

Successional dynamics of the bee community in a tropical dry forest: Insights from taxonomy and functional ecology

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Abstract

Despite the recent rapid growth of tropical dry forest succession ecology, most studies on this topic have focused on plant community attribute recovery, whereas animal community successional dynamics has been largely overlooked, and the few existing studies have used taxonomic approaches. Here, we analyze the successional changes in the bee community in a Mexican tropical dry forest, by integrating taxonomic (species, genus, and family diversity) and functional (sociability, nesting strategy, and body size) information for bees. Over one year, in a successional chronosequence (2–67 years after abandonment) we collected 469 individual bees, representing five families, 36 genera, and 69 species. Linear modeling showed decreases in taxonomic diversity with succession, more strongly so for species. Bee species turnover along succession ranged from moderate to high, decreasing slightly at intermediate stages. An RLQ analysis (ordination method that allows relating environmental variables with functional attributes) revealed clear relations between bee functional traits and the plant community. RLQ axis 1 was positively related to vegetation structural and diversity variables, and to eusociality, while solitary, parasociality, and ground nesting was negatively associated with it. Early successional fallows attract mostly solitary and parasocial bees; older fallows tend to attract eusocial bees with aerial nesting. The continuous taxonomic turnover observed by us and the functional analysis suggest that the disappearance of old fallows from agricultural landscapes would likely result in significant reductions and even local extinctions of particular bee guilds. Considering the low viability of preserving large mature tropical dry forest tracts, the conservation of older successional stands emerges as a crucial component of landscape management.

Abstract in Spanish is available with online material.

KEYWORDS

bee guilds, eusociality, flower visitors, nesting habit, parasociality, secondary succession, solitary bees

1 | INTRODUCTION

Tropical dry forest, one of the most extensive forest types in the tropics (Bullock, Mooney, & Medina, 1995; Dirzo, Young, Mooney, &

Ceballos, 2011), is currently under strong anthropogenic pressures, and its extent has decreased drastically (Miles et al., 2006; Sánchez-Azofeifa et al., 2005; Singh & Chaturvedi, 2018; Wright, 2005). Forest clearing to open agricultural fields and pastures for cattle,

one of the most impacting disturbances, has resulted in large biodiversity losses (Janzen, 1988; Quesada et al., 2009; Trejo & Dirzo, 2000). In the seasonally dry tropics, agricultural fields are frequently abandoned after a few years of use, giving way to forest recovery through secondary succession (Álvarez-Yépez, Martínez-Yrizar, Búrquez, & Lindquist, 2008; Dupuy et al., 2012; Powers, Becknell, Irving, & Pérez-Aviles, 2009).

The study of tropical dry forest succession has boomed in recent decades (Chazdon, 2014). However, the large majority of these studies have focused on the plant community; among other findings, these studies have shown that plant community assembly in old fields largely follows a repeatable pathway, provided there is homogeneity of environmental and social contexts (Arroyo-Rodríguez et al., 2017). Consequently, successional communities often recover to their pre-disturbance structure and functionality (Lebrija-Trejos, Meave, Poorter, Pérez-García, & Bongers, 2010; Poorter et al., 2016). Regrettably, the temporal dynamics of the animal component of successional communities has been largely overlooked. Despite reports demonstrating the ability of secondary vegetation to maintain mammal, avian, and insect populations (e.g., DeWalt, Maliakal, & Denslow, 2003; Martin & Blackburn, 2014; McShea et al., 2009; Taki, Okochi et al., 2013; Taki, Makihara et al., 2013), few studies have examined the potential of animal communities to reassemble (Avila-Cabadilla et al., 2014; Fraga-Ramírez, Suazo-Ortuño, Avila-Cabadilla, Alvarez-Añorve, & Alvarado-Díaz, 2017). The viability of the animal community is more uncertain when considering its complex relation with the plant community. Among the biotic interactions established between plants and insects, pollination is of paramount importance (Kearns, Inouye, & Waser, 1998; Ollerton, Winfree, & Tarrant, 2011; Wilcock & Neiland, 2002).

Bees are the main pollinators in tropical regions (Michener, 2006; Renner & Feil, 1993). Despite the ecological consequences of this fact, the recovery of the bee community along secondary succession has been rarely examined (Liow, Sodhi, & Elmqvist, 2001), and the few existing studies come mostly from temperate regions (Cairns, Villanueva-Gutiérrez, Koptur, & Bray, 2005; Corbet, 1995; Potts et al., 2003). These studies have shown that bee communities may respond rapidly to successional changes of vegetation attributes (Corbet, 1995; Kang & Bawa, 2003; Potts et al., 2003, 2005; Reyes-Novelo, Meléndez-Ramírez, Ayala, & Delfín-González, 2009; Steffan-Dewenter & Tscharntke, 2001). As succession progresses in the dry tropics, the structural complexity and floristic richness of vegetation tend to increase (Dupuy et al., 2012; Kennard, 2002; Lebrija-Trejos, Bongers, Pérez-García, & Meave, 2008; Maza-Villalobos, Balvanera, & Martínez-Ramos, 2011). In theory, the temporal development of the bee community should parallel such successional trajectory, as suggested by the well-known general relationships between vegetation structure complexity and composition, and the associated fauna (MacArthur & MacArthur, 1961; Montgomery & Chazdon, 2001). Yet, to date, no clear trend has been observed for apifauna behavior during forest recovery (Quesada et al., 2009). This is probably because many bee species can interact with a large number of plant species, but also a plant may receive a large number of visiting bee

species (Bullock, Martínez del Río, & Ayala, 1989; Perry & Starrett, 1980; Waser, Chittka, Price, Williams, & Ollerton, 1996).

The assessment of pollinators' functional traits may provide new insights on successional changes in bee communities (Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008; Moretti, de Bello, Roberts, & Potts, 2009; Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tscharntke, 2002; Williams et al., 2010). Functional traits are defined as those characters of an individual organism that are directly related to its performance (Díaz et al., 2007; Violle et al., 2007). In the case of bees, these insects have been grouped into functional guilds according to key morphological, ecological, physiological, and behavioral traits (Fontaine, Dajoz, Meriguet, & Loreau, 2006; Hoehn et al., 2008). Frequently used criteria for the classification of bee functional guilds are social habit (Fægri & van der Pijl, 1979; Meneses-Calvillo, Meléndez-Ramírez, Parra-Tabla, & Navarro, 2010), nesting strategy (Potts et al., 2005; Wcislo & Cane, 1996), feeding habit (Fægri & van der Pijl, 1979; Westrich, 1996), and body size (Greenleaf, Williams, Winfree, & Kremen, 2007; Hoehn et al., 2008). Thus, in studying successional trajectories of the apifauna structure, a functional approach may be a valuable supplement to the traditional taxonomic one (i.e., based on the assessment of individual species patterns; Moretti et al., 2009).

The goal of this study was to understand the successional changes in the bee community in a tropical dry forest of southern Mexico by using two perspectives, namely taxonomic and functional. We addressed the following questions: (a) What are the successional changes in the taxonomic diversity of the bee community in a tropical dry forest?, (b) What is the role played by functional bee traits in the successional development of these insects' community?, and (c) Which vegetation attributes are most strongly associated with changes in bee community structure along succession? Considering the monotonic successional increases in plant species richness and vegetation structural complexity (e.g., Kennard, 2002; Lebrija-Trejos et al., 2008; Mora et al., 2015), our first hypothesis was that the bee community diversity would follow a similar (i.e., increasing) pattern. However, there are also several theoretical reasons that would lead to the prediction of different (i.e., not increasing) patterns in bee community diversity. For one, ecological requirements of bees include resources as varied as pollen, nectar, resins, wax, and adequate nesting sites, and the availability of all these resources does not necessarily increase along succession. More importantly, different bee species or guilds use plant resources differentially. Therefore, we alternatively expected a continuous turnover of bee species along the successional gradient.

2 | METHODS

2.1 | Study area

The study was carried out in the surroundings of Nizanda (16°39'40"N, 95°00'40"W), Oaxaca State, southern Mexico (Supporting Information Figure S1). The regional climate is warm, subhumid, with an average total annual precipitation of 902.6 mm,

concentrating from June to mid-October, and a mean annual temperature of 27.6 °C (CLICOM Project, National Meteorological Service through CICESE, <http://clicom-mex.cicese.mx>). The prevailing vegetation is tropical dry forest, with varying degrees of conservation. Spread across this landscape, there are also numerous crop fields and increasingly larger areas of secondary vegetation in different stages of successional development (Pérez-García, Meave, Villaseñor, Gallardo-Cruz, & Lebrija-Trejos, 2010). Successional trends in this region were initially described by using a chronosequence approach (Gallardo-Cruz et al., 2012; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Lebrija-Trejos, Pérez-García, Meave, Poorter, & Bongers, 2011; Lebrija-Trejos et al., 2008), but the setting of permanent plots has allowed the subsequent continuous monitoring of vegetation development (Lebrija-Trejos, Meave et al., 2010).

2.2 | Site selection

The successional chronosequence was first established in 2003 (Lebrija-Trejos et al., 2008). In 2010, the chronosequence comprised 16 permanent plots with ages spanning from 7 to 67 yr. Fallow ages were determined through dendrochronology of canopy trees (Brienen et al., 2009). The plots have an approximate area of 900 m², and they were fenced to prevent livestock entry, while allowing free movement of native fauna. As the original chronosequence no longer included very young plots, an additional 2-year old plot was used in this study. Variables defining the plant community were canopy height (h), canopy cover (cov), basal area (BA), two true diversity measures (sensu Jost, 2006), namely diversity of order zero (⁰D; species richness) and diversity of order 1 (¹D; exp Shannon Index; Jost, 2010), and Pielou's evenness (*J'*). These variables were estimated for each secondary forest stand from the data collected in 2010, except for the additional plot, for which the estimation was based on the successional models constructed by Lebrija-Trejos et al. (2008). Community attributes were calculated in R (R Core Team 2018) using the *vegan* package (Oksanen et al., 2017).

2.3 | Data collection of the bee community

We sampled the bee community bimonthly over one year (July 2010–May 2011). Bee trapping was distributed across three periods during the day: morning (08:00–11:00 hr), afternoon (12:00–15:00 hr) and dusk (16:00–19:00 hr; no bee trapping was done in days with heavy rain). We trapped bees with aerial nets only when they landed on open flowers, as this action ensured the use of the plant resource by bees. When more than one individual of any given plant species occurred in the fallow, we selected the plant having the largest number of flowers in anthesis. We recorded date and time for each bee collection, along with the identity of the plant species on which they were captured.

Collected bees were classified according to social habit and nesting strategy, following Frankie, Newstrom, Vinson, and Barthell (1993), Michener (2006), and Neff (2008). Social habit was divided into three guilds: solitary, parasocial, and social bees.

Two nesting strategies were recognized: ground-nesters (mason bees) and aerial (cavity-) nesters. For each individual, we recorded the inter-tegular distance, as this is the best indicator of bee size (Moretti et al., 2009). Bee specimens were identified to genus or species level, whatever possible, but always distinguished as (morpho-) species. Bee specimens were deposited at the Hymenopterological Collection of the Alfonso L. Herrera Zoology Museum (Faculty of Sciences, National Autonomous University of Mexico, Mexico City).

2.4 | Analysis of taxonomic information

The data from the six censuses from each plot were merged to avoid temporal autocorrelation. Still so, it was possible that the analysis of diversity successional changes could be affected by unequal completeness among samples. First, we assessed completeness for the entire study system by estimating total number of bee species using the Mao Tau's procedure (Gotelli & Colwell, 2001), with the *wiqid* package (Meredith, 2015) in R. Then, we assessed the completeness of the apifauna recorded at each site (sample coverage) by estimating total number of bee species in them through extrapolation in the *iNEXT* package (Hsieh, Ma, & Chao, 2016) in R. Completeness so assessed ranged from a low value of 0.52 to a maximum of 0.93 (the maximum possible is 1.00). We then standardized the species richness estimates to the completeness at the mode of probability density (0.83). The same procedure was repeated for genus and family richness, for which completeness values were much higher (genus level range, 0.70–0.99; family level range, 0.92–0.99); in these cases, the standardized completeness for richness estimations used their respective modes of probability density (genus, 0.89; family, 0.99). We opted for a multi-level taxonomic approach because of the difficulty faced by many studies on tropical insect ecology to acquire species-level determinations, which makes them focus on higher taxonomic units, including sometimes the order level.

Taxonomic successional patterns in the bee community were analyzed for the species, genus, and family levels. To this end, we fitted generalized null, linear, quadratic, and additive models between successional age and true diversity values of three orders (⁰D, ¹D, and ²D), representing the effective number of taxa for three taxonomic levels (species, genera, or families). The construction of these models allowed us to explore different hypotheses: a null effect of age on the response variable, an increasing or decreasing effect, a maximum value of the response variable at intermediate successional ages, and an unrestricted response to age. Since estimated richness (⁰D), ¹D, and ²D are all positive, continuous variables, they were modeled with gamma and log-Gaussian distributions. For each response variable, there was more than one model supported by the data; thus, we also constructed an average model for each diversity variable based on their sample-corrected Akaike Information Criterion weights (AIC_{ccw}); model inclusion stopped when 95% of the cumulative weight was reached (Symonds & Moussalli, 2011). Model fitting was performed in R using packages *MASS* (Venables & Ripley, 2002), *betareg* (Cribari-Neto & Zeileis, 2010), and *mgcv* (Wood, 2017), and

model averaging was performed with the MUMIn package (Bartoń, 2016).

Finally, in order to identify the successional stages at which the largest compositional change in the bee community takes place, taxonomic temporal turnover was calculated (for the species level only) using the presence/absence of each species at each site. Baselga (2012) provides a method for partitioning dissimilarity measures into their turnover and nestedness components. Here, we used Sørensen's dissimilarity index and report the turnover component between pairs of sites of consecutive successional ages. The analysis was performed in R using the betapart package (Baselga, Olme, Villeger, Bortoli, & Leprieur, 2018). The resulting values were fitted to a Generalized Additive Model in order to achieve a more general pattern of the temporal faunistic changes; this was done in the mgcv package in R (Wood, 2017).

2.5 | Analysis of functional information

To analyze relationships between the ecological traits of bee species and vegetation attributes in the fallows, we conducted an RLQ analysis, which is a co-inertia-based ordination method that allows relating environmental variables with functional attributes (Dolédec, Chessel, Ter Braak, & Champely, 1996). RLQ analysis requires the construction of three matrices (**R**, **L**, and **Q**), one for each set of attributes, either for the vegetation or the bees, and one that establishes the link between them; in this way, it allows for the integrated examination of the structure of these three matrices, regardless of the type of data (i.e., qualitative or quantitative). Matrix **R** contains p values for plant community variables recorded at I sites (Supporting Information Table S1), whereas matrix **Q** comprises q values of the characteristics of J bee species (Supporting Information Table S2). Matrix **L** contains values for bee species abundances in the rows, and values for the vegetation of the sites where the bees were collected in the columns (Supporting Information Table S3), thus linking matrices **R** and **Q**.

In this study, rows of matrix **R** represented the nine selected fallows, whereas its columns represented the bee activity environment. In addition to fallow age and plant community structural and diversity attributes, we included in this matrix a measure of resource availability (number of species in flower), growth form of flowering species (tree, shrub, forb, and climber), and vertical position of the flowering plants in the community (understory or canopy). In turn, matrix **Q** contained bee species in the rows and their traits in the columns. Bee traits included social habit, nesting strategy, and ln-transformed mean body size (Supporting Information Table S2).

The first step in RLQ was a Correspondence Analysis (CA) of matrix **L**. We used the weights of sites and species obtained from the CA to fill in the rows of matrix **R** and the columns of matrix **Q**. The second step consisted in analyzing matrices **R** and **Q**. Matrix **R** was analyzed with a Principal Component Analysis (PCA), as all variables were quantitative (normality was tested with the Shapiro–Wilk test in all of them). Variables were standardized to account for the fact that they were measured in different units. In turn, as matrix

Q contained both quantitative and qualitative variables, it was analyzed through Hill and Smith's (1976) method. Through this procedure, RLQ maximizes the covariance between fallows and species (Dolédec et al., 1996; Ribera, Dolédec, Downie, & Foster, 2001) and allows performing the simultaneous ordination of these two sets.

We carried out two RLQ analyses, one including all bee species (68) and the other excluding 44 rare species (i.e., those with ≤ 5 individuals). In this way, we were able to assess the effect of rare species on RLQ results, given the alleged effect that such species can have on this procedure (Dray, Chessel, & Thioulouse, 2003), while recognizing that species elimination entails undesirable effects on the statistical power of the analysis. Abundance values were ln-transformed to achieve normality. We used a randomization test (1,000,000 permutations) proposed by Dray and Legendre (2008) to simultaneously test for the no-site (model 2) and no-bee attribute (model 4) effects. All calculations and graphs were obtained with the ade4 package (Dray, Dufour, & Thioulouse, 2018) in R.

3 | RESULTS

3.1 | Composition of the bee community

A total of 469 individual bees were trapped, which represented five families, 35 genera, and 68 species (Table 1). By far, Apidae was the best-represented family, with 21 genera (60.0% of the total), 38 species (55.9%) and 335 individuals (71.4%). Slightly over half of all individuals (55.6%) belonged to six species: *Apis mellifera*, *Ceratina nautlana*, *Heriades* sp., *Paratrigona guatemalensis*, *Trigona acapulconis*, and *T. fulviventris* (Supporting Information Table S3). In contrast, 31 species (45.6%) were represented by a single individual. The smoothed species accumulation curve does not become asymptotic; the estimated number of bee species, according to the 95% confidence upper limit obtained from the Mao Tau's procedure was ca. 80, indicating a completeness for the study system of at least 82.6% (Supporting Information Figure S2). Given the uneven taxonomic completeness across sites, true diversities were estimated using the extrapolated richness for each level, even though the difference between observed and estimated richness was negligible for higher taxa (Supporting Information Figure S3).

Average models constructed for bee species richness showed clear declining patterns for all three true diversity indices along successional age (Figure 1A–C, black lines). At the species level, null models were well supported, but in no case were the best-supported ones. Slightly different results were observed in the case of higher taxa (genus, family), for which the null models with gamma error were always the best-supported ones, albeit indistinguishable from their linear counterparts (Table 2). For all nine response variables (i.e., true diversity of three orders for the three taxonomic levels), additional models (either quadratic or additive, either gamma or log-Gaussian distribution) were included in the respective average model, but their effect was generally less important than that of those models having the highest AIC_w values. The inclusion of

TABLE 1 Bee community attributes and foraging patterns in secondary tropical dry forest stands in Nizanda, Oaxaca, Mexico. Upper part, abundance, and infra-family richness for each of the five bee families recorded. Lower part, distribution of the foraging bee individuals across plant growth forms. Numbers in parentheses are percentages relative to each row's total

	Andrenidae	Apidae	Colletidae	Halictidae	Megachilidae	Total
Abundance and infra-family observed bee richness						
Individuals	4 (0.9)	335 (71.4)	6 (1.3)	48 (10.2)	76 (16.2)	469
Species	1 (1.5)	38 (55.9)	2 (2.9)	13 (19.1)	14 (20.6)	68
Genera	1 (2.9)	21 (60.0)	2 (5.7)	6 (17.1)	5 (14.3)	35
Distribution of foraging bees across plant growth forms						
Tree	0	117 (81.3)	6 (4.2)	10 (6.9)	11 (7.6)	144
Shrub	0	102 (69.4)	0	18 (12.2)	27 (18.4)	147
Forb	3 (2.9)	62 (59.1)	0	14 (13.3)	26 (24.8)	105
Climber	1 (1.4)	54 (74.0)	0	6 (8.2)	12 (16.4)	73

three or more models in average models can be mainly ascribed to the limited sample size we had. The declining pattern of the diversity values along successional age decreases in strength with increasing taxonomical level, due to the preeminence attained by the null models at the genus and family levels.

Temporal turnover showed a nonlinear pattern, characterized by a high turnover both at the initial and most advanced stages of succession, with a decrease at intermediate stages (35–55 years after abandonment; Figure 2). Yet, more important than the nonlinear nature of this pattern is the fact that turnover was evident throughout the successional gradient, which implies a lack of compositional stability in the bee community associated to the recovery of the plant community.

3.2 | Traits of plants visited by bees

In the fallows, a total of 86 plant species were recorded with flowers in anthesis; among these, only 58 (67%) were visited by bees. Most of the 469 bee visits were recorded on shrubs and trees, while climbers were the least visited growth form (Table 1, Supporting Information Table S4). Bee visits to trees showed two peaks along the successional gradient (Supporting Information Table S3). One corresponded to young fallows and was largely accounted for by visits to the dominant early successional species *Mimosa tenuiflora*. The second peak was observed for the oldest fallows, which are characterized by the presence of both late-successional and mature forest tree species that attain sexual maturity, such as *Gliricidia sepium* and *Ceiba parviflora*.

3.3 | Relationship between bee traits and plant traits along the successional gradient

The percentage of total co-inertia (i.e., the link between bee traits and environmental variables) explained by the first two axes of RLQ was 99.18% (Table 3). The structure of the environmental matrix described by the RLQ analysis was similar to that described by the PCA (Figure 3B), except for the signs of the two-first axes. Moreover, a

larger similarity was observed between the first two RLQ axes and the results of the Hill-Smith ordination, since they both have the same sign (Figure 3C). Considering that these two analyses produced generally the same results, we hereafter only present and discuss those obtained with the RLQ analysis.

The first RLQ axis was positively related to vegetation structural variables (canopy height, canopy cover, and basal area), as well as to both true diversity values (0D and 1D) and Pielou's evenness (J'). The eusocial habit of bees had the strongest positive relation to the main axis of the RLQ analysis, while the solitary and ground-nesting habits had the strongest negative association with it (Figure 3A). Parasocial habit was the main bee trait positively related to the second RLQ axis, whereas body size and foraging activity on trees were negatively related, and foraging on shrubs positively related, to it. According to the randomization test, environment (vegetation) proved to be significantly related to the distribution of bee species across sites (model 2; $p = 0.043$), and bee traits affected bee species composition significantly (model 4; $p = 0.037$).

4 | DISCUSSION

The combination of a taxonomic approach focused on the diversity of bees in three taxonomic levels, and a functional approach relating bee functional traits with structural and diversity attributes of secondary vegetation, allowed us to gain insights on bee community succession that may not have been possible without having the two sets of results at sight.

4.1 | Insights from the taxonomy-based approach

Undoubtedly, one of the most unexpected results from this study was the reduction in taxonomic diversity in the second growth forest as succession proceeds. The reduction in the number of taxa was evident not only at the species level, but also at the genus level, whereas at the family level was this trend more subtle. This result leads to the rejection of our first hypothesis; indeed, as succession proceeds in

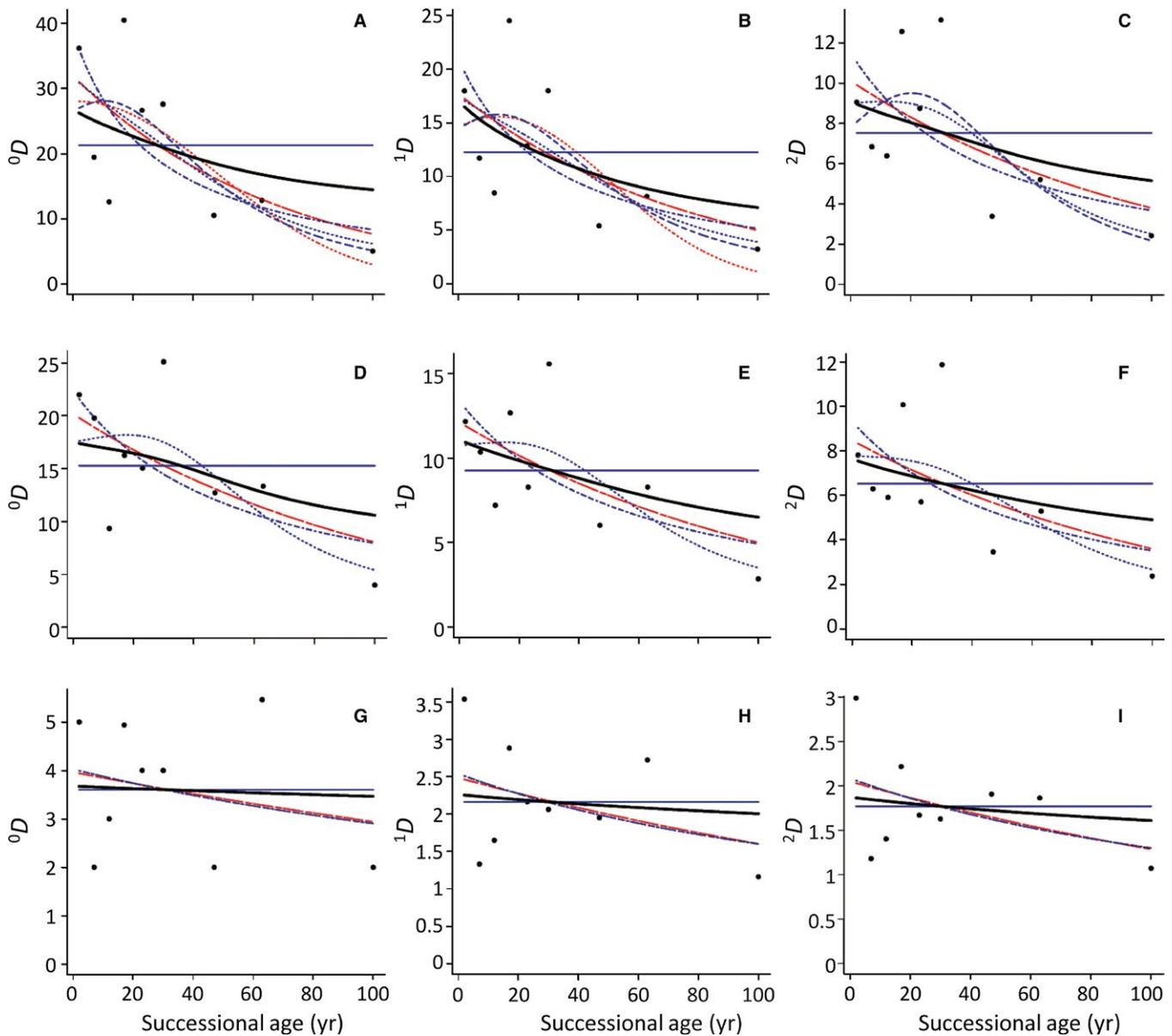


FIGURE 1 Successional patterns for the bee community true diversity at the species (A–C), genus (D–F), and family (G–I) levels. Diversity of order zero or species richness (0D ; A, D, G), diversity of order 1 (1D ; B, E, H), and diversity of order 2 (2D ; C, F, I) were estimated through a completeness analysis (Supporting Information Figure S3). These patterns resulted from constructing average models (black lines) that included null (solid line), linear (dashed), quadratic (dotted), and additive (dotdash) models, with gamma (blue) and log-Gaussian (red) error distributions

the tropical dry forest of Nizanda, follows host progressively lower bee diversity. Notably, all models examined by us that differ from the null model (constant richness) supported such decreasing pattern. In fact, the reason why the taxonomic richness reduction was modest according to the average models, is that in no case were we able to discard the null model, as it was as well or even better supported than the remaining ones. Yet, the fact that null models represented themselves a rejection of our first hypothesis must not be disregarded. In any case, this analysis is quite definite about the lack of an increasing pattern in bee diversity toward older fallows, despite the strong increasing trends in floristic diversity and structural complexity along succession in the same secondary forests (Lebrija-Trejos

et al., 2008; Lebrija-Trejos, Meave et al., 2010). It must be noted that even though the taxonomic richness patterns reported here oppose the findings of some previous studies, they are in line with those of other studies. For example, Steffan-Dewenter and Tscharntke (2001) found a significant increase in bee richness along the succession on an orchard meadow in Germany, although bee richness was also high in a young secondary field. In contrast, in a study of bee recovery in a temperate secondary forest in Japan (Taki, Okochi et al., 2013), the temporal dynamics of bee richness was best fitted to a null model, in closer agreement to our results. Moreover, when these researchers dissected bee richness in social and solitary guilds, the patterns became more complex, as the former guild was best described by a

TABLE 2 Models of successional change of estimated bee community true diversities (0D , true diversity of order zero, 1D , true diversity of order 1, and 2D , true diversity of order 2) included in the average models constructed for these response variables. True diversities were estimated through completeness analysis. AICc, Akaike Information Criterion corrected for sample size; AICcw, weights of corrected Akaike Information Criterion

Model (type, error)	Species		Genus		Family	
	Δ AICc	AICcw	Δ AICc	AICcw	Δ AICc	AICcw
0D						
Linear, gamma	0.00	0.408	1.32	0.124	4.22	0.050
Null, gamma	2.14	0.140	1.24	0.129	0.00	0.411
Linear, log-Gaussian	2.53	0.115	0.17	0.220	4.35	0.047
Additive, log-Gaussian	2.53	0.115	0.17	0.220	4.35	0.047
Null, log-Gaussian	3.05	0.089	0.00	0.240	0.10	0.392
Additive, gamma	3.19	0.083	3.91	0.034	4.22	0.050
Quadratic, gamma	4.16	0.051	4.67	0.023	10.66	0.002
Quadratic, log-Gaussian	9.22	0.004	6.30	0.010	11.04	0.002
1D						
Linear, gamma	0.00	0.369	0.33	0.179	3.22	0.084
Null, gamma	1.30	0.192	0.63	0.155	0.00	0.420
Null, log-Gaussian	2.32	0.115	0.00	0.212	0.67	0.301
Linear, log-Gaussian	2.61	0.100	0.31	0.181	4.11	0.054
Additive, log-Gaussian	2.61	0.100	0.32	0.181	4.11	0.054
Additive, gamma	3.23	0.073	3.06	0.046	3.22	0.084
Quadratic, gamma	4.12	0.047	3.48	0.037	9.87	0.003
Quadratic, log-Gaussian	8.94	0.004	6.16	0.010	11.14	0.003
2D						
Linear, gamma	0.00	0.244	0.34	0.243	2.62	0.116
Null, gamma	0.14	0.228	0.00	0.287	0.00	0.433
Null, log-Gaussian	0.57	0.184	0.75	0.198	1.27	0.230
Linear, log-Gaussian	1.61	0.109	2.25	0.093	4.32	0.050
Additive, log-Gaussian	1.61	0.109	2.25	0.093	4.32	0.050
Additive, gamma	2.85	0.059	3.67	0.046	2.62	0.116
Quadratic, gamma	2.97	0.055	4.20	0.035	9.62	0.004
Quadratic, log-Gaussian	6.12	0.011	8.02	0.005	11.50	0.001

null and an increasing model, whereas the latter best fitted a null and a decreasing one. In a non-successional context, Liow et al. (2001) report a pattern that is reminiscent to that described for Nizanda, as they recorded higher richness of bee species in disturbed than in undisturbed plots of tropical lowland forest in Malaysia and Singapore. Evidently, more studies are needed in tropical systems in order to make broad generalizations about the prevailing successional patterns in bee community richness.

Different reasons, having in common their relation to floral resource availability, may underpin this decreasing pattern in bee richness. A first likely explanation is that most plant species occurring in early successional communities have short life cycles and allocate abundant resources to reproduction (R strategists sensu Grime, 2006), and usually are very abundant but little diverse (Liow et al., 2001). Moreover, in early succession flowering periods are

generally longer than in older fallows (Kang & Bawa, 2003). A continuous flower availability may not only attract more individuals, but also more species that are active at different times of the year. Alternatively, the relative scarcity of both bee species and individuals in older fallows may derive, to some extent, from differential interannual flowering patterns. Early successional species tend to produce flowers every year (Bazzaz & Pickett, 1980). Conversely, late successional plants usually have supra-annual flowering patterns, that is, they tend to mast flower for short periods every two or more years (Bullock, 1992; Kang & Bawa, 2003), rendering flower availability less predictable in older successional stands.

At first sight, the decreasing taxonomic richness along succession appears to be in contradiction with the relatively constant turnover observed among fallows of successive ages. Actually, this is not necessarily the case, as long as taxonomic turnover encompasses

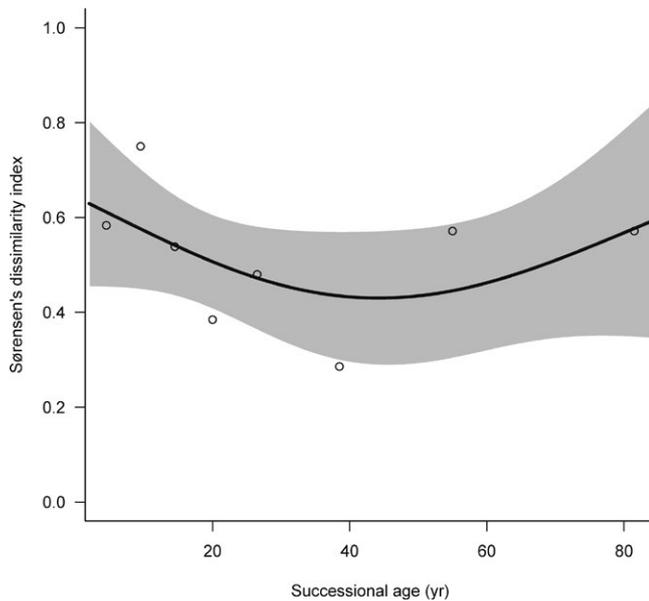


FIGURE 2 Temporal species turnover (Sørensen's dissimilarity index) between pairs of sites of consecutive successional ages. The black line represents the generalized additive model to which the index values were fitted. The gray area is the 95% Wald's confidence envelope

TABLE 3 Results of the RLQ analysis performed to analyze the relationship between bee traits, bee abundances, and vegetation attributes

Metric	Axis 1	Axis 2
Eigenvalue	0.62	0.07
Projected inertia (%)	89.50	9.67
Covariance	0.79	0.26
Correlation	0.22	0.17

consistently larger species losses than gains as vegetation recovers. Conversely, the fact that turnover dipped down at intermediate successional stages is more difficult to explain. Lebrija-Trejos et al. (2011) reported a higher microenvironmental heterogeneity at successional ages ranging between 20 and 40 years, and it is precisely in this period when the floristic enrichment of the plant community undergoes a significant acceleration, particularly through the establishment of numerous typical mature forest tree species (Lebrija-Trejos, Meave et al., 2010). The longer times needed by these species to achieve sexual maturity and initiate flower production may be related to the slight reduction in bee species turnover coinciding with this period.

The overall mismatch between the diversities of the bee and the plant communities may be also related to the high mobility of bees across the landscape. Bees are capable of visiting fallows both distant in geographical location and successional stage (Bommarco et al., 2010; Greenleaf et al., 2007). Environmental filtering in secondary forests may be mostly associated with resource availability and the way in which bees exploit them, rather than

with microenvironmental conditions (Díaz et al., 2007; Gathmann, Greiler, & Tschardtke, 1994; Moretti & Legg, 2009; Moretti et al., 2009). However, a better understanding of these patterns may be gained through the analysis of bee functional traits and their relationship with vegetation attributes.

4.2 | Insights from the functional trait-based approach

The RLQ analysis performed in this study seems to offer answers to the issues that remained unsolved by the taxonomic approach. Particularly, this analysis was revealing regarding the prominent role of vegetation diversity and structure (canopy height and cover, and basal area), as well as floral resources, on bee community diversity. Moreover, this analysis allowed us to assess the relevance of the examined functional bee traits, particularly of social and nesting habits.

The RLQ analysis allowed us to examine two null hypotheses: a non-relationship between the vegetation attributes and bee species composition, and a non-relationship between the latter and bee functional traits (models 2 and 4, respectively, sensu Dray et al., 2014). Both hypotheses were rejected by the analysis, which implies the existence of a clear association between vegetation and bee community attributes. Our study provides evidence for the two above-mentioned associations. Model 4 allowed us to evaluate how three bee functional traits, namely body size, social habit, and nesting habit, determine the development of the bee community. In turn, Model 2 showed a relatively high, positive correlation of the first RLQ axis with vegetation structure. The well-known positive associations of these variables with increasing successional age (Lebrija-Trejos et al., 2008), provide a strong ground to interpret axis 1 of the RLQ analysis as a synthesis of fallow age effects along vegetation recovery.

Body size is related to some aspects of plants' flowering activity. In a Costa Rican tropical dry forest, solitary bees with medium to large body size foraged preferentially in the upper canopy (Frankie & Rollin, 1979). This behavior agrees with our observation that large *Centris* bees are the most important pollinators of canopy trees (e.g., *Ceiba parviflora* and *Gliricidia sepium*) and climbers. Yet, not all large bees were exclusive canopy species; we often recorded *Xylocopa* bees visiting understory plants, as well as forbs and shrubs in early successional sites lacking a tree canopy. Bees of this latter genus are active all year round and display generalist feeding habits (Figueiredo, Gimenes, de Miranda, & Oliveira-Rebouças, 2013; Gerling, Velthuis, & Hefetz, 1989). Their large body size implies large energy requirements, and thus a dependence on resources from multiple sources.

Sociability is a very relevant aspect of bee ecology (Wilson & Hölldobler, 2005), and this trait also contributes to explaining the results of the functional RLQ analysis. The eusocial habit was positively related with the first RLQ axis, indicating that this guild tends to use more developed vegetation. Among the five eusocial species recorded, four belong to the Meliponini tribe (*Paratrigona*

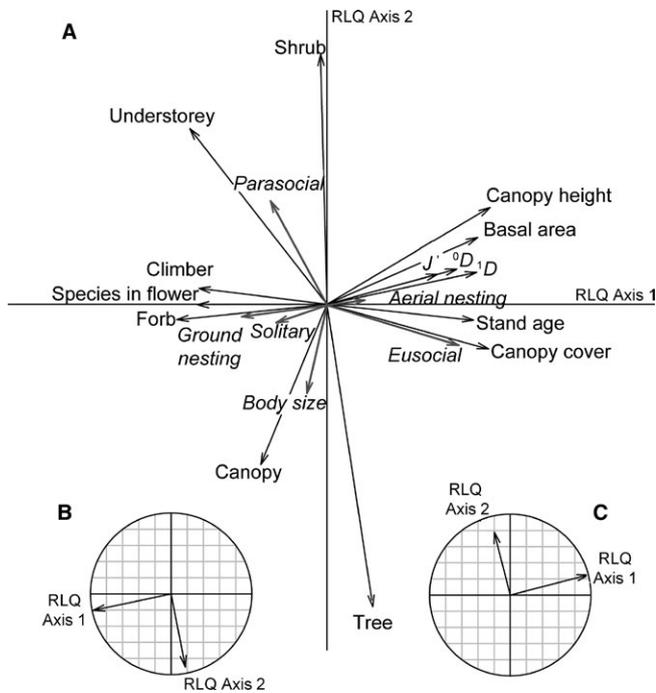


FIGURE 3 Results of the RLQ analysis. (A) RLQ biplot of the relationship between traits of the plant community and the bees in secondary tropical dry forest stands. The plant community plot was rescaled to fit that of the bee traits. Plant community attributes (regular font): $^{\circ}D$ (diversity of order zero), 1D (diversity of order 1), J' (Pielou's evenness), basal area, canopy height, canopy cover, stand age, species in flower, vegetation stratum (understorey, canopy), and plant growth forms (tree, shrub, forb, climber). Bee attributes (italics): body size, nesting guild (aerial nesting, ground nesting), and social guild (eusocial, parasocial, solitary). (B) First two axes of the PCA analysis of vegetation attributes (matrix **R**). (C) First two axes of the Hill-Smith's ordination of bee attributes (matrix **Q**)

guatemalensis, *Scaptotrigona mexicana*, *Trigona acapulconis*, and *T. fulviventris*). This result is consistent with previous reports showing that members of this tribe are more abundant and diverse in old-growth forest (Cairns et al., 2005; Fierro, Cruz-López, Sánchez, Villanueva-Gutiérrez, & Vandame, 2012; Liow et al., 2001; Taki, Makiyama et al., 2013). The other eusocial species recorded was *Apis mellifera*, which was particularly abundant at young and intermediate successional sites. This invasive species may potentially displace Meliponini bees (Cairns et al., 2005). Although the differential use of the fallows may represent an antagonistic relationship between *A. mellifera* and these native bees, it is more likely that it reflects the strong specialization of this tribe to mature forest conditions (Samejima, Marzuki, Nagamitsu, & Nakasizuka, 2004). Unlike the pattern displayed by eusocial bees, solitary and parasocial bees were mostly associated with young and intermediate fallows, and with the richness of plants bearing flowers, in agreement with the findings of Taki, Makiyama et al. (2013).

Nesting habit may also play an important role in determining successional changes in the bee community. The tendency of bees to construct nests in the vicinity of their foraging areas (Gathmann & Tschamtko, 2002) provides some clues for the interpretation of RLQ

results. This analysis showed a relationship between ground-nesting bees and a trend to forage on understory plants, as well as a relationship between aerial nesting and a tendency to forage in the canopy. Trees, either alive or dead, also provide bees with a substrate to construct their nests. Thus, it is surprising that the association between nesting habit and vegetation attributes was not very strong, which could be due to the broad distribution of some tree species along the successional gradient, some of which began to flower at early successional stages. In attempting to disentangle the relationship between nesting habits and succession, some studies have considered other habitat components, including substrate type and materials for nest construction (Potts et al., 2005). The assessment of the role of these variables is necessary, but more information on the regional apifauna, and its patterns of resource use is needed in order to pursue this line of research.

4.3 | Final remarks

Examination of the use of successional fallows by bees sheds new light on the problem of species coexistence in complex landscapes. The vegetation of Nizanda is a mosaic of contrasting patches of forests with different successional ages, including large (albeit vanishing) mature forest tracts, in addition to other non-forest communities (Gallardo-Cruz, Meave, Pérez-García, & Hernández-Stefanoni, 2010; Pérez-García, Meave, & Cevallos-Ferriz, 2012). Such landscape configuration is clearly associated with a heterogeneous resource availability, ranging from abundant and constant floral resources in young fallows, to scarcer, more patchy (both in time and space) resources in older stands.

A frequent assumption in studying succession is that recently abandoned sites, mostly dominated by pioneer plants, host a lower animal diversity and thus are less valuable for conservation, compared with late-successional sites. Although this may be true for many vertebrates (e.g., Hernández-Ordóñez, Urbina-Cardona, & Martínez-Ramos, 2015), this does not seem to be the case for bees, as young sites provide them with plenty of nourishment. In fact, from a purely taxonomic perspective one could incorrectly conclude that in agricultural landscapes with little, if any, mature forest coverage remaining, the presence of young fallows would suffice to conserve a high diversity of bee species, particularly of solitary and generalist bees. Yet, in many rural areas in the dry tropics such as Nizanda, there is a strong pressure to increase food production, which causes the reduction not only of mature forest cover, but also of the number of older fallows, as fallow time becomes reduced. The functional analysis performed by us clearly demonstrates that the disappearance of old fallows from the agricultural landscape would have profound implications, particularly regarding the reduction and potential local extinction of some types of bees, particularly those with eusocial and aerial nesting habits. The survival of these bee guilds in a region depends on the maintenance of structurally complex mature forests or older fallows hosting high plant species richness. As the preservation of large tracts of mature tropical dry forest seems less and less

viable every day, the conservation of older successional stands emerges as a crucial component of tropical landscape management (Chazdon et al., 2009). Based on the results derived from the combined taxonomic and functional approaches used in this study, we predict that the lower alpha (site level) bee diversity of older fallows is matched by a larger beta (between site) diversity, and thus a higher gamma diversity, as has been demonstrated for other agroforestry systems (Bandeira, Martorell, Meave, & Caballero, 2005). This possibility will have to be examined in future studies.

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DATA AVAILABILITY

Data available from Dryad Repository: <https://doi.org/10.5061/dryad.28hv53f> (Ramos-Fabiél, Pérez-García, González, Yáñez-Ordoñez, & Meave, 2018).

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REFERENCES

- Álvarez-Yépez, J. C., Martínez-Yrizar, A., Búrquez, A., & Lindquist, C. (2008). Variation in vegetation structure and soil properties related to land use history of old-growth and secondary tropical dry forests in northwestern Mexico. *Forest Ecology and Management*, 256, 355–366. <https://doi.org/10.1016/j.foreco.2008.04.049>
- Arroyo-Rodríguez, V., Melo, F. P., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., ... Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, 92, 326–340. <https://doi.org/10.1111/brv.12231>
- Avila-Cabadilla, L. D., Stoner, K. E., Nassar, J. M., Espirito-Santo, M. M., Alvarez-Añorve, M. Y., Aranguren, C. I., ... Sanchez-Azofeifa, G. A. (2014). Phyllostomid bat occurrence in successional stages of Neotropical dry forests. *PLoS One*, 9, e84572. <https://doi.org/10.1371/journal.pone.0084572>
- Bandeira, F. P., Martorell, C., Meave, J. A., & Caballero, J. (2005). The role of rustic coffee plantations in the conservation of wild tree diversity in the Chinantec region of Mexico. *Biodiversity and Conservation*, 14, 1225–1240. <https://doi.org/10.1007/s10531-004-7843-2>
- Bartoń, K. (2016). *MuMIn: Multi-model inference*. R package version 1.15.6. Retrieved from <https://CRAN.R-project.org/package=MuMIn>
- Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21, 1223–1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Baselga, A., Olme, C. D. L., Villeger, S., deBortoli, J., & Leprieux, F. (2018). *betapart: Partitioning beta diversity into turnover and nestedness components*. R package version 1.5.0. Retrieved from <https://CRAN.R-project.org/package=betapart>
- Bazzaz, F. A., & Pickett, S. T. A. (1980). Physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics*, 10, 351–345.
- Bommarco, R., Biesmeijer, J. C., Meyer, B., Potts, S. G., Pöyry, J., Roberts, S. P. M., ... Öckinger, E. (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2075–2082. <https://doi.org/10.1098/rspb.2009.2221>
- Brienen, R. J. W., Lebrija-Trejos, E., van Breugel, M., Pérez-García, E. A., Bongers, F., Meave, J. A., & Martínez-Ramos, M. (2009). The potential of tree rings for the study of forest succession in southern Mexico. *Biotropica*, 41, 186–195. <https://doi.org/10.1111/j.1744-7429.2008.00462.x>
- Bullock, S. H. (1992). Seasonal differences in nonstructural carbohydrate in two dioecious monsoon-climate trees. *Biotropica*, 24, 140–145. <https://doi.org/10.2307/2388667>
- Bullock, S. H., Martínez del Río, C., & Ayala, R. (1989). Bee visitation rates to trees of *Prockia crucis* differing in flower number. *Oecologia*, 78, 389–393. <https://doi.org/10.1007/BF00379114>
- Bullock, S. H., Mooney, H. A., & Medina, E. (1995). *Seasonally dry tropical forests*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9780511753398>
- Cairns, C. E., Villanueva-Gutiérrez, R., Koptur, S., & Bray, D. B. (2005). Bee populations, forest disturbance, and Africanization in Mexico. *Biotropica*, 37, 686–692. <https://doi.org/10.1111/j.1744-7429.2005.00087.x>
- Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: University of Chicago Press. <https://doi.org/10.7208/chicago/9780226118109.001.0001>
- Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E., & Miller, S. E. (2009). The potential for species conservation in tropical secondary forests. *Conservation Biology*, 23, 1406–1417. <https://doi.org/10.1111/j.1523-1739.2009.01338.x>
- Corbet, S. A. (1995). Insects, plants and succession: Advantages of long-term set-aside. *Agriculture, Ecosystems & Environment*, 53, 201–217. [https://doi.org/10.1016/0167-8809\(94\)00581-X](https://doi.org/10.1016/0167-8809(94)00581-X)
- Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, 34, 1–24.
- DeWalt, S. J., Maliakal, S. K., & Denslow, J. S. (2003). Changes in vegetation structure and composition along a tropical forest chronosequence: Implications for wildlife. *Forest Ecology and Management*, 182, 139–151. [https://doi.org/10.1016/S0378-1127\(03\)00029-X](https://doi.org/10.1016/S0378-1127(03)00029-X)
- Díaz, S., Lavorel, S., Chapin, F. S. III, Tecco, P. A., Gurrich, D. E., & Grigulis, K. (2007). Functional diversity at the crossroads between ecosystem functioning and environmental filters. In J. G. Canadell, G. Pataki, & L. F. Pitelka (Eds), *Terrestrial ecosystems in a changing world* (pp. 81–91). Berlin, Germany: Springer. <https://doi.org/10.1007/978-3-540-32730-1>
- Dirzo, R., Young, H. S., Mooney, H. A., & Ceballos, G. (2011). *Seasonally dry tropical forests: Ecology and conservation*. Washington, DC: Island Press. <https://doi.org/10.5822/978-1-61091-021-7>
- Dolédec, S., Chessel, D., Ter Braak, C. J. F., & Champely, S. (1996). Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics*, 3, 143–166. <https://doi.org/10.1007/BF02427859>
- Dray, S., Chessel, D., & Thioulouse, J. (2003). Co-inertia analysis and the linking of ecological data tables. *Ecology*, 84, 3078–3089. <https://doi.org/10.1890/03-0178>
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & ter Braak, C. J. F. (2014). Combining the fourth-corner and the

- RLQ methods for assessing trait responses to environmental variation. *Ecology*, 95, 14–21. <https://doi.org/10.1890/13-0196.1>
- Dray, S., Dufour, A.-B., & Thioulouse, J. (2018). *Analysis of ecological data: Exploratory and Euclidean methods in environmental sciences*. Retrieved from <http://pbil.univ-lyon1.fr/ADE-4>
- Dray, S., & Legendre, P. (2008). Testing the species traits-environment relationships: The fourth-corner problem revisited. *Ecology*, 89, 3400–3412. <https://doi.org/10.1890/08-0349.1>
- Dupuy, J. M., Hernández-Stefanoni, J. L., Hernández-Juárez, R. A., Tetetla-Rangel, E., López-Martínez, J. O., Leyequién-Abarca, E., Tun-Dzul, F. J., & May-Pat, F. (2012). Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. *Biotropica*, 44, 151–162. <https://doi.org/10.1111/j.1744-7429.2011.00783.x>
- Fægri, K., & van der Pijl, L. (1979). *The principles of pollination ecology*. Oxford, UK: Pergamon Press.
- Fierro, M. M., Cruz-López, L., Sánchez, D., Villanueva-Gutiérrez, R., & Vandame, R. (2012). Effect of biotic factors on the spatial distribution of stingless bees (Hymenoptera: Apidae, Meliponini) in fragmented Neotropical habitats. *Neotropical Entomology*, 41, 95–104. <https://doi.org/10.1007/s13744-011-0009-5>
- Figueiredo, N., Gimenes, M., de Miranda, M. D., & Oliveira-Rebouças, P. (2013). *Xylocopa* bees in tropical coastal sand dunes: Use of resources and their floral syndromes. *Neotropical Entomology*, 42, 252–257. <https://doi.org/10.1007/s13744-013-0121-9>
- Fontaine, C., Dajoz, I., Meriguet, J., & Loreau, M. (2006). Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, 4, e1.
- Fraga-Ramírez, Y., Suazo-Ortuño, I., Avila-Cabadilla, L. D., Alvarez-Añorve, M., & Alvarado-Díaz, J. (2017). Multiscale analysis of factors influencing herpetofaunal assemblages in early successional stages of a tropical dry forest in western Mexico. *Biological Conservation*, 209, 196–210. <https://doi.org/10.1016/j.biocon.2017.02.021>
- Frankie, G. W., Newstrom, L. E., Vinson, S. B., & Barthell, J. F. (1993). Nesting-habitat preference of select *Centris* bee species in Costa Rican dry forest. *Biotropica*, 25, 322–333. <https://doi.org/10.2307/2388790>
- Frankie, G. W., & Rollin, C. (1979). An experimental study on the foraging behavior of selected solitary bees species in Costa Rican dry forest (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society*, 52, 591–602.
- Gallardo-Cruz, J. A., Meave, J. A., González, E. J., Lebrija-Trejos, E. E., Romero-Romero, M. A., Pérez-García, E. A., ... Martorell, C. (2012). Predicting tropical dry forest successional attributes from space: Is the key hidden in image texture? *PLoS ONE*, 7, e30506. <https://doi.org/10.1371/journal.pone.0030506>
- Gallardo-Cruz, J. A., Meave, J. A., Pérez-García, E. A., & Hernández-Stefanoni, J. L. (2010). Spatial structure of plant communities in a complex tropical landscape: Implications for β -diversity. *Community Ecology*, 11, 202–210. <https://doi.org/10.1556/ComEc.11.2010.2.8>
- Gathmann, A., Greiler, H. J., & Tschardtke, T. (1994). Trap-nesting bees and wasps colonizing set-aside fields: Succession and body size, management by cutting and sowing. *Oecologia*, 98, 8–14. <https://doi.org/10.1007/BF00326084>
- Gathmann, A., & Tschardtke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71, 757–764. <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- Gerling, D., Velthuis, H. H. W., & Hefetz, A. (1989). Bionomics of the large carpenter bees of the genus *Xylocopa*. *Annual Review of Entomology*, 34, 163–190. <https://doi.org/10.1146/annurev.en.34.010189.001115>
- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589–596. <https://doi.org/10.1007/s00442-007-0752-9>
- Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties*. Chichester, UK: John Wiley & Sons.
- Hernández-Ordóñez, O., Urbina-Cardona, N., & Martínez-Ramos, M. (2015). Recovery of amphibian and reptile assemblages during old-field succession of tropical rain forests. *Biotropica*, 47, 377–388. <https://doi.org/10.1111/btp.12207>
- Hill, M. O., & Smith, A. J. (1976). Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon*, 25, 244–255.
- Hoehn, P., Tschardtke, T., Tylianakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B*, 275, 2283–2291. <https://doi.org/10.1098/rspb.2008.0405>
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Janzen, D. H. (1988). Tropical dry forests: The most endangered major tropical ecosystem. In E. O. Wilson (Ed.), *Biodiversity* (pp. 130–137). Washington, DC: National Academy of Science Press.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Jost, L. (2010). The relation between evenness and diversity. *Diversity*, 2, 207–232. <https://doi.org/10.3390/d2020207>
- Kang, H., & Bawa, K. S. (2003). Effects of successional status, habit, sexual systems, and pollinators on flowering patterns in tropical rain forest trees. *American Journal of Botany*, 90, 865–876. <https://doi.org/10.3732/ajb.90.6.865>
- Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, 29, 83–112. <https://doi.org/10.1146/annurev.ecolsys.29.1.83>
- Kennard, D. (2002). Secondary forest succession in a tropical dry forest: Patterns of development across a 50-year chronosequence in lowland Bolivia. *Journal of Tropical Ecology*, 18, 53–66. <https://doi.org/10.1017/S0266467402002031>
- Lebrija-Trejos, E., Bongers, F., Pérez-García, E. A., & Meave, J. A. (2008). Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. *Biotropica*, 40, 422–431. <https://doi.org/10.1111/j.1744-7429.2008.00398.x>
- Lebrija-Trejos, E., Meave, J. A., Poorter, L., Pérez-García, E. A., & Bongers, F. (2010). Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 267–275. <https://doi.org/10.1016/j.ppees.2010.09.002>
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, 91, 386–398. <https://doi.org/10.1890/08-1449.1>
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L., & Bongers, F. (2011). Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, 27, 477–489. <https://doi.org/10.1017/S0266467411000253>
- Liow, L. H., Sodhi, N. S., & Elmqvist, T. (2001). Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology*, 38, 180–192. <https://doi.org/10.1046/j.1365-2664.2001.00582.x>
- MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42, 594–598. <https://doi.org/10.2307/1932254>
- Martin, T. E., & Blackburn, G. A. (2014). Conservation value of secondary forest habitats for endemic birds, a perspective from two widely separated tropical ecosystems. *Ecography*, 37, 250–260. <https://doi.org/10.1111/j.1600-0587.2013.00234.x>

- Maza-Villalobos, S., Balvanera, P., & Martínez-Ramos, M. (2011). Early regeneration of tropical dry forest from abandoned pastures: Contrasting chronosequence and dynamic approaches. *Biotropica*, 43, 666–675. <https://doi.org/10.1111/j.1744-7429.2011.00755.x>
- McShea, W. J., Stewart, C., Peterson, L., Erb, P., Stuebing, R., & Gimán, B. (2009). The importance of secondary forest blocks for terrestrial mammals within an *Acacia*/secondary forest matrix in Sarawak, Malaysia. *Biological Conservation*, 142, 3108–3119. <https://doi.org/10.1016/j.biocon.2009.08.009>
- Meneses-Calvillo, L. M., Meléndez-Ramírez, V., Parra-Tabla, V., & Navarro, J. (2010). Bee diversity in a fragmented landscape of the Mexican neotropics. *Journal of Insect Conservation*, 14, 323–334. <https://doi.org/10.1007/s10841-010-9262-x>
- Meredith, M. (2015). *wiqid: Quick and dirty estimates for wildlife populations*. R package version 0.1.0. Retrieved from <https://CRAN.R-project.org/package=wiqid>
- Michener, C. D. (2006). *The bees of the world*. Baltimore, MD: John Hopkins University Press.
- Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., & Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33, 491–505. <https://doi.org/10.1111/j.1365-2699.2005.01424.x>
- Montgomery, R. A., & Chazdon, R. L. (2001). Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology*, 82, 2707–2718. [https://doi.org/10.1890/0012-9658\(2001\)082\[2707:FSCAAL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2707:FSCAAL]2.0.CO;2)
- Mora, F., Martínez-Ramos, M., Ibarra-Manríquez, G., Pérez-Jiménez, A., Trilleras, J., & Balvanera, P. (2015). Testing chronosequences through dynamic approaches: Time and site effects on tropical dry forest succession. *Biotropica*, 47, 38–48. <https://doi.org/10.1111/btp.12187>
- Moretti, M., de Bello, F., Roberts, S. P. M., & Potts, S. G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology*, 78, 98–108. <https://doi.org/10.1111/j.1365-2656.2008.01462.x>
- Moretti, M., & Legg, C. (2009). Combining plant and animal traits to assess community functional responses to disturbance. *Ecography*, 32, 299–309. <https://doi.org/10.1111/j.1600-0587.2008.05524.x>
- Neff, J. L. (2008). Components of nest provisioning behavior of solitary bees (Hymenoptera: Apoidea). *Apidologie*, 39, 30–45. <https://doi.org/10.1051/apido:2007055>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2017). *vegan: Community ecology package*. R package. ver. 2.4-3. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Pérez-García, E. A., Meave, J. A., & Cevallos-Ferriz, S. R. S. (2012). Flora and vegetation of the seasonally dry tropics of Mexico: Origin and biogeographical implications. *Acta Botanica Mexicana*, 100, 149–193. <https://doi.org/10.21829/abm100.2012.35>
- Pérez-García, E. A., Meave, J. A., Villaseñor, J. L., Gallardo-Cruz, J. A., & Lebrija-Trejos, E. E. (2010). Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, Mexico. *Folia Geobotanica*, 45, 143–161. <https://doi.org/10.1007/s12224-010-9064-7>
- Perry, D. R., & Starrett, A. (1980). The pollination ecology and blooming strategy of a neotropical emergent tree, *Dipteryx panamensis*. *Biotropica*, 12, 307–313. <https://doi.org/10.2307/2387702>
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., ... Rozendaal, D. M. A. (2016). Biomass resilience of tropical secondary forests. *Nature*, 530, 211–214. <https://doi.org/10.1038/nature16512>
- Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., & Willmer, P. (2005). Role of nesting resource in organizing diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30, 78–85. <https://doi.org/10.1111/j.0307-6946.2005.00662.x>
- Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., & Willmer, P. (2003). Response of plant-pollinator communities to fire: Changes in diversity, abundance and floral reward structure. *Oikos*, 101, 103–112. <https://doi.org/10.1034/j.1600-0706.2003.12186.x>
- Powers, J. S., Becknell, J. M., Irving, J., & Pérez-Aviles, D. (2009). Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. *Forest Ecology and Management*, 258, 959–970. <https://doi.org/10.1016/j.foreco.2008.10.036>
- Quesada, M., Sánchez-Azofeifa, G. A., Alvarez-Añorve, M., Stoner, K. E., Ávila-Cabadilla, L., Calvo-Alvarado, J., ... Sánchez-Montoya, G. (2009). Succession and management of tropical dry forest in the Americas: Review and new perspectives. *Forest Ecology and Management*, 258, 1014–1024. <https://doi.org/10.1016/j.foreco.2009.06.023>
- R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org>.
- Ramos-Fabiél, M. A., Pérez-García, E. A., González, E. J., Yáñez-Ordoñez, O., & Meave, J. A. (2018). Data from: Successional dynamics of the bee community in a tropical dry forest: Insights from taxonomy and functional ecology. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.28hv53f>.
- Renner, S. S., & Feil, J. P. (1993). Pollinators of tropical dioecious angiosperms. *American Journal of Botany*, 80, 1100–1107. <https://doi.org/10.1002/j.1537-2197.1993.tb15337.x>
- Reyes-Novelo, E., Meléndez-Ramírez, V., Ayala, R., & Delfín-González, H. (2009). Bee faunas (Hymenoptera: Apoidea) of six natural protected areas in Yucatan, Mexico. *Entomological News*, 120, 530–544. <https://doi.org/10.3157/021.120.0510>
- Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, 82, 1112–1129. [https://doi.org/10.1890/0012-9658\(2001\)082\[1112:EOLDAS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2)
- Samejima, H., Marzuki, M., Nagamitsu, T., & Nakasizuka, T. (2004). The effects of human disturbance on a stingless bee community in a tropical rainforest. *Biological Conservation*, 120, 577–587. <https://doi.org/10.1016/j.biocon.2004.03.030>
- Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., ... Cuevas-Reyes, P. (2005). Research priorities for Neotropical dry forests. *Biotropica*, 37, 477–485.
- Singh, J. S., & Chaturvedi, R. K. (2018). *Tropical dry deciduous forest: Research trends and emerging features*. Singapore, Singapore: Springer Nature.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tschardtke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421–1432. [https://doi.org/10.1890/0012-9658\(2002\)083\[1421:SDEOLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)
- Steffan-Dewenter, I., & Tschardtke, T. (2001). Succession of bee communities on fallows. *Ecography*, 24, 83–93. <https://doi.org/10.1034/j.1600-0587.2001.240110.x>
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65, 13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Taki, H., Makihara, H., Matsumura, T., Hasegawa, M., Matsuura, T., Tanaka, H., Makino, S., & Okabe, K. (2013). Evaluation of secondary forests as alternative habitats to primary forests for flower-visiting insects. *Journal of Insect Conservation*, 17, 549–556. <https://doi.org/10.1007/s10841-012-9539-3>

- Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T., & Makino, S. I. (2013). Succession influences wild bees in a temperate forest landscape: The value of early successional stages in naturally regenerated and planted forests. *PLoS ONE*, *8*, e56678. <https://doi.org/10.1371/journal.pone.0056678>
- Trejo, I., & Dirzo, R. (2000). Deforestation of seasonally dry tropical forest: A national and local analysis in Mexico. *Biological Conservation*, *94*, 133–142. [https://doi.org/10.1016/S0006-3207\(99\)00188-3](https://doi.org/10.1016/S0006-3207(99)00188-3)
- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. New York, NY: Springer. <https://doi.org/10.1007/978-0-387-21706-2>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, *116*, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Waser, N. M., Chittka, L., Price, M. V., Williams, N. M., & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology*, *77*, 1043–1060. <https://doi.org/10.2307/2265575>
- Wcislo, W. T., & Cane, J. H. (1996). Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology*, *41*, 257–286. <https://doi.org/10.1146/annurev.en.41.010196.001353>
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, & I. H. Williams (Eds.), *The conservation of the bees* (pp. 1–16). London, UK: Academic Press.
- Wilcock, C., & Neiland, R. (2002). Pollination failure in plants: Why it happens and when it matters. *Trends in Plant Science*, *7*, 270–277. [https://doi.org/10.1016/S1360-1385\(02\)02258-6](https://doi.org/10.1016/S1360-1385(02)02258-6)
- Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, *143*, 2280–2291. <https://doi.org/10.1016/j.biocon.2010.03.024>
- Wilson, E. O., & Hölldobler, B. (2005). Eusociality: Origin and consequences. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 13367–13371. <https://doi.org/10.1073/pnas.0505858102>
- Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). Boca Raton, FL: CRC Press. <https://doi.org/10.1201/9781315370279>
- Wright, J. S. (2005). Tropical forests in a changing environment. *Trends in Ecology & Evolution*, *20*, 553–560. <https://doi.org/10.1016/j.tree.2005.07.009>

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