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# High bee functional diversity buffers crop pollination services against Amazon deforestation

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## Abstract

Predicting outcomes of land use change on biodiversity and ecosystem services remains a key priority for ecologists, but may be particularly challenging in diverse tropical ecosystems. Trait-based approaches are a key tool to meet this challenge. Such approaches seek functional mechanisms underpinning species' responses to environmental disturbance and contributions to ecosystem services. Here, we use a functional trait approach to study effects of land use change on stingless bee communities and on pollination services to açaí palm (*Euterpe oleracea*, Arecaceae) in the Eastern Brazilian Amazon. We compared traits of stingless bees visiting açaí inflorescences across a land use intensity gradient (low to high forest cover) to determine: (1) the role of traits in bee species' responses to deforestation; (2) how deforestation affects functional composition of bee communities; and (3) whether bee traits better explain variation in açaí fruit production than species diversity metrics. We found that bee species' responses to deforestation were non-random and predicted by body size, with small-sized bees more susceptible to forest loss, and changes in functional diversity of bee communities were important for pollination services. However, not all changes in functional diversity were associated with forest loss. Together, these results suggest that: (1) large tracts of minimally disturbed tropical rainforest are vital for the conservation of diverse stingless bee communities; (2) efficient pollination is contingent on bee species not only having divergent trait values (functional dispersion), but also traits' relative abundance in communities (functional evenness); and (3) high functional diversity in stingless bee communities buffers açaí pollination services to loss of sensitive species. Thus, conservation strategies must focus on protecting wider biodiversity, not just ecosystem services, to guarantee conservation of native eusocial bee taxa. Doing so will safeguard crop pollination services, the pollination of native plant communities, and the long-term resilience of Amazon forest ecosystems.

**Key words:** land use change, functional complementarity, functional trait, ecosystem service, *Euterpe oleracea*, stingless bees

## 1. Introduction

The conversion of natural habitats into agricultural land is a major driver of global biodiversity loss (Foley et al., 2005). As a consequence we lose wild species that provide essential ecosystem services (Dainese et al., 2019). Understanding the impacts of land use change on biodiversity and ecosystem functioning (BEF) is key to devising land management practices that support wider biodiversity and ecosystem services in croplands (Kleijn et al., 2015). Much of the evidence for positive BEF relationships comes from plant communities (Tilman et al., 2014). In contrast, evidence from arthropod-mediated ecosystem services, such as pollination and pest control, remains mixed (Dainese et al., 2019; Kleijn et al., 2015; Ricketts et al., 2016), mainly due to continued uncertainty over underlying mechanisms (Bartomeus et al., 2018).

To provide a more mechanistic understanding of BEF relationships, ecologists have developed ‘trait-based’ approaches (Díaz and Cabido, 2001). These aim to identify morphological, physiological, and behavioral attributes of species (herein ‘traits’) that determine sensitivity to environmental change (‘response traits’), and contribute to specific ecological functions (‘effect traits’) (McGill et al., 2006). Trait-based approaches have been used to investigate impacts of land use and climate change on wild bee communities, and of bee diversity on pollination services (Giannini et al., 2020b; Williams et al., 2010; Woodcock et al., 2019). Despite recent advances, studies linking bee species’ environmental sensitivity and function (i.e., response-effect trait framework) remain scarce (but see Martins et al., 2015; Bartomeus et al., 2018). As such, trait-based approaches have so far failed to provide general predictions on how land use change alters bee pollination services (Bartomeus et al., 2018). We can improve this framework’s overall predictive power by testing it in diverse ecological contexts, especially where information on traits is limited, such as the tropics (Archer et al., 2014).

In tropical and subtropical regions, eusocial stingless bees (Hymenoptera: Apidae: Meliponini) are the dominant flower-visitor taxa in both natural and agricultural habitats (Bawa, 1990; Biesmeijer and Slaa, 2006), and vital crop pollinators (Heard, 1999). Most stingless bee taxa build their nests in trees and are generalist flower visitors (Roubik 1989). Yet, among species, there exists a striking diversity of morphological, physiological, and behavioral adaptations to maximize survival and resource exploitation in diverse tropical habitats (Hrncir and Maia-Silva, 2013), even allowing some species to thrive in human-modified landscapes (Jaffé et al., 2016). Nonetheless, many species are poorly adapted to forest loss, leading to precipitous declines in stingless bee abundance and diversity in degraded landscapes (Brosi et al., 2008; Ricketts et al., 2008). Unlike most other tropical insects, information on traits that could influence species’ responses to land use change is widely available for stingless bees, and recent studies have found that body size (Brown and De Oliveira, 2014; Mayes et al., 2019; Smith and Mayfield,

2018) and dominance interactions (Lichtenberg et al., 2017) influence species' local extinction risk. However, knowledge of the impacts of species loss on mechanisms driven by functional composition (e.g., niche complementarity) in stingless bee communities, and ecosystem functioning (e.g., crop pollination), remains limited.

Bee species vary in their contribution to pollination services based on differences in morphological (e.g., body size, hairiness; Larsen et al., 2005; Stavert et al., 2016), and physiological traits (e.g., thermal tolerance; Brittain et al., 2013), and behavior during flower visits (Martins et al., 2015). Yet, evidence on whether individual, or multiple traits best explain ecosystem functioning (Gagic et al., 2015) remains equivocal, with two hypotheses being prevalent in the literature. Firstly, if function is strongly linked to a particular range or level of a single trait ('trait state'), then that trait's abundance in the community will be the best predictor of ecosystem functioning ('functional identity' or 'mass ratio' hypothesis) (Garibaldi et al., 2015; Grime, 1998). Alternatively, if ecosystem function is dependent on the degree of complementarity among species' traits (e.g., spatio-temporal partitioning of flower visits), then function may be predicted by trait diversity ('functional complementarity' hypothesis) (Díaz and Cabido, 2001; Gagic et al., 2015). Under both hypotheses, if bee species' local extinction risk covaries with pollination function, then ecosystem services may be at risk under land use change (Larsen et al., 2005; Nicholson et al., 2019). On the other hand, if these variables are decoupled, for instance if functional redundancy is high and species are mutually replaceable, or if pollination is driven by common species, loss of sensitive species will not influence ecosystem service provision (Kleijn et al., 2015).

Here, we investigate how functional traits influence stingless bee responses to deforestation and pollination services to açaí palm (*Euterpe oleracea* Mart., Arecaceae) in the Eastern Brazilian Amazon, a global hotspot for stingless bee diversity (Pedro, 2014). Açaí fruit is vitally important for food security and rural livelihoods in the Amazon region (Brondízio 2008; Borges et al., 2020a), and, due to rapid growth in domestic and international demand, one of Brazil's most lucrative pollinator-dependent crops (Giannini et al., 2020a). It is produced in a wide range of contexts, from smallholder agroforestry systems in its native floodplain forest habitat to intensively managed plantations in uplands (Campbell et al., 2018). Pollinators, defined as species that visit both sexual morphs of palm inflorescences, include a diverse array of insects (bees, flies, wasps, beetles, and ants), that on average increase fruit yield by 80% relative to inflorescences where pollinators have been experimentally excluded (Campbell et al., 2018). Pollination services are positively related to pollinator species richness (Campbell et al., 2018). However, among pollinators, stingless bees are its most effective pollen vectors (Bezerra et al., 2020), and the only taxa whose visitation frequencies are dependent on surrounding forest cover (Campbell et al., 2018). Thus, pollination services may be contingent on a subset of environmentally sensitive stingless bees.

In this study, we address: (1) the role of functional traits in stingless bee species' responses to deforestation; (2) how deforestation affects functional composition of stingless bee communities; and (3) whether stingless bee traits or functional composition explain more variation in açaí fruit production than overall pollinator species diversity. We expect that stingless bee species' responses to deforestation are non-random and influenced by their functional traits, and not only lead to changes in species richness but also functional composition. For pollination services, we make three predictions. (i) If pollination services are enhanced by functional differences across a wide range of insect taxa (e.g., bees, flies, wasps, beetles), overall pollinator richness will remain the best predictor of açaí fruit production. (ii) If stingless bees are important pollinators, taxonomic or trait-based indices of stingless bee communities may replace or explain additional variation in pollination services on top of overall pollinator richness. (iii) Traits may interact with overall pollinator richness. This could occur if stingless bee trait diversity is a proxy of functional complementarity in wider flower-visitor communities, or behavioral interactions between stingless bees and other flower visitors have antagonistic or synergistic effects on pollination services (Carvalheiro et al., 2011).

## 2. Materials and methods

To investigate impacts of landscape structure (forest cover) and production system (upland or floodplain) on stingless bee communities and açaí pollination services, we focused on 18 sites used for intensive production of açaí palm fruit in the Amazon estuary region, close to Belém, Pará state, northern Brazil (Figure A1, Supplementary Materials). This region is characterized by large tracts of wet tropical rainforest, separated by large rivers and land cleared for agriculture (e.g., pasture, field crops), and urban settlements. Sampling took place between January and June 2016 to coincide with peak flowering periods of *E. oleracea*. The biodiversity and pollination datasets used here are the same as those presented in Campbell *et al.* (2018). Field sites included nine plantations of *E. oleracea* in upland habitats and nine floodplain areas under intensive management for fruit production, located at similar elevations (uplands = 8 ±0.4 m; floodplains = 4 ±0.3 m), with a minimum distance between sites of 500 m, and no spatial autocorrelation between sampled insect communities (for more details, see Campbell *et al.* 2018).

### 2.1 Field data collection

Açaí palm (*E. oleracea*) has large, branching monoecious inflorescences, with anthesis of unisex flowers occurring in two non-overlapping phases (i.e., temporal dichogamy) (Oliveira, 2002). At each site, three inflorescences with pistillate (female) flowers were selected for study.

We focused on pistillate rather than staminate (male) inflorescences as insect visitation to female inflorescences is a better predictor of fruit production (Campbell et al., 2018). Each inflorescence was observed three times (10 min observation periods), between 8 and 16 h, under calm (windspeed <5 kmph), dry conditions, and over a maximum of two consecutive days, during which all visits by stingless bees and other insects to five rachillae (branch-like structures on which sessile flowers are inserted; 50-300 female flowers per rachilla; 50-150 rachillae per inflorescence), were noted. Observations were immediately followed by a further ten minutes active sampling of flower-visiting insects on the same inflorescence using an entomological net and aspirator. All field sites were evenly sampled, with upland and lowland sites alternatively visited to avoid order effects, and a total sampling effort of 54 h across sites (observations plus active collection). All visits by stingless bees were determined to species, with voucher specimens deposited in the entomological collection held at Embrapa Amazônia Oriental (Belém, Brazil). Other insect visitors were identified to at least family level (for further details, see Campbell et al. 2018). Initial fruit set on tagged inflorescences was estimated by counting the total number of female flowers on three of the rachillae used during insect surveys, followed by counts of developing fruit approximately 90 days after flowering (range = 30-120 days).

## 2.2 Bee functional traits

We collected data on six functional traits of stingless bees (body size, tegument color, nest habit, colony size, foraging behavior, and diet breadth) that could influence their response to land-use change and role as crop pollinators, based on information available in the published literature and from discussions with experts (Table 1; for further details on trait methods, see Appendix A1, Supplementary Materials). Where appropriate, species with missing traits were assigned values of suitable proxies (e.g., sister species). As several traits may influence spatio-temporal resource partitioning in stingless bee communities (Table 1), we constructed trait diversity indices using all six traits (‘functional complementarity’ hypothesis, Table 1). However, single trait indices (‘functional identity’ hypothesis) were calculated for three traits (body size, foraging behavior, colony size) for which there exist *a priori* expectations of their importance for pollination efficacy in stingless bees, and sufficient variation in trait values among species (Table 1; Table A1, Supplementary Materials).

## 2.3 Land cover data

Surrounding landscape was characterized using a different land use cover classification to that used in Campbell et al. (2018). Here, we use an object-based image analysis of synthetic aperture radar satellite imagery from multiple satellite systems. We derived image composites from a time series of observations, which were then segmented into homogeneous regions (objects) and classified using the supervised random forests algorithm into several classes, including ‘preserved forest’ (i.e., diverse tree communities), ‘mixed agroforests’ (i.e., açaí intermixed with other tree species), and ‘intensive agroforest’ (i.e., açaí palm monoculture) (Ferreira-Ferreira et al., 2015; Resende et al. 2019; for more details see Appendix A2, Supplementary Materials). Supervised classification approaches are useful in human-modified tropical forest landscapes, where impacts on biodiversity do not always result from changes in overall forest cover, but rather from activities within forests (e.g., selective logging, fire, hunting) (Barlow et al., 2016). This is the case for açaí production in floodplains, where management involves the gradual removal of other tree species to increase palm densities in forests being exploited for fruit production (Freitas et al., 2015). In contrast, upland plantations are mostly situated in previously degraded lands (e.g., abandoned pasture) (Campbell et al., 2018). Area covered (hectares) by preserved forest was then calculated for each site at radii ranging from

100 to 1500 m in 100 m increments (mean, max and minimum forest cover at 500 m (out of 78.5 ha): 33.5, 63.6 and 0.8 ha).

## 2.4 Statistical analyses

### *2.4.1 Role of functional traits in stingless bee species' responses to deforestation*

We tested the effects of landscape (forest cover), farming system, and flower-visitor community metrics (species richness and abundance) on the probability of occurrence (presence/absence) of stingless bee species with different functional traits. Bee abundance data (visit frequencies and collected individuals) were pooled across repeat observations in field sites (*n*=18) and reclassified as presence/absence data, because species' abundances are more likely to reflect interspecific differences in foraging strategy (solitary or in groups), rather than population size in surrounding habitats (nest densities). To determine the scale of effect, we compared $R^2$ values of linear regressions of stingless bee richness and preserved forest cover in study sites at different spatial scales (Jackson and Fahrig, 2015). Furthermore, to understand deforestation impacts on wider flower-visitor communities, using the same data set, we also regressed total (all taxa) and other insect (e.g., other Hymenoptera, Diptera, Coleoptera, Lepidoptera) species richness and surrounding forest cover at the determined spatial radius.

Once we defined our scale of effect, we used methods detailed by Walker et al. (2012) to combine the three datasets that comprise the standard 'three corners' of environment-trait studies (site-by-species, species-by-traits, and site-by-environment matrices), into a single long-format dataset with one row per site-species combination, and all traits and environmental variables in separate columns. We did this to overcome the 'fourth corner' problem, the difficulty of ascribing joint effects of traits, which are properties of species, and environmental variables, which are properties of sites, on species' occurrences (Legendre et al., 1997). Under this format we could include trait-by-environment interactions (e.g., body size x forest cover) to simultaneously test their effects on stingless bee occurrence in study sites (Lichtenberg et al., 2017).

The importance of traits and environmental variables on stingless bee species occurrence was assessed using logistic regressions (binomial response) in the R statistical environment (R Core Team, 2019, ver. 3.6.2). Predictor variables included all six functional traits, preserved forest cover (at the *a priori* defined spatial scale), production system (floodplain or upland), and insect flower-visitor community variables (stingless bee abundance, wild insect abundance, stingless bee richness, and wild insect richness). Initial models showed high levels of collinearity (Variance Inflation Factor > 3). We dealt with this by removing insect richness variables which were collinear with forest cover (see Results). Two species with missing trait data were excluded from this analysis (*Celetrigona longicornis* (present in 3 of 18 sites) and *Dolichotrigona longitarsis* (1 site)*;* Table A1, Supplementary Materials) but retained in site-level estimates of species richness.

Candidate models included two-way interactions between traits and environmental variables (forest cover, production system) and were standardized using z-scores to facilitate cross-comparison of effect sizes. Model selection was performed using the 'dredge' function in the R package 'MuMin' (Barton, 2015), with corrected Akaike Information Criterion (AICc) values. Selected models were those with a delta AICc < 2 in comparison to the best model and were visually checked for assumptions of linear regressions using residual plots. As multiple models were selected, we used model averaging methods to summarize effects of included predictor variables. Variables in the average model with confidence intervals that did not overlap with zero were considered important predictors of stingless bee species occurrence. We used the full average or 'zero method' to estimate parameter estimates and confidence intervals as this approach limits influence of parameters which only occur sporadically in selected models (Anderson and Burnham, 2002).

### *2.4.2 Effects of deforestation on functional composition of stingless bee communities*

To explore relationships between landscape structure, species diversity, and trait composition (i.e., distribution and diversity of trait values) of stingless bee communities, we regressed single and multivariate trait-based indices against both forest cover (hectares) at the *a priori* defined spatial radius (see results) and stingless bee taxonomic diversity metrics (species richness, evenness – calculated using $E_{var}$). Significance ($\alpha$=0.05) of independent variables in linear regression models was assessed using F-tests and residuals visually checked for assumptions of Gaussian distribution and homoscedasticity.

Single trait indices, such as community-weighted means (CWM) that calculate mean trait values weighted by their relative abundance in a community, are a useful means of detecting shifts in trait values (‘trait states’) across land use gradients, and for testing ‘functional identity’ effects on ecosystem function (Gagic et al., 2015). We estimated CWMs for three traits for which we had *a priori* expectations of importance in pollination function: body size, foraging behavior, and colony size (Table 1).

Multivariate trait-based indices quantify trait diversity – the among-species variation in trait distributions – and are used to test for effects of functional complementarity on ecosystem functioning (Garibaldi et al., 2015). We used three multivariate indices that measure distinct components of functional diversity: (1) functional richness ($F_{Ric}$), the volume of multi-dimensional trait space occupied by a community (i.e., number of unique trait combinations) (Villéger et al., 2008); (2) functional evenness ($F_{Eve}$), the regularity of the abundance distribution within this volume (Villéger et al., 2008); and (3) weighted functional dispersion (herein, ‘$F_{Dis}$’), the dispersion (i.e., spread) of species and their relative abundance in multi-trait space (Laliberté and Legendre, 2010). To include all potential drivers of spatio-temporal complementarity in pollination services among stingless bee taxa, indices were calculated including all six traits using the 'dbFD' function in the *FD* package in *R* (Laliberté and Legendre, 2010).

### *2.4.3 Do stingless bee traits explain more variation in açaí fruit production than overall pollinator diversity?*

To investigate the influence of abundance, taxonomic diversity (all taxa) and trait-based indices (stingless bees) of flower-visitor communities on açaí fruit production, we constructed linear models ('stats' package in R) of logit-transformed average fruit set (weighted by average number of flowers per inflorescence) in study sites with the following predictor variables: visit frequencies and taxonomic richness of flower-visiting insects (stingless bees, and 'pollinator' species – insect morphospecies that visit both male and female inflorescences, collinear with total species richness: $\beta=0.68$, $F_{1,16}=216.7$, $P<0.001$, $R^2=0.93$); single (CWM body size, foraging behavior, colony size) and multivariate ($F_{Ric}$, $F_{Eve}$, $F_{Dis}$) trait-based indices of stingless bee communities; and all two-way interactions between functional (trait-based) and taxonomic diversity metrics. Prior to model selection, logit-transformed fruit set data were additionally standardized using z-scores to facilitate interpretation of predictor effects on the response variable. Model selection procedures were identical to those described previously, except that the maximum number of terms included in candidate models was limited to five to avoid problems of overfitting (n= 18). As before, selected models were tested for overdispersion and we visually checked their residuals for assumptions of linear models. Important predictors in selected models were those with confidence intervals that did not overlap zero. We additionally ran a simple regression model of fruit set and forest cover to test direct effects of landscape on fruit yield.

## 3. Results

### 3.1 Stingless bee communities visiting *açaí* inflorescences

A total of 33 species (16 genera) of stingless bees were collected on *E. oleracea* inflorescences. The most common genera (species totals) included: *Trigona* (5 species), *Trigonisca* (5), *Partamona* (4), *Plebeia* (3), and *Nannotrigona* (3) (for full species list, see Table A1, Supplementary Materials). Stingless bee species displayed extensive variation in trait values, with body size (inter-tegular distance, ITD) varying between 0.7 and 2.6 mm (median = 1.3 mm, IQR = 0.5 mm), colony size between 390 and 60000 adult bees, and diet breadth between 0.04 and 0.33 (Table A1). For categorical traits, 55% of species were classified as solitary foragers, and 39% as group foragers (no information for two species); 42% were exclusive ‘cavity-nesters’; and 70% had ‘dark’ teguments (Table A1).

### 3.2 Role of functional traits in stingless bee species’ responses to deforestation

Stingless bee species richness in study sites increased with surrounding forest cover (selected spatial scale = 400 m radii; $\beta$=0.16, $F_{1,16}$=8.65, *P*=0.009, $R^2$=0.35; for all spatial radii, see Table A2; Figure A2, Supplementary Materials). At the same spatial scale, total (all insect taxa) and other insect (excluding Meliponini) species richness also increased with surrounding forest cover (total: $\beta$=0.59, $F_{1,16}$=14.97, *P*=0.001, $R^2$=0.48; other insects: $\beta$=0.44, $F_{1,16}$=9.06, *P*=0.008, $R^2$=0.36).

Results from the average model of stingless bee species occurrence (based on all models <2 delta AICc from top model; for full list of selected models, see Table A3, Supplementary

Materials) showed that important predictors (confidence intervals that did not overlap zero) included forest cover, body size, nest habit, and the interaction between forest cover and body size (Table 2). As expected, stingless bee species occurrence was positively associated with surrounding forest cover, but body size influenced the slope of this relationship, with small species (ITD < 1.3 mm; below median value) more associated with preserved (high-forest) landscapes than larger species (Figure 1a). Nesting habit also influenced stingless bee species occurrence, with taxa that exclusively nest in tree cavities approximately 1.5 times less likely to be present in study sites (Figure A4, Supplementary Materials; Table 2).

### *3.3 Effects of deforestation on functional composition of stingless bee communities*

Differential effects of forest loss on species altered the functional composition of stingless bee communities. Communities surrounded by more forest had smaller community-weighted average body and colony sizes, and more solitary forager species, whereas communities in degraded landscapes were dominated by species with opposing traits (i.e. large, group-forager species, with populous colonies) (Figure 1b; Table 3), with high collinearity detected between single trait indices (Table A4, Supplementary Materials). However, no significant relationships were found between single trait indices and species richness ($P$ >0.05). In contrast, no significant effects of forest cover were detected on trait diversity indices, but functional richness and dispersion were positively associated with stingless bee species richness (Table 3; Figure A5). No significant effects of species evenness ($E_{var}$) were found on trait composition of stingless bee communities ($P$ >0.4).

### *3.4 Do stingless bee traits explain more variation in açaí fruit production than overall pollinator diversity?*

Mean fruit set on açaí inflorescences in study sites varied between 3 and 25%. Best models of fruit set included overall pollinator richness, CWM foraging behavior, and trait diversity indices ($F_{Eve}$, $F_{Dis}$) of stingless bee communities (Table 4). Inclusion of trait-based indices greatly improved model fit on fruit set beyond models including only taxonomic diversity metrics (overall pollinator richness: ΔAICc= 6.51; Table A5, Supplementary Materials). Fruit set increased with functional evenness ($F_{Eve}$) of stingless bee communities (Figure 2a). Fruit set also increased with overall pollinator richness, but only at sites with high functional dispersion ($F_{Dis}$) in stingless bee communities (Figure 2b, Table 4). An increase in $F_{Dis}$ indicates an increase in the relative abundance of bee taxa with low overlap in their trait distributions (i.e., more functional complementarity). Communities with low $F_{Dis}$ showed no clear relationship between pollinator richness and fruit set (Figure 2). Finally, the relationship between fruit set and forest cover was not significant ($\beta$=0.02, SE=0.01, $F_{1,16}$=2.63, $P$=0.124, $R^2$=0.14).

## 4. Discussion

Evidence for covariance between biodiversity and ecosystem services is mixed, due to high variability in species' responses to anthropogenic stressors and relative contributions to ecosystem services (Bartomeus et al., 2018; Kleijn et al., 2015), and differential spatio-temporal scales over which diversity effects are assessed (e.g., alpha vs. beta diversity, current vs. future contribution under environmental change) (Senapathi et al., 2015; Wilcox et al., 2017). Classifying organisms by measurable traits that influence their survival and performance provides a more mechanistic understanding of human impacts on biodiversity and ecosystem services (McGill et al., 2006). We found strong evidence that taxon-specific responses to Amazon forest loss of stingless bees that visit açaí inflorescences are non-random and predicted by body size. Furthermore, changes in functional diversity of stingless bee communities were important for pollination services, and provide support for the functional complementarity hypothesis of biodiversity-ecosystem functioning (BEF) relationships. However, not all changes in functional diversity were associated with deforestation. These results suggest that: (1) large tracts of minimally disturbed tropical rainforest are vital for the conservation of diverse bee communities; and (2) high functional diversity among bee communities may buffer açaí to loss of sensitive pollinator species. Conservation strategies must focus on protecting wider biodiversity, not just ecosystem services, to guarantee conservation of native bee taxa, that are essential for pollination of native plant communities, and the long-term resilience of tropical ecosystems.

### *4.1 Role of functional traits in stingless bee species' responses to deforestation*

As expected (Brosi et al., 2007; Brown and De Oliveira, 2014), stingless bee communities responded to deforestation at small spatial scales (400 m radii). Yet, we found substantial variation in taxon-specific responses, as small bees (ITD 0.7 ≤ 1.0 mm) were more susceptible to forest loss than medium or large-sized species. Body size influences bee responses to land use change (Benjamin et al., 2014; Gutiérrez-Chacón et al., 2018), including stingless bees (Mayes et al., 2019; Smith and Mayfield, 2018), because it is positively related with foraging range (Greenleaf et al., 2007). As a consequence, small bees require higher resource densities per unit area relative to species with similar needs but greater foraging ranges (Gutiérrez-Chacón et al., 2018). Body size may also influence meta-population dynamics in stingless bees, as nest establishment involves transfer of workers and materials between maternal and newly-established 'daughter' colonies (Roubik, 2006), and so occurs across short distances (<500 m) (van Veen and Sommeijer, 2000). As small species are expected to have the shortest relative dispersal distances, they are doubly affected by deforestation: having greatest difficulty in meeting colony resource requirements, and insufficient replacement of failed colonies by new arrivals from adjacent habitats (Brosi et al., 2007).

Body size was also related to foraging behavior (i.e., small bees tended to be solitary foragers). This was expected since previous studies have found that less competitive solitary foragers are restricted to forested landscapes with abundant resources (Brosi, 2009; Lichtenberg et al., 2017). As such, body size may act as a proxy for the effects of foraging behavior on local extinction risk. However, very small species, found here to be the most sensitive to deforestation, while classified as solitary foragers, may occupy feeding niches distinct from large bees, which may facilitate coexistence. For example, large species must initiate and end foraging earlier to avoid potentially lethal heat stress (Pereboom and Biesmeijer, 2003), leading to temporal complementarity in foraging activities. Likewise, small and large species may visit the same food patches, but due to variation in individual and colony level resource requirements (Hubbell and Johnson, 1977), small species may continue foraging long after large bees have moved on to other more rewarding food patches (Biesmeijer and Slaa, 2004; Hrncir and Maia-Silva, 2013; Oliveira et al., 2014). Thus, we expect the influence of body size on species responses to deforestation to be primarily related to the differential dispersal abilities of small and large bees.

Low occurrence of tree cavity nesters (14 of 33 species) across study sites suggested such species may be poorly adapted to human disturbance (Ferreira et al., 2015; Gutiérrez-Chacón et al., 2018). Specifically, because of widespread historic logging activities (i.e. targeted removal of large trees in which these species build their nests; Eltz et al., 2003), as well as destruction of nests for honey collection (Carvalho-Zilse and Nunes-Silva 2012), even forested landscapes in the Amazon estuary region may support disproportionately low numbers of cavity-nesting bees. In contrast, non-tree cavity nesters (e.g., species with external nests, belowground nests, inquilines of other insect nests), may encounter potential nest sites in similar densities across different landscapes, and be less frequently targeted by honey gatherers. To test this, future research should use standardized sampling methods to compare bee communities and nesting opportunities in Amazon forests under differing levels of human disturbance, as conducted in other tropical regions (Eltz et al., 2003; Silva et al., 2013).

Finally, the lack of evidence of effects of açaí production system (i.e., upland or floodplain) on bee species occurrence probabilities suggests that, despite the very different processes by which native vegetation is lost in floodplains (selective removal of other tree species to enrich palm stands) and uplands (clear cut followed by conversion into agricultural land use) (Brondízio 2008), the influence of traits on bee species' responses was consistent across study sites. Identifying strong response traits, as found here, can provide invaluable information on local extinction risk and help guide conservation planning (Bartomeus et al., 2018). Nonetheless, as our results are from a single crop and study region, to make general predictions on stingless bee responses to deforestation, further assessments are required, ideally that synthesize species and trait data from multiple regions (e.g., Borges et al., 2020b). Furthermore, because of these limitations, our findings likely represent a considerable simplification on the complex ecological reality, where multiple traits have non-additive effects on bee responses to forest loss, including traits not considered here, such as brood type (combs or clusters), which may delimit minimum cavity size for tree nesting species, and should be explored in future studies.

### *4.2 Effects of deforestation on trait composition in stingless bee communities*

Loss of sensitive taxa under deforestation not only led to changes in species richness, but also provoked changes in functional composition of bee communities, with average body size inversely related to surrounding forest cover. Non-random community disassembly is expected to impact functional diversity (Larsen et al., 2005), and while we found no direct effect of forest cover, two components of functional diversity were positively related to species richness (which was associated with forest cover). Specifically, the positive correlation between functional richness and taxonomic richness suggested high functional uniqueness (and low functional redundancy) among bee taxa (Garibaldi et al., 2015). However, functional complementarity may be conditional on species' relative abundances in communities (Gagic et al., 2015). Consistent with this, species richness and functional dispersion covaried in this study, as species in diverse communities were also more dispersed (i.e., spread out) in multi-trait space, as a product of both their divergent trait distributions and more regular abundances (Laliberté and Legendre, 2010). On the other hand, we found no evidence that variation in functional evenness, the regularity of abundance in occupied trait space, was explained by changes in either surrounding forest cover, or species richness. In summary, local extinction of small-bodied bees under forest loss caused important changes in the functional composition of stingless bee communities. However, effects on functional diversity were less accentuated than effects on species richness or functional composition.

### *4.3 Do stingless bee traits explain more variation in açaí fruit production than overall pollinator diversity?*

The fact that functional diversity of stingless bee communities explained more variation in açaí fruit set than taxonomic diversity metrics, underlines the vital importance of these insects for high crop yields, providing strong support for the functional complementarity hypothesis. In contrast, evidence for functional identity effects was limited to a non-significant positive association between fruit set and group foraging behavior. The importance of individual traits likely depends on the focal crop and its compatibility with different flower-visitor taxa ('trait matching') (Garibaldi et al., 2015). While large bees carry more pollen than other insect taxa (Bezerra et al., 2020), *E. oleracea* inflorescences present several morphological and phenological adaptations (e.g., exposed reproductive structures, bimodal nectar production in unisex flowers) that allow them to be efficiently pollinated by a diverse guild of nectar-feeding insects, not just stingless bees (Campbell et al., 2018; Oliveira, 2002). As such, it is expected that pollination services are enhanced by multiple traits that increase niche complementarity in pollinator communities, rather than individual traits that influence per visit pollination efficacy (i.e., number of pollen grains deposited). This also may explain why overall pollinator species richness remained an important predictor of fruit production, as it likely reflected important functional differences among non-bee visitor taxa.

Evidence for functional complementarity came from positive effects of functional evenness and functional dispersion in stingless bee communities on fruit set, although the latter was dependent on high overall pollinator species richness. These findings suggest efficient pollination is contingent on bee species not only having divergent trait values (functional dispersion), but also traits' relative abundance in communities (functional evenness). For example, complementarity in foraging activities of different sized bee species across variable weather conditions may improve stability of pollination services (Brittain et al., 2013). This may be particularly important in crops such as açaí palm that flower during the tropical wet season where heavy rainfall causes substantial reductions in insect visitation rates. However, functional differences can only improve stability if bee visits are regularly distributed across environmental gradients (i.e., not clumped). Other traits that may contribute to functional complementarity in stingless bee communities include tegument color, colony size, foraging behavior, and nest habit (for mechanisms, see Table 1), although evidence from observational studies on crop flowers is lacking.

We expected that effects of functional dispersion would depend on overall pollinator richness because trait diversity was calculated for a subset of flower-visitor species. As such, trait diversity in stingless bees may serve as a proxy measure for functional complementarity in wider pollinator communities. Alternatively, bee species in communities with low functional dispersion may have specific traits that reduce visitation by other insects (i.e., antagonistic effects). One such trait may be group foraging behavior, as functional dispersion tended to be lowest in degraded landscapes, where group forager taxa (e.g., *Trigona* species) were most dominant. Under these conditions, group foragers may partially buffer pollination services from loss of sensitive species, as they remain abundant on farms with low surrounding preserved forest cover, and are among the palm's most efficient pollen vectors (Bezerra et al., 2020). However, in diverse communities, due to dominance interactions, these taxa may suppress visitation of other insects, particularly other stingless bees, potentially reducing pollen flow between inflorescences. While several studies have found synergistic effects of species interactions on pollination services (Carvalheiro et al., 2011; Greenleaf and Kremen, 2006), antagonistic effects have also been reported in stingless bees (Heard, 1999). Importantly, not all group forager taxa show aggression to heterospecific flower visitors (e.g., *Partamona, Scaptotrigona*), but may still suppress the abundance of other insects by occupying all available feeding spots (Hrncir and Maia-Silva, 2013). To investigate these hypotheses, future studies should include the traits of other insect flower-visitor taxa, an important step given most trait databases are heavily biased towards bees (Rader et al., 2016; Woodcock et al., 2019), and seek to understand how dominance interactions affect pollen transfer between inflorescences, for example using pollen analogues (e.g., fluorescent dyes) (Hass et al., 2018).

### *4.4 Implications for bee conservation and ecosystem services in açaí production landscapes*

Açaí production landscapes increasingly resemble palm monocultures interspersed with native forest fragments of variable size and configuration. Consequently, production areas support depauperate plant and animal communities relative to adjacent forest habitats (Freitas et al., 2015; Moegenburg and Levey, 2002), and are increasingly dependent on these habitats for ecosystem service providers (Campbell et al., 2018). Here, we found that deforestation led to changes not only in species richness of stingless bees visiting açaí inflorescences, but also in bee functional composition, because small bees are most vulnerable to local extinction caused by loss of natural habitat.

Nonetheless, pollination services were best explained by stingless bee functional diversity, which showed less accentuated declines with forest loss, and may buffer açaí to pollinator species loss. As such, the amount of forest required to safeguard pollination services may fall below thresholds needed to protect the most vulnerable bee species from local extinction. Furthermore, from a strictly applied perspective, growers could increase bee functional diversity using managed colonies. Specifically, the number of colonies and species used could be tailored to maximize important elements of functional diversity (dispersion, evenness) following assessments of wild bee communities. However, sensitive (small-sized) stingless bees are essential pollinators of many native plant species (Bawa, 1990), including important crops (Giannini et al., 2020a), and are expected to be more resilient to impacts of climate change than larger bees (Aguirre-Gutiérrez et al., 2016; Giannini et al., 2020b). Further, overall pollinator species richness remained an important predictor of pollination services and increased with surrounding forest cover. As such, Amazon forest conservation guarantees both pollination services provided by wild insects, including stingless bees, and the long term resilience of plant-pollinator interactions and crop pollination services (Senapathi et al., 2015).

In summary, we identify bee species at high risk of local extinction from Amazon forest loss, reinforcing the importance of preserved landscapes (70-80% forest cover) for bee conservation and ecological resilience in Amazon forests. This is in solid agreement with existing Brazilian environmental legislation where landowners in the Brazilian Amazon are required by law to maintain up to 80% of their property as native vegetation (Brazilian Native Vegetation Protection Law, 2012). Given that many açaí growers own and manage land parcels of relatively small size

(<50 ha), conservation of native forest habitats must be done collectively to be effective. Importantly, our estimates of forest cover included only areas of low-disturbed native forest. Thus, for these conservation actions to be effective, only preserved forest habitats should be considered in the designation of legal reserves in uplands, and to estimate habitat integrity in floodplains being managed for açaí fruit production (mostly classified as Areas of Permanent Protection, APPs) (Metzger et al., 2019). With these steps, açaí production landscapes can continue to bring important economic benefits to rural communities in the Eastern Brazilian Amazon whilst incentivizing the conservation and restoration of essential forest habitats for biodiversity, including vital ecosystem service providers, such as native stingless bees.

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## TABLES & FIGURES

**Table 1.** Traits used to classify stingless bee species visiting *Euterpe oleracea* inflorescences. In this table, we define traits by their measurement (continuous or categorical), relevance as response traits to land use change (R) and ecosystem functioning (EF), whether they were used to test 'functional complementarity' (FC) and 'functional identity' (FI) hypotheses, and supporting references from the bee trait literature. For more details on trait measurement and categorization methods, see Appendix A1, Supplementary Materials.

| Trait | Measurement | Links with Responses/Ecosystem function | FC | FI | Noted references |
|---|---|---|---|---|---|
| Body size | Intertegular distance (mm) | **R:** Robust predictor of maximum foraging range in bees; **EF:** Influences pollen loads, compatibility with floral structures ('trait matching'), and spatio-temporal complementarity in resource use. | X | X | Greenleaf et al. (2007);<br>Garibaldi et al. (2015);<br>Pereboom & Biesmeijer (2003) |
| Foraging behavior | Group forager? ('no', 'yes') | **R:** Group foragers dominate limited resources in degraded landscapes; **EF:** Numerically-dominant species may drive pollination services; group foragers may reduce visitation by more effective pollinator taxa. | X | X | Lichtenberg et al. (2017);<br>Kleijn et al. (2015);<br>Heard (1999) |
| Colony size | No. adult bees | **R:** Determines colony resource demands and intake capacity; **EF:** Numerically-dominant taxa may drive pollination services. | X | X | Hubbell & Johnson (1977);<br>Elizalde et al. (2020) |
| Nesting habit | Cavity nester? ('no', 'yes') | **R:** Species which exclusively nest in tree cavities may be more sensitive to deforestation; **EF:** spatial complementarity in resource use (e.g., forest border vs. crop interior). | X |  | Roubik (2006);<br>Brosi et al. (2007, 2008, 2009) |
| Tegument color | Light colored? ('no', 'yes') | **R:** Regulates habitat use - darker species restricted to shaded habitats (e.g., forests) due to difficulties with thermal regulation in open habitats; **EF:** spatio-temporal complementarity in resource use (e.g., open vs. shaded crop areas, early vs late initiation of foraging activities). | X |  | Pereboom & Biesmeijer (2003) |
| Diet Breadth | Normalized degree in bee-plant networks | **R:** Specialists are more sensitive to land use change – but opposing relationship found for stingless bees as mediated by dominance interactions; **EF:** Species with low diet breadth may carry less heterospecific pollen. | X |  | Bommarco et al. (2010);<br>Lichtenberg et al. (2017); |

**Table 2.** Effects of forest cover (ha at 400 m radius), *Euterpe oleracea* production system (PS): floodplain or upland, flower visitor community (abundance of stingless bees, other insect taxa), and influence of functional traits on stingless bee species occurrence probability. Functional traits: Body size: ITD (mm), Tegument: light colored? ('no', 'yes'), Foraging behavior (FB): group forager? ('no', 'yes'), Nest habit: cavity nester? ('no', 'yes'), Diet breadth: normalized degree, between 0 and 1). Two-way interactions are indicated with ':'. All predictors were standardized (z-scores) to facilitate cross-comparison of effect sizes. Coefficients (β), standard errors (SE), Confidence Intervals (95%), and Importance values (sum Akaike weights) are from the averaged model (45 models < 2 ΔAICc, Table A3, Supplementary Materials). Terms with confidence intervals that do not overlap with zero are shown in bold.

| Covariate | β | SE | Lower | Upper | Importance |
|---|---|---|---|---|---|
| (Intercept) | -1.46 | 0.12 | -1.70 | -1.22 | 1.00 |
| **Nest habit (ref: no cavity)** | **-1.13** | **0.37** | **-1.85** | **-0.42** | **1.00** |
| Body size | -0.59 | 0.42 | -1.40 | 0.23 | 1.00 |
| **Forest** | **0.57** | **0.22** | **0.13** | **1.00** | **1.00** |
| **Body size: Forest** | **-1.47** | **0.53** | **-2.50** | **-0.44** | **1.00** |
| Foraging behavior (ref: solitary) | 0.61 | 0.37 | -0.10 | 1.33 | 0.93 |
| Colony size | 0.35 | 0.26 | -0.16 | 0.86 | 0.85 |
| Production system (ref: floodplain) | -0.33 | 0.31 | -0.94 | 0.28 | 0.70 |
| Abundance (Meli.) | 0.22 | 0.28 | -0.33 | 0.77 | 0.52 |
| Diet breadth | -0.19 | 0.34 | -0.85 | 0.46 | 0.39 |
| Body size: PS | -0.34 | 0.73 | -1.76 | 1.08 | 0.27 |
| FB: PS | 0.26 | 0.58 | -0.89 | 1.41 | 0.23 |
| CS: PS | -0.10 | 0.29 | -0.66 | 0.46 | 0.17 |
| Nest: Forest | -0.05 | 0.20 | -0.44 | 0.35 | 0.10 |
| Tegument | 0.02 | 0.09 | -0.16 | 0.19 | 0.08 |
| Abundance (other) | 0.01 | 0.07 | -0.13 | 0.14 | 0.04 |
| Nest: PS | 0.01 | 0.08 | -0.15 | 0.16 | 0.02 |
| FB: Forest | 0.00 | 0.08 | -0.16 | 0.16 | 0.02 |

**Table 3.** Effects of forest cover (ha at 400 m radii) on: a) community-weighted mean (CWM) traits of stingless bees with *a priori* expectations for pollination services; b) trait diversity indices of stingless bee communities; and c) relationships between stingless bee species richness and functional diversity metrics. Coefficients (β), standard errors (SE), F-values (d.f. = 1,16), p-values (<0.05 in bold), and $R^2$ values are presented for all models.

| **Linear model** | **β** | **SE** | **F** | ***P*** | **$R^2$** |
|---|---|---|---|---|---|
| *a) Single traits (CWM) vs. Forest cover* | | | | | |
| Body size | -0.009 | 0.003 | 8.82 | **0.009** | 0.36 |
| Colony size | -1319 | 593 | 4.95 | **0.041** | 0.24 |
| Foraging behavior | -0.011 | 0.005 | 4.83 | **0.043** | 0.23 |
| *b) Trait diversity vs. Forest cover* | | | | | |
| $F_{Ric}$ | 0.010 | 0.007 | 2.03 | 0.173 | 0.11 |
| $F_{Eve}$ | 0.000 | 0.004 | 0.00 | 0.981 | 0.00 |
| $F_{Dis}$ | 0.001 | 0.001 | 1.03 | 0.326 | 0.06 |
| *c) Trait diversity vs. Species richness* | | | | | |
| $F_{Ric}$ | 0.093 | 0.015 | 36.63 | **<0.001** | 0.70 |
| $F_{Eve}$ | 0.023 | 0.014 | 2.80 | 0.113 | 0.15 |
| $F_{Dis}$ | 0.014 | 0.004 | 12.01 | **0.003** | 0.43 |

**Table 4.** Selected linear models (<2ΔAICc from best model) of *Euterpe oleracea* fruit set in study sites. Predictors include total pollinator richness (PR), stingless bee trait diversity indices ($F_{Dis}$, $F_{Eve}$), and community-weighted trait values of foraging behavior (CWM FB; reference level= 'solitary forager'). Two-way interactions are indicated with ':'. Predictor variables (95% confidence intervals) were standardized (z-scores) to facilitate comparison of regression coefficients and those with confidence intervals that do not overlap with zero are shown in bold.

| Mod. | Intercept | Poll. Rich | $F_{Dis}$ | $F_{Eve}$ | CWM FB | $F_{Dis}$: PR | AICc | Delta | Wgt |
|---|---|---|---|---|---|---|---|---|---|
| 1 | -0.34 | **0.92** (0.75) | **-0.88** (0. 71) | **1.19** (0.66) | | **2.61** (1.66) | 34.21 | 0.00 | 0.58 |
| 2 | -0.30 | **1.42** (0.86) | **-0.88** (0.65) | **1.18** (0.59) | 0.76 (0.77) | **2.13** (1.59) | 34.88 | 0.66 | 0.42 |

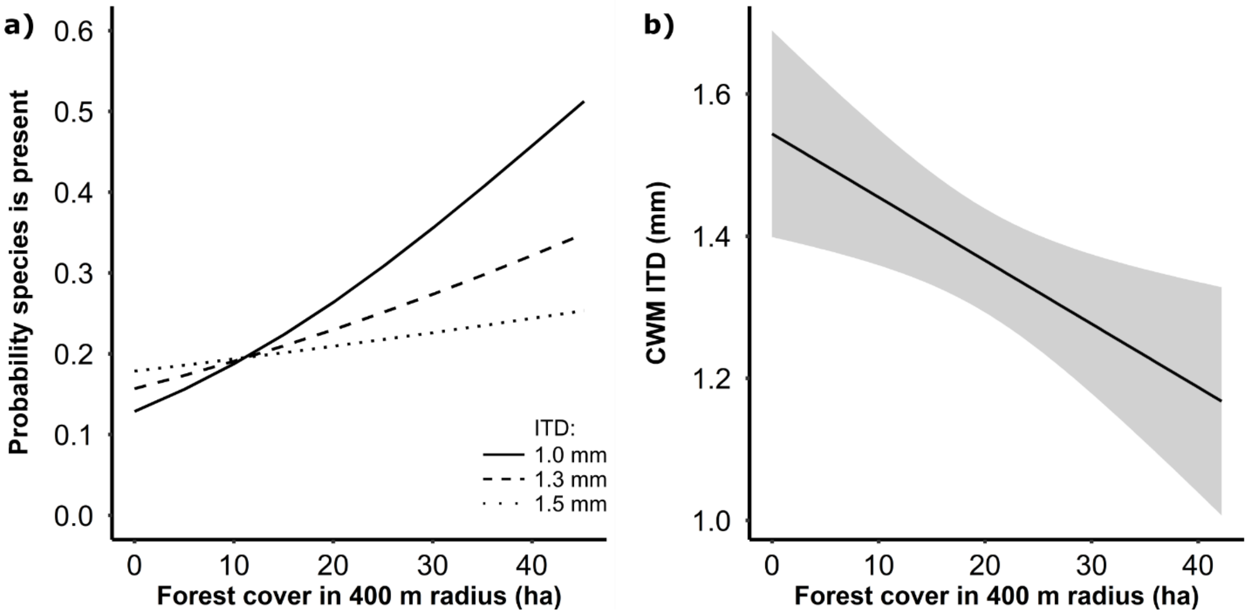

**Figure 1.** Effects of forest cover surrounding *Euterpe oleracea* agroecosystems on a) probability of occurrence of stingless bee species with different body sizes; and b) community-weighted mean (CWM) body size. Forest cover was measured within 400 m radii (data for 18 study sites denoted by tick marks) and ITD (inter-tegular distance; measured in mm), was used as a proxy of bee body size. Curves in panel a) show predicted probabilities for lower quartile (1.0 mm), median (1.3 mm) and upper quartile (1.5 mm) body sizes among recorded Meliponini species when all other traits and site variables are held at their mean values (for lines with 95% confidence intervals, see Figure A3, Supplementary Materials). Shaded areas in panel b) show 95% confidence intervals.

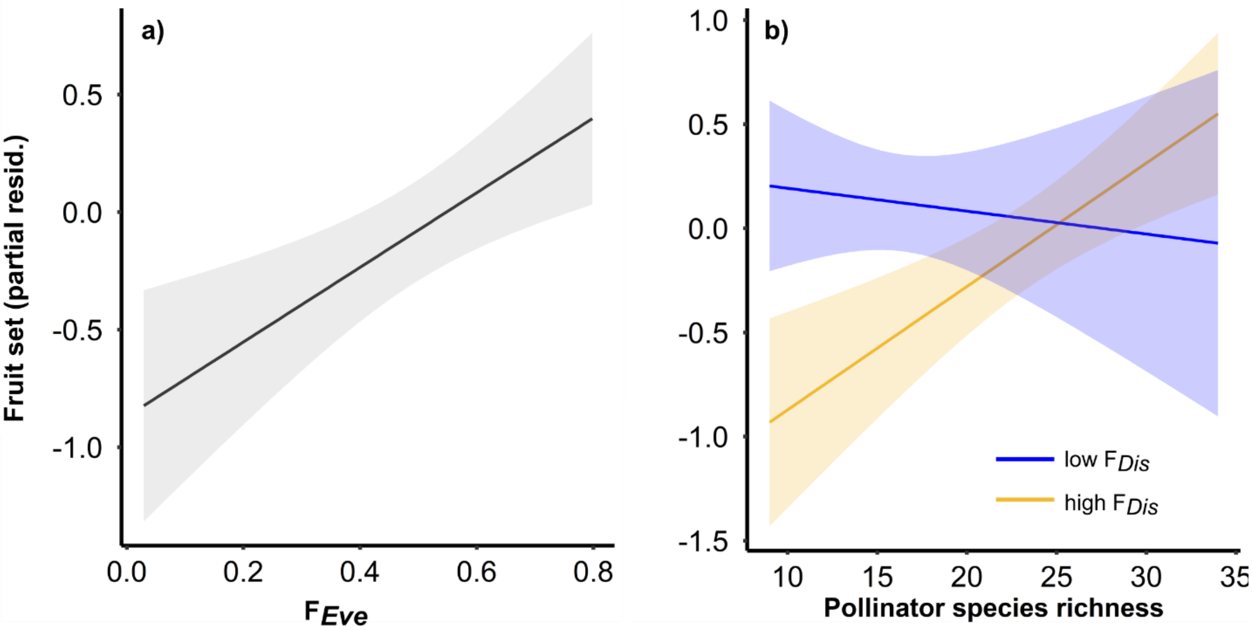

**Figure 2.** Relationships between *Euterpe oleracea* fruit set (z-scores) and a) functional evenness ($F_{Eve}$) of stingless bee communities; and b) pollinator species richness under differing levels of functional dispersion ($F_{Dis}$) in stingless bee communities. Lines show predicted relationships from the best model when all other predictors are held at their mean values (Table 4); and in b) lower quartile (0.12) and upper quartile (0.23) values of $F_{Dis}$ in stingless bee communities. Shaded areas indicate 95% confidence intervals.