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ARTICLE

ECOLOGICAL APPLICATIONS
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Tree identity and canopy openness mediate oil palm biodiversity enrichment effects on insect herbivory and pollination

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Abstract

As the extent of oil palm (*Elaeis guineensis*) cultivation has expanded at the expense of tropical rainforests, enriching conventional large-scale oil palm plantations with native trees has been proposed as a strategy for restoring biodiversity and ecosystem function. However, how tree enrichment affects insect-mediated ecosystem functions is unknown. We investigated impacts on insect herbivory and pollination in the fourth year of a plantation-scale, long-term oil palm biodiversity enrichment experiment in Jambi, Sumatra, Indonesia. Within 48 plots systematically varying in size (25–1600 m^2) and planted tree species richness (one to six species), we collected response data on vegetation structure, understory insect abundances, and pollinator and herbivore activity on chili plants (*Capsicum annuum*), which served as indicators of insect-mediated ecosystem functions. We examined the independent effects of plot size, tree species richness, and tree identity on these response variables, using the linear model for random partitions design. The experimental treatments were most associated with vegetation structure: tree identity mattered, as the species *Peronema canescens* strongly decreased (by approximately one standard deviation) both canopy openness and understory vegetation cover; whereas tree richness only decreased understory flower density. Further, the smallest plots had the lowest understory flower density and richness, presumably because of lower light availability and colonization rates, respectively. Enrichment influenced herbivorous insects and natural enemies in the understory to a lesser extent: both groups had higher abundances in plots with two enrichment species planted, possibly because higher associated tree mortality created more habitat, while herbivores decreased with increasing tree species richness, in line with the resource concentration hypothesis. Linking relationships in structural equation models showed that the negative association

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between *P. canescens* and understory vegetation cover was mediated through canopy openness. Likewise, canopy openness mediated increases in herbivore and pollinator insect abundances. Higher pollinator visitation increased phytometer yield, while impacts of insect herbivores on yield were not apparent. Our results demonstrate that even at an early stage, different levels of ecological restoration influence insect-mediated ecosystem functions, mainly through canopy openness. These findings suggest that maintaining some canopy gaps while enrichment plots develop may be beneficial for increasing habitat heterogeneity and insect-mediated ecosystem functions.

KEYWORDS
biodiversity, chili pepper (*Capsicum annuum*), ecosystem functions, ecosystem services, EFForTS-BEE, herbivores, natural enemies, pollinators, restoration, TreeDivNet

INTRODUCTION

In landscapes dominated by oil palm (*Elaeis guineensis*, Arecaceae), biodiversity is much lower than in natural forests (Barnes et al., 2017; Savilaakso et al., 2014), which negatively impacts ecosystem functions and services (Clough et al., 2016; Dislich et al., 2016; Grass et al., 2020; Qaim et al., 2020). With oil palm expanding at the expense of forests (Koh & Wilcove, 2008; Vijay et al., 2016), landscape biodiversity and ecosystem functioning is declining, which has led to calls to halt or reverse these trends (Wilcove & Koh, 2010). The United Nations recently declared 2021–2030 the "Decade on Ecosystem Restoration" aiming to reverse degradation in ecosystems worldwide (Gann et al., 2019), joining the increasing number of international initiatives on forest restoration, such as the Bonn Challenge in 2011 and the New York Declaration on Forests in 2014, which aim to restore forest ecosystems for recovering ecological integrity and carbon sequestration (Suding et al., 2015). As oil palm is grown in tropical regions that are among Earth's richest biodiversity hotspots, oil palm landscapes are a compelling priority for ecological restoration (Meijaard et al., 2018; Mittermeier et al., 2011). Therefore, methods of improving biodiversity and ecosystem function in these landscapes are needed (Darras et al., 2019; Foster et al., 2011; Koh et al., 2009).

The link between biodiversity and ecosystem function is an important topic in ecological research (Benayas et al., 2009; Cardinale et al., 2006), with practical relevance in conservation and agroecology (Manning et al., 2019). Diversified agroecosystems can contribute significantly to the provision of important ecosystem functions such as pollination and biocontrol (Kremen & Miles, 2012), but they can also contribute ecosystem disservices like increased herbivory (Grossman et al., 2018; Wielgoss et al., 2014; Zhang et al., 2007). Understanding trade-offs in such services and disservices from increasing semi-natural habitat is important in restoration and agricultural management, but research rarely examines the associated ecological processes and interactions behind these outcomes (Saunders, 2020).

Insects play an important role in providing ecosystem services and disservices in agroecosystems. Pollination by insects contributes to the yield of nearly 70% of major crops (Klein et al., 2007), while biocontrol of agricultural pests by insect natural enemies also plays a major role in agricultural production, especially in tropical agroecosystems. Oil palm cultivation has been found to have a negative impact on pollinator and biocontrol-associated insect species (Lucey & Hill, 2012; Nurdiansyah et al., 2016; Rizali et al., 2019). Recent conservation efforts around oil palm have promoted the introduction of high-value conservation areas (Senior et al., 2015) but the conditions under which conservation measures are effective in promoting ecosystem functions are not well known. Remnant riparian fragments within oil palm landscapes do not appear to promote biocontrol services, but also do not increase herbivory disservices (Gray & Lewis, 2014; Woodham et al., 2019). However, the outcome of enrichment or restoration of tree biodiversity in oil palm plantations for insect-mediated ecosystem functions is still an area of developing research (Luke et al., 2020).

In this study, we investigate the effects of different levels of mixed-species tree planting on pollination, biocontrol, and herbivory functions from flying insects using an experimental tree biodiversity framework. Our study makes use of a long-term biodiversity enrichment experiment (Teuscher et al., 2016; Zemp et al., 2023) in Sumatra, Indonesia, within the Ecological and Socio-economic Functions of Tropical Lowland Rainforest Transformation Systems (EFForTS) collaborative research center (Drescher et al., 2016). In the experiment, an oil palm monoculture has been enriched with multiple native tree species in experimental plots, systematically varying plot size and planted tree species richness, allowing for the partitioning of the effects of tree species richness, identity, and plot size (Teuscher et al., 2016). To estimate effects on pollination and herbivory related to yield, we used phytometer plants, that is, standardized, transplanted individuals used to indicate differences in environmental conditions between experimental sites, which can be effective for assessing ecological restoration (Dietrich et al., 2013). We used the random partitions analysis approach (Bell et al., 2009) to examine direct associations between our measured ecological variables and the experimental enrichment treatments. To further explore potential mediating ecological pathways that may explain significant associations with enrichment, we tested hypothesized relationships of ecosystem functions outlined in Figure 1 and Table 1, using covariance-based structural equation models (SEM). This approach can help disentangle interrelated ecological variables by comparing the covariance of observed data to the theoretical covariance of a proposed system of relationships (Grace, 2008).

METHODS

Study site

We conducted our study in the fourth year of the EFForTS biodiversity enrichment experiment (EFForTS-BEE), which was established in December 2013 in Jambi province of the island of Sumatra, Indonesia (Teuscher et al., 2016). The site is located at 103.25° E, and 1.95° S in a region formerly dominated by lowland dipterocarp forest (Laumonier et al., 2010) and receives on average 2235 ± 385 mm of annual rainfall (Drescher et al., 2016). The experiment covers an area of approximately 160 ha and is embedded within a conventionally managed industrial oil palm plantation. The surrounding landscape is dominated by oil palm monoculture with some patches of rubber, fallow lands, orchard, and secondary forests (Korol et al., 2021).

The biodiversity enrichment experiment uses an array of enrichment plots established within oil palm monoculture (example photo in Figure 1) to test the effects of mixed-species tree planting and natural regeneration as strategies for increasing biodiversity and ecosystem functioning (Teuscher et al., 2016). The experiment systemically varies plot size and planted tree species richness following a random partitions design (Bell et al., 2009; Teuscher et al., 2016). The plots were assigned among four categories of sizes (quadrats of 5 × 5, 10 × 10, 20 × 20, and 40 × 40 m) and were further partitioned into levels of planted tree species richness (1, 2, 3, and 6 species), which forms blocks where each species is represented in equal proportion. We did not include plots with no planted trees (i.e., zero diversity) mentioned in Teuscher et al. (2016), as the focus of our study was the ecological effects of different levels of tree diversity restoration. Therefore, our analysis included the 48 plots with one or more tree species planted. At intermediate levels of diversity (two and three species), plot species composition was assigned randomly without replacement from the species pool. A diagram of the enrichment experiment design of the plots used in this study is presented in Appendix S1: Figure S1. This setup allows for separation of the effects of plot size, tree species richness, and tree species identity without the need for a full factorial design (Bell et al., 2009).

Enrichment plots were established by thinning oil palms in the plots by 40% on average, although the number of felled oil palms depended on the plot size (Gérard et al., 2017). Enrichment tree seedlings were planted in a 2 m grid within the plot and the plot was protected by a perimeter fence. Planted tree species were *Archidendron jiringa* (Fabaceae), *Parkia speciosa*, (Fabaceae), *Peronema canescens* (Lamiaceae), *Durio zibethinus* (Malvaceae), *Dyera polyphylla* (Apocynaceae), and *Shorea leprosula* (Dipterocarpaceae). At each level of diversity, each species was equally abundant, and individuals of the same species were spaced as far apart as possible. After tree planting, typical oil palm plantation management, including fertilizer and pesticide applications were halted within the plots for the experiment. Weeding was continued within the plots until 2.5 years after plot establishment, which allowed 1.5 years of natural vegetation development before the earliest sampling of this study, in November 2017. Further details about the experiment can be found in Teuscher et al. (2016) and Zemp, Gérard, et al. (2019); Zemp et al. (2023).

Plot field data collection

Vegetation structure variables

We estimated average flower density of each plot from 288 flower transect surveys (six transects per plot), conducted in November/December, in the period prior to the phytometer experiment in February 2018. In three rounds, a pair of surveyors each walked a random 10 m transect within each plot, identifying and counting all flower units (single flowers or inflorescences) within 1 m of either side of the transect. Transects were allowed to change direction to conform to space limitations of the plot, for example, to stay within small plots or when

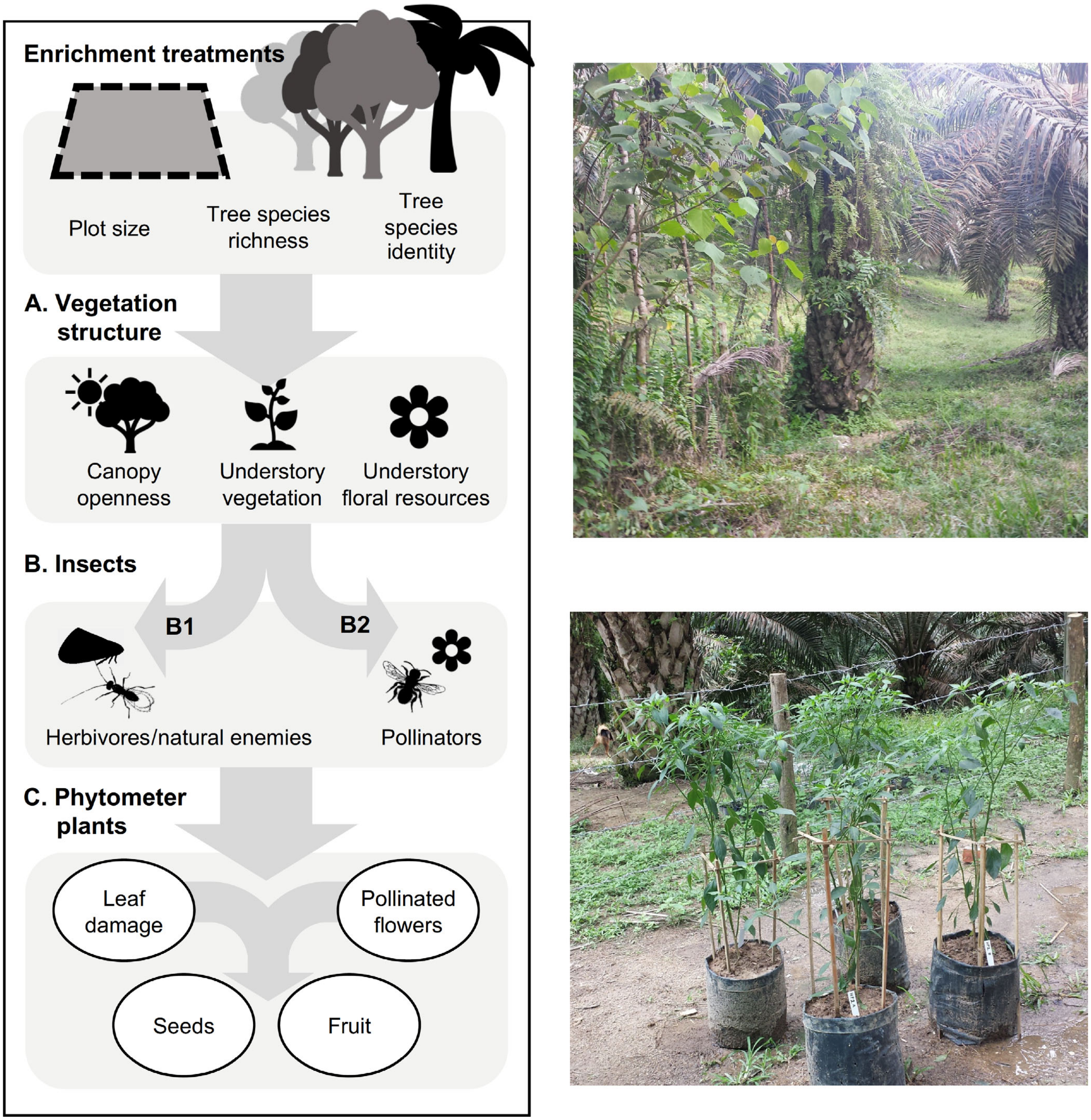

FIGURE 1 Diagram of hypothesized flow of effects from enrichment treatments to levels of endogenous variables: (A) vegetation structure, (B) insects-level ecosystem functions, and (C) phytometer plant-level ecosystem functions. Upper-right photo shows example of an enrichment plot (left side of photo) within oil palm context. Plot is 20 × 20 m and is planted with one enrichment tree species, *Parkia speciosa* (Fabaceae). Lower-right photo demonstrates phytometer plant setup as it would be in each enrichment plot. Photo credit: Kevin Li.

transects were near plot borders. We estimated plot flower richness with data from these transects in combination with a spatially stratified quadrat survey of flowering species only, which was conducted in January 2018. The supplemental quadrat surveys ensured that we sampled species richness over a large and spatially representative proportion of each plot. In these, we counted flowering species in 5 × 5 m quadrats, sampling the entirety of the 25 m^2 plots and placing 1 quadrat in the 100 m^2 plots, 3 quadrats in the 400 m^2 plots, and 13 quadrats in the 1600 m^2 plots. The total sampled areas of the plots larger than 25 m^2 were therefore 25%, 19%, and 20% of the total plot area, respectively. The quadrats were stratified in space so that one quadrat was always

TABLE 1 Ecological response (endogenous) variables, with transformation used, interaction level, and hypothesized driver in structural equation models.

Endogenous variable	Trans-formation	Level	Hypothesized relationships
Canopy openness	Logit	A	Plot size, tree species identity*
Understory vegetation cover	None	A	Canopy openness, tree species identity*
Understory flower richness	Log	A	Canopy openness, understory vegetation cover, plot size*
Understory flower density	Log	A	Canopy openness, understory vegetation cover, tree species richness*, plot size*
Herbivore abundance	Log	B1	Understory vegetation cover, canopy openness, natural enemy abundance, tree species richness*, non-linear tree species richness*
Natural enemy abundance	Log	B1	Understory vegetation cover, canopy openness, herbivore abundance, non-linear tree species richness*
Chili pollinator abundance	Log	B2	Understory flower richness, understory flower density, canopy openness, understory vegetation cover
Chili flower visits	Log	B2	Chili pollinator abundance, understory flower richness, understory flower density, canopy openness, understory vegetation cover
Chili fruit-flower ratio	Log	C	Chili flower visits, chili leaf damage, canopy openness
Chili leaf damage	None	C	Herbivore abundance, plot size*
Fruit per chili plant	Log	C	Chili fruit-flower ratio, chili leaf damage, canopy openness
Seeds per chili fruit	None	C	Chili flower visitors, chili leaf damage

Note: Interaction levels correspond to those presented in Figure 1: A = Vegetation structure; B1 = Herbivore and natural enemy insects; B2 = Pollinator insects; C = Insect-mediated ecosystem functions in phytometer plants. Asterisk (*) indicates significant biodiversity enrichment treatment from random partitions results.

placed in the plot center and additional quadrats were placed randomly within equal divisions of the enrichment plot. We used the Chao asymptotic species richness estimator and a small sample bias correction (Chiu et al., 2014) to project estimates of plot flower richness from the combined transect and quadrat survey samples. Extrapolated richness values ranged from 0.0 to 5.3 additional species (mean = 0.5), or 0%–89% of original values (mean = 9%).

In March–May 2018, we estimated percent coverage of vegetation below a height of 1.3 m in 5 × 5 m subplots in each enrichment plot. These subplots were conducted separately from the floral abundance and richness surveys and were part of a series of vegetation surveys within a randomly placed 5 × 5 m sublot in each enrichment plot (Sachsenmaier, 2018). Vegetation coverage estimation was based on consensus by two observers and excluded coarse woody debris, bare ground, senescent plants, leaf litter, or the phytometer plants. Canopy openness, which quantifies the fraction of sky not blocked by vegetation, was measured in April–May 2018 using hemispherical photos following recommended practices (Beckschäfer et al., 2013) and processed using the program ImageJ (Schindelin et al., 2012) with the "Hemispherical" plugin (Beckschäfer, 2015). For larger plots, we took multiple measurements in a spatial array following Teuscher et al. (2016), taking three photos in 400 m^2 plots and seven photos in 1600 m^2 plots, and averaged across measurements to represent light availability over the entire plot.

Survey of understory flying insects

We estimated abundances of herbivorous and natural enemy (predatory and parasitoid) insects from sweep net surveys of the herbaceous vegetation layer, conducted in the enrichment plots on non-rainy days, from November to December 2017, during a mild rainy season. Within the understory vegetation of each plot, a surveyor made five evenly spaced sweeps, covering ca. 1 m of vegetation each, along a randomly placed 5 m transect using a 32 cm diameter sweep net (BioForm, Nuremburg, Germany). All flying insects (i.e., excluding Formicidae) were collected and individually preserved on site in 1.5 mL Eppendorf tubes with 70% ethanol. We identified samples to family using a binocular microscope and general and region-specific guides (Bosuang et al., 2017; Goulet et al., 1993; Johnson & Triplehorn, 2004). We used family information to classify individuals as herbivores, predators, or other functional groups (Appendix S2: Table S1), which form the basis of the herbivore and natural enemy abundance variables in our models. We conservatively excluded families with mixed trophic niches (approximately one-third of families) from our counts of herbivore and natural enemy abundances.

Phytometer plants

We estimated the ecosystem functions of pollination and herbivory using phytometer plants, which we set in the enrichment plots. We selected *Capsicum annuum* (chili pepper) as a phytometer plant species because of its potential shade tolerance (Pouliot et al., 2012), its widespread home garden cultivation in this region (Prabowo et al., 2016), and the potential for generalist pollinators to increase fruit quality and yield (Roldán Serrano & Guerra-Sanz, 2006). We raised 1500 individuals of a locally available variety of *C. annuum* from seeds. During a growth period outside the enrichment plots, we applied NPK fertilizer and pesticide (imidacloprid, deltamethrin, mancozeb, and abamectin) following local practices to standardize growing conditions and control pest damage before transfer to field sites. Applications of insecticides were in the form of foliar spray mainly focused on host plants near the nursery, rather than the chili plants themselves, to reduce insecticide transfer into the plots.

In early February 2018, we selected four healthy individuals of comparable size to place in each of the 48 enrichment plots (192 total). We selected this period because it coincided with a drier period between peak rainy seasons, which facilitated pollinator observations without being too dry, that is, avoiding the driest period from July to August (Drescher et al., 2016). We halted pesticide application 1 week prior to placement in the plots and only watered as conditions required thereafter. Immediately prior to placement, we removed any flowers that had already opened to ensure pollination could be attributed to plot conditions. We placed four chili plants together with plant stems forming a 60 cm square at approximately the plot center in a location receiving at least partial sunlight and free from encroaching vegetation (exemplary photo in Figure 1). Plants were kept in their original polyethylene containers to isolate them from local soil conditions.

Monitoring insect functions and phytometer plants

During 5 weeks from February to March 2018, we conducted flower visitor observations while the chili plants bloomed in the field. Once a week for each plot on non-rainy days, a pair of observers counted flower visits by flying insects and number of unique flying insect visitors over a 5-min period between 9:00 and 15:00, for a total of 25 observation minutes. We allowed a 1-min acclimatization period before each observation to reduce the effect of disturbance. After each observation session, we counted the number of chili flowers and visually estimated the percent of total leaves with damage. The damage estimate was arrived at by consensus between the two observers and, for rapid assessment, encompassed all forms of damage, including insect herbivory, discoloration, distortion, spotting, or mildew.

We began harvesting ripe fruits after week 5, continuing until all fruits were collected. For each plant, we counted the number of harvested fruits and selected a random subset of 10 fruits to count the number of seeds per fruit. We estimated pollination and fruiting success by calculating the fruit-flower ratio of the plot, which was the total number of fruits divided by the total number of flowers observed over the 6 weeks prior to final harvest.

Analysis

We tested the strength of associations between the experimental enrichment treatments and the response variables in Table 1 by applying the random partitions linear modeling procedure (Bell et al., 2009). We then tested hypothesized ecological pathways (summarized in Table 1) with SEMs within the levels of direct and indirect effects proposed in Figure 1: (a) the effects of experimental enrichment treatments on plot vegetation structure; (b1) effects on herbivore and natural enemy insects, and (b2) on pollinator insects; and (c) herbivory and pollination functions in the phytometer plants. These levels divide our study system into thematic modules centered around ecosystem functions of interest, which present tractable systems of hypothesized relationships that can be tested within the assumptions of the maximum likelihood-based SEM framework (Grace, 2008), given our relatively small sample size ($n = 48$ plots).

Analyses were conducted with R statistical software (R Core Team, 2022). We estimated flower richness using the "vegan" package (Oksanen et al., 2022). Following recommended practices (Gotelli & Ellison, 2004; Warton & Hui, 2011), we applied appropriate transformations (Table 1) to the response variables to meet assumptions for linear models (i.e., normal distribution of residuals), which is recommended for both the partition analysis and maximum likelihood-based SEM (Bell et al., 2009; Grace, 2006). We checked this assumption by viewing simulated model residuals in quantile-quantile plots using the package DHARMa (Hartig, 2019). All variables were mean centered and unit variance scaled for comparability of effect sizes.

Random partitions analysis

The experimental treatments were assigned according to the linear model for random partitions design (Bell et al., 2009), which was adapted to EFForTS-BEE (Teuscher et al., 2016; Zemp, Ehbrecht, et al., 2019) and analyzed using code available in the supplementary material of Bell et al. (2009). The design allowed us to separately quantify the effects of tree species identity, tree species richness (linear and nonlinear effects), and plot size on the ecological response variables. The overall model is specified as:

$$y = \beta_0 + \beta_{\mathrm{LR}} x_{\mathrm{LR}} + \left(\Sigma_i{}^6 \beta_i x_i\right) + \beta_{\mathrm{NLR}} x_{\mathrm{NLR}} + \beta_P x_P + e, \qquad (1)$$

where y is the ecological response variable; β_0 is the model intercept; x_{LR} is the planted enrichment tree species richness treated as a continuous variable ("linear richness"); x_i is an indicator of the presence or absence of species i from among the six enrichment tree species originally planted at the outset of the experiment; x_{NLR} is the "non-linear richness", that is, the effects of specific richness levels as factors; x_P is the enrichment plot size as a factor; and e is a normally-distributed error term. The method estimates the β coefficients using sequential models in the order presented in Equation (1), fitting subsequent models to the residuals of the preceding model. When the data are fit in this order, the linear effect of species richness term is fit first and the remaining variability in the residuals is attributed to the subsequent model terms in turn. Done this way, the random partitions design ensures that the nonlinear species richness term β_{NLR} is orthogonal to species identity effects (β_i). The β_{NLR} term therefore quantifies the deviation from the linear richness expectation that is also not attributed to tree species identity and, hence, represents interaction importance at different levels of species richness. Coefficients for each enrichment tree species i are estimated relative to the "average" species effect, which does not require the contribution of each species to the response to be directly measurable. Demonstrations and further details on the model are available in Bell et al., 2009. We analyzed all variables in Table 1 as the response variable y in Equation (1).

SEMs

We built four separate SEMs representing the hypothesized flow diagram of enrichment treatment effects (Figure 1), presented in Table 1 as the drivers of each endogenous (response) variable. These hypotheses and supporting information are described in more detail in Appendix S3. We followed a "weight of evidence" approach (Grace, 2020), which involves building models based on prior knowledge and making ecologically-sound adjustments using multiple lines of evidence. After removing unsupported links, we compared plausible intermediate models to test whether the significant effects of tree enrichment treatments identified in the random partitions analysis (Table 1, marked with asterisks) were mediated by ecosystem function variables.

We fit SEMs by maximum likelihood estimation using the "lavaan" package (Rosseel, 2012). We assessed model distinguishability with the Vuong variance (ω^2) test using the package "nonnest2" (Merkle, You, Schneider, & Seongho, 2016). For distinguishable models, we used robust alternative likelihood ratio test variants for nested (LR) and non-nested (Z) model comparisons (Merkle, You, & Preacher, 2016; Vuong, 1989). We report the χ^2 exact fit index of the final models, as well as the Swain small sample size correction adjusted for our sample size ($n = 48$) (Rosseel, 2020). In the *SEM results* section, we present overviews of the final models and a narrative summary of the comparisons testing alternative model structures. Full model results, additional approximate fit measures, and details about model comparisons are presented in Appendix S3.

RESULTS

Plot data summaries

Across all plots and transects, we found a total of 21 understory vegetation species with flowers. At this stage of the experiment, the planted enrichment tree species had not matured enough to produce flowers except for a few individuals of *A. jiringa*. The two most abundant flower species were the invasive species *Miconia crenata* (Melastomataceae) and *Asystasia gangetica* (Acanthaceae) which accounted for 57 and 21% of all flower units, respectively. Flower density had a mean of 0.71 (±0.41 standard deviation) flower units/m^2. We found a mean vegetation coverage of 70 (±15 SD) % in 5 × 5 m subplots. Plot canopy openness had a mean of 10 (±8.2 SD) %.

On the 48 transects, we identified a total of 934 insect individuals representing 68 families in 11 orders. Of these, 231 individuals were from 20 families (6 orders) that were exclusively herbivorous, and 260 individuals were from 23 families (6 orders) that were exclusively predatory or parasitic, that is, natural enemies (more information in Appendix S2: Table S1). Mean sweep net herbivore count was 4.8 (±4.5 SD), and mean natural enemy count was

5.4 (±3.6 SD). From the cumulative 25 min of phytometer plant monitoring at each plot, we observed 89 pollinator individuals (plot mean = 1.9 ± 2.2 SD) making a total of 327 chili flower visits (plot mean = 6.8 ± 9.5 SD).

Phytometer plants produced an average of 0.56 (±0.39 SD) fruits per observed flower (fruit-flower ratio). Average plant damage was 41.5 (±10.7 SD) % of total leaves affected, with insect herbivory reported in 94% of observations, while discoloration, distortion, spotting, and mildew were reported in 72%, 41%, 66%, and 3% of observations, respectively. We harvested 3108 fruits (plant mean = 18.9 ± 23.2 SD). Based on a subset of the fruit harvested (n = 1287), we calculated a mean of 41.1 (±12.8 SD) seeds per fruit. We excluded six outlier plants (from among five plots) that never produced any flowers from fruit and seed calculations.

Enrichment treatment effects from the random partitions analysis

Effects of linear tree species richness

Tree species richness as a linear predictor ("linear richness") explained significant variability in flower density (Appendix S4: Table S1) and herbivore abundance (Appendix S4: Table S2) in random partitions models. In both cases, linear richness had a negative effect (Figure 2a).

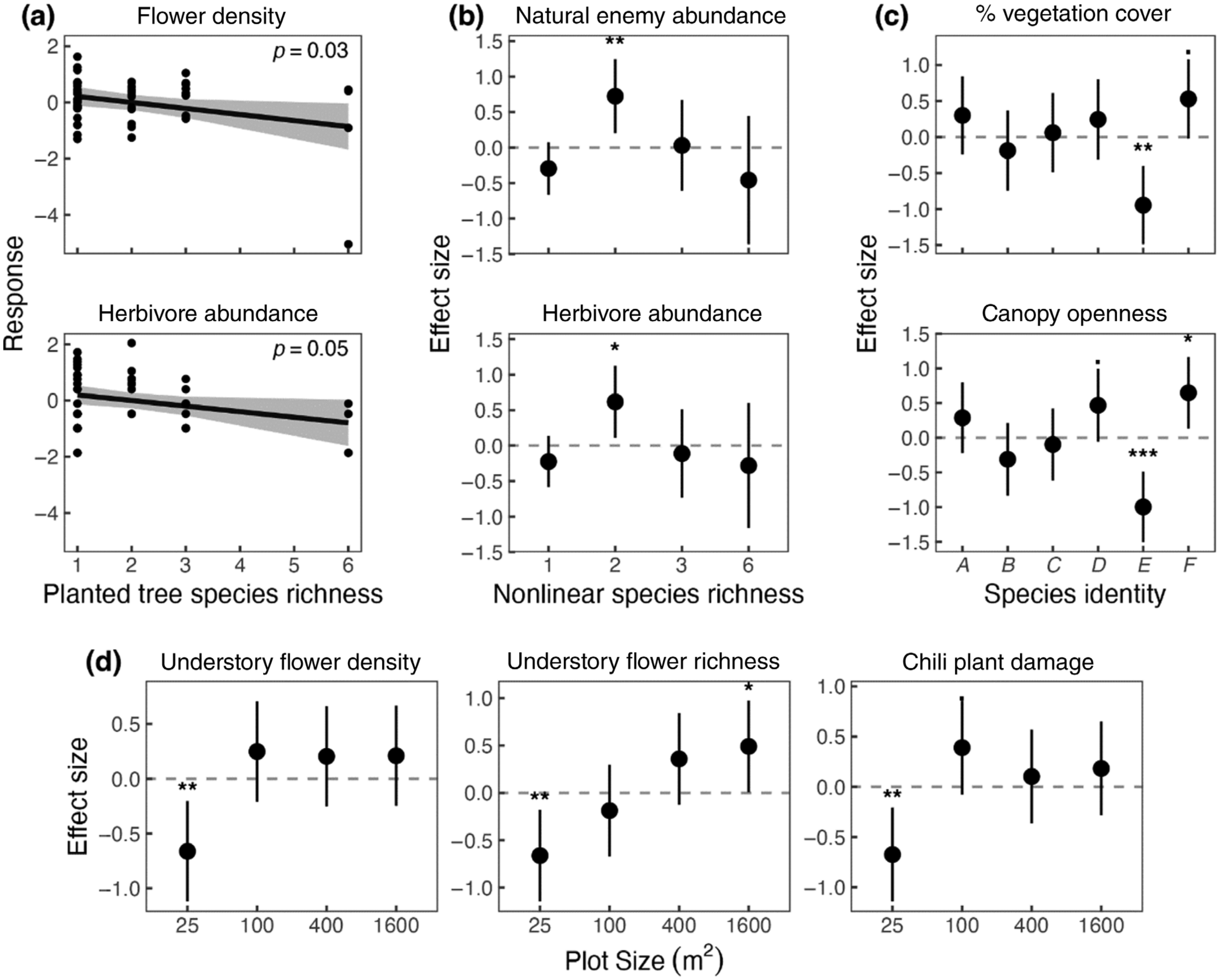

FIGURE 2 Contributors ($p < 0.05$ in Appendix S4: Tables S1–S3) for (a) linear richness effect (illustrated by estimated regression slope and 95% CI), (b) species identity effect coefficients, (c) nonlinear richness effect coefficients, and (d) plot size effect coefficients. All effect sizes are for normalized, mean-centered, and unit variance-scaled variables. Letter codes for species identities are A: *Parkia speciosa*, B: *Archidendron jiringa*, C: *Durio zibethinus*, D: *Dyera polyphylla*, E: *Peronema canescens*, F: *Shorea leprosula*. Effect coefficients are shown with 95% CI. Symbols indicate p-value levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ·$p < 0.10$.

The linear richness model coefficient for flower density was $\beta_{LR} = -0.21 \pm 0.10$ standard error ($p = 0.03$) and the coefficient for herbivore abundance was $\beta_{LR} = -0.20 \pm 0.10$ ($p = 0.050$).

Effects of tree species identity

Planted tree species identity had a significant effect on canopy openness and vegetation cover (Appendix S4: Tables S1 and S2). *Peronema canescens* significantly decreased canopy openness ($\beta_i = -1.0 \pm 0.25$, $p < 0.001$) while *Shorea leprosula* contributed to significant increase in canopy openness ($\beta_i = 0.65 \pm 0.26$, $p = 0.02$) (Figure 2c). These same species identity effects were mirrored in vegetation cover, though only the negative effect of *P. canescens* was significant ($\beta_i = -0.95 \pm 0.27$, $p = 0.001$) while the positive effect of *S. leprosula* was marginally significant (Figure 2c).

Effects of non-linear tree species richness

The number of tree enrichment species as a categorical variable ("non-linear species richness") also explained significant variability in herbivore and natural enemy insect abundance (Appendix S4: Table S2). Two-tree species treatments had a significant positive effect on herbivores ($\beta_{NLR} = 0.62 \pm 0.25$ $p = 0.02$) and natural enemies ($\beta_{NLR} = 0.72 \pm 0.26$, $p = 0.008$) (Figure 2c).

Effects of plot size

Plot size significantly affected understory flower density, flower richness, and chili plant damage (Appendix S4: Tables S1 and S3). For all these variables, the smallest plot size (25 m^2) had a significant negative effect (flower density: $\beta_P = -0.66 \pm 0.23$, $p = 0.006$; flower richness: $\beta_P = -0.66 \pm 0.24$, $p = 0.008$; and chili plant damage: $\beta_P = -0.67 \pm 0.23$, $p = 0.006$) (Figure 2d). The largest plot size (1600 m^2) also had a significant positive effect on flower richness ($\beta_P = 0.49 \pm 0.24$, $p = 0.047$).

No effects with tree enrichment

Some response variables did not have significant relationships with any experimental treatments. At the insect level, pollinator abundance and number of phytometer flower visits did not have significant associations with treatments (Appendix S4: Table S2); and at the phytometer level, fruit-flower ratio, fruit per plant, and seeds per fruit did not have significant associations with treatments (Appendix S4: Table S3).

SEM results

Effects on vegetation structure

The final vegetation structure SEM suggests that tree species identity (*P. canescens*) directly decreased canopy openness, which in turn increased understory vegetation (Figure 3a). Species identity is represented by *P. canescens* presence in our SEMs since this species had the most consistent effect in the random partitions analysis. We found strong support that canopy openness fully mediated a positive effect of *P. canescens* on understory vegetation coverage, as an alternative SEM with only a direct effect of *P. canescens* on understory vegetation coverage fit significantly worse than the final model ($Z = -2.60$, $p = 0.005$, see Appendix S3: Figure S1a and Table S1 for more details). We found that canopy openness contributed positively to flower richness, but plot size also remained a significant positive variable in model comparisons. Tree species richness as a continuous variable had a significant negative relationship with understory flower richness, as was the case in the random partitions analysis results. There was marginal evidence that canopy openness partially mediated the positive effect of plot size on understory flower richness, as the final model with both canopy openness and plot size influencing flower richness fit marginally better than an alternative model where plot size was removed ($LR = 3.390$, $p = 0.0542$); however, this difference was only marginally distinguishable ($\omega^2 = 0.061$, $p = 0.095$). Positive effects of plot size on canopy openness and of canopy openness on understory flower density were marginally significant ($p < 0.10$) in the final model. The global fit index of the final model was $\chi^2(7) = 4.558$, $p = 0.714$; Swain $\chi^2(7) = 3.986$, $p = 0.875$, indicating an adequate model fit to the data, that is, model-implied covariances were not significantly different from the empirical data ($p > 0.05$), with no omitted relationships (Grace, 2020).

Effects on insect abundance and ecosystem functions

In the herbivore and natural enemy insect SEM, two-species tree richness remained a significant positive predictor of both herbivore and natural enemy insect abundance (Figure 3b), supporting the links indicated by the random partitions analysis. There was marginal support ($p = 0.054$) for a negative effect of linear tree species

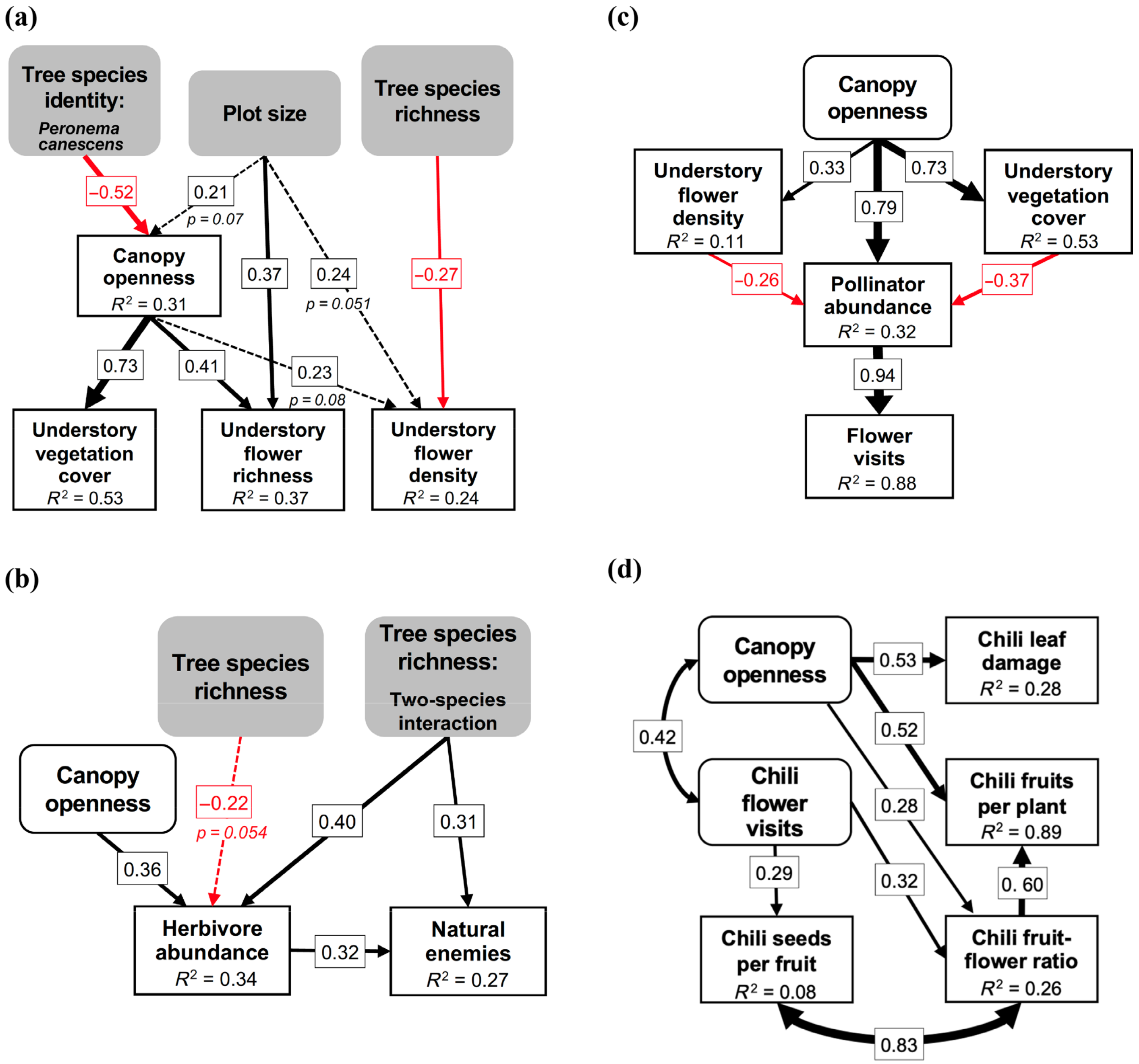

FIGURE 3 Diagrams of structural equation models of (a) vegetation structure, (b) herbivore and natural enemy ecosystem functions, (c) pollinator ecosystem functions, and (d) phytometer ecosystem functions. Rounded boxes represent exogenous variables in the model, that is, those without regressions, and those with gray fill represent enrichment treatment variables. Square boxes represent endogenous variables, that is, dependent variables in regressions. All effect sizes are for normalized, mean-centered, and unit variance-scaled variables. Single-headed arrows represent independent variable relationship with the standardized effect size in the associated box. Double-headed arrows represent model-fitted standardized covariance terms. Arrow widths are scaled by effect size. Solid arrows indicate relationships with $p < 0.05$ and dashed arrows indicate marginally significant ($p < 0.10$) relationships, with the p-value given beneath the effect size.

richness on herbivore abundance, with no supported mediating pathways through other hypothesized links. Canopy openness was also a positive predictor of herbivore abundance but did not have a significant direct link to natural enemy abundance. We did not find significant relationships with understory vegetation cover or understory flower richness. In comparing alternative SEM formulations (Appendix S3: Figure S1b and Table S1), we found significant support against natural enemy abundance fully mediating the effect of two-species tree richness on herbivore abundance (LR $= 4.608$, $p = 0.024$). In our final model, herbivores partially mediate the effects of two-species tree richness on natural enemies with a significant positive effect (Figure 3b), consistent with a bottom-up hypothesis (Scherber et al., 2010). Our final model had the best global fit of all candidate models considered ($\chi^2(5) = 2.241$, $p = 0.815$, Swain $\chi^2(5) = 2.126$, $p = 0.832$) and is consistent with one of our ecologically-based hypotheses, though Vuong variance tests (see the *SEMs* section) indicated that our data could not distinguish between fits with other intermediate models (Appendix S3: Table S1).

In the pollinator insect SEM, we find that flower density and vegetation cover both had a negative effect on pollinator abundance, while canopy openness had a strong positive effect (Figure 3c). Pollinator abundance was the major positive driver of the number of chili flower visits, accounting for 88% of variability as the only independent variable. There was not strong evidence that other variables played significant mediating roles. An alternative SEM in which canopy openness did not have a direct link to pollinator abundance and only influenced vegetation cover and flower density did not fit better ($Z = 16.054$, $p < 0.001$, Appendix S3: Figure S1c and Table S1), suggesting that the two understory vegetation variables partially mediated the effect of canopy openness. The final pollinator insect global fit was $\chi^2(4) = 1.177$, $p = 0.882$, Swain $\chi^2(4) = 1.115$, $p = 0.892$.

Effects on ecosystem functions in phytometer plants

The final phytometer SEM (Figure 3d) supported a significant positive link between pollinator visits to chili flowers and the chili fruit-flower ratio; the latter in turn having a positive effect on the seeds per fruit. We included a covariance term between canopy openness and flower visits, which was significant and positive, reflecting the finding of the pollinator SEM. Based on modification indices, we added a covariance term between seeds per fruit and the fruit-flower ratio. This additional term indicated high positive correlation (0.83) and may reflect shared mechanisms related to pollination success and plant resource allocation (Knight et al., 2006). On the other hand, flower visits explained only 8% of variance in seeds per fruit. Canopy openness had significant positive effects on the fruit-flower ratio and the number of fruits per plant. We did not find significant relationships between herbivore abundance and plant damage. In intermediate models, we included enrichment plot size as a predictor of plant damage (Appendix S3: Figure S1d, Table S1), which was suggested by the random partitions results. However, we found that an SEM where canopy openness fully mediated the effect of plot size on leaf damage had moderately better fit than an SEM where plot size was the only driver ($\mathrm{LR} = -1.628$, $p = 0.052$). When both variables were included in the leaf damage regression, the model was indistinguishable from the full mediation model ($\omega^2 = 0.031$, $p = 0.164$) but plot size was not a significant predictor ($p > 0.10$). We therefore removed plot size as a variable from the final model, which had a global fit of $\chi^2(4) = 5.610$, $p = 0.230$, Swain $\chi^2(4) = 5.253$, $p = 0.262$.

DISCUSSION

We investigated the biodiversity enrichment effects of the EFForTS-BEE (Teuscher et al., 2016) on ecosystem functioning with random partitions analysis (Bell et al., 2009) and tested for indirect effects using SEMs. Through the random partitions approach, we found canopy openness and understory vegetation cover to be negatively and positively associated with planted *Peronema canescens* and *Shorea leprosula* trees, respectively (Figure 2c), lower flower richness and density in smaller plots (Figure 2d), and lower flower richness with higher planted tree richness (Figure 2a). We found positive tree species interaction effects on understory herbivore and natural enemy insects (Figure 2b), while effects on pollinator activity and phytometer plant functions were mostly not significant. However, SEMs revealed that the vegetation structure variables, namely the positive effect of canopy openness, mediated enrichment effects on insect abundances and functions (Figure 3b,c) to phytometer plants (Figure 3d). Our results demonstrate that the effects of biodiversity enrichment, focusing on ecosystem functions associated with understory herbivore, natural enemy, and pollinator insects, are not always directly correlated with enrichment treatments, but rather may be mediated through multiple interacting pathways.

Effects on vegetation structure

The positive effect of canopy openness explained different degrees of variability in the understory vegetation variables in the SEM. Canopy openness completely mediated enrichment effects on understory vegetation cover (Figure 3a). In this same model, flower richness was directly and positively related to plot size, as predicted by island biogeography theory (MacArthur & Wilson, 1963), but this effect was also partially mediated through canopy openness. This indirect effect of plot size can be explained by oil palm thinning that was part of the experimental setup and design, as more palms were felled in larger plots initially, increasing canopy openness (Gérard et al., 2017; Khokthong et al., 2019). Likewise, canopy openness also positively influenced understory flower density in our SEM results.

Our final vegetation structure SEM results (Figure 3a) demonstrate that tree species identity can play an influential role in determining downstream effects. The SEM confirms that the presence of *P. canescens* directly decreased canopy openness, which in turn played important mediating roles for herbaceous vegetation variables. This fast-growing, early successional species performed very well in experimental plots (Zemp, Gérard, et al., 2019) and was an important driver of stand structural complexity, a measure of vegetation structure that is correlated to canopy openness (Zemp, Ehbrecht, et al., 2019). On the other hand, *S. leprosula* is a primary forest species and had low survival rates (Zemp, Gérard, et al., 2019). Mortality-induced canopy gaps may therefore explain this species' positive association with canopy openness in the random partitions analysis results. Species identity can be a key factor in tree biodiversity experiments associated with selection effects (Ebeling et al., 2008; Grossman et al., 2018); nevertheless, it is not commonly considered in comparing ecosystem functions across agroforestry systems (e.g., Steffan-Dewenter et al., 2007). Measures to diversify agricultural landscapes may therefore do well to consider life history traits and performance of enrichment tree species when anticipating downstream effects on insect-mediated ecosystem functions.

Effects on insect abundance and ecosystem functions

We found evidence that canopy openness played a role in determining herbivore and pollinator abundance. Some studies have found positive herbivore responses to increased canopy openness in forests, which is attributed to increased understory leaf growth or changes in microclimate (Basset et al., 2001; Franc & Götmark, 2008). Indeed, our SEM showed that canopy openness had a positive effect on herbivore and pollinator abundance, though the latter was partly mediated by the negative effect of understory vegetation cover (Figure 3c). This negative effect may reflect additional aspects of habitat outside of understory vegetation that were favorable for pollinators, for example, availability of nesting sites in bare soil or dead wood (Proctor et al., 2012; Rodríguez & Kouki, 2015). Outside of increasing vegetation growth, canopy openness may also promote warmer, sunnier environments that can create favorable ovipositioning sites and reduce larval development times of herbivore and pollinating insects (Wirth et al., 2008).

A negative effect of flower density also partially mediated the relationship between canopy openness and pollinator abundance (Figure 3b). This may suggest that co-flowering species in the plot competed with phytometer plants for pollinators (Knight et al., 2005). This dilution effect could indicate a depauperate pollination landscape where pollination services are a finite resource due to limited pollinator populations, leading to pollination competition (Holzschuh et al., 2011; Knight et al., 2005; Veddeler et al., 2006). This is also suggested by the low number of pollinator individuals we observed during the monitoring period, which is in line with findings on butterflies (Lucey & Hill, 2012) and bees (Power et al., 2022) in oil palm plantations; while the lack of enrichment effects on pollinator abundance and visitation could also indicate that the different levels of enrichment did not significantly improve habitat at this stage. On the other hand, as we took measures to reduce insecticide effects in the field, we do not expect this to bias the enrichment effects (Obregon et al., 2021).

Two-species enrichment treatments had a significant positive effect on both herbivore and natural enemy understory insects (Figure 2b), which was not mediated through canopy openness (Figure 3b). As this factor represents species interactions in the random partitions framework (Bell et al., 2009), this suggests interactions between two species of trees have additional positive effects not associated with canopy openness. Zemp, Gérard, et al. (2019) concurrently analyzed planted tree performance within these plots and found that trees in two-species plots experienced higher mortality, which they attributed to a selection effect that led to competitive dominance of better-performing species in this environment. However, they also found that underyielding in these plots (due to tree mortality) was only apparent after an initial period of overyielding in the first year. This initial period of growth may have contributed to more dead wood on these plots, creating habitat conditions that promoted higher insect populations (Seibold et al., 2016). Seibold et al. (2016) also found that the positive effects of dead wood on the arthropod community were independent of a strong positive effect of canopy openness, which aligns with our finding that canopy openness did not mediate the effect of two-species interactions on herbivores and natural enemies (Figure 3b). However, more data are needed to determine whether dead wood is the ecological variable mediating the effect of two-species interactions.

We represent the connection between herbivore and natural enemy abundances as a bottom-up relationship in our final SEM, that is, herbivores drive natural enemies (Figure 3b). This model had the best global fit, but we could not formally compare alternative models based on our data. Nevertheless, the positive bottom-up relationship between herbivore and natural enemy abundances was consistent with a lack of a density-dependent relationship that might be expected in top-down control; though this can also depend on other controlling factors of predator and prey populations, such as environmental sensitivity (Levins & Schultz, 1996) or spatial heterogeneity (Tscharntke, 1992). The negative effect of tree species richness on herbivore abundance, though marginal, is also consistent with hypothesized associational effects of plant species diversity on insect herbivores, in which the likelihood of a host plant being found by pests increases with low diversity due to host concentration (Grossman et al., 2018).

These results suggest that insect herbivores respond more strongly to habitat changes related to biodiversity enrichment than natural enemies. Although stronger top-down effects may be more prevalent generally (Vidal & Murphy, 2018), this is not always the case (Denno et al., 2003; Scherber et al., 2010; Schuldt et al., 2017). This might be related to the young age of plant biodiversity experiments, to heterogeneity across natural enemy groups, or to other moderating effects such as intraguild predation (Grossman et al., 2018; Staab & Schuldt, 2020).

Effects on ecosystem functions in phytometer plants

Our results suggest that the variation in pollination ecosystem function was attributed to flower visits in the enrichment plots. We found positive effects of flower visits on the fruit-flower ratio, which in turn increased the number of fruits produced (Figure 3c). As flower visits were a positive driver of successful development from flowers to fruit (Figure 3d), we may infer that fruit loss during development was not a major factor for the phytometer chili plants (Bos et al., 2007). This may indicate that plants were not under major stress and could explain why leaf damage did not have the expected negative impact on fruit and seed variables. Pollinator visits only explained a small portion of seeds per fruit, though a study in sweet peppers has shown this has a major effect (Roldán Serrano & Guerra-Sanz, 2006). However, we also found a strong positive correlation between the fruit-flower ratio and seeds per fruit, which could indicate our model may not be capturing more complex interactions due to plant resource allocation in response to pollination and other biotic or abiotic effects (Bos et al., 2007; Knight et al., 2006).

We found no relationships between herbivore abundance and phytometer plant damage or the fruit to flower ratio (Figure 3d). We note that our herbivore samples were not taken at the same time as phytometer fruit development, so short-term temporal variability may have masked an effect. Our simple metric of damage potentially included effects of fungi and other pathogens, though insect herbivory was by far the most prevalent form of damage we observed (94% of observations). However, we did find some evidence that increased canopy openness could explain a positive effect of plot size on leaf damage. Light gaps can moderate herbivory effects on plants by promoting leaf growth, which presents a target for more herbivore attack (Norghauer et al., 2008), reflecting the "plant vigor hypothesis" (Price, 1991). Canopy openness also had positive relationships with fruiting success indicators in the phytometer plants (fruit flower ratio and number of fruits), suggesting that canopy openness did indeed increase plant vigor. Nevertheless, plant tolerance of herbivory may depend on many factors, including environmental stress and nutrients (Wise & Abrahamson, 2007), which may explain why leaf damage did not have significant impacts on fruit and seed production.

Canopy openness mediates early biodiversity enrichment effects on ecosystem functions

At 4 years, the progression of this enrichment experiment was still relatively early (Zemp, Ehbrecht, et al., 2019), and our finding of the importance of canopy openness reflects an early successional forest (Holmes & Matlack, 2017). Canopy openness appears to play an important role in driving ecosystem functions at all the ecosystem levels we examined. In many cases, canopy openness was both a direct and indirect driver of ecosystem functions (e.g., on pollinator abundance and through flower density and vegetation cover). In other cases, canopy openness appears to fully mediate the effect of an enrichment treatment variable (e.g., canopy openness explained the negative correlation between understory vegetation cover and *P. canescens*). Based on the ecosystem functions we observed affecting the phytometer plants, the trends in our findings could suggest an eventual trade-off between net beneficial insect activity, namely from pollination services, and other ecosystem functions related to tree growth, as exemplified by the fast-growing species *P. canescens*, which lead to canopy closure (Zemp, Ehbrecht, et al., 2019). A similar dynamic may be behind an initial increase in oil palm yield adjacent to enrichment plots, which Gérard et al. (2017) attributed to light and other resource availability resulting from oil palm thinning, which remained significant five years after planting (Zemp et al., 2023).

Decreased canopy openness is an expected effect of forest restoration, as it is associated with structural complexity and productivity that is characteristic of mature natural forests (Lamb et al., 2005; Zemp, Ehbrecht, et al., 2019). As tree growth continues to close canopy gaps, our results suggest understory vegetation cover and flower richness, which was strongly driven by canopy openness, may decrease, though decreases in flower richness may be dampened for large plots. Our findings also suggest herbivore abundance may decrease with decreasing canopy openness, which in turn may lead to lower natural enemy abundance. These patterns highlight the important role canopy gaps play in enrichment ecosystems, as they do in natural forest habitats (Bouget & Duelli, 2004). Methods of maintaining patches of canopy openness, such as through selective tree felling (Basset et al., 2001), could be one way to increase favorable environments for insect-mediated ecosystem functions in restoration projects, though further research is needed on which ecosystem functions may be favored and how this relates to specific restoration goals.

However, on a longer timescale, predominant dynamics may shift based on changing communities (Luong et al., 2019). Plot understories were dominated by invasive pantropical plants (Rembold et al., 2017). However, continued tree growth and spontaneous establishment of shade-adapted plant species through seed dispersal may add complexity and diversity to plots (Arroyo-Rodríguez et al., 2009; Staab & Schuldt, 2020). This could create more heterogeneous habitats for insects, in turn promoting higher diversity of specialist herbivores and more stable populations of associated natural enemies (Root, 1973). Larger-scale dynamics may also play a role as plot communities become more established. For example, as some plots develop into sources for pollinator populations, this could shift the dynamic between flower density and pollination services from dilution to resource concentration in nearby plots, reflecting processes closer to that observed in more natural heterogeneous landscapes (Jauker et al., 2009).

Conclusions

The importance and prevalence of restoration approaches is increasing in oil palm and other ecologically simplified land uses, as demonstrated by the current “Decade on Ecosystem Restoration” declared by the United Nations (Gann et al., 2019). Our findings provide insight into how enrichment may affect ecosystem functions in early stages of restoration in oil palm. We demonstrate that the effects of different levels of biodiversity enrichment treatments on ecosystem functions of herbivory, natural enemy biocontrol, and pollination may be mainly indirect, that is, mediated by changes in vegetation structure or canopy cover. In addition, enrichment species traits may play an important role, as we found that fast-growing trees (i.e., *Peronema canescens*) drove decreasing canopy openness, which in turn mediated effects on herbivores, natural enemies, and pollinators. We observed a net benefit for phytometer plants through insect-mediated pollination function with no apparent negative effect of herbivory; however, as this was driven by canopy openness, an eventual trade-off with forest complexity and the emergence of new patterns will likely occur as biotic communities continue to develop. Our results demonstrate that, even at early stages of the restoration of highly simplified oil palm environments, differences in tree biodiversity enrichment can have a substantial effect on ecosystem functioning. As our findings of the influence of canopy demonstrate, the ability of enrichment to enhance vegetation complexity had the greatest effect, reflecting the dynamics of forest succession, while tree species richness per se played less of a role in ecosystem functioning at this stage. Moving forward, our results suggest that maintaining heterogeneity in canopy openness in restoration plots may be important for supporting increased ecosystem functioning and improving habitat diversity.

AUTHOR CONTRIBUTIONS

Kevin Li, Ingo Grass, and Teja Tscharntke designed the study. Dirk Hölscher and Holger Kreft designed the enrichment experiment, which was maintained under the supervision of Delphine Clara Zemp. Kevin Li, Lena Sachsenmaier, and Hendrik Lorenz collected data with guidance by Delphine Clara Zemp, Dirk Hölscher, Fuad Nurdiansyah, Holger Kreft, Ingo Grass, and Teja Tscharntke. Kevin Li performed analysis and drafted the manuscript with input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Li et al., 2023) are available in GRO.data at https://doi.org/10.25625/MZP7HQ.

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SUPPORTING INFORMATION

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

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