CONSERVATION ECOLOGY – ORIGINAL RESEARCH

Re-establishment of cavity-nesting bee and wasp communities along a reforestation gradient in southern Amazonia

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Abstract
Global initiatives to reforest degraded areas have intensified in recent years, in an attempt to reverse the environmental impacts of habitat loss on species and ecosystem provided by them. However, the effectiveness of such reforestation initiatives in re-establishing biodiversity is still poorly understood. Here, we test how reforestation type and intensity applied to deforested areas affect the reestablishment of communities of cavity-nesting bees and wasps. We deployed experimental trap-nests along a reforestation gradient of increasing structural similarity to primary forest, after 18 years of reforestation. We found that reestablishment, in terms of abundance and richness of both bees and wasps, was greatest at an intermediate point along the reforestation gradient. However, these communities were highly dissimilar to primary forest, and recovery of intact insect community composition was only achieved when reforestation was more similar in structure to natural forests. This effect was more pronounced for bees than for wasps. Our findings suggest that along the reforestation gradient, services provided by wasps will be more easily recovered than those provided by bees. Our results have important implications for the challenges of restoring and maintaining species biodiversity as well as their associated ecosystem services.

Keywords Ecosystem-services · Rainforest · Reforestation · Forest regeneration gradient · Pollination

Introduction

The global decline in biodiversity due to land-use intensification has reached alarming levels in recent years (Usubiaga-Liaño et al. 2019), particularly in tropical regions that have a high potential for agricultural productivity (Peters et al. 2019). In the Amazon rain forest, the largest and most diverse tropical forest in the world, thousands of hectares of primary forest are converted to crop land and livestock grazing every year (Lierop et al. 2015; Austin et al. 2017). While this provides short-term economic gain for the landholder, it comes at a longer-term socioeconomic cost of declining biodiversity and loss of ecosystem services (Balmford et al. 2011; Menzler-Hokkanen 2018). This will have direct impacts on human well-being, as these services are essential for the sustainable production of food and forestry product (Pinho et al. 2017). Therefore, there is a pressing need for the development and implementation of strategies that can promote the maintenance of biodiversity and its related ecosystem services (Chazdon 2013; Sloan and Sayer 2015).

To mitigate threats from historical land-use conversion, global initiatives aim to restore over 350 million hectares

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of deforested land by 2030 (Bonn Challenge 2019). However, the effectiveness of reforestation in the recovery of biodiversity and ecosystem functioning is still little studied (Majer 2009). Most restoration initiatives focus solely on re-creating vegetation structure and composition, and implicitly assume that animal communities will reassemble naturally (Derhé et al. 2016). Recovery of species interactions has only become a restoration target, in its own right, very recently (Audino et al. 2014). In many cases, the recovery of degraded areas may fail if the planted tree species or the reforestation processes used do not provide the resources necessary for the reintroduction of fauna and consequently the reestablishment of the networks of interactions necessary for the maintenance of these environments (Antonini et al. 2016; Araujo et al. 2018a; Brito et al. 2018).

The reestablishment of pollinators not only improves seed-set in flowering species but also increases the rate and spatial extent of out-crossing, with a consequent increase in the genetic variability of pollinated species (Camacho and Franke 2002). More than 100,000 species of animals are pollinators, but bees are recognized as being especially important in many systems (McGregor 1976; Kremen et al. 2002; Farinha 2015). Bees potentially pollinate up to 70% of all flowering species in the world (Klein et al. 2007), and in tropical forests these rates can reach up to 90% (Kerr et al. 1996). Bees are also key for agriculture since they contribute to food production in 75% of all cultivated species in the world (Klein et al. 2007). It is less well recognized, but wasps can also play an important role in pollination because adults also collect floral resources to supply their nutritional demands (Bohart and Menke 1976). However, the main role of this group is in the biological control of invertebrate species, many of which are considered pests in agricultural crops (Tylianakis et al. 2005; Buschini and Woiski 2008; Saunders 2016). The role of natural enemies has attracted a lot of attention in recent years, given the potential for sustainable biological control solutions in combating agricultural pests (van Lenteren et al. 2018; Tougeron and Tena 2019), rather than traditional chemical control (Desneux et al. 2007; Gill et al. 2012; Pignati et al. 2017).

Bees and wasps vary widely in terms of their behaviours, social organization (solitary, parasitic, or social), nesting habitat (users of pre-existing cavities, soil excavators or nest builders in exposed locations) and food diet (specialists or generalists) (Goulet and Huber 1993; Silveira and Almeida 2002). During and after reforestation, several factors may affect successful population establishment, such as prey availability, floral resource diversity, nesting sites and microclimatic conditions (Klein et al. 2002; Tylianakis et al. 2006; Rubene et al. 2015). Species nesting in natural cavities are more likely to establish when there is a greater availability of deadwood (Tscharntke et al. 1998). Solitary bees and wasps spend most of their adult lifetime building nests and provisioning resources for their offspring (Morato and Martins 2006). Thus, differences in forest structure, such as those caused by different types of reforestation during the forest recovery process, can have parallel cascading effects on the establishment and composition of bee and wasp communities (Araújo et al. 2018b).

Here we investigate how differences in forest structure along a gradient of reforestation approaches affect the establishment of cavity-nesting bees and wasps that have different food requirements, but similar nesting habits. We expect that as reforested areas become more similar to natural conditions, both bee and wasp abundance and richness will increase, but with varying community-level responses between the two groups. We predict that bee communities will recover more slowly along the gradient of reforestation. Although they feed exclusively on plants (primary producers) the availability of specific food resources required by some species occurs in environments with a more complex structure. By contrast, for wasp communities we predict that food resources will increase more quickly along the reforestation gradient since the reestablishment of vegetation cover allows rapid colonization of arthropod prey species (primary and secondary consumers). Consequently, we predict that the degree of community dissimilarity between reforested areas and natural forests will diminish more rapidly for wasps than for bees, with a corresponding shift from species replacement processes to nestedness processes as the dominant drivers of species turnover. Our results have important implications for strategies for the recovery and conservation of ecosystem services such as pollination and biological control in human-modified landscapes.

Materials and methods

Study area

We selected sampling sites to reflect a gradient of reforested habitats at São Nicolau farm (9°48′S 58°15′W, elevation 254 m above sea level), located in the southern Amazonia in the municipality of Cotriguaçu, Mato Grosso, Brazil. The farm covers 10,000 ha, of which 7200 ha remains as primary forest, 300 ha was converted to pasture for cattle grazing, 2000 ha had been cleared and re-planted 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 2300 mm of precipitation. The original phytophysiognomy is the Tropical
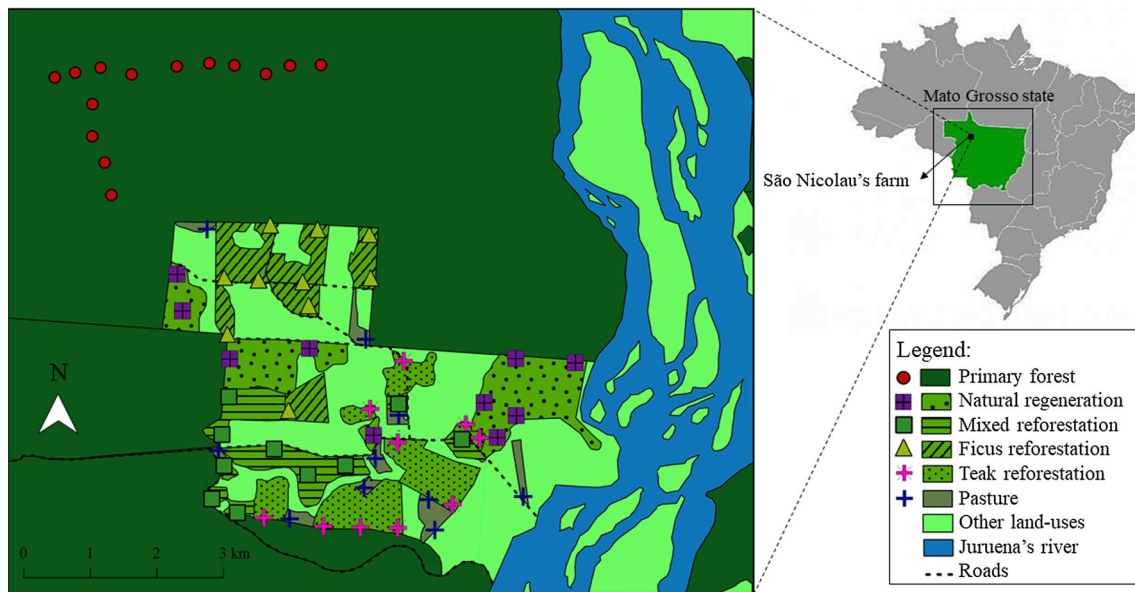
Fig. 1 Map showing the spatial arrangement of the 64 sampling sites established in six different habitat types at the São Nicolau farm, municipality of Cotriguaçu, State of Mato Grosso, Brazil: pasture, teak reforestation, fig reforestation, mixed reforestation, natural regeneration and primary forest

Open Ombrophilous Forest, Submontane formation with Palmeiras (Rodrigues et al. 2011).

Experimental design

We classified vegetation cover into six broad treatment categories, ranging from completely cleared to completely intact. We recognise there is a gradient of tree cover and forest structure within these categories, but we used them only for site selection in a stratified random manner, to ensure complete coverage of the reforestation gradient. The six forest cover types were: (1) pasture (PA) dominated by pasture grasses (not more than 50 cm tall; (2) teak reforestation (TR) consisting of monodominant stands of the exotic *Tectona grandis* (Verbenaceae); (3) fig reforestation (FR) consisting of monodominant stands of the native *Ficus maxima* (Moraceae); (4) mixed reforestation (MR) consisting of planted native tree species; (5) secondary regeneration (SR) without cattle or anthropogenic interference, where vegetation has recovered naturally; and (6) primary forest (PF) consisting of undisturbed primary forest that we used as the reference habitat. 'Other' non-treatment land uses in the study area (Fig. 1) included various additional types of reforestation using different combinations of tree species, as well as conservation protection zones. For detailed information see (Araújo et al. 2020).

Within each of the six forest cover categories, we randomly selected 10 sampling sites ($n = 14$ in the case of the primary forest) based on feasibility of access and logistical constraints (64 sites in total, see Fig. 1). To minimise spatial

dependence among sites, all sampling sites of the same category were at least 500 m apart, based on the typical foraging distances estimated for cavity-nesting bees and wasps (Klein et al. 2004; Zurbuchen et al. 2010). The distance of 500 m was also maintained, whenever possible, between treatments of different categories, but due to spatial limitations six sites had pairwise distances to another nearby site that were less than 500 m (ranging from 375 to 450 m). Site replicates of each habitat type were spatially interspersed among replicates of all other degraded forest types (Fig. 1), but this was not possible for primary forest sites due to logistical issues with permission for site access. To address this issue, all statistical analyses incorporated explicit tests of spatial autocorrelation.

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) at least 50 m from the nearest habitat edge. Trap-nests were covered with a plastic rain cover and placed at a height of 1.5 m above the ground attached to trees (in pasture, the trap-nests were attached to wooden stakes) (Tylianakis et al. 2006).

Trap-nest design and sampling

Each trap-nest consisted of one block (30 cm length × 7 cm height × 12 cm width) made of wood (*Cedrela 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).

Black paperboard tubes were inserted into each hole to create a removable sleeve (Araújo et al. 2018b).

We recognize that different species of cavity-nesting bees and wasps prefer holes of widely varying diameters. Therefore, to provide artificial nests that could be occupied by a diverse array of species, we chose a range of diameters from 8 to 20 mm based on the findings from past trap nest studies of these taxa in the tropics (Araújo et al. 2018b; da Rocha-Filho et al. 2017; Flores et al. 2018; Klein et al. 2002; Morato and Campos 2000). We did not expect this range of hole diameters to sample all species present, as our goal was not a complete inventory of the fauna, but instead was designed to be highly standardised across treatment comparisons. Across all sites, a total of 320 trap-nests were placed out, containing 12,800 nest tubes.

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 °C 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 "Acknowledgements"). The voucher specimens were deposited in the Invertebrate Collection of the Universidade Federal of Mato Grosso, Brazil.

Vegetation structure

At each of the 64 sites we marked out a 10×10 m plot in which we measured five components of vegetation structure: tree abundance (i.e., number of individuals with a diameter at breast height [DBH] greater than or equal to 15 cm), tree richness (i.e., number of species), shrub abundance (i.e., number of individuals with DBH less than 15 cm), shrub richness, and average height of trees.

Statistical analyses

Quantifying the forest structure gradient across sites

We used the five measures of vegetation structure described above to construct a single composite variable representing the gradient of variation in forest structure across the 64 sites. For this, we mean-centred and standardized vegetation structure measurements due to differences in unit scales of measure, and performed a correlation-based Principal Components Analysis (PCA) using the function 'prcomp' in the 'stats' package in R v.3.5.2 (R Core Team 2018). We used the values of the first axis of the PCA (PC1) as a composite

variable representing the position of each of the 64 sites along a reforestation gradient (RG). For the purposes of analysis, we rescaled the minimum and maximum PC1 scores to a scale of 0 to 10, which does not alter the relative dissimilarity in forest structure among sites.

Testing variation in the abundance and richness of solitary bees and wasps along the reforestation gradient

For the purposes of univariate analyses, repeated samples through time were pooled into a single value per trap-nest (given the very high number of zero values in some seasonal samples). To evaluate the completeness of sampling across treatments, we constructed collector curves and extrapolated the nest-trap sampling effort ($n = 10$) for all treatments using the iNEXT function of the iNEXT package (Hsieh et al. 2019) in R. We tested the effect of the reforestation gradient on abundance and richness of bees and wasps (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. 2014). In the full model for each response variable, we specified a fixed polynomial effect of the reforestation gradient (i.e., including a quadratic term in the regression function) to account for potential non-uniformity in response. In the richness models, we also specified a 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' ($n = 64$) to account for the non-independence 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.

In our study area, we recognize that the proximity of different land-use types (in a mosaic around the reforestation treatment type) could influence the occupation of trap nests by bees and wasps. To take this potential effect into account, we generated circular buffers (250 m radius) around each trap nest location and performed a supervised land-use classification of the images, using the Bhattacharya classifier to quantify the land use area of the following classes: teak reforestation, ficus reforestation, mixed reforestation, natural regeneration, pasture, and primary forest. Using forest regeneration values (PCA values) as a measure to assess the influence of the proportion of adjacent land uses within the buffer area, we create a weighted average value considering the proportion of land use area present around the respective trap nests site, which we call 'surrounding land-use context'. We performed the procedures of mosaic, segmentation, and classification of images in the SPRING 5.3 software and the extraction of landscape metrics in ArcGis 10.5 software. We included 'surrounding land use context' as a covariate in

alternative model fitting, to evaluate if land-use context had complementary or confounding effects on the interpretation of forest regeneration models.

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 and Linden 2019). We determined the minimum adequate model(s) by comparing Akaike Information Criterion corrected (AICc) values and AICc weights (AICcWt) for sub-models consisting of (1) the polynomial RG model, (2) the polynomial RG + surrounding land-use context alternative model, (3) a linear RG model, (4) a linear RG + surrounding land-use context alternative model or (5) a null, intercept-only model. Models within 2 ΔAICc 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 and 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 (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).

Testing variation in community composition along the reforestation gradient

For the purposes of multivariate analyses, we pooled species abundance data for all five trap-nests per site to create a single community-level sample for each of the 64 sampling sites. To investigate changes in the composition of bee and wasp communities along the reforestation gradient, a species dissimilarity matrix based on the Bray–Curtis distance metric was calculated among the 64 sampling sites (Legendre and De Cáceres 2013). From this, we calculated the average pairwise dissimilarity of each sample to the centroid of the primary forest (control) samples using the function 'vegdist' in the 'vegan' v.5-5 package (Oksanen et al. 2019). This response measure, therefore, reflects 'dissimilarity to primary forest' in terms of species composition.

We tested the effect of the reforestation gradient on bee and wasp 'dissimilarity to primary forest' using separate linear models (LMs) with a gaussian error structure (and identity-link function). We specified a fixed polynomial effect of the reforestation gradient and as described above we carried out model simplification using AIC comparisons of polynomial, linear and null sub-models. Finally, we estimated the coefficient of determination of final models using the 'rsq' v.1.1 package (Zhang 2018).

When we found significant variability in community dissimilarity along the reforestation gradient, we partitioned

total community dissimilarity into two components of turnover and nestedness: (1) 'balanced variation in abundances', which is analogous to species replacement in incidence-based patterns, and (2) 'abundance gradients', which is analogous to nestedness in incidence-based patterns (dBC-bal and dBC-gra, respectively) (Baselga 2013). We calculated the components of beta diversity taking the *average* of habitat samples in pairwise comparisons with primary forest samples (as the reference control). To evaluate the components of beta diversity of bees and wasps we used the betapart package v1.4-1 (Baselga and Orme 2012). As before, we tested the effect of the RG on the components of beta diversity (dBC-bal and dBC-gra) using the same LM model approach as described above.

In the final model for all univariate and multivariate responses, we assessed potential spatial autocorrelation in raw response values and in the residuals of the final best-fit models, by calculating spatial correlograms for Moran's I values in the 'ncf' v.1.2-6 package (Bjornstad and Jun Cai 2018). This approach tests for any systematic spatial dependence in the data that cannot be explained by fixed predictor effects in the model (Elith and Leathwick 2009).

Results

Quantifying the FRG across sites

The PCA ordination based on five vegetation structure variables produced a strong gradient of variation in forest structure across forest types (Fig. 2). A two-dimensional representation of the data explained 81.2% of the variation in vegetation structure among the sites and described a dominant gradient along PCA axis 1 from pasture sites, to Teak, Fig, and mixed reforestation sites, and then natural secondary regeneration and primary forest sites (Fig. 2). Eigenvectors for PCA axis 1 (Tables S1 and S2) indicated that this gradient was characterized by a composite measure of increasing tree abundance, tree richness, shrub abundance, shrub richness, and tree height (Fig. S1).

The cavity-nesting fauna

From the total of 12,800 artificial cavities available for nesting during the study period, 2143 (16.74%) were occupied by solitary bees or wasps. We recorded 26 wasp species (3525 individuals emerging from 1813 nests) belonging to the families Crabronidae, Pompilidae, Sphecidae and Vespidae, and 14 bee species (1286 individuals emerging from 330 nests) belonging to the families Apidae and Megachilidae (Table 1, Fig. S2). Vespidae and Apidae were the families with the greatest number of species (nine and 11 species, respectively), and together represented 50% of the
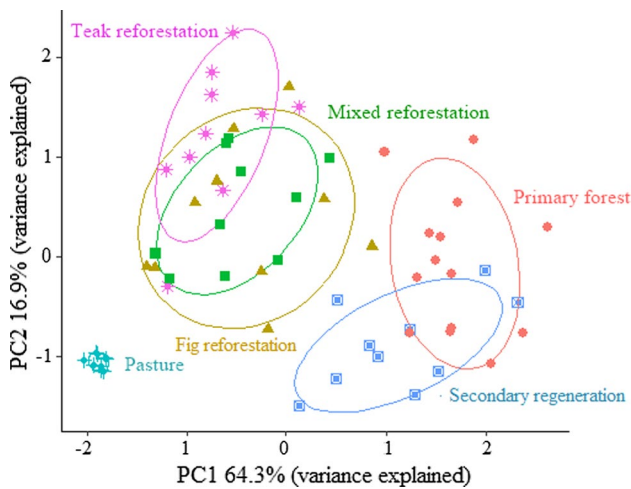
Fig. 2 Biplot of Principal Components Analysis (PCA) axes 1 and 2 showing the gradient of variation in forest structure across the reforestation treatments (see Table S2 for eigenvalues). Forest structure varies strongly along PC1 (left to right) with the change in the type of reforestation from open pasture, to teak, fig, and mixed reforestation treatments, to higher-intensity secondary regeneration and primary forest. We refer to this gradient along PC1 as the 'reforestation gradient'. Ellipses are for illustrative purposes only

total number of nesting species. Crabronidae was the family with the greatest number of occupied cavities (623), followed by Pompilidae and Sphecidae (both with 497), totaling 52.26% of all nests.

Effects of the reforestation gradient on abundance and richness of bees and wasps

Abundance per trap-nest varied significantly among habitat types for both bees and wasps, but there was no simple monotonic relationship along the forest regeneration gradient (Fig. 3a, b). Instead, the best-fit GLMM model for both bee abundance (AICc weight = 0.90, Table S3) and wasp abundance (AICc weight = 1.00, Table S3) was a hump-shaped (quadratic) relationship (Fig. 3, Table 2, Table S3), indicating that highest abundance per trap-nest was found at intermediate levels of reforestation, such as in mixed reforestation and natural secondary regeneration sites (Fig. 3). The inclusion of 'surrounding land-use context' as a covariate in the models for an abundance of bees and wasps, as well as the best fit-models found for the other response variables, did not change the best-fit model (Table S3).

Species richness trends for both bees (AICc weight = 0.98, Fig. 3c, Table S3) and wasps (AICc weight = 1.00, Fig. 3d, Table S3) mirrored the hump-shaped relationships along the reforestation 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 2). Independent of sample abundance effects, richness was significantly higher at intermediate levels of forest regeneration (Table 2, Table S3), such as in mixed reforestation and natural secondary regeneration sites (Fig. 3).

Bee and wasp compositional responses

Both bee and wasp communities showed significant variation in community 'dissimilarity to primary forest' along the reforestation gradient (Fig. 4a, b). For bees, stochastic variation among sites was high, and even within the primary forest the local scale site-to-site dissimilarity was ca 70—90%. Nevertheless, there was still statistical evidence that compositional dissimilarity declined significantly among habitat types as well, from ca 92% on average in the pasture to ca 82% on average in the natural secondary and primary forest along with the RG (Fig. 4a). The reforestation gradient trend was best explained by the linear LM model (AICc weight = 0.70, Table 2, Table S3). For wasps, the quadratic model was a significantly better fit to the data (AICc weight = 1.00, Table 2, Table S3), and community dissimilarity to primary forest declined dramatically from > 90% in pasture habitats to < 30% in natural secondary habitats and among sites within the primary forest (Fig. 4b).

Partitioning the components of total community dissimilarity showed that variation in composition was predominantly explained by species replacement processes (dBC-bal) rather than nestedness (dBC-gra) for both bees and wasps (Fig. 4c–f). More importantly, the relative components of dissimilarity varied significantly, themselves, across the reforestation gradient (Table S3). In bee communities, dissimilarity was dominated by turnover (ca 80–90% on average; Fig. 4c), with pasture and primary forest sites at the two ends of the reforestation gradient showing the highest values, while reforested sites at intermediate points along the RG had significantly lower turnover (quadratic LM, AICc weight = 0.61; Table S3, Fig. 4c). By comparison, nestedness had only a minor contribution to total dissimilarity (ca 5–20% on average, Fig. 4E), but values still increased significantly along with the RG (linear LM, AICc weight = 0.64, Table S3, Fig. 4D).

In wasp communities, turnover also explained most of beta diversity (37%), albeit to a lesser degree than for bees, whereas nestedness explained just 27%. However, only turnover was related (negatively) to the reforestation gradient (quadratic LM, AICc weight = 0.6, Table S3, Fig. 4e). The nestedness component did not show significant variation along the reforestation gradient (the linear LM had the greatest weight, AICc weight = 0.42, Table S3, but the reforestation gradient coefficient was not significantly different from zero, $t = -1.481$, $p = 0.14$, Table 2, Fig. 4f).

Table 1 Abundances of each species of solitary bee and wasp nesting in different habitat types along the reforestation gradient in southern Amazonia between August 2016 and July 2017

	Family	Species	Habitats					
			PA	TR	FR	MR	NR	PF
Bees	Apidae	*Centris* (*Hemisiella*) *tarsata* Smith, 1874				10		
		Centris (*Hemisiella*) *trigonoides* Lepeletier, 1841		51	8	10	1	47
		Centris (*Heterocentris*) *analis* (Fabricius, 1804)					22	6
		Euglossa (*Euglossa*) *cognata* Moure, 1970					19	
		Euglossa chlorina Dressler, 1982		16		24		6
		Euglossa despecta Moure, 1968		15		4		20
		Euglossa (*Euglossa*) *townsendi* Cockerell, 1904			21			8
		Tetrapedia sp1		4	9	9	6	19
		Tetrapedia sp2					3	3
	Megachilidae	*Anthodioctes vilhenae* Urban, 1999	15	260	208	136	31	12
		Megachile (*Austromegachile*) *sejuncta* Cockerell, 1927		3				14
		Megachile (*Chrysosarus*) sp.		8		12	28	
		Megachile (*Chrysosarus*) *turpis* Mitchell 1930	4	10	6	49	9	20
		Megachile (*Melanosarus*) *brasiliensis* Dalla Torre, 1896		107	8		1	
Wasps	Crabronidae	*Trypoxylon* (*Trypargilum*) *lactitarse* Saussure, 1867	10	180	75	170	154	250
		Trypoxylon nitidum nitidum F. Smith, 1856	18	111	42	86	101	71
		Trypoxylon punctivertex Richards, 1934	11	41	36	9	22	55
		Trypoxylon xanthandrum Richards, 1934					4	2
		Trypoxylon (*Trypoxylon*) *asuncicola* Strand, 1910					4	2
	Pompilidae	*Auplopus sp1*		108	7	33	12	35
		Auplopus sp2		40	27	29	13	52
		Priochilus sp1		48	136	63	88	202
		Priochilus sp2			24	11		1
	Sphecidae	*Podium agile* Kohl, 1902						1
		Podium foxii Kohl, 1902						2
		Podium rufipes Fabricius 1804	1	69	16	77	130	332
		Penepodium egregium (Saussure, 1867)					3	
		Penepodium goryanum (Lepeletier 1845)		2	1			2
		Isodontia sp.			4	5	7	7
	Vespidae	*Monobia angulosa* Saussure			3	4		3
		Pachodynerus argentipilis Willink & Roig-Alsina, 1998		2		16		
		Pachodynerus brevithorax (Saussure, 1852)		5				
		Pachodynerus gianelli (Gribodo, 1891)					9	
		Pachodynerus grandis Willink & Roig-Alsina, 1998		4		11		4
		Pachodynerus guadulpensis (Saussure, 1853)		10		9	23	11
		Pachodynerus nasidens (Latreille, 1812)	6	77	10	10	11	4
		Parazumia surinama (von Schulihess, 1903)					4	
		Zethus alessandroi Lopes, 2015						12
		Zethus proximus Fox, 1899	3	54				7
		Zethus smithii (de Saussure, 1855)		35	2	15	21	95
		Total abundance	68	1260	650	802	726	1305
		Total richness	8	24	19	23	25	31

PA pasture, *TR* teak reforestation, *FR* fig reforestation, *MR* mixed reforestation, *SR* secondary regeneration, *PF* primary forest

(A) Bees

(B) Wasps

(C)

(D)

Forest regeneration gradient

Treatments:

+ Pasture ✳ Teak reforestation ▲ Fig reforestation ■ Mixed reforestation ⊠ Secondary regeneration ✹ Primary forest
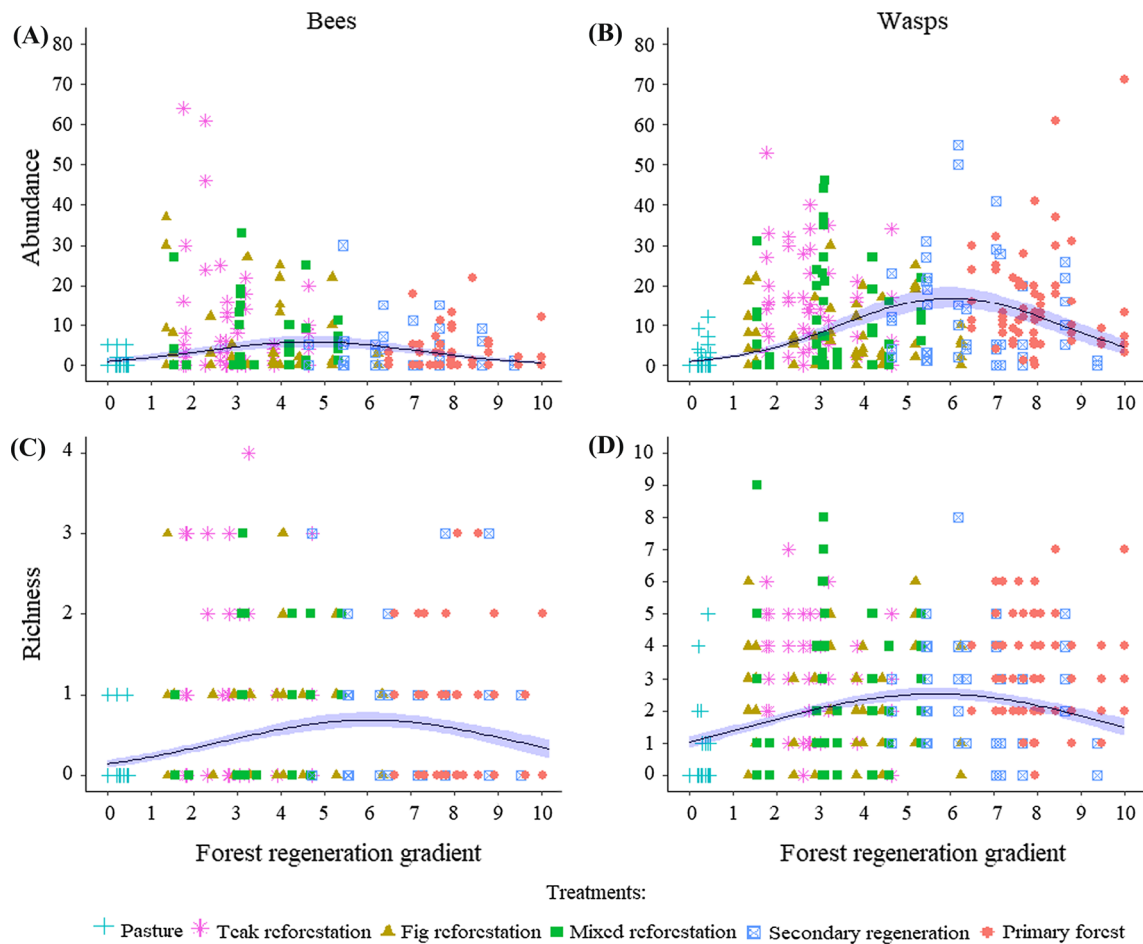
Fig. 3 Variation in **a** bee abundance, **b** wasp abundance, **c** bee richness and **d** wasp richness along the reforestation gradient (re-scaled PCA axis 1 values; see Fig. 2). Note the varying y-axis scales for richness. Fitted lines represent the mean (± SE) estimated from the final best-fit GLMM model using the 'predict' function in R, while holding significant covariate effects constant at their mean value

Analysis of spatial autocorrelation

In the bee univariate and multivariate analyses, there was no significant spatial autocorrelation of responses that was not already accounted for by the predictor variables in our models (i.e., no spatial autocorrelation of model residuals; Fig. S3). In the wasp analyses, however, we found significant spatial autocorrelation of model residuals for species richness and for turnover (dBC-bal) (Fig. S4). For the wasp richness model, richness values were more similar than expected by chance alone for sites < 500 m apart, and less similar than expected by chance alone for sites > 8000 m apart. For the wasp turnover model, dBC-bal values were less similar than expected by chance alone for sites > 9000 m apart (Fig. S4). Together, these results suggest, first, that the closer proximity of a few adjacent treatment replicates and, second, more-distant spatial separation of the primary forest sites from the regenerating sites in our sampling design, explain a portion of the deviance in two of the wasp response models.

Discussion

Restoration of functioning forest ecosystems requires the reassembly of diverse networks of interacting organisms, not just the replanting of vegetation. Across a reforestation gradient (RG) in southern Amazonia, we found that cavity-nesting bee and wasp communities benefited from reforestation, but recovery of abundance, richness and composition did not always increase monotonically with the reforestation process, nor respond in a similar manner between different functional groups of bees and wasps. We discuss the functional significance of these findings in the context of conserving and restoring insect biodiversity and ecosystem services within degraded tropical landscapes.

An important initial finding, albeit one that is broadly recognized across many study systems (Araújo et al. 2018b, 2019; Flores et al. 2018; Kruess and Tscharntke 2002), is that the nesting rate of solitary bees and wasps is extremely low in severely impacted and/or strongly simplified habitats,

Table 2 Parameter estimates from the final best-fit generalised linear mixed model (GLMM) or linear model (LM) model (as appropriate) for each response variable: (a) bee abundance, (b) bee richness, (c) bee community dissimilarity, (d) bee community turnover (dBC-bal), (e) bee community nestedness (dBC-gra), (f) wasp abundance, (g) wasp richness, (h) wasp community dissimilarity, (i) wasp community turnover and (j) wasp community nestedness (dBC-gra)

Response variable	Intercept [± SE]	RG [± SE]	Quadratic term	Cov. abundance [± SE]	R^2 GLMM (M)	R^2 GLMM (C)	R^2 GLM
Bees							
(a) Abundance	− 0.034 [± 0.590]	**0.761** [± 0.240]	**− 0.080** [± 0.020]	–	14%	22%	–
(b) Richness	− 2.189 [± 0.340]	**0.531** [± 0.140]	**− 0.044** [± 0.010]	0.058 [± 0.005]	31%	39%	–
(c) Community dissimilarity	0.927 [± 0.020]	**0.010** [± 0.003]	–	–	–	–	13%
(d) Turnover	0.866 [± 0.050]	**0.046** [± 0.020]	**0.005** [± 0.002]	–	–	–	11%
(e) Nestedness	0.064 [± 0.030]	**0.016** [± 0.007]	–	–	–	–	10%
Wasps							
(f) Abundance	− 0.120 [± 0.320]	**0.981** [± 0.150]	**− 0.081** [± 0.010]	–	38%	66%	–
(g) Richness	0.332 [± 0.170]	**0.313** [± 0.070]	**− 0.027** [± 0.010]	0.033 [± 0.002]	43%	51%	–
(h) Community dissimilarity	0.953 [± 0.050]	**0.191** [± 0.020]	**0.012** [± 0.002]	–	–	–	71%
(i) Turnover	0.588 [± 0.040]	**0.072** [± 0.020]	0.004 [± 0.002]	–	–	–	35%
(j) Nestedness	0.332 [± 0.040]	0.011 [± 0.007]	–	–	–	–	3%

RG linear coefficient of the fitted reforestation gradient, *Cov.* covariate, *SE* standard error; *R2* coefficient of determination (for GLMM shown as both marginal, M, and conditional, C, values). Bold values mean *p*-value < 0.05

such as pasture (nest occupancy rates approximately ten times lower than typical in adjacent forested systems). Reforestation of pasture habitats with any form of woody vegetation, regardless of tree species composition or structure, resulted in a marked increase in the abundance and richness of bees and wasps in trap-nests. Here, we are implicitly assuming that higher trap-nest occupancy corresponds with higher abundance in the environment. However, we did not measure the frequency of cavity nesting in natural substrates in our study. One caveat is that a greater availability of naturally occurring cavities could reduce occupancy in artificial nests. We suspect this is unlikely to be responsible for the low trap-nest occupancy in degraded pasture habitats, because our anecdotal observations suggested that naturally occurring cavities are likely to be rare, rather than common, in pasture. Forest environments, on the other hand, are likely to have greater food resources and nesting site availability (Matos et al. 2016; Flores et al. 2018). All other things being equal, then, we expect that trap-nest occupancy is a reasonable proxy for abundance at a site, but will be influenced by variation in a wide range of factors including nest site availability and environmental conditions that affect the colonization of bees and wasps (Hilário et al. 2012; Araújo et al. 2020).

Among the forested habitat types, ranging from exotic teak plantations to natural regeneration and primary rainforest, our initial prediction was that abundance and richness of bees and wasps would increase in direct proportion to the degree of recovery of vegetation structure along the reforestation gradient. The observed findings were quite different from our prediction. We found that abundance and richness, of both bees and wasps, increased linearly up to a peak at intermediate levels of the reforestation gradient, typical of mixed reforestation and natural secondary regeneration, but then decreased at higher levels of the reforestation gradient, typical of primary forest. This hump-shaped trend of greatest bee and wasp trap-nesting success in environments with intermediate levels of disturbance has also been found in other studies (Tylianakis et al. 2006; Buschini and Woiski 2008; Gikungu et al. 2015; Araújo et al. 2018). We suggest that the variation in abundance and richness of bees and wasps along the reforestation gradient reflects variation in the availability of food resources and the suitability of habitat structure. Structurally simplified environments, such as pasture habitats and exotic monoculture forests of fig and teak, may have comparatively low environmental suitability for re-establishing bees and wasps that nest in cavities (Gathmann and Tscharntke 2002; Flores et al. 2018). Abundance and richness were particularly variable in teak plantations, however, which previous studies have shown was related to strong heterogeneity in resource pulses associated with leaf and flowering phenology (Araújo et al. 2020). On the other hand, in more structurally complex types of reforestation with open canopies (e.g., mixed reforestation and natural regeneration) the high light penetration to the forest floor allows a greater development of ruderal plants over time (Buschini and Woiski 2008; Evans et al. 2018;
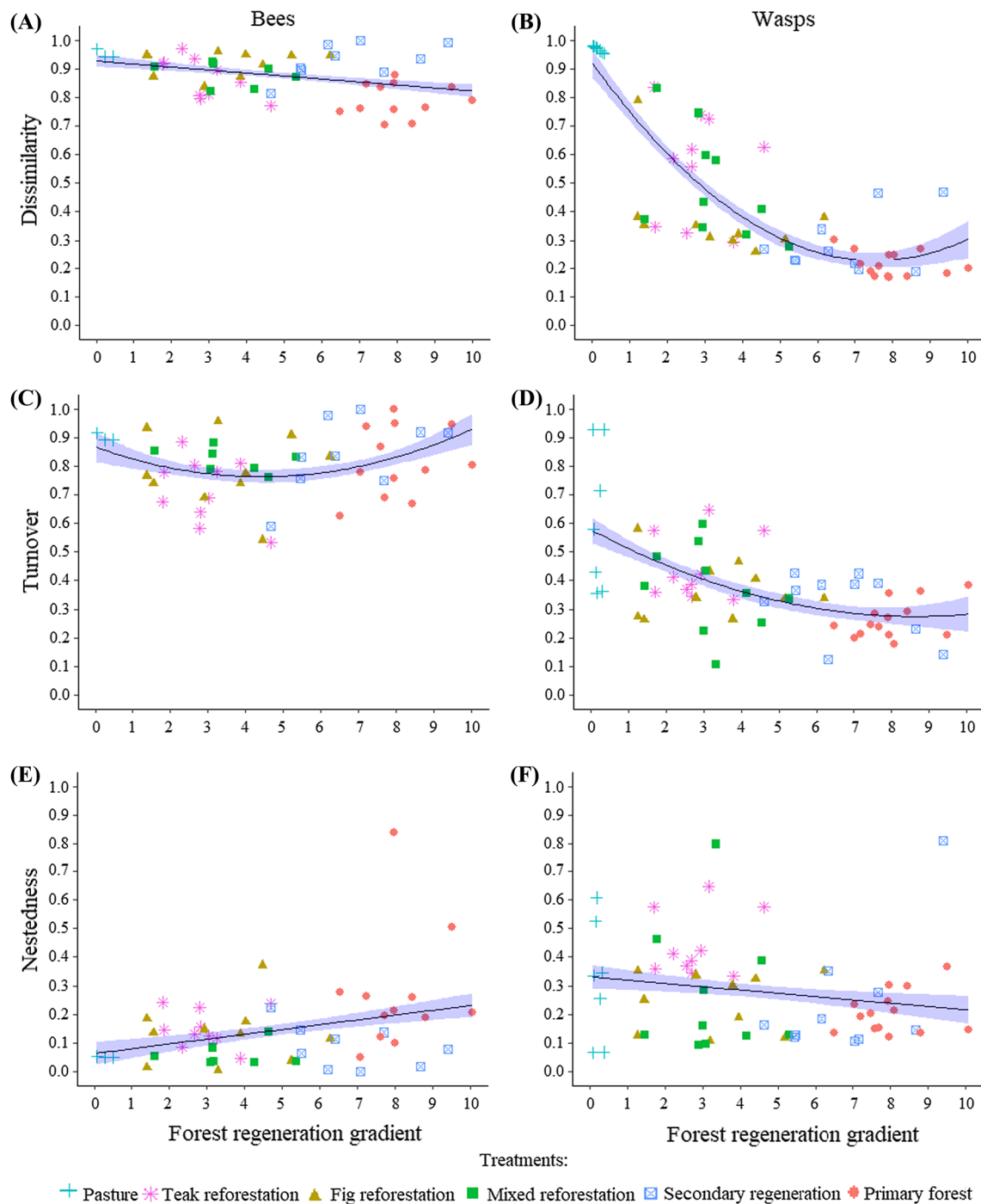
Fig. 4 Variation in **a** bee community dissimilarity, **b** wasp community dissimilarity, and partitioned components of **c** bee species turnover, **d** wasp species turnover, **e** bee nestedness and **f** wasp nestedness along the reforestation gradient (re-scaled PCA axis 1 values; see

Fig. 2). Note the varying y-axis scales. Fitted lines represent the mean (± SE) estimated from the final best-fit GLMM model using the 'predict' function in R

Araújo et al. 2020). Because of their ability to supply pollen and nectar to various species of bees, wasps and their prey, the high occurrence of ruderal plants could favor these insects more in regenerating forests than the primary forests (Fye 1972; Araújo et al. 2018, 2019).

Although intermediate levels of reforestation apparently provided optimal conditions in terms of the abundance and richness of nesting bees and wasps, this does not take into account the identities of the colonizing species. Reforestation may still impose restrictions on community reassembly

processes if rare or specialist primary forest species fail to establish, which appeared to be the case in our data. Our measure of bee and wasp compositional dissimilarity to primary forest showed a monotonic decline with increasing forest structural complexity along the reforestation gradient. The higher dissimilarity among bee and wasp communities in more simplified environments is likely caused by a reduction in plant diversity and a consequent reduction in the variety of food resources and nesting structures (Ebeling et al. 2012; Antonini et al. 2016). As such, we might expect these environments to be occupied by species with fewer food and environmental restrictions, such as generalist species. Previous studies have also found that these types of changes in the structure of bee and wasp communities in simplified habitats can lead to changes in ecosystem functions (predation by wasps and pollination by bees) (Ebeling et al. 2012). Therefore, the degree of recovery of forest structure is likely to be a strong predictor of not only the recovery of community composition in bees and wasps but also their associated ecosystem services (Araújo et al. 2018b; Flores et al. 2018), although we do not have functional rate measures for our system.

Community responses to reforestation varied markedly between bees and wasps. For bees, community reassembly was not strongly associated with forest structural similarity to primary forest. However, the power to detect such changes is admittedly low in our data set due to the low abundance of bees in our samples, which is a common pattern across tropical regions using the trap nesting methodology (Araújo et al. 2018b; Loyola and Martins 2006, 2011; Flores et al. 2018; Wilson et al. 2020). Substantially more sampling effort would be required for bees to provide greater statistical power. Another possibility for future studies is that an even broader range of cavity diameters might be required to effectively sample the fauna in this region since some small solitary bees may have a preference for small hole diameters and may not use larger existing cavities that would require greater resource expenditure in nest building (Krombein 1967). For wasps, community reassembly was much more rapid with increasing forest structural complexity, than for bees. Wasp community dissimilarity declined sharply from low to intermediate levels of reforestation, with mixed reforestation and natural secondary regeneration having wasp communities that were extremely similar to those in primary forest. This suggests that wasp community responses to reforestation are more rapid than for bee communities. Some studies with solitary bees and wasps show that tree species composition is not the main factor affecting the choice of nesting sites for these groups (Morato and Martins 2006). Certainly, this may be true for predatory wasps, but not necessarily for many species of bees that demand specific resources (e.g., oligolectic bees) (Loyola

and Martins 2008). Even though wasps might feed on particular prey, such as spiders, caterpillars, cockroaches and grasshoppers (Krombein 1967), they tend to be relatively generalist in predating a broad range of species within these groups. This almost certainly allows them to colonize and survive in habitats with a much broader range of conditions and resources than bees, which are more directly dependent on floral resources that often have a narrow window of temporal availability (Tscharntke et al. 1998; Villanueva-Gutierrez and Roubik 2004). Therefore, for bees, the restrictions may be greater in their choice of nesting sites. Taken together, this suggests that different approaches (and degrees of intensity) of habitat restoration will have differing effects on the recovery of functional groups within insect communities (Araújo et al. 2018b, 2019). Hence, some ecosystem services (e.g., biological control) are probably more rapidly established than others (e.g., pollination).

The patterns of faunal dissimilarity that we observed among sites were predominantly determined by species replacement processes (in which community change is driven by varying species preferences for distinct habitats or environments), rather than by nestedness processes (for instance, progressive loss of species that are most sensitive to disturbance, without replacement by new species). However, the relative magnitude of this difference varied between bees and wasps, and across the reforestation gradient. For bees, the degree of turnover, relative to nestedness, was substantially higher than for wasps. Moreover, the degree of nestedness in bee community composition increased along the reforestation gradient, as we had predicted, but this was not matched by a corresponding monotonic decline in the relative contribution of species turnover. Instead, there was a complex U-shaped trend in turnover along the reforestation gradient. Potentially this might stem from relatively high community heterogeneity within primary and secondary forest habitats, and/or relatively low sample abundances. Natural forests provide a larger variety of microhabitats and possibly greater availability of natural cavities that may allow species with different resource requirements to co-occur, such as specialist species (Tylianakis et al. 2005; Flores et al. 2018). In fact, many bee species are specialized on a small number of plants (Villanueva-Gutierrez and Roubik 2004). So, we suggest that the greater turnover from site to site within primary and secondary forest habitats may be due to the greater capability to provide resources for more specialized species, although this remains to be tested. For wasps, the relative contribution of turnover processes was higher in relation to nestedness but differed once again from our expectations, as both components of beta-diversity declined monotonically with increasing forest regeneration. This suggests that wasp turnover is comparatively low between habitats (compared to bee communities), and at least among the

more structurally complex reforestation types wasp communities are largely subsets of the same species found in primary forest.

Our findings have important implications for restoration management in degraded tropical landscapes. Deforested pastures and re-planted sites with highly simplified forest structure, such as teak and fig reforestation, provide a low diversity of food and nesting resources, culminating in a low potential for the effective recovery of bee and wasp communities. In many ways, our study site also represented a 'best-case scenario', in the sense that the restoration sites were all relatively close in proximity to unmodified continuous forest sites. In other regions of the tropics in which degraded areas are many times larger in extent, the restoration outcomes may be even worse. Unfortunately, reforestation schemes focus predominantly on these types of monocultures, or on low diversity tree assemblages, that promote the rapid establishment of vegetation cover (Lugo 1992) at the expense of potential long-term biodiversity value. We suggest that greater importance must be placed on the choice of the tree species involved since this can alter the dynamics of ecological succession and determine the reassembly trajectory of associated faunal communities (Chazdon and Guariguata 2016). It was notable that even in the mixed reforestation habitats, the re-planting of a considerable number of native tree species was still not comparable to natural secondary succession. This suggests that special attention should be given to the characteristics of planted species that might be more conducive to establishing conditions that facilitate natural plant recruitment. Highly structured habitats (with greater richness, abundance, and three-dimensional complexity) will provide a greater long-term benefit for the conservation of solitary bees and wasps, and the ecosystem services provided by them (Araújo et al. 2018b). These same benefits have also been shown to extend to a wide range of other taxa, in other studies (Steffan-dewenter et al. 1997; Lassau et al. 2005; Paolucci et al. 2017). Thus, although reforestation through natural regeneration processes may not present satisfactory short-term recovery of tree cover, compared with manual re-planting (Aide et al. 1995, 1996), they tend to be more efficient in the medium- to longer-term for re-establishing a more diverse fauna and flora (Aide et al. 1995). Our study showed that after about 17 years of forest recovery, naturally recovered habitats were more effective in re-establishing natural wasp communities than planted forest sites. From a management perspective, natural regeneration is also an attractive strategy in the recovery of degraded areas due to the low costs involved (Chazdon and Guariguata 2016). In our study, the relatively close proximity to continuous forest certainly contributed to successful community re-assembly. In sites that are more distant from propagule sources, the active mixed planting of natural species may be the most favourable approach for environmental recovery. Thus, the choice of approach needs to be selected with much caution, taking into account the history of land use, the availability of seed banks and the arrival of propagules from colonizing sources.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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