

The authors declared no conflicts of interest in relation to this work.

## Authors' contributions

J.B.R. Alencar and C.R.V. da Fonseca conceived the idea; C.R.V. da Fonseca identified recorded species; F.B. Baccaro, J.B.R. Alencar and D.M. Marra formulated the research questions and analysed the data; J.B.R. Alencar wrote the article with substantial collaboration from all authors.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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Accepted 25 July 2021

Editor/associate editor: Raphael Didham