



# Is being green what matters? Functional diversity of cavity-nesting bees and wasps and their interaction networks with parasites in different reforestation types in Amazonia

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**Abstract.** 1. Understanding the processes that shape biotic interactions within biological communities helps us to develop strategies for the establishment of ecological communities and to rehabilitate the functionality of degraded environments.

2. We evaluated the functional diversity of cavity-nesting bees and wasps and their interaction networks established with nest parasites in different types of reforestation in Southern Amazonia. To do so, we used bee and wasp trap-nests to sample six different types of environments: pasture, teak reforestation, fig reforestation, mixed reforestation, natural regeneration and primary forest.

3. Although the bees' functional diversity indices evaluated did not vary between reforestation types and natural forests, the functional traits of these insects were quite different in reforestation with planting species, especially teak. For wasps, we observed lower functional diversity in pasture, fig plantation and mixed reforestation. Moreover, we observed that while teak reforestation presented the highest parasite richness, parasitism rate and diversity of interactions, natural regeneration shows higher interaction specialisation.

4. Our results indicate that the simplification of the structure of reforested environments contributes to increase the divergence in the functional diversity of cavity-nesting bee and wasp community and the interactions they establish with their parasites in relation to natural environments. However, these differences can be reduced by structuring the environment. Thus, natural regeneration can be a favourable strategy if the degraded areas are not severely impacted and present proximity to the source of propagules.

**Key words.** Functional traits, network, parasite–host interaction, rainforest, reforestation.

## Introduction

Biological communities are composed by species that interact with each other in different ways, forming complex

ecological networks, in which species are denoted by nodes and their interactions by links (Dáttilo & Rico-Gray, 2018; Osorio-Canadas *et al.*, 2018). In recent years, studies of these interaction networks have greatly improved our understanding as to the importance of the organisation of such networks on the stability of ecological communities (Harvey *et al.*, 2017). Mainly in the face of increasing biodiversity loss through the conversion of natural environments into highly anthropized landscapes (Costanza *et al.*, 2014), understanding the effect of

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these changes on the pattern of interaction of these communities has been the goal of many ecologists (Tylianakis *et al.*, 2006; Falcão *et al.*, 2015; Campião & Dáttilo, 2020; Silva *et al.*, 2020). This because changes in species composition and also ecological interactions mismatches may compromise ecosystem functionality (Esquivel-Muelbert *et al.*, 2019; Fei *et al.*, 2017; Wood *et al.*, 2019). In fact, biological communities can naturally change, since environments can experience instabilities that promote the exclusion of resident species and the arrival of new ones (Bramon Mora *et al.*, 2020). But the intense modifications of the natural landscapes in the last decades by the land-use have led to the exclusion of biological groups strongly linked to human well-being, such as pollinators, seed dispersers and biological control agents (Potts *et al.*, 2010; Hua *et al.*, 2016). In an attempt to mitigate the environmental and socioeconomic impacts caused by the loss of these services, environmental recovery projects have taken place around the world in recent years (Chazdon & Guariguata, 2016).

During the process of recovering vegetation cover from degraded areas worldwide, two strategies are commonly used: reforestation with planting species process (active strategy) and natural regeneration process (passive strategy) (Holl & Aide, 2011). Regardless of the process performed, both aim to restore the functional diversity, biodiversity and ecosystem dynamics (Aronson *et al.*, 2006). Despite the emergence of restoration ecology, proposed in the mid-1990s (Suding *et al.*, 2015; Beiroz *et al.*, 2019), most studies in recovered areas concentrate on restoring species diversity but do not evaluate parameters that can, in fact, promote an exam of the quality of these systems (Audino *et al.*, 2014; Cisneros *et al.*, 2015; Beiroz *et al.*, 2018). Thus, functional and ecological information, such as the recovery of individuals with traits that allow them to perform the activities associated with their group and the establishment of interactions between biological species are still limited. In the process of environmental restoration, the attributes used in the vegetal recovery can strongly regulate the established fauna due to the presence of conditions that allow them exploring these resources or not (Olito & Fox, 2015). Thus, variations in the characteristics of individuals (functional traits) that can be attributed to a species, such as phenological, morphological, physiological, reproductive or behavioural (Kissling *et al.*, 2018; Esquivel-Muelbert *et al.*, 2019), can be suggested to evaluate the community abilities in using the environment or its vulnerability to environmental changes (Laliberte & Legendre, 2010; Palma *et al.*, 2015).

Bees and wasps together make up more than 40 000 species worldwide (Michener, 2000; O'Neill, 2001). Beyond to the variety of nesting behaviour (digging, natural cavities, exposed-nesting, parasitic) (Krombein, 1967), social organisation (solitary, semi-social, eusocial, cleptoparasites and parasitoids) (Silveira & Almeida, 2002) and larval diet (pollen, spiders, cockroaches, caterpillars and grasshoppers) (Krombein, 1967; Michener, 2000; O'Neill, 2001) that these Hymenoptera present, they play an important ecological and economic role in both natural and cultivated systems (Tylianakis *et al.*, 2005; Araújo *et al.*, 2018a,b, 2020; Flores *et al.*, 2019; Giannini *et al.*, 2020). Due to their pollination activities, bees are responsible for the reproduction of up to 90% of the species of flowering plants in

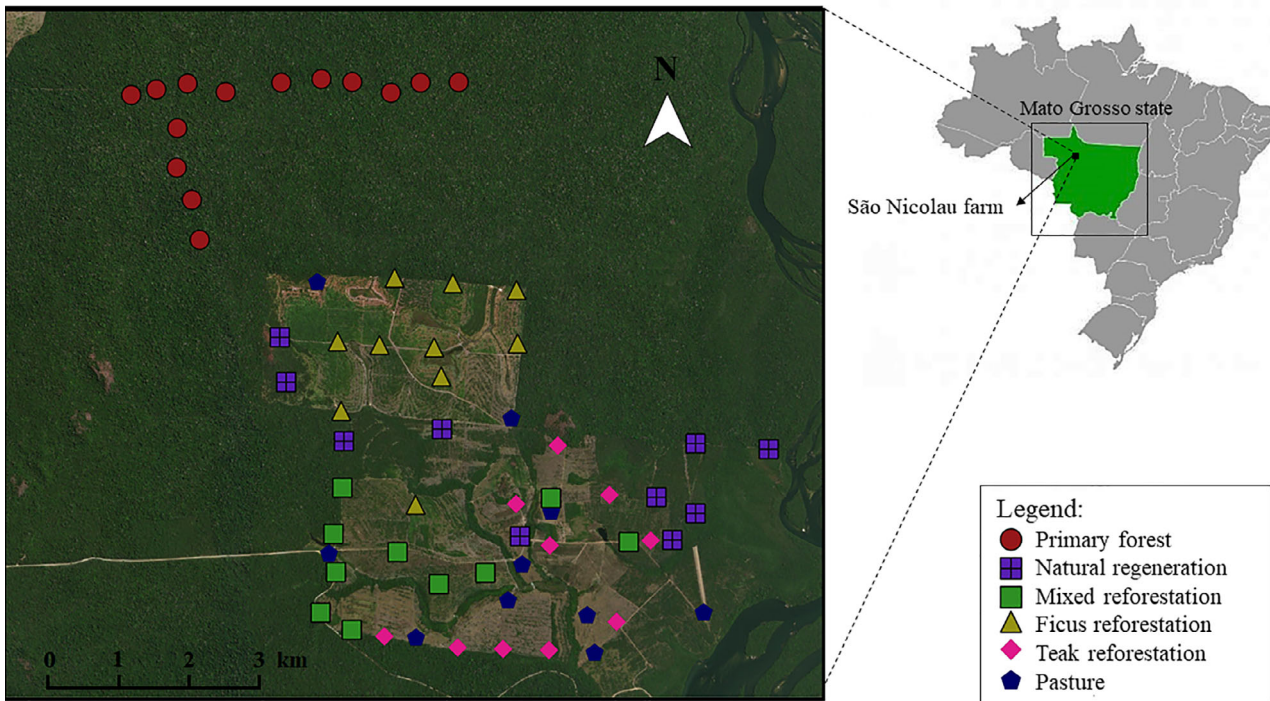
tropical regions (Ollerton *et al.*, 2011) and 75% of cultivated plants (Klein *et al.*, 2007). Although wasps can also play a role in pollination, the main activity of this group is the biological control of several species of invertebrates, many considered as pests in agricultural crop (Tylianakis *et al.*, 2005; Saunders, 2016). As far as we know, there are no studies evaluating the efficiency of different types of reforestation in restoring the functionality of introduced species or the interactions that they establish in the new environments. Understanding these factors is a key element to promote the efficiency of the efforts used in projects that aim to re-establish the local biodiversity and its associated services. Bees and wasps that nest in cavities form an interesting model for studies of this purpose. Their nesting strategy allows the use of trap-nests to sample not only the characteristics of the species that occur in the region but also the interactions that they establish with other organisms, such as parasites associated with their nests (Tylianakis *et al.*, 2006, 2010; Osorio-Canadas *et al.*, 2018; Araújo *et al.*, 2018a,b).

In this study, we evaluated whether different reforestation types used in the recovery of degraded areas from pastures also differ in their capacity to recover the functional diversity of cavity-nesting bees and wasps and the interactions that these species establish with their nest parasites. Due to their different food specialisation and different ecological functions, we evaluated the functional diversity of bees and wasps separately. However, we evaluated the interactions of both groups with the parasites together, because our interest was to assess the effects of reforestation on the host–parasite relationship. Our hypothesis is that the vegetation structure used in the reforestation process from pasture areas influences the capacity of these new environments to recover the functional diversity of cavity-nesting bees and wasps and to restore the structure of the interaction networks with the parasites associated with their nests, once the plant species used on reforestation process can shape the established communities. Our predictions are that: reforestations with a more diverse vegetation structure will present (i) functional diversity of bees and wasps, (ii) parasite richness, and (iii) parasitism rates more uniform (similar) to those found in primary forests. We also predict that the plant diversity used in reforestation favours a greater similarity in parasite species composition, (iv) and greater similarity of their interactions with cavity-nesting bees and wasps in relation to the primary forests. Finally, (v) we predict that increasing plant structure may favour the establishment of more specialised networks than those present in simplified environments.

## Materials and methods

### Study area

We conducted this study at the São Nicolau Farm (9°48'S, 58°15'W, 254 m), located in the municipality of Cotriguaçu, northern Mato Grosso State, Brazil (Fig. 1). The study region is characterised as a tropical rainforest within the southern Brazilian Amazonia, not being subject to seasonal inundation. Of the farm's 10 000 ha, 2800 ha were converted and used as cattle pasture between the 1980s and 1990s. In the years 1999 and



**Figure 1.** Map showing the spatial arrangement of our 64 sites established in six different types of habitats at the São Nicolau farm, municipality of Cotriguaçu, State of Mato Grosso, Brazil: pasture, teak, reforestation, fig reforestation, mixed reforestation, natural forest and primary forest.

2000, 2000 ha of grazing area was replanted with various tree species. In the same period of revegetation, 500 ha of pasture were abandoned for their reversion in secondary forest by the process of natural succession, leaving 300 ha of active pasture for cattle grazing. The farm still has 7200 ha of primary forest (Araújo *et al.*, 2020). The climate of the region is the AW type, according to the Köppen classification (warm and humid), with an average annual temperature of 24°C, 85% humidity, and 2300 mm of precipitation (Rodrigues *et al.*, 2011).

#### Experimental design

We collected data on six different landscapes: (i) Pasture (PA): landscape dominated by great predominance of planted grasses (not more than 50 cm tall) used as food for cattle. This landscape is characterised by a very high incidence of light and the absence of leaf litter accumulation. We used pasture in our design as a ‘starting point’ of forest succession under different reforestations (Supporting Information Fig. S.1a); (ii) teak reforestation (TR): monoculture of *Tectona grandis* (Verbenaceae) of nearly 17 years, an exotic tree that loses/sheds its leaves annually. During the collection period on this landscape, leaves were green, allowing little light penetration in the understory. Moreover, the understory is open and has an abundant leaf litter accumulation (Supporting Information Fig. S.1b); (iii) fig reforestation (FR): monoculture of native species, *Ficus maxima* (Moraceae), of nearly 17 years and performed with seedlings obtained from native seeds in our study area. This landscape

presents some gaps formed by dead trees, which are characterised by grasses and shrubs. The understory has plants of varying sizes and low leaf litter accumulation (Supporting Information Fig. S.1c); (iv) mixed reforestation (MR): mixed reforestation with tree species obtained from native seeds in our study area, including *Handroanthus chrysotrichus* (Bignoniaceae), *Tabebuia roseoalba*, *Handroanthus impetiginosus*, *Cedrela fissilis* var. *macrocarpa* (Meliaceae), *Cordia alliodora* (Boraginaceae), *Simarouba amara* var. *typica* (Simaroubaceae), *Spondias mombin* var. *globosa* (Anacardiaceae), *Hevea brasiliensis* var. *acreana* (Euphorbiaceae), and *Schizolobium parahyba* var. *amazonicum* (Fabaceae). This reforestation presents understory of low shrubs and low leaf litter accumulation (Supporting Information Fig. S.1d); (v) natural regeneration (NR): Secondary forest formed by the natural regeneration process of nearly 17 years without the presence of cattle or anthropogenic interference. The understory of natural regeneration forest is extremely dense, with vegetation higher than 5 m; there is a low leaf litter accumulation and light incidence (Supporting Information Fig. S.1e); (vi) primary forest (PR): our control, defined as ‘terra-firme’ and closed-canopy forest without the influence of seasonal flooding from larger rivers. The understory is relatively open and very biodiverse, and the canopy varies between 30 and 40 m tall with some trees reaching up to 50 m (Supporting Information Fig. S.1f).

Within each of the six landscapes, we randomly selected 10 sampling sites ( $n = 14$  in the case of the primary forest) based on the feasibility of access and logistical constraints (64 sites in total, Fig. 1). Based on the typical foraging distances estimated for cavity-nesting bees and wasps (Gathmann &

Tsharnke, 2002; Klein *et al.*, 2004; Zurbuchen *et al.*, 2010), our sites were sampled at least 500 m apart from any other site to minimise spatial dependence among sites, following the distance used in previous bee and wasp works in the same study area (Araújo *et al.*, 2019, 2020). Site replicates of each forest type were also spatially interspersed among replicates of all other degraded forest types (Fig. 1). Because permission to sample was only available for one spatial location in the northwest of the study region (but only 1–3 km from the nearest degraded forest sites; Fig. 1), the primary forest sites could not be interspersed. To address this issue, we used the same approach as Araújo *et al.* (2020), incorporating tests of spacial autocorrelation in all statistical analyses (see in statistical analyses).

At each of the 64 sites, we marked out five equidistant points 50 m apart on a line transect (oriented along the primary forest) and installed experimental trap-nest blocks constructed of wood (*Cedrela fissilis*, Meliaceae) with holes drilled into them. Trap-nests were placed at a height of 1.5 m above the ground attached to trees or wooden stakes (Araújo *et al.*, 2019).

#### *Trap-nest design and sampling*

We considered each trap-nest as one woodblock (30 cm length × 7 cm height × 12 cm width) with 10 holes each of four sizes, 8, 12, 16 and 20 mm diameter, randomly distributed across the block surface and drilled to 100 mm deep (Supporting Information Fig. S.2). We inserted an appropriate black cardboard tube in each hole to create a removable sleeve. Our methodology for the construction of trap nests was based on previous studies of survey of solitary bees and wasps that nest in cavities (Araújo *et al.*, 2018a,b). To prevent ant and termite attacks on the traps, we use an anti-pest glue (type Tanglefoot) around their substrate. We placed, across all sites, a total of 320 trap-nests, containing 12 800 nest tubes. We inspected the traps every 20 days between August 2016 and July 2017, and those occupied were collected and replaced by another trap with the same measurements. In the laboratory, the trap nests brought from the field were placed in test tubes, closed with cotton, and kept in a dark room at temperatures of between 20°C and 25°C until the emergence of adults. After emergence, we pinned the insects, quantified the number of cells built and identified the specimens. Voucher specimens were deposited in the Invertebrate Collection of the Federal University of Mato Grosso (Araújo *et al.*, 2020).

#### *Functional community structure among habitats*

We compiled ecological and morphological traits of all species recorded in our study. Our traits were selected based on information available in the literature that demonstrated their importance in carrying out activities. For bees, we evaluated: (i) wing length, (ii) body size, (iii) posterior tibia length, (iv) nesting material, (v) tongue length, and (vi) pollen-carrying structures (see Supplementary Table S1 and S2). As for wasps, we measured: (i) wing length, (ii) body size, (iii) posterior tibia length, (iv) mandibular length, and (v) larval diet (see Supplementary Table S1 and S3). These traits were selected because they included several ecological

attributes of bees and wasps that are known to influence their functional roles in the assembly. The wing length correlates with the foraging ability of the individual within the landscape (Spaethe & Weidenmüller, 2002; Greenleaf *et al.*, 2007). The mean body size reflects the resource availability within the landscape and it is positively related to the distance of foraging (Goulson, 2010; Persson & Smith, 2011). Individuals with longer posterior tibia may have a greater ability to handle food (e.g. pollen and prey) in a shorter period of time, reflecting greater agility in the provision of resources for their offspring (Michener, 2000; Eggenberger *et al.*, 2019). Nesting materials reflect the specialisation of nesting individuals on resources necessary for the construction of their nests, the limitation of these resources may affect the occurrence of these individuals in the environment (Michener, 2000). The tongue length is related to food preferences, determining accessibility to food resources (pollen and nectar), and their handling time in flowers with different depths of the corolla (Harder, 1985; Goulson *et al.*, 2010). Pollen-carrying structure can affect the amount of pollen transported, affecting the foraging duration and the range supported on each trip (Michener, 2000; Araújo *et al.*, 2018a,b; Eggenberger *et al.*, 2019). The mandibular length is related to the size of the prey capable of being captured by the individual, indicating its predation capacity (Michener, 2000; Blanke, 2019). The larval diet can indicate a feed restriction on a specific type or group of prey, limiting the occurrence of individuals in the environment (Coudrain *et al.*, 2014). For all species in which emerged more than 20 females, we randomly selected 20 individuals to take the measures of all traits cited above. For all those species that emerged less than 20 females, we measured all females. For species that did not show female emergence, we measured all males available. The measurements of the insect's body parts were made on a millimetre scale, using Leica Application Suite software version 2.0.

We characterised the functional composition of bee and wasp communities at each site by computing the following functional indices: (i) trait average – indicative of the most common trait in a community. For continuous traits, we computed the trait average as the weighted community mean (mean of the trait values of all species in the community weighted by their abundance) using dbFD function. In the case of categorical traits, we converted each level of the trait into a separate variable and we calculated the proportion of individuals of each species accounting for each level; (ii) functional richness (FRic) – which provides a measure of the amount of niche space filled by community species; (iii) functional evenness (uniformity) (FEve) – which provides a measure of the evenness of the distribution of abundance in the space of the filled niche; (iv) functional dispersion (FDis) – which provides a measure of functional trait diversity and reflects the extent to which species within a community differ in their traits (Mason *et al.*, 2005; Laliberté & Legendre, 2010). We quantified the weighted community mean and functional indices using the Gower dissimilarity coefficient in the 'FD' package v. 1.0-12 package (Laliberté *et al.*, 2014).

#### *Parasitism rate and host–parasite network structure*

We expressed the parasitism rate as the percentage of cells that were parasitised. We used a network approach to understand the

relationship between host and parasite. We first built network of species interactions recorded at the brood-cell level for each site of each habitat. Of the 64 sites sampled, 54 showed interaction with parasites. Of these, we used only 44 for the analysis because 10 networks had less than  $2 \times 2$  species, which we considered too small to generate meaningful values of network structure (Murphy, 2016). We then computed the following quantitative metrics related to networks specialisation: (i) *The specialisation index  $H_2'$* , a measure of the degree of complementary specialisation at the network level. This metric, which accounts for the interaction frequency (number of parasitised brood cells) of each species, is not affected by network size and ranges between 0 (maximum generalisation) and 1 (maximum specialisation) (Blüthgen *et al.*, 2006); (ii) *diversity of host–parasite interactions*, this index is derived from Shannon’s diversity index and ranges from 0 (no diversity) to infinity (Bascompte *et al.*, 2005) and estimates the degree to which a community is rich in species and interactions (and how these interactions are distributed among all species) (Corro *et al.*, 2019); (iii) *number of compartments*, this metric measures subgroups of species of one trophic level that interact more frequently with a group of species of another trophic level (Bascompte *et al.*, 2005); (iv) *Nestedness*, this metric estimates the degree which species engaged in few interactions are connected to a subset of generalist species with more interactions (Corso *et al.*, 2011); (v) *Connectance*, this metric quantifies the proportion of established interactions relative to all possible interactions (Jordano, 1987); and (vi) *Niche overlap*, this metric also quantifies the similarity between species regarding their partners from another trophic level (i.e., interaction functional redundancy) (Messeder *et al.*, 2020). Values near 0 indicate no common use of niches and 1 indicates a perfect niche overlap (Cornell, 2011). The significances as to results were assessed by randomization, using the *r2dtable* null model based on the Patefield algorithm. This null model uses fixed marginal totals to distribute the interactions and produce a set of networks where all species are randomly associated (Patefield, 1981). Network analyses were performed using the *networks.list* function in the ‘*bipartite*’ v. 2.15 package (Dormann *et al.*, 2008).

### Statistical analyses

We used general linear models (GLMs) to analyse the effect of reforested environments on functional indices, parasite richness, parasitism percentage and network indices. In order to estimate significant differences in the response variables between the primary forest and reforestation types, we fixed the first (our control) as the intercept of the analysis. This allowed us to directly contrast reforestation with undisturbed environments. In the parasite richness and parasitism percentage models, we also specified a fixed covariate effect for ‘occupation’ (i.e., number of cavities occupied by bees and wasps) to account for any variation in richness and/or parasitism percentage that could be attributed solely to variation in sample occupation. We used Gaussian for continuous dependent variables, Poisson for discrete dependent variables and Binomial for proportion dependent variables. We tested each model for overdispersion of residuals and, where

necessary, overdispersed models were fit using quasibinomial or negative binomial error distribution, according to the dependent variable. Following the construction of the model for each response variable, we contrast the proposed model against the null model using the ‘*AICcmodavg*’ v. 2.3-1 package (Mazerolle & Linden, 2019), in order to find the best-fit model for our response variables. We determined the minimum adequate model(s) by comparing Akaike Information Criterion corrected (AICc) values and AICc weights (AICcWt) for proposed models and null models (intercept-only model). Models within 2  $\Delta$ AICc units of the top model (i.e. the model with the lowest AICc and highest AICcWt values) were considered to have equivalent explanatory power (Burnham & Anderson, 2002) (Supplementary Table S4 and S5). Due to the lower nesting rate of bees, our analyses of FEve produced a high amount of ‘NA’. Therefore, for this group, we do not include these indices in the statistical models. In addition, pasture treatment presented an extremely low number of occupations of bees and parasites associated with the nests (see Table 1). Thus, we did not include this treatment in the GLMs analyses for functional diversity indices. In the models for all response variables, we assessed potential spatial autocorrelation in raw response values and in the residuals of the models, by calculating spatial correlograms for Moran’s I values in ‘*ncf*’ v.1.2-6 package (Bjornstad & Cai, 2018).

We tested the variation in the composition of *parasites* and *parasite–host interactions* among habitats by performing permutational multivariate analyses of variance (PERMANOVA) with 1000 permutations (Anderson, 2001) on the abundance of data (parasite/parasite–host interaction) standardised to proportion, using Bray–Curtis dissimilarity index with the *adonis* function in ‘*vegan*’ v. 2.5-7 package (Oksanen *et al.*, 2020). Standardisation was necessary, as we were more interested in relative similarity/dissimilarity patterns than down weighting abundant species or interactions (Clarke & Warwick, 2001). When the result was significant, we assessed the differences between ‘Control vs. Treatments’, by pairwise comparisons with adjusted *P*-value using Bonferroni correction (Paolucci *et al.*, 2017). Additionally, we also assessed within-group homogeneity using PERMDISP (Warton *et al.*, 2012). We used the first two axis of principal coordinates analyses (PCoA) to visualise graphically significant differences in PERMANOVA and treatment clusters. All analyses were performed in R version 3.5.1 (R Team Core, 2018).

## Results

### General description of the community

From the total of 2000 (2800 in PF) trap-nests available in each sampled treatment, 23.96% were occupied in PF, 24.99% in TR, 17.10% in MR, 16.45% in NR, 13.80% in FR and 1.5% in PA. We recorded 26 host wasp species (1813 nests, 3525 individuals) belonging to the families Crabronidae, Pompilidae, Sphecidae and Vespidae, and 14 host bee species (330 nests, 1286 individuals) belonging to the families Apidae and Megachilidae that nested among sampled habitats (Supporting Information Table S.6). We also found 26 parasite species



belonging to 14 families of four orders (Coleoptera, Diptera, Hymenoptera, and Neuroptera) which parasitised 11.27% of the constructed cells (349 nests, 543 cells) (Supporting Information Table S.6). Among the families of parasite species, Mutillidae showed the highest number of species ( $n = 4$ ), followed by Ichneumonidae, Chrysididae, Bombyliidae and Meloidae (all with three species). Of the breeding cells parasitised, 77.16% ( $n = 419$ ) were in wasp nests and 22.84% ( $n = 124$ ) were in bee nests.

#### Effects of different types of reforestation on bee and wasp functional diversity

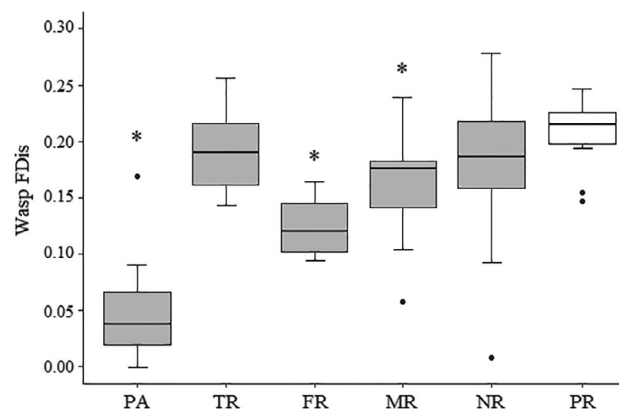
Regardless of the reforestation process used, we found that all reforested sites had higher functional diversity of bees compared to severely impacted environments such as pasture. Nonetheless, several bee traits were different in treatments with active planting of species (TR, FR, and MR). In general, bee species found in TR, FR and MR were specialised in using resins for nest construction and in transporting the pollen using leg and abdomen scopae. They also presented smaller posterior tibia. In addition, FR bees presented lower tongue length (Table 1). On the other hand, in NR, only the structure used to transport pollen varied in relation to primary forest. The species of this treatment were more specialised in transporting the pollen in the abdomen scopae. The different reforestation processes did not differ in their FRic and FDis for this group (Table 1).

In wasps, the treatments PA, TR, MR, and NR presented a community characterised by reduced wing length, smaller body size and lower mandibular length. PA and TR also presented wasps with smaller posterior tibia. The reforestations that had active process of planting of species showed a lower proportion of cockroach hunting species and a higher proportion of spider hunting and caterpillar-hunting species. The secondary regeneration treatments not only presented a greater proportion of spider and caterpillar-hunting species but also of cockroach-hunting species (Table 1). In relation to the indices of functional diversity of the community, pasture, fig, and mixed reforestation supported lower FDis (Table 1; Fig. 2). We did not find differences for the other indices evaluated (Table 1).

#### Parasitism and network structure in different types of reforestation

We found that the parasite richness and the percentage of parasitism varied among the different types of reforestation. Teak reforestation was the treatment with a greater number of parasite species and a higher percentage of parasitised cells (Table 2; Fig. 3a, b, respectively). Although we did not identify differences in the percentage of parasitism of the cells constructed in the pasture area, this treatment showed lower richness of parasite species (Fig. 3a; Table 2).

We did not find differences between the treatments in relation to the composition of the parasite species associated with the nests of solitary bees and wasps (PERMANOVA:  $R^2 = 0.12$ ,  $P = 0.06$ ; PERMDISP:  $F = 0.75$ ,  $P = 0.58$ ). However, we found



**Figure 2.** Variation in Wasp Functional dispersion among different types of reforestation in southeast of the Amazon rainforest. Treatments: pasture (PA), teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), natural regeneration (NR) and primary forest (PF). Asterisks (\*) on the boxes mean significant differences ( $P \leq 0.05$ ) in relation to the primary forest (our control).

differences in the identity of the interactions established between parasites vs. hosts (PERMANOVA:  $R^2 = 0.12$ ,  $P = 0.002$ ; PERMDISP:  $F = 3.340$ ,  $P = 0.005$ ). The heterogeneity in the dispersion within the treatments occurred due to the high variability of the pasture samples (Supporting Information Fig. S.3). When we ran PERMDISP without pasture, we did not find significant differences ( $F = 2.481$ ,  $P = 0.06$ ). Through pairwise comparison, we have identified that even the composition of the teak reforestation and pasture parasites were not different from those found in primary forest. The identity of the interactions that these species established with their hosts differed in these environments in relation to those found in primary forest (Table 2; Fig. 4a,b).

Regarding the structure of interaction networks, we found that the observed values for the indices were significantly different from the random values in more than 50% of the networks, with the exception of connectance and diversity of interactions in MR and Niche Overlap in PF and NR. In these cases, the differences in observed and randomised values ranged from 25% to 37% of the networks (Supplementary Table S7 and S8). Moreover, we found that fig reforestation and natural regeneration present higher specialisation values ( $H_2'$ ) in their parasite and host interactions than those recorded in primary forests. We also identified greater diversity of interactions in teak reforestation and higher nestedness in fig reforestation (Table 2; Fig. 5a–c, respectively). For the other network descriptors, we did not identify any significant variation.

#### Analysis of spatial autocorrelation

We found no significant spatial autocorrelation of model residuals in the analysis of any of the response variables of bee and wasp functional diversity (Supplementary Figs. S4 and S5, respectively) or network descriptors (Supplementary Fig. S6).

**Table 2.** Summary of general linear model outputs analysing the effect of different types of reforestations in Southeast of the Amazon Forest (reference level: Primary forest) on recovery of (a) parasite richness; (b) parasitism percentage; (c) H2'; (d) Connectance; (e) diversity of interactions; (f) niche overlap; (g) compartments; (h) Nestedness and (i) composition of parasite–host interaction.

Variable	Pasture		Teak reforestation		Ficus reforestation		Mixed reforestation		Secondary regeneration	
	Estimate ± SE	t-value	Estimate ± SE	t-value	Estimate ± SE	t-value	Estimate ± SE	t-value	Estimate ± SE	t-value
(a) Parasite richness	<b>-1.966 ± 0.50</b>	<b>-1.966</b>	<b>0.539 ± 0.21</b>	<b>2.531</b>	0.048 ± 0.24	0.202	0.202 ± 0.23	0.877	-0.094 ± 0.25	-0.374
(b) Parasitism (%)	0.254 ± 0.55	0.458	<b>0.385 ± 0.18</b>	<b>2.122</b>	0.194 ± 0.22	0.859	0.312 ± 0.20	1.504	0.118 ± 0.22	0.536
(c) H2'	-	-	0.040 ± 0.12	0.323	<b>0.370 ± 0.15</b>	<b>2.464</b>	0.154 ± 0.13	1.182	<b>0.328 ± 0.14</b>	<b>2.31</b>
(d) Connectance	-	-	-0.053 ± 0.05	-0.965	-0.032 ± 0.60	-0.529	0.011 ± 0.05	0.201	0.043 ± 0.60	0.704
(e) Diversity of interactions	-	-	<b>0.584 ± 0.18</b>	<b>2.084</b>	-0.122 ± 0.20	-0.598	0.1911 ± 0.19	0.976	0.052 ± 0.20	0.256
(f) Niche overlap	-	-	0.583 ± 0.47	1.229	-0.209 ± 0.60	-0.347	0.678 ± 0.49	1.375	0.747 ± 0.50	1.48
(g) Compartments	-	-	0.249 ± 0.27	0.897	0.364 ± 0.29	1.237	0.030 ± 0.31	0.099	-0.018 ± 0.32	-0.055
(h) Nestedness	-	-	-0.862 ± 4.51	-0.191	<b>10.785 ± 4.99</b>	<b>2.161</b>	2.414 ± 4.79	0.503	-3.506 ± 4.99	-0.703
(i) Pairwise Permanova		$r^2$		$r^2$		$r^2$		$r^2$		$r^2$
		<b>0.08</b>		<b>0.06</b>		0.04		0.05		0.08

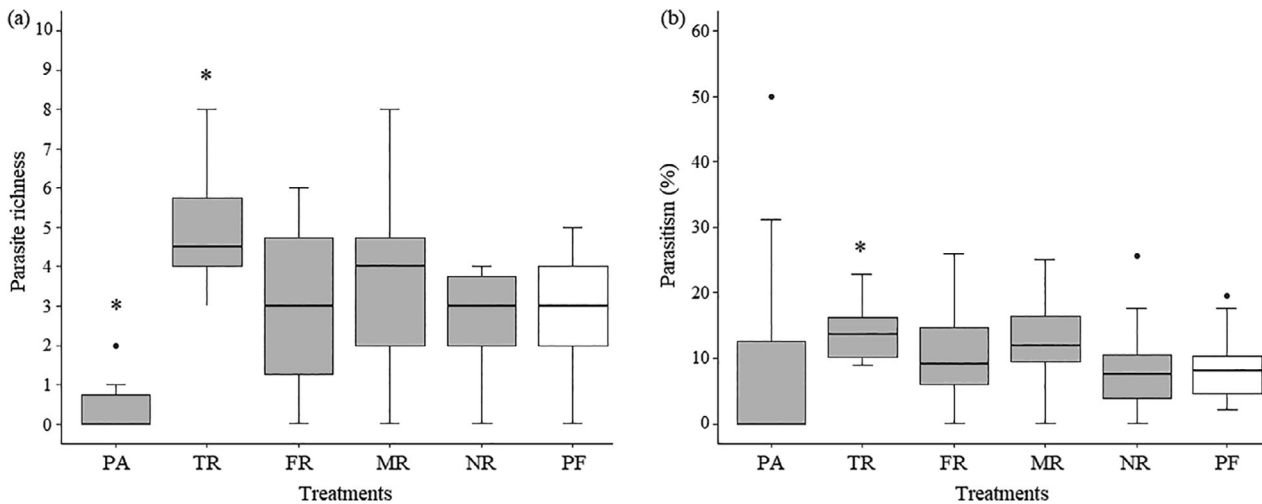
Significant values ( $P \leq 0.05$ ) are marked in bold.

## Discussion

The loss of biodiversity due to land-use has been the main factor disturbing ecosystem functionality (Laliberte & Legendre, 2010; 2010; Rader *et al.*, 2014). In fact, studies have shown that changes in vegetation cover influence the distribution pattern of communities and exert selective pressure on their individuals, such as bees and wasps (Tylianakis *et al.*, 2007; Flores *et al.*, 2018, 2019; Araújo *et al.*, 2018a,b, 2020). The conditions imposed by planting reforestation resulted in a cavity-nesting bee and wasp community often composed by functional traits that are different from those found in primary forests, which could modify the natural patterns of provided services by these organisms. Variations in the functional traits of other groups of Hymenoptera have also been reported in reforestation plantations (Santoandré *et al.*, 2019). Beyond the simplified structure of reforestation (teak and fig plantings), the features of planted species (species mix planting) exerted significant pressures that modified functional traits for both bee and wasp groups in primary forests. For example, bee species specialised in resin collection may be more selective in choosing the visited plants (Pinto *et al.*, 2019) and individuals with less ability to handle pollen grains in the field, such as those with the smaller posterior tibia, may spend more time and energy to meet the nutritional requirements of their offspring (Eggenberger *et al.*, 2019). These factors can culminate in a lower pollination efficiency community. Also, in addition to the lower capacity of foraging and predation, which results in less efficiency in capturing prey (Greenleaf *et al.*, 2007; Goulson *et al.*, 2010), wasps with different food habits possibly interfere in the group's ability to provide biological control services. Highly modified environments typically undergo changes in the mechanisms that shape the structure of biological communities (Temperton & Zirr, 2004). In modified environments, such as those with active planting of species in the present study, niche restriction due to modification of the natural structure may displace the functional characteristics of the established species (Mayfield *et al.*, 2010). Thus, even though the establishment of a vegetation cover has contributed to the increase of functional diversity of communities such as wasps, their assemblages were composed by species whose functional traits are different from those expected in primary forests. Therefore, even the establishment of vegetation cover has contributed to the increase in wasps' functional diversity, both bee and wasp groups were composed of species whose functional traits are different from those expected in primary forests.

Although the reforestation types have changed the patterns of functional traits of both groups, cavity-nesting bees and wasps responded differently in regards to recovering the functional diversity of their communities. In our study, the no difference in FRic and FDis of bees suggests that either species of primary forest and species of reforestations have high functional redundancy in relation to each other, or that substitution for functionally distinct species may have contributed to similar functional diversity values between these environments (Rosenfeld, 2002; Magnago *et al.*, 2014). Based on the differences in the traits of bee communities established in the planting reforestations and the primary forest community, our results corroborate with the latter. This implies that although the forest structure applied in





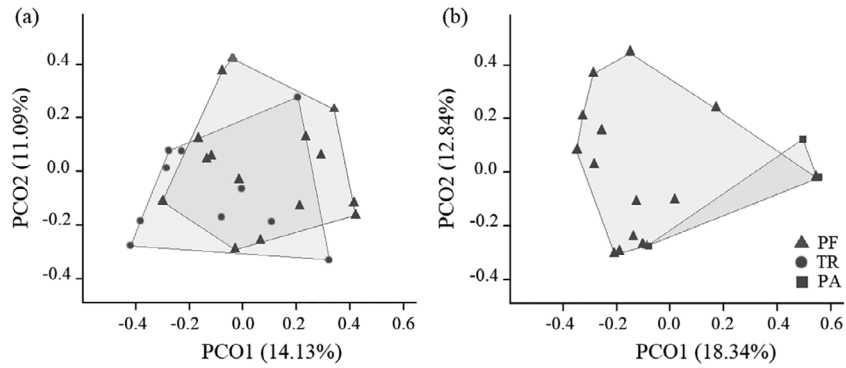
**Figure 3.** Variation in (a) parasite richness and (b) parasitism percentage among different types of reforestation in southeast of the Amazon rainforest. Treatments: pasture (PA), teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), natural regeneration (NR) and primary forest (PF). Asterisks (\*) on the boxes mean significant differences ( $P \leq 0.05$ ) in relation to the primary forest (our control)

the impacted areas contributes to improve their functional diversity, the cavity-nesting bee communities present in these reforestations have different environmental functionalities in relation to primary forest species. Forest structure by itself does not appear to be a good predictor of functional diversity in the bee community (Brito *et al.*, 2018). These insects appear to be strongly associated with local abiotic factors, such as variations in temperature, humidity, and precipitation (Andrade-Silva *et al.*, 2014; Giangarelli *et al.*, 2014), and other habitat characteristics, such as canopy and understory density and exposure to sunlight (Taki *et al.*, 2008). These parameters are already known to result in biological losses, especially of insects (Hanski & Cambefort, 1991). Thus, our results demonstrate that, for cavity-nesting bees, more variables must be taken into consideration to evaluate the effectiveness of the recovery of functional diversity values.

Wasp communities presented lower functional FDis in environments like fig and mixed reforestations. Previous studies have shown that these reforestations are more subject to greater exposure to light and heat due to their open canopy (Falcão *et al.*, 2015). High temperatures and light intensity are factors that can act as environmental filters (Holl, 1999). Thus, the structure of tree species involved in plantations are of great importance in restoring cavity-nesting wasps with traits found in undisturbed environments. This helps to explain the high modification of the features of the wasp community in teak, even with this treatment presenting FDis similar to natural conditions. Unlike *Ficus*, pollinated exclusively by wasps Agaonidae, a parasitic group (Schiffler, 2002; Kjellberg *et al.*, 2005), *Tectona grandis* flowers can be visited by a wide variety of insects, including Sphecidae, Vespidae and Megachilidae (Tangmitcharoen *et al.*, 2006, 2009), families reported in our study. However, its flowers are only available for specific periods, with subsequent loss of leaves (given the deciduous characteristic of teak) and strong structural changes in this treatment over time (Falcão *et al.*, 2015; Araújo *et al.*, 2019). Certainly, this structural

variation can direct the reestablishment of resources, e.g., prey species, that support these conditions. Regardless of the type of reforestation, all of them, to some degree, had wasp communities functionally distinct from natural conditions, but no differences were reported for indexes FEve and FRic. This may suggest that the niche space is being similarly occupied by wasps in the different reforestation types (Audino *et al.*, 2014; Correa *et al.*, 2019).

Changes in the functional structure found in the host communities present in the different treatments have demanded specialised traits for the establishment of host–parasite interactions such as, for example, the types of food resource offered to their offspring and body size. Consequently, we expected to find that the variation of these traits could exert changes in the interactions of parasite species with their hosts. However, our expectations were not corroborated. Studies of the relationships between functional diversity and ecological interaction networks are rare (Osorio-Canadas *et al.*, 2018), and most network studies are focused on taxonomic changes in communities (Kaarinen & Roslin, 2011; Staab *et al.*, 2016). Although changes in the community composition may change the composition of interactions between species (Albrecht *et al.*, 2007; Tylianakis *et al.*, 2007), the extent of these changes acting over networks of interactions is still uncertain (Kaarinen & Roslin, 2011; Staab *et al.*, 2016; Dáttilo & Vasconcelos, 2019). An explanation for the low changes in the organisation of species interactions between most of the treatments analysed could be the high generality of the parasite communities in the choosing of their hosts. This can be supported by the high occurrence of Chrysididae and Ichneumonidae emerged in collected bee and wasp nests. In addition to parasitising a wide variety of hosts, such as caterpillar/or pupae of butterflies, solitary bees and wasps (Townes, 1958; Kimsey & Bohart, 1991), Chrysididae larvae can also develop at the expense of food (moth and beetle larvae, aphids, spiders, insects and thrips) stored in wasp nests of the families Vespidae, Sphecidae and Crabronidae (Martynova &

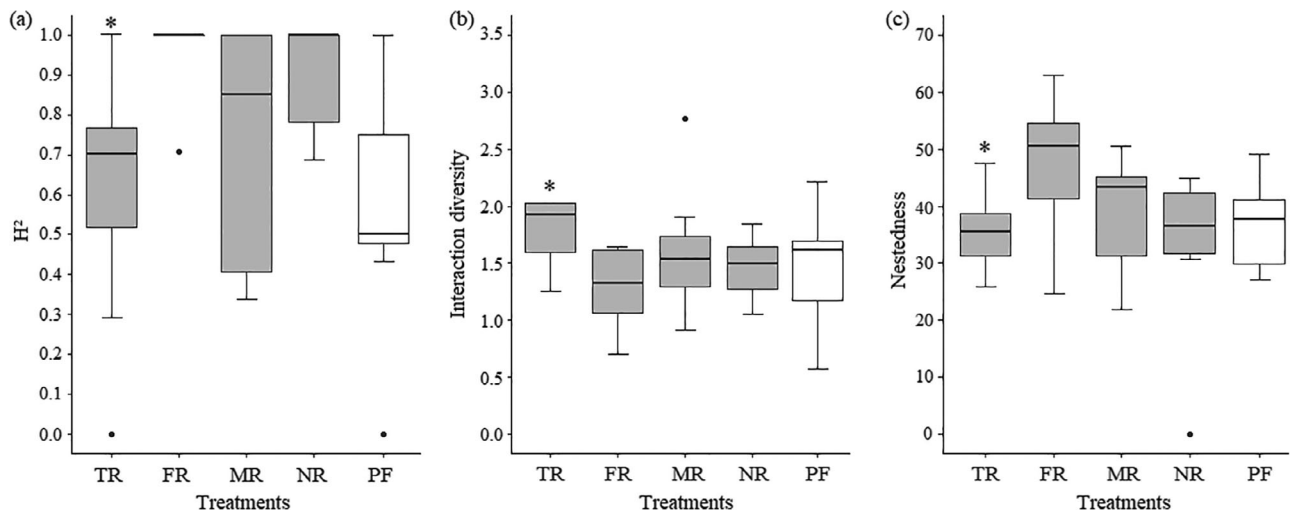


**Figure 4.** PCoA samples of parasite–host composition according to treatments (a) teak reforestation and (b) pasture against primary forest (control), based on Bray–Curtis dissimilarity index.

Fateryga, 2015). Therefore, specific functional traits do not seem to be the main modulators of the interactions for most of the parasites found in the present study.

Some studies relate the increase in host–parasite interactions with the increase in productivity and/or structure of environments (Albrecht *et al.*, 2007; Tylianakis *et al.*, 2010; Swanson *et al.*, 2011). In the temperate region, a high occurrence of bees and wasps with solitary and parasitic behaviour was reported in early successional stages forests (Taki *et al.*, 2013). Although our study was carried out in the tropical region, this helps to explain the high parasite richness and parasitism rate in teak. Even being a monoculture, reforestations with *Tectona grandis* present a temporal explosion of resources which promote a high variation in the occurrence of cavity-nesting bees and wasps (Araújo *et al.*, 2020). Since host availability has been considered as a predictor of increased parasitism rate (Fox, 2004; Gamfeldt *et al.*, 2005), the high occurrence of bees and wasps in specific periods may have shaped the parasite’s success in teak. The

greater richness of parasites in this treatment may explain its greater diversity of interaction with bees and wasps, since a greater number of parasites allows the establishment of new connections (Lewis, 2014; Falcão *et al.*, 2015). The high diversity of interactions in teak reflects an important result, where the functional role of host species seems to be quite redundant for their parasites. In environments with a higher occurrence of parasites, such as teak, the low specificity in the choice of hosts may be a characteristic that favoured their reestablishment (Morris *et al.*, 2004). Another hypothesis that could be considered is the abundance of community components. Rocha-Filho *et al.* (2019) observed that woody savannah areas, which had more abundant trap-nesting bee and wasp species, presented lower degree of host–parasite specialisation than seasonal semi-deciduous forest areas, which had few abundant trap-nesting wasp species. In woody savannah areas, the most abundant parasite attacked more host species in comparison to seasonal semi-deciduous forest areas. In fact, the number of generalist species



**Figure 5.** Variation in (a)  $H^2$ , (b) Diversity of interactions and (c) Nestedness among different types of reforestation in southeast of the Amazon rain-forest. Treatments: teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), natural regeneration (NR) and primary forest (PF). Asterisks (\*) on the boxes mean significant differences ( $P \leq 0.05$ ) in relation to the primary forest (our control).

tends to increase in more simplified environments (Dáttilo *et al.*, 2011; Falcão *et al.*, 2015), while more specialised species tend to be more prevalent in habitats which are more structurally diverse, due to increased habitat availability (Tylianakis *et al.*, 2006; Araújo *et al.*, 2018a,b). This may explain the greater specialisation of parasites in secondary regeneration. Although the parasite communities are not different among the environments, the greater structural complexity of these environments apparently contributes to the establishment of more specialised parasitic behaviour, probably due to the variety of resources (hosts) available. In environments with favourable conditions, it is expected that the species will show preferences in choosing their hosts (Tylianakis *et al.*, 2007; Lewis, 2014). However, fig reforestation also showed greater specialisation in the established interactions. Disturbed/modified environments can induce shifts in species composition and also ecological mismatches (Esquivel-Muelbert *et al.*, 2019; Wood *et al.*, 2019), which may compromise the natural ecosystem functionality (Fei *et al.*, 2017; Wood *et al.*, 2019). The lower richness of hosts in fig reforestation possibly directed the parasites to species that could provide food for the development of their offspring, such as pollen and prey. In this case, it would be “apparent specialisation” (Tylianakis *et al.*, 2010; Souza *et al.*, 2018) since the sampled parasite community showed great flexibility regarding the use of available resources, based on the different host nests that these insects were able to parasitize in this study. The “apparent specialisation” can be supported by the higher nestedness values found in fig reforestation. The high values of this index are linked to treatments that have greater redundancy of interactions, i.e. species capable of performing the same functions (Tylianakis *et al.*, 2010). Thus, parasites related to a specific resource (e.g., pollen), even being able to colonise nests of several species, can narrow their relationships in environments when its occurrence is low. Consequently, these species could be identified as specialists in interaction networks given the presence of few interaction options.

## Conclusion

The structure of reforestation affected the functional diversity of cavity-nesting bees and wasps and consequently their ability to provide their related services to the level of natural environments (primary forest). But regardless of the type of reforestation used, all of them contributed to increase functional diversity of cavity-nesting bees and wasps in relation to the impacted areas. Here, we found that functional diversity does not seem to shape the interactions between cavity-nesting bees and wasps and the parasites associated with their nests, since the most common parasites have a wide range of hosts (Chrysididae and Ichneumonidae). However, in simplified reforestations, such as teak, we observed that the frequency of encounter between parasite and host seems to be favoured by the specific concentration of treatment resources over time, promoting the high occurrence of bees and wasps in a short period of time. In environments not severely impacted and near to natural forests, as in our study, natural regeneration is certainly a favourable strategy to increase the similarity of the functional traits of the restored bee and wasp

communities to the natural habitats, as well as their levels of parasite–host interaction. In this case, natural forest can act as a source of propagules, favouring the establishment of conditions close to natural ones. In degraded environments surrounded by simplified landscapes, such as monocultures, mixed planting of natural species may be the most appropriate alternative, but planted species should be evaluated. In our study, we approached the traits as a filter capable of limiting the occurrence of the species in the environment. Thus, the main focus was to investigate the role of different types of reforestation in the reorganisation of communities restored under new conditions. But there is still a lot to investigate about the establishment of functional diversity in reforested environments. A suggestion for new studies to address phylogenetic diversity together with functional diversity to investigate the relationship between species that make up the new communities.

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## Authors contributions

G.J.A. and T.J.I. conceptualization, G.J.A. conducted the experiment, G.J.A. Data curation, G.J.A. and W.D. formal analyses, T.J.I. funding acquisition, G.J.A. and T.J.I. Investigation, T.J.I. supervision, G.J.A. validation, G.J.A. Writing (original draft preparation), G.J.A., D.S.T., W.D. and T.J.I. Writing (review and editing).

## Data availability statement

Data available on request due to privacy/ethical restrictions

## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1** Traits of solitary bees and wasps used in the functional diversity analysis for species that nested in trap nests in different types of reforestation in southeastern Amazonia between August 2016 and July 2017

**Table S2** Functional traits for each bee species based on measurements, laboratory observations and literature source.

**Table S3** Functional traits for each wasp species based on measurements, laboratory observations and literature source.

**Table S4** Comparison of the likelihood of model fit for linear and null models of the bee response variables against the effect of different types of reforestations in Southeast of the Amazon Forest. Separate models were run for FDis, FRic, wing length, body length, posterior tibia length, tongue length, pollen-carrying structures and nesting materials. K: the number of estimated parameters for each model, AICc: Akaike Information Criterion corrected;  $\Delta$ AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to  $\Delta$ AICc.

**Table S5** Comparison of the likelihood of model fit for linear and null models of the wasp response variables against the effect of different types of reforestations in Southeast of the Amazon Forest. Separate models were run for FDis, FRic, FEve, wing length, body length, posterior tibia length, mandibular length, larval diet and nesting materials. K: the number of estimated parameters for each model, AICc: Akaike Information Criterion corrected;  $\Delta$ AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to  $\Delta$ AICc.

**Table S6** Abundance of hosts (bees and wasp) and parasites species identified from trap nests at different types of reforestation in southeastern Amazonia between August 2016 and July 2017. PA = Pasture; TR = *Teak* reforestation; FR = *Ficus* reforestation; MR = Mixed reforestation; NR = Natural regeneration and PF = Primary forest.

**Table S7** Percentage of matrices analysed with observed index values significantly different ( $\leq 0.05$ ) from randomised null models. The significance of observed results was tested by constructing 1000 randomised networks with identical margin totals as the empirical networks and comparing the observed and random values using the null model 'r2d'.

**Figure S1** An illustrative representation of the six treatment types sampled at São Nicolau farm, municipally of Cotriguaçu, Mato Grosso state – Brazil: (a) pasture, (b) teak reforestation, (c) ficus reforestation, (d) mixed reforestation, (e) natural regeneration and (f) primary forest.

**Figure S2** Trap-nest sample used to collect solitary bees and wasps in six different types of habitats at the São Nicolau farm, municipality of Cotriguaçu, state of Mato Grosso, Brazil.

**Figure S3** Graphic representation of test for homogeneity of multivariate dispersions (*PERMDISP*) for interaction composition between parasite–host among treatments.

**Figure S4** Spatial correlograms showing the degree of spatial autocorrelation (Moran's I) among sites for each of the raw response measures for bee traits (a, c, e, g, i, k, m, o, q, s), and the corresponding residuals of the GLM model appropriate to each response (b, d, f, h, j, l, n, p, r, t).

**Figure S5** Spatial correlograms showing the degree of spatial autocorrelation (Moran's I) among sites for each of the raw response measures for wasp variates (a, c, e, g, i, k, m), and the corresponding residuals of the GLM model appropriate to each response (b, d, f, h, j, l, n).

**Figure S6** Spatial correlograms showing the degree of spatial autocorrelation (Moran's I) among sites for each of the raw response measures for indexes of the host–parasite networks

(a, c, e, g, i), and the corresponding residuals of the GLM model appropriate to each response (b, d, f, h, j).

## References

- Albrecht, M., Duelli, P., Müller, C., Kleijn, D. & Schmid, B. (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, **44**, 813–822.
- Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.
- Andrade-Silva, A.C.R., Nemésio, A., Freitas, F. & Nascimento, F.S. (2014) Spatial-temporal variation in orchid bee communities (Hymenoptera: Apidae) in remnants of arboreal caatinga in the Chapada Diamantina Region, State of Bahia, Brazil. *Neotropical Entomology*, **41**(4), 296–305. <https://doi.org/10.1007/s13744-012-0053-9>.
- Araújo, G.J., Fagundes, R. & Antonini, Y. (2018a) Trap-nesting hymenoptera and their network with parasites in recovered Riparian forests Brazil. *Neotropical Entomology*, **47**(1), 26–36. <https://doi.org/10.1007/s13744-017-0504-4>.
- Araújo, G.J., França, G., Messias, M.C.T. & Antonini, Y. (2018b) Restore it, and they will come: trap-nesting bee and wasp communities (Hymenoptera: Aculeata) are recovered by restoration of riparian forests. *Journal of Insect Conservation*, **22**(2), 245–256. <https://doi.org/10.1007/s10841-018-0058-8>.
- Araújo, G.J., Storck-Tonon, D. & Izzo, T.J. (2019) Is planting trees enough? The effect of different types of reforestation on the offspring of *Trypoxylon (Trypargilum) lactitarse* (Hymenoptera: Crabronidae) in the Southern Amazon. *Neotropical Entomology*, **48**(4), 572–582. <https://doi.org/10.1007/s13744-019-00682-9>.
- Araújo, G.J., Stork-Tonon, D. & Izzo, T.J. (2020) Temporal stability of cavity-nesting bee and wasp communities in different types of reforestation in southeastern Amazonia. *Restoration Ecology*, **28**(6), 1528–1540. <https://doi.org/10.1111/rec.13250>.
- Aronson, J., Floret, C., Floc'h, E., Ovalle, C. & Pontanier, R. (2006) Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. II. Case studies in Southern Tunisia, Central Chile and Northern Cameroon. *Restoration Ecology*, **1**(3), 168–187.
- Audino, L.D., Louzada, J. & Comita, L. (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? *Biological Conservation*, **169**, 248–257. <https://doi.org/10.1016/j.biocon.2013.11.023>.
- Bascompte, J., Melia, C.J. & Sala, E. (2005) Interaction strength combinations and the overfishing. *PNAS*, **102**, 5443–5447.
- Beiroz, W., Barlow, J., Slade, E.M., Borges, C., Louzada, J. & Sayer, E.J. (2019) Forest ecology and management biodiversity in tropical plantations is influenced by surrounding native vegetation but not yield: a case study with dung beetles in Amazonia. *Forest Ecology and Management*, **444**, 107–114. <https://doi.org/10.1016/j.foreco.2019.04.036>.
- Beiroz, W., Sayer, E., Slade, E.M., Audino, L., Fagundes, R., Louzada, J. & Barlow, J. (2018) Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. *Ecological Indicators*, **95**, 518–526. <https://doi.org/10.1016/j.ecolind.2018.07.062>.
- Bjornstad, O. N. & Cai, J. (2018) Spatial nonparametric covariance functions. R package version 1.2.3.
- Blanke, A. (2019) The early evolution of biting–chewing performance in hexapoda. *Insect Mouthparts*. Charm: Springer.
- Blüthgen, N., Menzel, F. & Blüthgen, N. (2006) Measuring specialization in species interaction networks. *BMC Ecology*, **6**(9), 1472–6785. <https://doi.org/10.1186/1472-6785-6-9>.

- Bramon Mora, B., Shin, E., CaraDonna, P.J. & Stouffer, D.B. (2020) Untangling the seasonal dynamics of plant-pollinator communities. *Nature Communications*, **11**(1), 4086. <https://doi.org/10.1038/s41467-020-17894-y>.
- Brito, T.F., Contrera, F.A.L., Phifer, C.C., Knowlton, J.L., Brasil, L.S., Maués, M.M. & Silva, D.P. (2018) Effects of habitat type change on taxonomic and functional composition of orchid bees (Apidae: Euglossini) in the Brazilian Amazon. *Journal of Insect Conservation*, **22**, 451–463. <https://doi.org/10.1007/s10841-018-0073-9>.
- Burnham, K. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*. Heidelberg: Springer.
- Campião, K.M. & Dáttilo, W. (2020) Biological drivers of individual-based anuran-parasite networks under contrasting environmental conditions. *Journal of Helminthology*, **94**, E167. <https://doi.org/10.1017/S0022149X20000504>.
- Chazdon, R.L. & Guariguata, M.R. (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica*, **48**(6), 716–730.
- Cisneros, L.M., Fagan, M.E. & Willig, M.R. (2015) Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, **21**, 523–533. <https://doi.org/10.1111/ddi.12277>.
- Clarke, K. & Warwick, R. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd Edn. Primer-E, Plymouth.
- Cornell, H. (2011) Niche overlap. I. *Encyclopedia of Theoretical Ecology* (s. 848p). (ed. by A. Hastings and L.J. Gross). Berkeley: University of California Press.
- Correa, C.M.A., Braga, R.F., Puker, A. & Korasaki, V. (2019) Patterns of taxonomic and functional diversity of dung beetles in a human-modified variegated landscape in Brazilian Cerrado. *Journal of Insect Conservation*, **23**(1), 89–99. <https://doi.org/10.1007/s10841-018-00118-6>.
- Corro, E.J., Ahuatzin, D.A., Jaimés, A.A., Favila, M.E., Ribeiro, M.C., López-Acosta, J.C. & Dáttilo, W. (2019) Forest cover and landscape heterogeneity shape ant-plant co-occurrence networks in human-dominated tropical rainforests. *Landscape Ecology*, **34**(1), 93–104. <https://doi.org/10.1007/s10980-018-0747-4>.
- Corso, G., Araújo, A.I.L. & Almeida, A.M. (2011) Connectivity and nestedness in bipartite networks from community ecology. *Journal of Physics: Conference Series*, **285**(1), 1–6. <https://doi.org/10.1088/1742-6596/285/1/012009>.
- Costanza, R., Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S. & Turner, R.K. (2014) Changes in the global value of ecosystem services. *Global Environmental Change*, **26**(1), 152–158. <https://doi.org/10.1016/j.gloenvcha.2014.04.002>.
- Coudrain, V., Schüepp, C., Herzog, F., Albrecht, M. & Entling, M.H. (2014) Habitat amount modulates the effect of patch isolation on host-parasitoid interactions. *Frontiers in Environmental Science*, **2**, 1–8. <https://doi.org/10.3389/fenvs.2014.00027>.
- Dáttilo, W. & Rico-Gray, V. (2018) *Ecological Networks in the Tropics*. Charm: Springer International Publishing. <https://doi.org/10.1007/978-3-319-68228-0>.
- Dáttilo, W., Sibinel, N., Falcão, J.C.F. & Nunes, R.V. (2011) Ant fauna in an urban remnant of Atlantic Forest in the municipality of Marília, State of São Paulo, Brazil Article. *Bioscience Journal*, **27**(3), 494–504.
- Dáttilo, W. & Vasconcelos, H.L. (2019) Macroecological patterns and correlates of ant-tree interaction networks in neotropical savannas. *Global Ecology and Biogeography*, **28**(9), 1283–1294. <https://doi.org/10.1111/geb.12932>.
- Dormann, C.F., Gruber, B. & Fründ, J. (2008) Introducing the bipartite package: analyzing ecological networks. *R News*, **8**(1), 8–11. <https://doi.org/10.1159/000265935>.
- Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S. & Moretti, M. (2019) Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *Journal of Animal Ecology*, **88**(10), 1522–1533. <https://doi.org/10.1111/1365-2656.13051>.
- Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J.W., Feldpausch, T.R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B.S., Marimon-Junior, B.H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J. & Phillips, O.L. (2019) Compositional response of Amazon forests to climate change. *Global Change Biology*, **25**(1), 39–56. <https://doi.org/10.1111/gcb.14413>.
- Falcão, J.C.F., Dáttilo, W. & Izzo, T.J. (2015) Forest ecology and management efficiency of different planted forests in recovering biodiversity and ecological interactions in Brazilian Amazon. *Forest Ecology and Management Journal*, **339**, 105–111. <https://doi.org/10.1016/j.foreco.2014.12.007>.
- Fei, S., Desprez, J.M., Potter, K.M., Jo, I., Knott, J.A. & Oswalt, C.M. (2017) Divergence of species responses to climate change. *Science Advances*, **3**(5), e1603055. <https://doi.org/10.1126/sciadv.1603055>.
- Flores, L.M.A., Zanette, L.R.S. & Araujo, F.S. (2018) Effects of habitat simplification on assemblages of cavity nesting bees and wasps in a semiarid neotropical conservation area. *Biodiversity and Conservation*, **27**, 311–328. <https://doi.org/10.1007/s10531-017-1436-3>.
- Flores, L.M.A., Zanette, L.R.S., Boscolo, D. & Araújo, F.S. (2019) Landscape structure effects on bee and wasp assemblages in a semiarid buffer zone. *Landscape Online*, **76**, 1–17. <https://doi.org/10.3097/LO.201976>.
- Fox, J.W. (2004) Modelling the joint effects of predator and prey diversity on total prey biomass. *Journal of Animal Ecology*, **73**, 88–96.
- Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2005) Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecology Letters*, **8**, 696–703. <https://doi.org/10.1111/j.1461-0248.2005.00765.x>.
- Gathmann, A. & Tsharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764.
- Giangarelli, D.C., Aguiar, W.M. & Sofia, S.H. (2014) Orchid bee (Hymenoptera: Apidae: Euglossini) assemblages from three different threatened phytophysiognomies of the subtropical Brazilian Atlantic Forest. *Apidologie*, **46**, 71–83. <https://doi.org/10.1007/s13592-014-0303-4>.
- Giannini, T.C., Costa, W.F., Borges, R.C., Miranda, L., Costa, C.P.W., Saraiva, A.M. & Imperatriz Fonseca, V.L. (2020) Climate change in the Eastern Amazon: crop-pollinator and occurrence-restricted bees are potentially more affected. *Regional Environmental Change*, **20**(9), 1–12. <https://doi.org/10.1007/s10113-020-01611-y>.
- Goulson, D. (2010) *Bumblebees, Behavior and Ecology*. Oxônia: Oxford University Press.
- Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L. & Darvill, B. (2010) Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology*, **47**(6), 1207–1215. <https://doi.org/10.1111/j.1365-2664.2010.01872.x>.
- Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**(3), 589–596. <https://doi.org/10.1007/s00442-007-0752-9>.
- Hanski, I. & Cambefort, Y. (1991) *Dung Beetle Ecology*. Princeton: Princeton University Press.
- Harder, L.D. (1985) Morphology as a predictor of flower choice by bumble bees. *Ecology*, **66**(1), 198–210.
- Harvey, E., Gounand, I., Ward, C. & Altermatt, F. (2017) Bridging ecology and conservation: from ecological networks to ecosystem

- function. *Journal of Applied Ecology*, **54**(2), 371–379. <https://doi.org/10.1111/1365-2664.12769>.
- Holl, K.D. & Aide, T.M. (2011) When and where to actively restore ecosystems? *Forest Ecology and Management*, **261**(10), 1558–1563. <https://doi.org/10.1016/j.foreco.2010.07.004>.
- Holl, K.D. (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica*, **31**(2), 229–242.
- Hua, F., Wang, X., Zheng, X., Fisher, B., Wang, L., Zhu, J., Tang, Y., Yu, D.W. & Wilcove, D.S. (2016) Opportunities for biodiversity gains under the world's largest reforestation programme. *Nature Communications*, **7**(1), 12717. <https://doi.org/10.1038/ncomms12717>.
- Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–162.
- Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist*, **129**(5), 657–677.
- Kaartinen, R. & Roslin, T. (2011) Shrinking by numbers: landscape context affects the species composition but not the quantitative structure of local food webs. *Journal of Animal Ecology*, **80**(3), 622–631. <https://doi.org/10.1111/j.1365-2656.2011.01811.x>.
- Kimsey, L. & Bohart, R.M. (1991) *The Chrysidid Wasps of the World*. Oxônia: Oxford University Press.
- Kissling, W.D., Ahumada, J.A., Bowser, A., Fernandez, M., Fernández, N., García, E.A., Guralnick, R.P., Isaac, N.J.B., Kelling, S., Los, W., McAra, L., Mihoub, J.B., Obst, M., Santamaria, M., Skidmore, A.K., Williams, K.J., Agosti, D., Amariles, D., Arvanitidis, C., Bastin, L., de Leo, F., Egloff, W., Elith, J., Hobern, D., Martin, D., Pereira, H.M., Pesole, G., Peterseil, J., Saarenmaa, H., Schigel, D., Schmeller, D.S., Segata, N., Turak, E., Uhlir, P.F., Wee, B. & Hardisty, A.R. (2018) Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. *Biological Reviews*, **93**(1), 600–625. <https://doi.org/10.1111/brv.12359>.
- Kjellberg, F., Jusselin, E., Hossaert-Mckey, M. & Rasplus, J. (2005) Biology, ecology and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae). I. *Biology, Ecology and Evolution of Gall Inducing Arthropods* (s. 539–572). (ed. by A. Raman, C.W. Schaefer and T.M. Withers). Plymouth: Science Publishers Inc.
- Klein, A.M., Tscharntke, T. & Steffan-Dewenter, I. (2004) Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *Journal of Animal Ecology*, **73**(3), 517–525.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Krombein, K.V. (1967) *Trap-Nesting Wasps and Bees: Life Histories, Nests and Associates*. Washington: Smithsonian Press.
- Laliberte, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits A distance-based framework for measuring from multiple traits functional diversity. *Ecology*, **91**(1), 299–305.
- Laliberté, E., Legendre, P. & Shipley, B. (2014) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version, 1–26.
- Lewis, O.T. (2014) Antagonistic interaction networks are structured independently of latitude and host guild. *Ecological Letters*, **27**, 340–349. <https://doi.org/10.1111/ele.12235>.
- Magnago, L.F.S., Edwards, D.P., Edwards, F.A., Martins, V., Laurance, W.F., Magrach, A. & Gerais, M. (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. *Journal of Ecology*, **102**, 475–485. <https://doi.org/10.1111/1365-2745.12206>.
- Martynova, K.V. & Fateryga, A.V. (2015) Chrysidid wasps (Hymenoptera, Chrysididae) parasites of eumenine wasps (Hymenoptera, Vespidae: Eumeninae) in Crimea. *Entomological Review*, **95**(4), 472–485. <https://doi.org/10.1134/S0013873815040090>.
- Mason, N.W.H., Moullot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112–118.
- Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. & Vesik, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431. <https://doi.org/10.1111/j.1466-8238.2010.00532.x>.
- Mazerolle, M.J. & Linden, D. (2019) Model Selection and Multimodel Inference Based on (Q)AIC(c). R Package ‘AICcmodavg’ version 3.2-1
- Messeder, J.V.S., Guerra, T.J., Dáttilo, W. & Silveira, F.A.O. (2020) Searching for keystone plant resources in fruit-frugivore interaction networks across the neotropics. *Biotropica*, **52**, 1–14. <https://doi.org/10.1111/btp.12804>.
- Michener, C.D. (2000) *The Bees of the World*. Baltimore: The Johns Hopkins University Press.
- Morris, R.J., Lewis, O.T. & Godfray, H.C.J. (2004) Experimental evidence for apparent competition in a tropical forest food web. *Nature*, **428**, 310–313.
- Murphy, M.V. (2016) *Interactive Effects of Land-Use Change and Rainfall Decline on Insect Species Networks*. Perth: University of Western Australia.
- O'Neill, K.M. (2001) *Solitary Wasps: Behavior and Natural History*. Ithaca: Comstock Publishing Associates.
- Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Szoecs, E. (2020) Package ‘vegan’. I: CRAN.
- Olito, C. & Fox, J.W. (2015) Species traits and abundances predict metrics of plant-pollinator network structure, but not pairwise interactions. *Oikos*, **124**(4), 428–436. <https://doi.org/10.1111/oik.01439>.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Osorio-Canadas, S., Arnan, X., Bassols, E., Vicens, N. & Bosch, J. (2018) Seasonal dynamics in a cavity-nesting bee and wasp community: shifts in composition, functional diversity and host-parasitoid network structure. *PLoS One*, **13**, 1–18. <https://doi.org/10.1371/journal.pone.0205854>.
- Palma, A.D., Kuhlmann, M., Roberts, S.P.M., Potts, S.G., Hudson, L.N., Lysenko, I., Newbold, T., Purvis, A. & Luca, B. (2015) Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. *Journal of Applied Ecology*, **52**, 1567–1577. <https://doi.org/10.1111/1365-2664.12524>.
- Paolucci, L.N., Schoederer, J.H., Brando, P.M. & Andersen, A.N. (2017) Fire-induced forest transition to derived savannas: cascading effects on ant communities. *Biological Conservation*, **214**, 295–302. <https://doi.org/10.1016/j.biocon.2017.08.020>.
- Patefield, W.M. (1981) Algorithm AS 159: an efficient method of generating random RxC tables with given row and column totals. *Journal of the Royal Statistical Society*, **30**, 91–97.
- Persson, A.S. & Smith, H.G. (2011) Bumblebee colonies produce larger foragers in complex landscapes. *Basic and Applied Ecology*, **12**(8), 695–702. <https://doi.org/10.1016/j.baee.2011.10.002>.

- Pinto, A.R., Silveira, G.C., Gaglianone, M.C. & Freitas, L. (2019) Abrupt decrease in the diversity of Euglossini bees (Hymenoptera: Apidae) in a montane rainforest. *Journal of Apicultural Research*, **58** (5), 682–693. <https://doi.org/10.1080/00218839.2019.1637223>.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**(6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- R Team Core (2018) *R: A Language and Environment for Statistical Computing*. Vienna, Austria. <https://www.R-project.org/>.
- Rader, R., Bartomeus, I., Tylianakis, J.M. & Lalibert, E. (2014) The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity. *Diversity and Distributions*, **20**, 908–917. <https://doi.org/10.1111/ddi.12221>.
- Rocha-Filho, L.C., Moure-Oliveira, D., Carvalho, S.M., Frantini-Silva, W. & Augusto, S.C. (2019) Diversity and host-parasite interactions of cavity-nesting Hymenoptera communities in the Brazilian Savannah. *Journal of Insect Conservation*, **23**(4), 651–665.
- Rodrigues, D.J., Izzo, T.J. & Battistola, L. (2011) *Descobrimos a Amazônia Meridional: Biodiversidade da Fazenda São Nicolau*. Fundação Araucária. Curitiba: Pau e Prosa Comunicação.
- Santoandré, S., Filloy, J., Zurita, G.A. & Bellocq, M.I. (2019) Ant taxonomic and functional diversity show differential response to plantation age in two contrasting biomes. *Forest Ecology and Management*, **437**, 304–313. <https://doi.org/10.1016/j.foreco.2019.01.021>.
- Saunders, M.E. (2016) Resource connectivity for beneficial insects in landscapes dominated by monoculture tree crop plantations. *International Journal of Agricultural Sustainability*, **14**(1), 82–99. <https://doi.org/10.1080/14735903.2015.1025496>.
- Schiffler, G. (2002) Fig wasps (Hymenoptera: Agaonidae) associated to *Ficus mexiae* Standl (Moraceae) in Lavras, Minas Gerais, Brazil. *Neotropical Entomology*, **31**(4), 653–655. <https://doi.org/10.1590/S1519-566X2002000400022>.
- Silva, C.V.C., Silva Goldas, C., Dáttilo, W., Dröse, W., Souza Mendonça, M. & Podgaiski, L.R. (2020) Effects of time-since-fire on ant-plant interactions in southern Brazilian grasslands. *Ecological Indicators*, **112**, 106094. <https://doi.org/10.1016/j.ecolind.2020.106094>.
- Silveira, F.A. & Almeida, E.A.B. (2002) *Abelhas Brasileiras: Sistemática e Identificação*. Belo Horizonte: Fundação Araucária.
- Souza, C.S., Maruyama, P.K., Aoki, C., Sigrist, M.R., Raizer, J., Gross, C.L. & de Araujo, A.C. (2018) Temporal variation in plant-pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. *Journal of Ecology*, **106**(6), 2409–2420. <https://doi.org/10.1111/1365-2745.12978>.
- Spaethe, J. & Weidenmüller, A. (2002) Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insectes Sociaux*, **49**(2), 142–146. <https://doi.org/10.1007/s00040-002-8293-z>.
- Staab, M., Bruelheide, H., Durka, W., Michalski, S., Purschke, O., Zhu, C.D. & Klein, A.M. (2016) Tree phylogenetic diversity promotes host–parasitoid interactions. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 1–9. <https://doi.org/10.1098/rspb.2016.0275>.
- Suding, B.K., Higgs, E., Palmer, M., Callicott, J.B., Anderson, C.B., Gutrich, J.J., Hondula, K.L., Lavefor, M.C., Larson, B.M.H. & Randall, A. (2015) Committing to ecological restoration. *Science*, **348**, 638–640. <https://doi.org/10.1126/science.aaa4216>.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B. & Swanson, F.J. (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, **9**(2), 117–125. <https://doi.org/10.1890/090157>.
- Taki, H., Kevan, P.G., Viana, B.F., Silva, F.O. & Buck, M. (2008) Artificial covering on trap nests improves the colonization of trap - nesting wasps. *Journal of Applied Ecology*, **132**, 225–229. <https://doi.org/10.1111/j.1439-0418.2007.01237.x>.
- Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T. & Makino, S. (2013) Succession influences wild bees in a temperate forest landscape: the value of early successional stages in naturally regenerated and planted forests. *PLoS ONE*, **8**(2), e56678. <https://doi.org/10.1371/journal.pone.0056678>.
- Tangmitcharoen, S., Takaso, T., Siripatanadilox, S., Tasen, W. & Owens, J.N. (2006) Insect biodiversity in flowering teak (*Tectona grandis* L.f.) canopies: comparison of wild and plantation stands. *Forest Ecology and Management*, **222**(1–3), 99–107. <https://doi.org/10.1016/j.foreco.2005.10.040>.
- Tangmitcharoen, S., Tasen, W., Owens, J.N. & Bhodthipuks, J. (2009) Fruit set as affected by pollinators of teak (*Tectona grandis* L. f.) at two tree spacings in a seed orchard. *Songklanakarin Journal of Science and Technology*, **31**(3), 255–259.
- Temperton, V.M. & Zirr, K. (2004) Order of arrival and availability of safe sites: an example of their importance for plant community assembly in stressed ecosystems. I: V.M. Temperton. *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice*. (ed. by R.J. Hobbs, T. Nuttle and S. Halle), pp. p. 285–304. Washington: Island Press.
- Townes, H. (1958) Some biological characteristics of the Ichneumonidae (Hymenoptera) in relation to biological control. *Journal of Economic Entomology*, **51**, 650–652.
- Tylianakis, J.M., Klein, A.M. & Tscharntke, T. (2005) Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology*, **86**(12), 3296–3302. <https://doi.org/10.1890/05-0371>.
- Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation*, **143**, 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>.
- Tylianakis, J.M., Tcharntke, T. & Klein, A.M. (2006) Diversity, ecosystem function, and stability of parasitoid-host interactions across a tropical habitat gradient. *Ecology*, **87**(12), 3047–3057.
- Tylianakis, J.M., Tcharntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*, **445**, 202–205. <https://doi.org/10.1038/nature05429>.
- Warton, D.I., Wright, S.T. & Wang, Y. (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, **3**, 89–101. <https://doi.org/10.1111/j.2041-210X.2011.00127.x>.
- Wood, T.J., Gibbs, J., Graham, K.K. & Isaacs, R. (2019) Narrow pollen diets are associated with declining Midwestern bumble bee species. *Ecology*, **100**(6), e02697. <https://doi.org/10.1002/ecy.2697>.
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, **143**(3), 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>.

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