

RESEARCH ARTICLE

# Temporal stability of cavity-nesting bee and wasp communities in different types of reforestation in southeastern Amazonia

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Global initiatives to recover degraded areas have intensified in recent years. However, the effectiveness of different reforestation practices in restoring habitat stability and essential resources for species over time is poorly known. We tested the degree of temporal stability of bee and wasp communities reestablishment in different types of forest regeneration compared to intact primary forest in southern Amazonia. Using trap-nest sampling, we collected, during 12 months, information about the nesting species in six different types of treatments: pastures, teak reforestation, fig and mixed native species, natural regeneration forest, and forest primary. We observed that in all reforested treatments, the abundance and richness of both bees and wasps were greater than in pasture sites. However, not all reforestation strategies had the same degree of effectiveness in maintaining the stability of bee and wasp communities over time than observed in primary forest communities. The high temporal variation in teak structure promoted high instability in bee and wasp communities over time. In contrast, reforestation using perennial species, such as fig or mixed species, resulted in a greater temporal stability of bee and wasp communities, although dissimilarity to primary forest remained high. Communities in natural regeneration were the most similar to primary forest, with high similarity of species composition and high temporal stability across seasons. Our findings suggest that reforestation strategies that promote increased complexity of vegetation structure, and better resemble “natural” forests in the provision of habitat resources throughout the year, will better restore and maintain communities through time.

**Key words:** ecosystem services, environmental stability, reforestation, solitary bees and wasps, temporal variation

## Implications for Practice

- Temporal biodiversity metrics can potentially be used as a tool to assess the stability of recovered environments in the maintenance of reestablished species.
- Bees and wasps are key species in the functioning of the ecosystem due to the pollination and biological control services that they perform, respectively, so understanding the factors that contribute to the continuous maintenance of these insects is essential for the success of recovered environments.
- Activities related to food production are strongly dependent on ecosystem services carried out by biological species, especially pollination services and biological control of herbivores. Therefore, developing techniques that promote the stability of these services is of great importance to promote agricultural activities.

extinctions and the disappearance of species that are associated with the maintenance of essential ecosystem services (Cardinale et al. 2012). Beyond the direct and indirect consequences for the environment, the loss of ecosystem services also has a large socioeconomic impact on human health and well-being (Chazdon 2008; Lewis et al. 2015; Chazdon & Guariguata 2016; Gilby et al. 2018). Estimates show that the value of ecosystem services lost due to land use change may be as high as \$20 trillion per year (Costanza et al. 2014). As a result, increasing concern has focused on potential policy initiatives to facilitate the recovery of degraded areas (Pistorius & Freiberg 2014; Suganuma & Durigan 2015).

In recent years, a broad range of studies has been carried out to evaluate the effectiveness of human-modified environments

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## Introduction

The scale of human impacts on tropical forests continues to grow at a rapid rate (Senior et al. 2019). The increasing loss and degradation of tropical forests leads to a chain of local

in the maintenance and/or recovery of biodiversity, predominantly focusing on pollinators due to their importance in human food production (Tylianakis et al. 2006; Buschini & Woiski 2008; Williams et al. 2010; Gikungu et al. 2015; Flores et al. 2018; Araújo et al. 2018a). Most monitoring studies evaluating the restoration of fauna in disturbed areas normally use discrete point-comparisons with primary forests (PFs) as reference sites to compare their effectiveness (Cristescu et al. 2012). However, they rarely consider the degree of temporal variation in biological communities over time, and whether restored habitats provide temporal stability of resources for species with varying life histories and phenologies.

As seasonal variation in climatic conditions are more or less predictable over the year in tropical forests, the life cycles of tropical forest species have evolved in response to the stability of habitat and resource conditions (Visser et al. 2010; Bradshaw et al. 2011). Consequently, turnover in local community composition is observed through time since different types of resources required by resident species may be available at different time periods (Hawkins & Sedell 1981; Basilio et al. 2006). This temporal heterogeneity in species occurrence can be a problem in studies, which aim to compare environmental impacts on biodiversity in different habitat types (Wolda 1978; Tylianakis et al. 2005). It occurs because the time scale of sampling may lead to an unbalanced estimate in the relative importance of analyzed spatial and temporal parameters (Roubik 2001; Summerville & Crist 2005). Particularly in tropical regions, the relatively low seasonal variation in temperature (compared to other temperate regions of the world) has led to the assumption that biodiversity sampling can be carried out over short time scales and inferred to be representative of all time points (Tylianakis et al. 2005). However, if seasonal partitioning of resources is high in intact tropical forests, but lower in degraded forests due to the replacement of specialists by generalists (Tylianakis et al. 2005), then spatial point-comparisons of diversity between degraded and natural habitats will underestimate biodiversity loss due to temporal turnover.

Bees are considered to be the most efficient pollinators in many systems (Klein et al. 2002; Kremen et al. 2002), pollinating up to 90% angiosperms in tropical forests (Ollerton et al. 2011). Wasps are also important pollinators and, at the same time, they provide additional ecosystem services through the biological control of various invertebrate species, many pests of crops (Klein et al. 2007; Santoni & Del Lama 2007; Rezende et al. 2014). Worldwide, bees and wasps, together, reach more than 40,000 identified species (Evans & Eberhard 1970; O'Neill 2001). Although they have different levels of social organization, approximately 85% of bees and wasps present solitary behavior (Batra 1984; Martins & Pimenta 1993). These hymenopterans also have different nesting habits, with many species that dig their nests in the ground or build them in cavities present in dead wood (Krombein 1967). For the cavity-nesting species, the nest-trap methodology is widely used for their monitoring since it allows to survey only the species that occur in the studied region, excluding those that are just transiting (Assis & Camillo 1997; Araújo et al. 2018b; Araújo

et al. 2019). In natural environments, the community composition of bees and wasps is closely correlated with availability of food, nesting sites, and favorable microclimatic conditions (Loyola & Brito 2006; Tylianakis et al. 2006; Araújo et al. 2018b). Temporal variation in resources and environmental conditions over time is frequently reflected in variation in species composition (Matos et al. 2016), acting as environmental filters that influence the colonization or persistence of healthy populations in disturbed habitats (Loyola & Martins 2006; Antonini et al. 2016; Matos et al. 2016; Araújo et al. 2019).

In degraded livestock pasture habitats formed following the destruction and clearing of rainforest in southern Amazonia, subsequent reforestation can lead to the reestablishment of semi-natural forest conditions and the parallel recovery of bees and solitary wasps (Araújo et al. 2019). However, the type of reforestation strategies employed can have a large influence on the rate of recovery of resources and environmental conditions, affecting the composition of local species (Suganuma & Durigan 2015; Martínez-ramos et al. 2016; Wheeler et al. 2017). Although some studies have evaluated the success of reforestation in the recovery of cavity-nesting bee and wasp communities (Klein et al. 2002; Buschini & Woiski 2008; Gikungu et al. 2015; Matos et al. 2016; Araújo et al. 2018b), so far little is known about the effectiveness of reforestation in supporting natural temporal heterogeneity of resource and conditions, and its influence on the temporal stability of pollinator and biological control communities.

Here, we investigate how different types of reforestation affect the temporal stability of the reestablished community of solitary bees and wasps that nest in cavities, with varying requirements for phenological resources and environmental conditions, relative to the intact tropical forest. We sampled communities at regular intervals, which allowed us to incorporate the temporal dimensions of community turnover in the study of bee and wasp community recovery among treatments. Our study system in southeastern Amazonia exhibits comparatively stable temperature regimes throughout the year, but has marked variation in rainfall. This seasonal climatic variation can affect environmental conditions as well as the availability of resources for bees (pollen and nectar) and wasps (arthropod prey), therefore temporal turnover in community parameters is expected to occur in mature undisturbed forest. In degraded areas, reduced vegetation complexity may limit the availability of essential resources at certain times of the year, leading to higher temporal variation in community composition compared to intact forests. On the other hand, degraded habitats are often dominated by generalist rather than specialist species (Araújo et al. 2018b; Araújo et al. 2019), and environments with more generalist species could mean lower temporal heterogeneity. For this reason, we hypothesize that the type of reforestation in an area affects the recovery of the natural dynamics of the species communities over time. With this, we predict that (1) reforestation with more diverse vegetation structure will facilitate the recovery of environmental conditions and availability of resources across seasons, promoting temporal stability of bee and wasp communities through time, relative to intact forest;

and (2) the temporal patterns of beta diversity between reforested habitats and natural forest will decrease with increasing diversity of reforested vegetation, with a corresponding shift from turnover processes to nestedness processes along the reforestation gradient.

## Methods

### Study Area

We selected sampling sites at São Nicolau farm (9°48'S, 58°15'W, elevation 254 m above sea level), located in the municipality of Cotriguaçu, Mato Grosso, Brazil. Positioned in the arc of deforestation of Amazon Forest, the farm covers 10,000 ha. Of these, 7,200 ha remains as PF, 300 ha was converted to pasture for cattle grazing, 2,000 ha had been cleared and replanted with various species of trees, and 500 ha of previously cleared land was left to natural forest recovery (Fig. 1). The prior land use of all reforested plantation areas and natural secondary forests was cattle grazing pasture, before the establishment of forestry between 1999 and 2000 (Rodrigues et al. 2011). The regional climate is the AW type, according to the Köppen classification (warm and humid), with an average annual temperature of 24°C, 85% humidity, and 2,300 mm of precipitation. The original phytophysiognomy is the Tropical Open Ombrophilous Forest, Submontane formation with Palmeiras (Rodrigues et al. 2011).

### Experimental Design

We selected six categories of habitats, ranging from completely cleared to completely intact. The six habitats types were: (1) pasture (PA), dominated by pasture grasses (up to 50 cm tall), with

very high light incidence, almost no woody vegetation, and lack of a leaf litter layer; (2) teak reforestation (TR), consisting of monodominant stands of the exotic *Tectona grandis* (Verbenaceae), characterized by an open understory, deciduous leaf-fall pattern in the dry season, and deep leaf litter layer; (3) fig reforestation (FR), consisting of monodominant stands of the native *Ficus maxima* (Moraceae), sourced from local seed provenance and characterized by mixed-age understory shrubs, a thin leaf litter layer, and some patches of grasses; (4) mixed reforestation (MR), consisting of planted native tree species, including *Tabebuia chysotricha* (Bignoniaceae), *T. roseo-alba*, *T. impetiginosa*, *Cedrela fissilis* (Meliaceae), *Cordia alliodora* (Boraginaceae), *Simarouba amara* (Simaroubaceae), *Spondias mombin* (Anacardiaceae), *Hevea brasiliensis* (Euphorbiaceae), and *Schizolobium amazonicum* (Fabaceae), with an understory of low shrubs and grasses, and limited leaf litter accumulation; (5) secondary regeneration, without cattle or anthropogenic interference, where vegetation has recovered naturally, resulting in an extremely dense understory taller than 5 m, and low light incidence; and (6) PF, consisting of undisturbed PF that we used as the reference habitat. PF in the region is defined as *terra-firme* (upland) rainforest, typically with a closed-canopy of 30–40 m (emergent to 50 m) and an open but diverse understory.

Within each of the six forest cover categories, we selected 10 sampling sites ( $n = 14$  in the case of PF) based on feasibility of access and logistical constraints (64 sites in total, see Fig. 1). To minimize spatial dependence among sites, all sampling sites were at least 500 m apart, based on the typical foraging distances estimated for cavity-nesting bees and wasps (Gathmann & Tsharntke 2002; Klein et al. 2002; Zurbuchen et al. 2010). The distance of 500 m was also maintained, whenever possible, between treatments of different categories. Site replicates of each forest type were spatially interspersed among

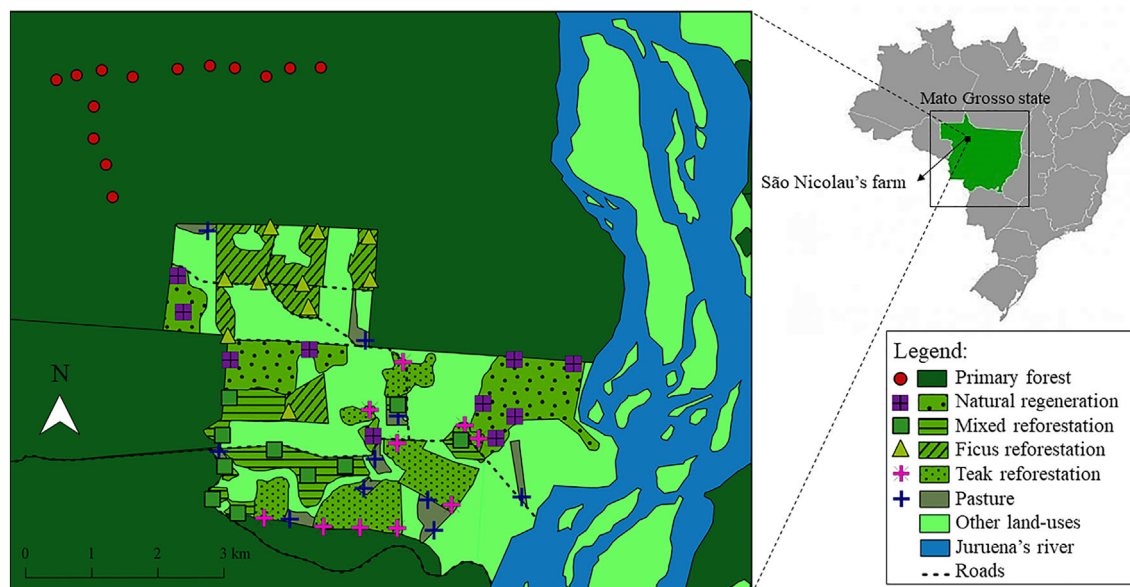


Figure 1. Map showing the spatial arrangement of our 64 sites established in six different types of habitats at the São Nicolau farm, municipality of Cotriguaçu, state of Mato Grosso, Brazil: pasture, teak reforestation, fig reforestation, mixed reforestation, natural forest, and primary forest.

replicates of all other degraded forest types (Fig. 1), but this was not possible for PF sites due to logistical issues with permission for site access. To address this issue, all statistical analyses incorporated explicit tests of spatial autocorrelation. Due to limitations in the study areas, sites in the same category presented different distances from the PF, to ensure that this variation did not tend to our data, we use generalized linear mixed models (GLMMs) and permutational multivariate analysis of variance (PERMANOVA) to verify possible effects of these variations in the distance of the Primary Forest between sites of the same category (see Tables S1 and S2, Supporting Information, respectively).

At each of the 64 sites, we marked out five equidistant points 50 m apart on a line transect, and installed experimental trap-nests (i.e. 320 trap-nests in total). Trap-nests were placed at a height of 1.5 m above the ground attached to trees (in pasture, the blocks were attached to wooden stakes) (Fig. 2).

### Trap-Nest Design and Sampling

Each trap-nest consisted of one block (30 cm length  $\times$  7 cm height  $\times$  12 cm width) made of wood (*C. fissilis*, Meliaceae) with 10 holes of each of four sizes, 8, 12, 16, and 20 mm diameter, haphazardly distributed across the block and drilled to 100 mm deep (40 holes in total per block) (Fig. 2). Black paper-board tubes were inserted into each hole to create a removable sleeve (Araújo et al. 2018b). In total, 320 trap-nests (12,800 nest tubes) were placed out among the 64 study sites.

We inspected the traps at 20-day intervals between August 2016 and July 2017, and occupied nest tubes were collected and replaced by a new tube of the same size on each sampling event. Occupied nest tubes were placed in glass test tubes in the laboratory, which were closed with cotton wool and kept in a dark room at temperatures between 20 and 25°C until the emergence of adults (ensuring that we discriminated host bees and wasps from any parasitoid insects that emerged). After emergence, we pinned the insects, quantified the number of cells

built, and sent the specimens for identification by taxonomic specialists (see Acknowledgments section). The voucher specimens were deposited in the Invertebrate Collection of the Universidade Federal de Mato Grosso, Brazil.

### Collecting Climatic Variation Over Time

To quantify temporal variation in seasonal climatic conditions, we extracted the daily climatic data of the region during the whole study period (11 variables): average minimum temperature, average daily mean temperature, average maximum temperature, precipitation, average days without rain, minimum relative humidity, maximum relative humidity, evapotranspiration, solar radiation, wind speed and soil water availability, and quantified the monthly averages of each variable (Table S3). We extracted these data from Cotriguaçu-MT, Brazil, available at [https://rp5.ru/Weather\\_in\\_the\\_world](https://rp5.ru/Weather_in_the_world).

### Statistical Analyses

**Quantifying Climatic Variation Over Time.** We had no a priori evidence for a single climate variable that would represent an “ideal” indicator of climatic variation over time. Therefore, we used the 11 climate variables described above to construct a single composite variable representing a seasonal climate gradient across months. For this, the 11 climate variables were normalized to account for the different unit scales of measure, and we performed a correlation-based principal components analysis (PCA) using the function “prcomp” in R version 3.5.1. To obtain the seasonal climate gradient, we used the values of the first axis of the PCA (PC1) comprising loadings of the 11 measured variables for each of the 12 months sampled. For the purposes of analysis, we rescaled the minimum and maximum PC1 scores to a scale of 0 to 10 (from dry season to wet season), which does not alter the relative dissimilarity in forest structure among sites.



Figure 2. 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.



## Testing the Degree of Temporal Variation in Solitary Bees and Wasp Communities Among Different Reforestation Types

### *Abundance and Richness of Species*

We tested the variation in abundance and richness of bees and wasps over time (separately) using generalized linear mixed models (GLMMs) with a Poisson error structure (and log-link function) in the “lme4” v.3.1-147 package (Bates et al. 2015). In the full model for each response variable, we specified treatments (six categories of forest cover) and seasonal climate gradient, plus their interaction, as fixed predictor effects. A second-order polynomial function was specified for seasonal climate gradient, to account for potential nonuniformity of response. In the richness models, we also specified an additional fixed covariate effect for “abundance” (i.e. number of individuals) to account for any variation in richness that could be attributed solely to variation in sample abundance. Each model included a random intercept for “sites” ( $n = 64$ ) in order to account for the nonindependence of the five trap-nests located within each site. We tested each model for overdispersion of residuals, and where necessary overdispersed models were fit using a negative binomial error distribution.

Following the construction of the full model for each response variable (i.e. Bees: richness and abundance, Wasps: richness and abundance), we carried out a model simplification process using the “AICcmodavg” package (Mazerolle & Linden 2019). We determined the minimum adequate model(s) by comparing Akaike information criterion corrected (AICc) and Akaike information criterion corrected weight (AICcWt) values for submodels consisting of (1) the full polynomial seasonal climate gradient model, (2) a linear seasonal climate gradient model, or (3) a null, intercept-only model. Models within 2  $\Delta$ AICc units of the top model (i.e. the model with the lowest AICc value) were considered to have equivalent explanatory power (Burnham & Anderson 2002). We estimated the final model coefficients using restricted maximum likelihood (REML) estimation. For the final model, we used the approach of Nakagawa and Schielzeth (2013) to estimate absolute model fit using marginal  $R^2$  GLMM (variance explained by just the fixed effects) and conditional  $R^2$  GLMM (variance explained by both fixed and random effects).

**Bee and Wasp Composition.** Because not all sites had species nesting during every 20-day collection period, we pooled temporal samples into four categories of climatic seasonality over time which were defined as “seasons”: start of rainy season (SR; November, December, and January), end of rainy season (ED; February, March, and April), start of dry season (SD; May, June, and July), and end of dry season (August, September, and October) (Gikungu et al. 2015; Araújo et al. 2018b). We tested if bee and wasp species composition differed among the six forest type treatments and among the four seasons by performing permutational multivariate analyses of variance with 1,000 permutations (PERMANOVA; Anderson 2001) on abundance data, using Bray–Curtis dissimilarity index using the “adonis” function. To account for the nonindependence of repeated seasonal measures at each site, we

included “site” as a random effect in the model, using the “strata” function. When the among-group tests were significant in PERMANOVA, we assessed if within-group dispersion was homogeneous using PERMDISP (Warton et al. 2012). We assessed differences between Treatment levels by pairwise comparisons with adjusted  $p$  values after Bonferroni correction using “pairwise.adonis2” function (Martinez Arbizu 2019). When we found significant differences we partitioned total Bray–Curtis dissimilarity into its components balanced variation in abundances (dBC-bal), which is analogous to species replacement in incidence-based patterns, and in abundance gradients (dBC-gra), which is analogous to species nestedness in incidence-based patterns (Baselga 2013). We visualized clustering of treatment plots using principal coordinates analyses (PCoA), and for significant differences according to PERMANOVA. We evaluated the change in turnover (dBC-bal) and nestedness (dBC-gra) of species among the comparisons (control vs. treatment) using the PERMANOVA.

In all cases, we assessed potential spatial autocorrelation in raw response values and in the residuals of the final best-fit models for all variables, by calculating spatial correlograms for Moran’s  $I$  values in ncf v.1.2-6 (Bjornstad 2018). All analyses were performed in R version 3.5.1 (R Core Team 2018).

## Results

### Trap-Nest Occupation by Bees and Wasps

In total, of the 12,800 cavities available for nesting during the period of study, 2,143 (16.74%) were occupied by solitary bees or wasps. We recorded 26 wasp species (1,813 nests; 3,525 individuals) belonging to the families Crabronidae, Pompilidae, Sphecidae, and Vespidae, and 14 bee species (330 nests; 1,286 individuals) belonging to the families Apidae and Megachilidae (Table S4). Vespidae and Apidae were the families with the greatest numbers of species (9 and 11 species, respectively), and together they represented 52.50% of the total number of nesting species. Crabronidae was the family with the greatest numbers of occupied cavities (623), followed by Pompilidae and Sphecidae (both with 497), totalling 52.26% of all nests.

### Quantifying the Temporal Gradient in Seasonal Components of Climate

The PCA ordination based on 11 climate measures produced a strong composite seasonal climate gradient across months (Fig. 3). A two-dimensional representation of the data (Fig. 3) explained 80.94% of the variation in climate, with dry months from May until October to the left of PC axis 1, and wet months from November until April to the right of PC axis 1 (see Table S5). PC1 is referred to as the seasonal climate gradient.

### Temporal Variation in Abundance and Richness of Bees and Wasps

We found that abundance varied significantly among reforestation treatments for both bees and wasps (Table 1), but treatment differences were not consistent across time. Moreover, there was

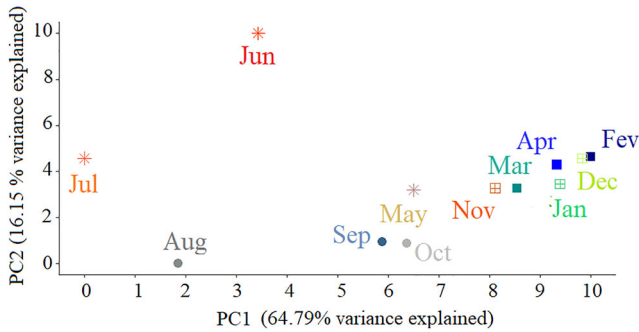


Figure 3. Biplot of principal components analysis (PCA) axes 1 and 2 showing the seasonal climate gradient variation across the months. The climate varies strongly along PC1 (dry season to wet season) with the change in months. We refer to this gradient along PC1 as the “seasonal climate gradient.”

no simple monotonic variation in abundance with seasonal time period along the seasonal climate gradient (Fig. 4A & 4B). Instead, the best-fit GLMM model for both bee abundance (AICc weight = 0.81, Table S6) and wasp abundance (AICc weight = 0.72, Table S6) was a hump-shaped (quadratic) relationship for seasonal climate gradient without interaction with treatments (Fig. 4A & 4B, Tables 2 and S6). Among the treatments, we found that pasture had the lowest bee abundance, whereas abundance in TR was higher than that found in PF (control).

We did not identify differences in bee abundance between FR, MR, and natural regeneration (NR) in relation to temporal variation in abundance at PF (Fig. 4A, Table 1). In general, all the habitats presented greater bee abundance around the intermediate portion of the seasonal climate gradient, which was characterized by the transition period after the end of the dry season (Fig. 3). Meanwhile, for wasps, we found that treatments FR, MR, and pasture (PA) had lower capacity to ensure consistent abundance through time, since for TR and NR we did not find differences in relation to PF (Fig. 4B, Table 1). Unlike bees, wasp nesting rates in all habitat types were higher at high values

of the PC1 seasonal climate gradient, corresponding to the December to April rainy season (Fig. 4B). Species richness trends for both bees (AICc weight = 0.95, Fig. 4C, Table S6) and wasps (AICc weight = 0.83, Fig. 4D, Table S6) mirrored the hump-shaped relationships through the seasonal climate gradient that were observed in the abundance data, even after accounting for potentially spurious effects due to variation in sample abundances between trap-nests (significant covariate effects for abundance in Table 1). However, bee richness did not vary between the different types of treatments and PF as occurred for wasp richness (Table 1). As for abundance, the highest bee richness, for all habitats, also occurred around the intermediate portion of the seasonal climate gradient (Fig. 4C). For wasps, we found that all the treatments had lower stability to ensure consistent richness through time in relation to the PF. However, as for the abundance of this group, the highest values of richness were among the PC1 values, which are characterized by the end of rainy season (Fig. 4D).

### Bee and Wasp Compositional Responses Along Temporal Variation Among Treatments

We observed high dissimilarities in bee species composition between all different reforestation types and PF. All comparisons “control versus treatment” differed in species composition along seasonal climate gradient (Table 2a–c, Fig. 5A–E). For wasps, only NF forest types had similar species composition with PF throughout the seasonal climate gradient (Table 2f–j, Fig. 5F–J).

For bees, the beta dissimilarity between control and treatments was derived mainly from turnover in all pairs of comparisons (Table 3a–e). With the PERMANOVA dissimilarity comparisons of species turnover between “control versus treatment,” we verified that the species involved in the turnover process between each treatment were different from the species involved in turnover in PF. We did not find differences in species dissimilarity in the nestedness process between treatments and PF (see values of PERMANOVA, Table 3). For wasps, although the beta dissimilarity was also predominantly

**Table 1.** Parameter estimates from the final best-fit mixed model (GLMM) for each response variable: (a) bee abundance, (b) wasp abundance, (c) bee richness, (d) wasp richness. CVG, linear coefficient of the fitted climate variation gradient; Cov., covariate;  $R^2$ , coefficient of determination (for GLMM shown as both marginal, M, and conditional, C, values). Bold values mean  $p$ value < 0.05.

| Fixed Factors              | (a) Bee Abundance                  | (b) Wasp Abundance                  | (c) Bee Richness                   | (d) Wasp Richness                   |
|----------------------------|------------------------------------|-------------------------------------|------------------------------------|-------------------------------------|
|                            | Estimate ( $\pm$ SE)               | Estimate ( $\pm$ SE)                | Estimate ( $\pm$ SE)               | Estimate ( $\pm$ SE)                |
| Primary forest (intercept) | <b>−1.46 <math>\pm</math> 0.46</b> | <b>1.91 <math>\pm</math> 0.20</b>   | <b>−2.22 <math>\pm</math> 0.25</b> | <b>0.21 <math>\pm</math> 0.09</b>   |
| Teak reforestation         | <b>1.23 <math>\pm</math> 0.49</b>  | 0.03 $\pm$ 0.28                     | 0.02 $\pm$ 0.28                    | <b>−0.35 <math>\pm</math> 0.11</b>  |
| Fig reforestation          | 0.25 $\pm$ 0.50                    | <b>−0.72 <math>\pm</math> 0.28</b>  | −0.06 $\pm$ 0.29                   | <b>−0.25 <math>\pm</math> 0.12</b>  |
| Mixed reforestation        | 0.23 $\pm$ 0.49                    | <b>−0.66 <math>\pm</math> 0.28</b>  | −0.21 $\pm$ 0.30                   | <b>−0.30 <math>\pm</math> 0.11</b>  |
| Natural regeneration       | −0.11 $\pm$ 0.52                   | −0.32 $\pm$ 0.28                    | 0.07 $\pm$ 0.28                    | <b>−0.37 <math>\pm</math> 0.11</b>  |
| Pasture                    | <b>−2.45 <math>\pm</math> 0.59</b> | <b>−3.05 <math>\pm</math> 0.33</b>  | −0.34 $\pm$ 0.33                   | <b>−1.98 <math>\pm</math> 0.25</b>  |
| CVG                        | <b>1.07 <math>\pm</math> 0.17</b>  | <b>0.14 <math>\pm</math> 0.06</b>   | <b>0.31 <math>\pm</math> 0.10</b>  | 0.02 $\pm$ 0.04                     |
| Quadratic-term (CVG)       | <b>−0.10 <math>\pm</math> 0.01</b> | <b>−0.03 <math>\pm</math> 0.006</b> | <b>−0.03 <math>\pm</math> 0.01</b> | <b>−0.01 <math>\pm</math> 0.005</b> |
| Cov. abundance             | –                                  | –                                   | <b>0.09 <math>\pm</math> 0.01</b>  | <b>0.05 <math>\pm</math> 0.005</b>  |
| $R^2$ GLMM(M)              | 67.14%                             | 64.53%                              | 19.47%                             | 21.27%                              |
| $R^2$ GLMM(C)              | 72.16%                             | 78.08%                              | 19.47%                             | 21.27%                              |

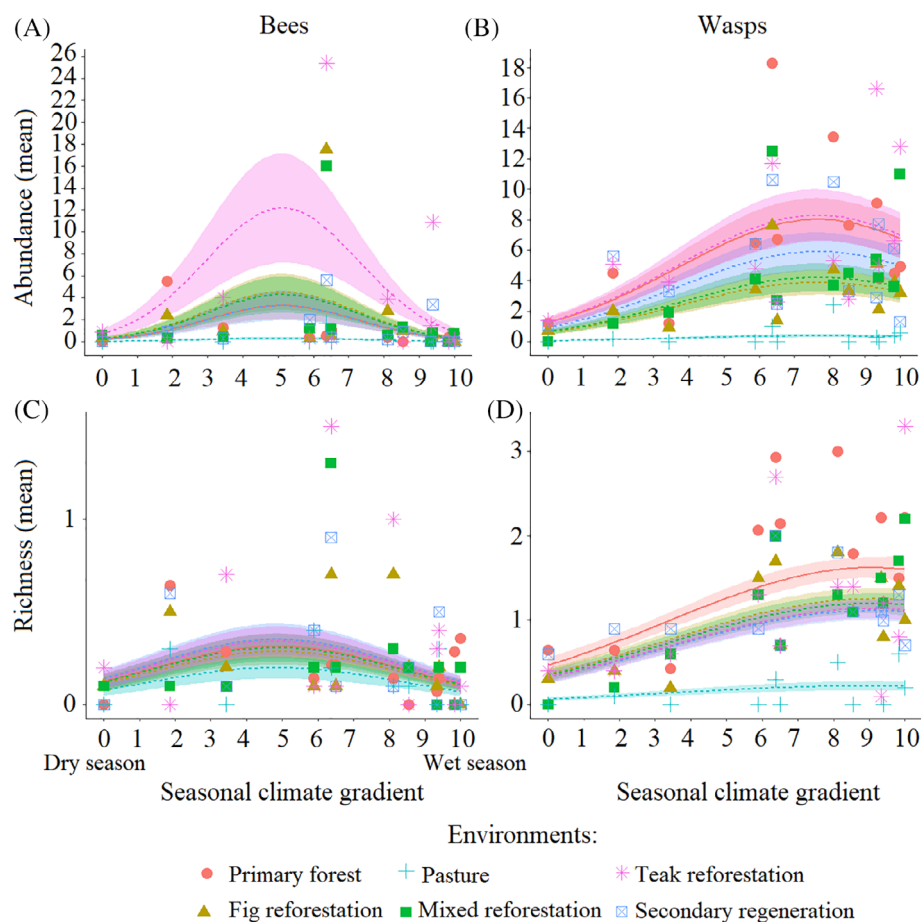


Figure 4. Variation in (A) bee abundance, (B) wasp abundance, (C) bee richness, and (D) wasp richness along temporal variation (rescaled PCA axis 1 values; see Fig. 2).

**Table 2.** Bee and wasp compositional differences along temporal variation between primary forest (control) and reforestations (treatments). PERMANOVA, permutational multivariate analyses of variance with Bonferroni correction; PERMDISP, within-group permutational dispersion;  $R^2$ , coefficient of determination for PERMANOVA; F, ratio of two variances between-group comparisons. Bold values mean  $p$ value < 0.05.

| <i>Bee Composition Along Temporal Variation</i>  |                  |                  |                  |                  |                  |
|--------------------------------------------------|------------------|------------------|------------------|------------------|------------------|
|                                                  | (a) PF versus PA | (b) PF versus TR | (c) PF versus FR | (d) PF versus MR | (e) PF versus NR |
| PERMANOVA                                        | $R^2$            | $R^2$            | $R^2$            | $R^2$            | $R^2$            |
| Treatment                                        | <b>0.12</b>      | <b>0.08</b>      | <b>0.09</b>      | <b>0.09</b>      | <b>0.06</b>      |
| Seasons                                          | <b>0.24</b>      | <b>0.18</b>      | <b>0.11</b>      | <b>0.15</b>      | <b>0.16</b>      |
| Treatment * Seasons                              | <b>0.06</b>      | <b>0.12</b>      | <b>0.12</b>      | <b>0.15</b>      | 0.08             |
|                                                  | F                | F                | F                | F                | F                |
| PERMDISP                                         | <b>12.59</b>     | 2.06             | 1.67             | 3.16             | 0.51             |
| <i>Wasp Composition Along Temporal Variation</i> |                  |                  |                  |                  |                  |
|                                                  | (f) PF versus PA | (g) PF versus TR | (h) PF versus FR | (i) PF versus MR | (j) PF versus NR |
| PERMANOVA                                        | $R^2$            | $R^2$            | $R^2$            | $R^2$            | $R^2$            |
| Treatment                                        | <b>0.1</b>       | <b>0.06</b>      | <b>0.07</b>      | <b>0.03</b>      | <b>0.009</b>     |
| Seasons                                          | <b>0.155</b>     | <b>0.15</b>      | <b>0.18</b>      | <b>0.16</b>      | 0.17             |
| Treatment * Seasons                              | <b>0.04</b>      | <b>0.04</b>      | <b>0.04</b>      | <b>0.03</b>      | 0.04             |
|                                                  | F                | F                | F                | F                | F                |
| PERMDISP                                         | 3.4              | <b>5.22</b>      | 0.3              | 3.05             | 1.25             |

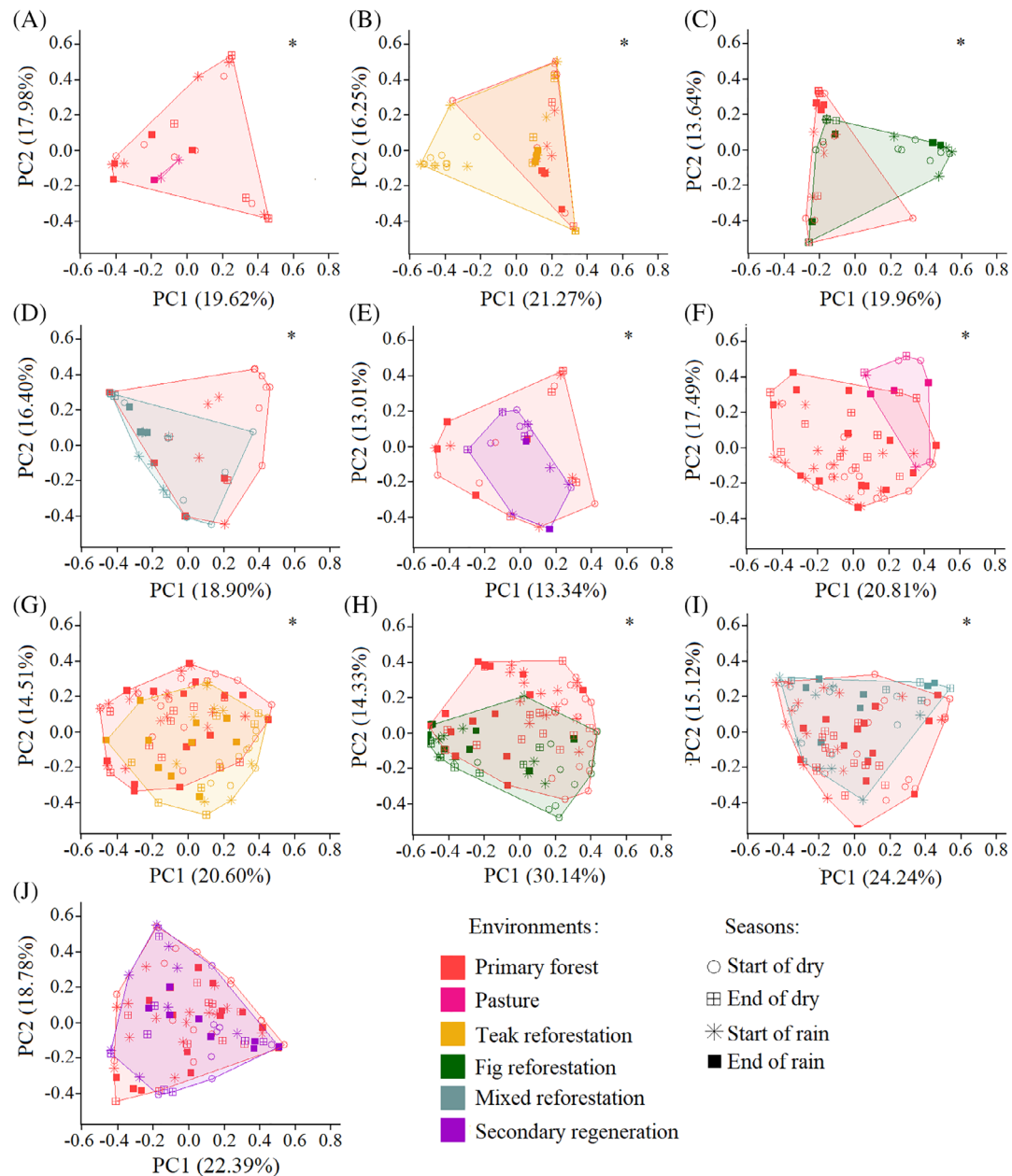


Figure 5. PCoA pairwise comparisons of species composition between "treatments versus control" for bee: (A) pasture vs. primary forest; (B) teak reforestation vs. primary forest; (C) fig reforestation vs. primary forest; (D) mixed reforestation vs. primary forest; and (E) natural regeneration vs. primary forest; and for wasps: (F) pasture vs. primary forest; (G) teak reforestation vs. primary forest; (H) fig reforestation vs. primary forest; (I) mixed reforestation vs. primary forest, based on Bray-Curtis dissimilarity index. Asterisks indicate significant differences ( $p < 0.05$ ): The composition in control was different when comparing treatment along seasonal variation.

explained by turnover, the relative variation in this component was lower than for bees. We found that all planted reforestation treatments had different wasp species involved in the turnover process when compared to PF. By contrast, for NF areas, the species involved in turnover did not differ from PF (see values of PERMANOVA, Table 3). We found no differences for species dissimilarity involved in nestedness between treatments and PF (see Table 3).

#### Analysis of Spatial Autocorrelation

We found no significant spatial autocorrelation of model residuals in the analysis of any of the response variables (Fig. S1).

#### Discussion

All types of reforestation studied were successful in maintaining a greater diversity of bees and wasps throughout the temporal



**Table 3.** Bee and wasp compositional differences in turnover and nestedness process along temporal variation between primary forest (control) and reforestation (treatments). PERMANOVA, permutational multivariate analyses of variance with Bonferroni correction; PERMDISP, within-group permutational dispersion;  $R^2$ , coefficient of determination for PERMANOVA. Bold values mean  $p$ value < 0.05

| <i>Bray–Curtis Dissimilarity of Bees</i>  |                  |                  |                  |                  |                  |
|-------------------------------------------|------------------|------------------|------------------|------------------|------------------|
|                                           | (a) PF versus FR | (b) PF versus TR | (c) PF versus NR | (d) PF versus MR | (e) PF versus PA |
| Turnover                                  | 0.91             | 0.87             | 0.92             | 0.89             | 0.93             |
| PERMANOVA ( $R^2$ )                       | <b>0.14</b>      | <b>0.11</b>      | <b>0.08</b>      | <b>0.14</b>      | <b>0.14</b>      |
| Nestedness                                | 0.04             | 0.06             | 0.03             | 0.04             | 0.03             |
| PERMANOVA ( $R^2$ )                       | −0.52            | −0.29            | −0.37            | −0.61            | −0.15            |
| <i>Bray–Curtis Dissimilarity of Wasps</i> |                  |                  |                  |                  |                  |
|                                           | (f) PF versus FR | (g) PF versus TR | (h) PF versus NR | (i) PF versus MR | (j) PF versus PA |
| Turnover                                  | 0.62             | 0.66             | 0.01             | 0.57             | 0.82             |
| PERMANOVA ( $R^2$ )                       | <b>0.11</b>      | <b>0.13</b>      | <b>0.29</b>      | <b>0.04</b>      | <b>0.17</b>      |
| Nestedness                                | 0.17             | 0.14             | 0.22             | 0.2              | 0.1              |
| PERMANOVA ( $R^2$ )                       | −0.08            | −0.2             | −0.01            | −0.01            | −0.07            |

partition of complementary resources and conditions in seasonal climate gradient, when compared to degraded areas (pasture). These results demonstrate that the efforts used in the reforestation process from degraded areas are contributing to the recovery of similar patterns to those found in natural environments, as the variation in environmental conditions that allows maintenance continues in the process of colonization of different species through seasonal variation. Even with different intensities, the pattern in species colonization remained the same among the treatments throughout the analyzed period, differing from that found for other types of habitats (Tylianakis et al. 2005). Nevertheless, the responses of bees and wasps were different in relation to the types of environments along temporal variability. Even both being excellent indicators of environmental quality (Klein et al. 2002; Loyola & Martins 2006; Williams et al. 2010), these groups present different sensitivities to environmental variations in relation to each other. While bees are strongly dependent on the availability of floral resources for nesting, wasps need a broad variety of prey (Klein et al. 2007; Batista Matos et al. 2013; Araújo et al. 2018a). Thus, the observed differential pattern is probably related to the different capacities that the treatments present in establishing the diverse dietary requirements required by the solitary bees and wasps over time.

In our study, the end of the dry season was marked by an increase in the richness and abundance of bees, while for wasps the peaks occurred in the rainy season in all forest treatments. This pattern has also been observed in other tropical environments (Assis & Camillo 1997; Melo & Zanella 2012; Batista Matos et al. 2013; Matos et al. 2016; Oliveira & Gonçalves 2017; Flores et al. 2018; Araújo et al. 2018a, 2018b). However, among treatments, teak was the habitat with lower temporal stability of nesting rates across seasons. In this treatment, bees showed a high variation in abundance throughout the seasonal climate gradient. This is probably due to the high structural variation of this treatment in the function of the total deciduous characteristic of the species (Tangmitcharoen et al. 2006; Tonini

et al. 2009; Araújo et al. 2019). The variation in the occurrence of these insects is strongly related to the availability of environmental conditions and food resources presented by habitats (Klein et al. 2002, 2007). Certainly, the highest bee abundance in teak at the end of the dry season was due to the presence of certain flowering plants, which allowed the occurrence of some species with low restriction to exposure to light and heat (Batista Matos et al. 2013; Stangler & Hanson 2015). However, the conditions imposed by these environments do not appear to be favorable for wasps, presumably due to the low availability of prey capable of tolerating the conditions of exposed environments given leaf loss of teak plants during this period. However, environmental conditions imposed by teak do not appear to be favourable for wasps. This possibly is related to the low availability of their prey in tolerating the environmental variations imposed by these environments, since the loss of leaves exposes the interior of the treatment to high temperatures that can limit the occurrence of some arthropods (Lister & Garcia 2018; Harris et al. 2019). However, with the beginning of the rainy season, the availability of an open understory with few woody shrubs certainly contributed to the increase of resources and establishment of appropriate climatic conditions in teak, which might have ensured its high wasp abundance during this period. (Gikungu et al. 2015; Rhoades et al. 2018). This shows that the effectiveness of teak reforestation in the continuous maintenance of these insects depends constantly on the action of adjacent environments in the dynamics of the source-sink to provide resources for these environments, such as short-term development plants.

In fact, the simplification of habitat in some degraded environments may lead to “overproduction” of resources for certain generalist species of bees and wasps in specific periods (Tylianakis et al. 2005; Buschini & Woiski 2008; Araújo et al. 2018a). However, an intense and a continuous impact, such as constant grazing by cattle, probably resulted in low pasture productivity in the production of resources for bees and wasps throughout all seasons (Hall et al. 1992; Dunne

et al. 2011). As in teak, the direct exposure to high temperatures in pasture may be among the main factors to contribute to the low colonization rate by species. Higher average temperatures are correlated with higher fluctuations of local temperatures, such as those caused by sites exposed to direct sunlight (Murcia 1995). Due to thermo-sensitive characteristics, most species of bees and wasps cannot compensate for high temperature fluctuations (Fye 1972). Besides reducing their colonization capacity, the exposure of nesting species to the high environmental variations present in these environments can affect the development of their offspring and, consequently, affect the survivability of these individuals (Araújo et al. 2019).

The patterns of temporal variation in bee abundance were similar between PF, FR, MR, and NR. This suggests greater stability of these reforestations in the maintenance of conditions required by this group. However, for wasps, only NR maintained the similar abundance to PF. In the present study, the PF probably acted as source of propagules for colonization in NR (Aide et al. 1995, 1996). The perennial characteristic of species of FR and MR may have contributed to the greater stability in the abundance of bees in relation to teak. This characteristic may have provided greater stability to environments by dampening the effects of climatic variation within these habitats, such as temperature and humidity (Stangler & Hanson 2015). Thus, environmental stability may be a process that contributed to the establishment of natural dynamics of bees, even in simplified environments like fig. However, the planting of perennials and trees does not appear to have been sufficient to ensure the maintenance of wasps. Therefore, recovery of structural parameters of vegetation does not present the same efficiency on the maintenance of both groups. This possibly occurs because vegetation structure attributes are not sufficient in themselves to provide the necessary conditions and resources that ensure the establishment and availability of prey used by wasps, such as spiders (Souza & Parentoni 2004), grasshoppers (Chambers et al. 1996), lepidopteran caterpillars (Kitahara et al. 2008), and several other arthropods (Krombein 1967). Although reforestations with fig monocultures or mixed polycultures of native tree species provide greater stability of vegetation structure than teak reforestation, they are still insufficient to ensure equivalent densities of wasps at all seasonal time points that would expect from those observed in PFs, even after of almost 20 years of community recovery.

As in previous studies, the temporal variation did not affect the bee species richness among the treatment types (e.g. Matos et al. 2016). For wasps, reforestation allowed greater species richness through seasonal variation than pasture, but have not been able to secure similar richness to that present PF. It demonstrates that the reestablishment of the species richness of the groups is also affected differently over time by the environmental heterogeneity presented by reforestations (Araújo et al. 2018a). But independent of the group, more heterogeneous environments tend to be more constant for these insects over time due to the different sources of resources and conditions that they can offer (Antonini et al. 2016; Araújo et al. 2018b; Araújo et al. 2019).

The success in recover the dynamics of the species composition present in the PFs throughout the temporal variation was only reached in the areas of NR and it was only for wasps. This suggests that planted reforestations have low ability to provide adequate conditions and resources required by the species present in the environment without disturbance. Although reforestations like fig and mixture of native species have better stabilities in their structures than teak, these environments present less environmental heterogeneity than the primary environments. This might have contributed to limited resource diversity through temporal variation which led to the establishment of a community with different requirements than those present PFs (Roubik 2001; Meléndez et al. 2016; Araújo et al. 2018b). The variation in species composition within habitats occurs because important resources are available at different times (Cane & Payne 1993). The high environmental heterogeneity of the Amazon forest allows for a great diversity of available resources throughout the temporal variation (Morato & Campos 2000), allowing the occurrence of species with specific requirements, such as specialized bees, regarding the use of the resource (Meléndez et al. 2016). Thus, areas of NR possibly have not yet been able to establish a heterogeneity that allows the occurrence of resources necessary to house a bee community similar to that of the PF as they were for the wasp community. Prey required by the wasps present in primary environments apparently are less affected by the variation of vegetation than pollen, nectar, and oil required by bees (Fye 1972; Araújo et al. 2018a; Araújo et al. 2019). Then, during the NR process, faster recovery of this group is expected than the floral resources, and the recovery of the resources used by bees in tropical forests may occur later.

Differences in species composition among habitats corroborate the hypothesis that the species turnover within the taxa increases with increasing environmental dissimilarity (Harrison et al. 1992), as in the case of the present study. New communities of bees and wasps were established in all reforestations with active planting of species. Our results highlight the importance of using the three diversity metrics present in our study (abundance, richness, and species composition) in the environmental assessment process. If we had drawn our conclusions only with the results of richness and abundance, we would probably conclude that reforestations were effective in the recovery process over the temporal variation, especially those using teak. However, the high turnover values obtained between reforestation and PF shows that these new environments are contributing to the reestablishment of communities of bees and wasps distinct from those present in the PF over time. The establishment of a new community and turnover dynamics in the temporal variation reflects that the reforestations are assuming characteristics different from those present in the PFs. It is known that during the ecological succession process there may be changes in the composition of the colonizing species due to the variation in the availability of resources and conditions throughout this period (Veddeler et al. 2005; Bragagnolo et al. 2007). However, we do not know if the variation in species composition found in our study is occurring due to the formation of new habitats created from the active planting of trees or if this

variation is due to the process of succession that is still occurring in these environments. Given the lower values of turnover and greater nestedness presented by wasp, the processes that ensure the recovery of this group seem faster recovered than bees. This corroborates with other studies that report that species of bees present in PF present greater sensitivity to environmental changes than wasps (Morato & Campos 2000; Batista Matos et al. 2013; Stangler & Hanson 2015; Araújo et al. 2018b).

Although climatic variation has exerted a strong effect on the colonization capacity of bees and wasps, the pattern of occupation of these insects over time was not influenced by the type of reforestation. An exception was the monodominant teak reforestation. The high variation within the structure of this treatment promotes low ability to ensure a constant dynamic of colonization by these insects in these environments, different from that expected in natural patterns. The increase of the temporal stability of reforested environments in Amazon forest may be favored by active planting of native tree species. Knowledge about the effectiveness of these novel environments in the recovery of biodiversity over time is still very scarce. Our study has indicated that different types of reforestation may present similar variations in the colonization capacity of bees and wasps, and the structure of these reforestations is the main factor that guarantees the success in the recovery of the natural composition of the community along the temporal variation.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Spatial correlograms showing the degree of spatial autocorrelation (Moran's I) among sites for each of the raw response measures for bees and wasps (a, c, e, and g), and the corresponding residuals of the final best-fit GLMM model appropriate to each response (b, d, f, and h).

**Table S1.** Parameter estimates from the generalized linear mixed model (GLMM) for each response variable: (a) wasp abundance, (b) wasp richness, (c) bee abundance, and (d) bee richness among site of the same category but different distances from Primary Forest.

**Table S2.** Wasp and bee compositional differences between sites from same category but different distances from Primary Forest through permutational multivariate analyses of variance (PERMANOVA).

**Table S3.** Mean climatic data value of the municipality of Cotriguaçu-MT, Brazil during August 2016 to July 2017 obtained on the website [https://rp5.ru/Weather\\_in\\_the\\_world](https://rp5.ru/Weather_in_the_world).

**Table S4.** Abundance of species of solitary bees and wasps that nested at different reforested forests in southeastern Amazonia between August 2016 and July 2017.

**Table S5.** The rescaled values of each month in terms of the principal component (PC1).

**Table S6.** Comparison of model likelihood for null, linear, and quadratic models of bee and wasp abundance and richness for *treatments* and *CVG* variables.

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