Check for updates

Received: 1 February 2024 | Accepted: 18 October 2024

DOI: 10.1111/1365-2664.14851

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

RESEARCH ARTICLE

Cacao grafting increases crop yield without compromising biodiversity

Carolina Ocampo-Ariza[1,2] | Sophie Müller[1] | Fredy Yovera[2,3] | Evert Thomas[2] | Justine Vansynghel[2,4] | Bea Maas[5] | Ingolf Steffan-Dewenter[4] | Teja Tscharntke[1]

[1]Agroecology and Functional Agrobiodiversity, University of Göttingen, Göttingen, Germany

[2]Bioversity International, The Americas—Lima Office, Lima, Peru

[3]Cooperativa Agraria Norandino Ltda, Piura, Peru

[4]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany

[5]Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria

Correspondence
Carolina Ocampo-Ariza
Email: carocampoa@gmail.com

Funding information
Bundesministerium für Wirtschaftliche Zusammenarbeit und Entwicklung, Grant/Award Number: GIZ—81219430; Center of Biodiversity and Sustainable Landuse at the University of Göttingen; Deutsche Forschungsgemeinschaft, Grant/Award Number: TS 45/42-1 and STE 957/27-1

Handling Editor: Ricardo Solar

Abstract

1. Yields of tropical tree crops decline with time, often forcing smallholders to establish new deforestation-derived plantations. Consequently, alternative strategies reconciling crop yield and biodiversity conservation are essential. Grafting is a common propagation method to boost yield in crops as cacao, but it alters tree structure potentially affecting associated insect diversity.
2. We investigated how grafting affects cacao yield and biodiversity, modulated by local management and landscape, that is shade-tree cover and distance to nearest forest. Within nine organic agroforests in Peru, we monitored the number of pods yielded over 2 years by ~190 trees per plot, and compared production levels with non-grafted trees. We collected arthropods on 54 trees shortly after grafting and replicated surveys in the dry and rainy season, with standardized diurnal and nocturnal inspection of tree branches. We expected grafting would increase yield after a brief gap, while the arthropod community associated with freshly grafted cacao would differ from that of full-grown cacao trees.
3. Cacao grafting increased yields after 2 years by an average of 45% more than adjacent non-grafted trees. Compared to non-grafted trees, arthropod abundance was 25% lower 3 months after grafting and 12% lower after 6 months, indicating a recovery of arthropod communities shortly after grafting. Similar patterns were observed for species richness (22% and 12%) and Hill–Shannon diversity (18% and 13%). Abundance of phytophagous insects (mainly aphids) was unchanged with grafting. However, we found 46% fewer beetles and 39% fewer predatory arthropods (mainly spiders) on young—but not old—grafted cacao, indicating a possible decrease in pest control services by predatory arthropods at early grafting stages.
4. We observed richer, more diverse, but less abundant arthropods during nocturnal surveys than on diurnal surveys. Arthropods were richer, more abundant and diverse in the rainy season than in the dry season. Increasing shade-tree cover decreased arthropod diversity but did not affect species richness or abundance.

Carolina Ocampo-Ariza and Sophie Müller contributed equally to the development of this manuscript.

Shorter distances from forest decreased richness and diversity, but not abundance, possibly due to higher pressure from vertebrate predators nearby forests.

5. *Synthesis and applications*. Grafting is a successful approach for rejuvenating old, unproductive cacao trees, enhancing smallholder income opportunities and thus reducing pressure for new deforestation-based plantations. Grafting briefly reduced arthropod abundance and diversity, but recovered in a short time. Hence, rejuvenation of cacao trees by grafting should be promoted and implemented as a promising strategy for more sustainable social-ecological cacao management, with economic and ecological benefits for smallholders.

KEYWORDS
agricultural sustainability, crop productivity, ecological regeneration, native cacao, smallholders

1 | INTRODUCTION

Yield gaps in smallholder farming are a major challenge in tropical commodity production, often associated with high levels of poverty and deforestation (Clough et al., 2009; Steffan-Dewenter et al., 2007; Wurz et al., 2022). Addressing yield gaps of tropical tree cash crops without sacrificing agrobiodiversity is challenging, given that common strategies to enhance yield focus on intensifying agricultural practices through monocultures, due to expected yield benefits (Wessel & Quist-Wessel, 2015), despite evidence that agroforestry with intermediate shade-tree cover supports higher biodiversity, and associated ecosystem services at little cost for crop yield (Clough et al., 2011; Rakotomalala et al., 2023). Reductions in crop yield are often linked to the impact of pests and diseases, plant ageing and unsustainable management practices, which tend to force smallholders to abandon plantations and sustain their income by establishing new cropland, at the cost of remaining forests (Ivanova et al., 2020; Ruf et al., 2015). Strategies that increase the productive life of already existing commodity crops without compromising biodiversity have the greatest potential to sustainably address yield gaps and reduce the pressure on surrounding natural habitats.

Grafting is a long-used management technique to asexually propagate vegetable plants, which allows for the rapid rehabilitation of old, unproductive plants (e.g. Rivard & Louws, 2008; Toledo-Hernández et al., 2023). Grafting may recover yield due to the introduction of younger and vitalized tissue, but may also bring additional features of flavour, productivity or resistance to extreme environmental conditions associated to its genetic makeup (e.g. Kyriacou et al., 2020; Nawaz et al., 2016; Rivard & Louws, 2008). However, although multiple studies have evaluated the effect of vegetable and fruit tree grafting on growth and productivity (e.g. Kyriacou et al., 2020; Nirosha et al., 2023; N'zi et al., 2023), the benefits for cacao yield are much less well documented.

The technique consists in combining two plants of one or more species, by implanting a scion—a branch section with one or more active buds—onto a host plant known as the rootstock, gradually replacing the crown of the tree with a completely new species or variety (Marattukalam & Saraswathyamma, 1992). Consequently, the old complex plant crown is replaced by a much-simplified crown dominated by young meristematic tissue from the scion, while the grafted tissue benefits from the fully developed root system of the mother plant. This young tissue is more vulnerable to herbivores given its lower lignification, and high nutrient and water content, and therefore may be expected to be visited more frequently by phytophagous insects (Basset, 2001; Conceição et al., 2019; Cuevas-Reyes et al., 2004). Moreover, a simplified crown structure with fewer branches than adult plants likely reduces the plant's structural heterogeneity and availability of refuges and other resources for arthropods, such as spiders (Lawton, 1983). These changes are likely local and may be counterbalanced by a quick recolonization from surrounding vegetation (Klein et al., 2002). To our knowledge, there is no assessment so far about how grafting, in combination with different management of surrounding vegetation, affects arthropod communities on tree crops and cacao yields.

In addition, other factors influence the composition of arthropods, such as season (e.g. Guerrero et al., 2003; Wagner, 2001) and daytime (e.g. Basset, 2001; Costa & Crossley Jr., 1991; Hoehn et al., 2008). In cacao, previous studies have shown higher numbers of flying arthropods at night (Young, 1986), or more flower visitors in the rainy season (Tarmadja, 2015). Furthermore, the occurrence of shade in agroforestry systems can provide habitats for tropical forest animals from adjacent forests and can benefit ecosystem services such as pollination or biological pest control (Rice & Greenberg, 2000; Schroth & Harvey, 2007; Tscharntke et al., 2011).

In cacao, grafting has been used for several decades as an alternative to improve plant yield, bean quality and resistance to adverse environmental conditions (Ceccarelli et al., 2022; N'zi et al., 2023). Frequently, new plantations are established with grafted seedlings, or such seedlings are used to replace dead plants within a plantation. In recent years, rehabilitation of old, unproductive plantations, whereby large areas or entire plantations of resident cacao trees are grafted simultaneously is increasingly being applied (Somarriba et al., 2021; Zavaleta et al., 2022). Grafting is preferred given its lower cost and higher success rate than other drastic strategies such as renovating through replanting—ca. USD $5000 for replanting vs. USD $1350 for renovating the tree crown through grafting or rehabilitating the crop through fertilization of soils with mineral nutrients and other fertilizers, in coffee agroforestry (USAID, 2017; Wiegel et al., 2020). However, there is no published data quantifying the success of large-scale grafting and the time it takes to achieve higher yields. Since grafted cacao is less productive during the first 1–2 years, as the branches grow and mature, initiatives to reconvert entire plantations represent an economic risk for smallholders, who rely mainly on income from their crops and who represent ca. 90% of cacao producers worldwide (Voora et al., 2019). Therefore, the consequences of cacao grafting for crop yield and economic stability as well as for biodiversity must be considered together.

Here, we assessed the effects of grafting and graft age on yield and arthropod biodiversity on cacao trees grafted with fine-flavour native cacao genotypes in agroforests from Piura, Peru. We hypothesized that grafting could positively influence cacao yield as soon as cacao trees start being productive, from the second year after grafting onwards. We also hypothesized that the change in plant architecture resulting from the canopy pruning associated with grafting negatively impacts overall arthropod abundance, as a result of decreased crown area and resource availability and heterogeneity. Finally, we expected grafting to decrease arthropod diversity, through a higher dominance of herbivorous taxa which would benefit more than other arthropod guilds from the new meristematic tissue as a food resource.

2 | MATERIALS AND METHODS

2.1 | Study area and design

We selected nine cacao agroforests from smallholder farmers associated with the agrarian cooperative Norandino, located around the village of La Quemazón (5°18′44.2″ S, 79°43′08.3″ W), at 245 m.a.s.l. in the department of Piura, Peru. The region is characterized by a native vegetation of seasonally dry tropical forests, with annual average temperatures of 25.4°C, ranging between 16.3°C mean temperature minima in August and 33.0°C mean maximum temperature in January (reference period: 1981–2010). Mean annual precipitation is 489.5 mm, concentrated between January and April (91%; 445.6 mm) with a precipitation peak in March (SENAMHI, 2020). Under these environmental conditions, cacao must be grown under year-round irrigation, normally performed by gravity.

The agricultural landscape is dominated by a matrix of rice fields grown seasonally and perennial cacao agroforests. Agroforests include cacao trees of ca. 3.5 m, shaded by a combination of fruit trees (e.g. *Inga* spp., Citrus spp., *Mangifera indica*, *Persea americana*) and timber trees (e.g. *Cedrela odorata*, *Prosopis palida*, *Tectonia grandis*). The selected agroforests had an average size of 0.57 ha ± SD 0.38 ha, and were located along a distance gradient to the nearest forest patch, ranging between 681 m and 1249 m (Appendix S1; Ocampo-Ariza et al., 2022).

Within each agroforest, areas of ca. 0.2 ha were grafted with different genotypes of the fine or flavour cacao variety *Gran Blanco de Piura* between 2019 and 2020 (Thomas et al., 2023; Tscharntke et al., 2023). We performed three grafts per tree from up to three different genotypes selected for their high productivity and compatibility (Vansynghel et al., 2023). Grafting success is known to vary with management and biological factors (e.g. N'zi et al., 2023), and in our case not all grafts succeeded. Some trees had to be re-grafted 3 months after the first attempt. As a result, in each agroforest there were cacao trees with grafts of two different ages (hereafter "graft age"): (1) young grafted cacao, grafted in August 2019 and (2) old grafted cacao, done ca. 3 months before the young grafted cacao (April–May 2019). Additionally, each agroforest had (3) non-grafted trees, used as control, which were either never grafted or grafted several years ago with unidentified genotypes without any selection towards high yield. We selected two trees of each age category for a total of six experimental trees per agroforest. In all grafted trees, the crown of the rootstock was largely pruned or completely removed approximately 1 month before the start of the arthropod sampling. As a result, plant architecture was largely simplified and the foliage remaining was mostly dominated by young leaves. We drastically pruned non-grafted trees to make their crown volume similar to that of grafted trees, but the tree's foliage was dominated by adult leaves and lignified branches. Despite the drastic pruning, the crown of old, non-grafted plants remained larger in comparison to that of grafted cacao. We calculated the crown volume of each cacao plant following (Frank, 2010), which showed an average reduction of 65% from experimental non-grafted trees ($12.38 \pm 7.00\,\text{m}^3$, $n = 18$) to old grafted cacao ($4.32 \pm 3.96\,\text{m}^3$, $n = 18$) and of 85% to the young grafted cacao ($1.74 \pm 1.52\,\text{m}^3$, $n = 18$). All pruning was performed in the months when it is typically done in the region, as suggested by the cooperative Norandino Ltda. Crown volume reduction could negatively impact the plant's yield in the short term due to an overall lower availability of flowers from the cut branches and a higher initial investment of the trees in vegetative growth. However, the 2-year gap between grafting and yield assessments (see below) likely avoids any drastic short-term effects from pruning on our yield assessments.

We evaluated the canopy cover of shade-trees (hereafter "shade-tree cover") above each experimental tree using a Taotronics® Fish-eye lens adapted to a smartphone. We attached the smartphone to a selfie stick, took a picture at a standard height of ca. 3.30 m, and quantified the percentage cover of shade-tree canopy in pictures with the software GIMP. Shade-tree cover above experimental cacao trees ranged between 0% and 85.8%. We measured the distance in a straight line of each agroforest from the nearest (secondary) large area of tropical dry forest using satellite imagery (Ocampo-Ariza et al., 2022). Distance from forest is known to affect the diversity and function of arthropod communities in agricultural areas (Klein et al., 2006). The nearest forest was composed of two patches of seasonally dry tropical forest covering an average surface of 142.89 ± 81.15 km^2. This average patch size is characteristic of the fragmented forests in the Piura region (Fremout et al., 2020; Linares-Palomino & Alvarez, 2005). All research was developed under permit number 0519-2019-MIN AGRI-SERFOR-DGGSPFFS.

2.2 | Arthropod sampling

We collected arthropods four times on each cacao tree: twice in the dry season (December 2019; with young and old cacao grafts being three and 6 months old, respectively) and twice in the rainy season, between February and April 2020 (with young and old cacao grafts being 6 and 9 months old, respectively). In each season, one sampling round was done in the morning (07:00–11:00) and the second one at night (19:00–00:00) on different days and times for each tree. Each sampling round combined two methods to target either sessile or mobile arthropods, each performed for 10 min. First, we manually collected arthropods using tweezers and brushes from branches, trunk and leaves around the tree, from the base of the trunk to the top of the tree's crown. Second, we used a modified branch beating method, in which we shook the branches of cacao trees, and caught all fallen insects into a beating tray of 72 cm diameter with a plastic bottle containing 70% alcohol in the middle (www.bioform.de). Branch beating and manual collection significantly differed in arthropod abundance and richness (paired *t*-test—abundance: $t = 2.077$; $p = 0.039$. Species richness: $t = 15.66$; $p < 0.001$; $n = 216$ visits to all trees; Appendix S3), but we merged the data from both methods for all analyses to achieve a more comprehensive data base. As a result, for each study tree there were four replicates for data analysis.

We sorted all collected arthropods into morphospecies and identified them mostly to family level using several taxonomic keys (Aguilera & Casanueva, 2005; Arnett Jr. & Thomas, 2000; Choate & Choate, 1999; Gibb & Oseto, 2006; Nieves-Aldrey et al., 2006; Schaefer, 2018). All morphospecies were classified into one of three foraging guilds: (1) Phytophagous arthropods, including sap suckers and plant chewers; (2) natural enemies, including predatory and parasitic arthropods and (3) others, including mostly nectar or pollen feeders and detritivores which could not be included in the two previous groups. Since the third group included <5% of the collected arthropods, we excluded it from further analyses. None of the methodologies used in this arthropod sampling or in any other parts of our study required approval from animal ethics committees.

2.3 | Cacao yield assessments

We monitored the potential yield of all grafted trees (ca. 0.2 ha per agroforest) in six visits starting in January 2021, that is 2 years after grafting. Since we assessed yield on the whole grafting plots and only knew the precise age of grafts on our four experimental trees, we made no distinction between graft ages. The visits were performed every 4 months starting at the beginning of the harvesting peak and repeated three times per year (January, May and September) to cover two full years of harvest. In each visit, we counted per tree the number of healthy fruits with >13 cm of length. These fruits were considered to be harvestable in the next 4 months, without being at risk of abortion by the tree, based on the average size of pods from this cacao variety (Thomas et al., 2023).

All ripe pods per visit were harvested and weighted fresh. We calculated the expected dry weight of each pod, by multiplying the fresh weight by 0.4 (Villalobos Rodríguez & Orozco Estrada, 2012), considered to be the standard percentage of change after drying and fermenting cacao. Then, we calculated a pod index (IM) for each genotype per plantation, representing the number of pods necessary to obtain 1 kg of dry cacao: $\mathrm{IM} = \frac{N \times 1000\ \mathrm{g}}{\mathrm{FW}_N \times 0.4}$, where N is the number of harvested and weighted cacao pods, and FW_N the sum of fresh weights from such pods. We used the IM to estimate the final annual yield per hectare (Y_i) which could be obtained from all pods counted per year per agroforest (*Np*), as: $Y_i = \sum_{j=0}^{n} \frac{Np}{\mathrm{IM}}$, where j is each of the genotypes found per plantation. We estimated a density per hectare of 1100 cacao trees in an agroforest, planted at a distancing of roughly 3 × 3 m. We used this estimation to scale up Y_i to a hectare, according to the number of trees assessed in each agroforest.

We compared the estimated yield in grafted plots with the yield of the remaining—non-grafted—portion of the land owned by each farmer. To do so, we obtained information from the annals of the Norandino Ltda. Cooperative about the total annual yield delivered by each producer. Since several producers distribute their yield among multiple buyers, including the cooperative, we could only use the information from four farmers which deliver all their production to Norandino Ltda. We acknowledge that this biases our comparisons between grafted and non-grafted trees to agroforests under high-quality management and monitoring. However, we are confident that this guarantees that the comparisons presented are accurate.

We subtracted Y_i from the total annual yield reported by each farmer. The result corresponds to the yield of the rest of the farm, excluding the grafted area. We calculated the area corresponding to this yield in non-grafted portions of the farms by subtracting the size of the grafted plots (0.144 ha in three cases and 0.125 ha in the fourth) from the total size of the farmers' properties, and extrapolated to yield per 1 ha as described above.

2.4 | Data analysis

All analyses were performed in R v. 4.2.2 (R Core Team, 2022) in RStudio (Posit Team, 2023). We quantified the diversity of arthropod communities on the study trees using Hill diversity numbers in the package *hillR* (Chao et al., 2014; Li, 2018; Roswell et al., 2021), since raw species richness is widely considered to be an insufficient measurement of biodiversity when sampling is limited (Roswell et al., 2021). Hill diversity numbers calculate the effective number of species in a community, by accounting differently for rare species (Jost, 2006). As such, we will refer hereafter to *species richness* as the number of morphospecies that we identified on each tree ($q=0$); *diversity* as the effective species richness weighing all species according to their abundance using the Shannon-Wiener diversity index, and *dominance* as the effective species richness giving less weight to rare species, based on the Simpson index (Jost, 2006; Roswell et al., 2021).

We used generalized linear mixed-effects models (GLMM) in the package *glmmTMB* (Magnusson et al., 2017) to evaluate the effect of graft age, season, time of the day, distance to forest, shade-tree cover above cacao trees, and all two-way interactions involving graft age on the abundance and diversity of arthropods on cacao trees. We used the identity of each agroforest and cacao tree as a random effect in the model, to account for potential differences in variance among agroforests. We inspected model fits with the package *DHARMa* (Hartig, 2017), and adapted the distribution for the models accordingly. For models of abundance and species richness we used a negative binomial distribution, whereas for the diversity and dominance variables, we used an inverse Gaussian and Gamma distribution, respectively (Zuur et al., 2009). We performed model selection using *MuMIN::dredge*, and report the variables included in all the best models, and quality measures in Appendix S2. We averaged the best models ($\Delta\text{AIC} \leq 2$) using *MuMIn::model.avg* (Barton, 2015), extracted estimates (i.e. incidence rate ratios), *p*-values and confidence intervals using *sjPlot* (Lüdecke, 2017), and plotted our results using *ggplot2* (Wickham, 2011).

We repeated the same model structure to assess abundance changes of the most common arthropod groups: beetles (Coleoptera; 11.54% of all arthropods collected), ants (Hymnoptera: Formicidae; 22% of collected arthropods), spiders (Araneae; 19.25%), aphids (Hemiptera: Aphididae; 15.06%), and two functional groups composed by multiple taxa, namely other phytophagous insects (all insects with a sap-sucking or herbivorous diet, excluding aphids), and other potential natural enemies (parasitoids and all arthropods with predatory diets, excluding spiders). In all cases, we run post hoc Tukey HSD tests to evaluate the differences between all pairs of graft ages. Finally, we used a GLMM to compare annual cacao yield before and after grafting. Since we only had complete yield information for four of our plots (see “Cacao yield assessments” above), the replication and extent of gradients of forest distance (681–824.5 m) and shade-tree cover (43%–78%) were too limited for conclusive analyses. Therefore, the model only included the two grafting categories (Grafted vs. Non-grafted) as a fixed effect, and the identity of our plots as a random effect. All data used in these analyses, as well as R scripts with statistical analyses and data preparation are available from the GRO.Data repository https://doi.org/10.25625/CVUEPO (Ocampo-Ariza et al., 2024).

3 | RESULTS

3.1 | Effects of grafting on overall arthropod diversity

We collected 10,249 arthropods, grouped in 491 morphospecies from 18 orders. Out of these, 2475 (24.15%) could be classified as natural enemies and 3138 (30.61%) as phytophagous insects. Natural enemies were dominated by spiders (79.72%), whereas phytophagous insects were dominated by aphids (49.20%). Ants represented 21.98% of all caught arthropods and 92.6% of all Hymenoptera, but were not classified as either predatory or phytophagous since most of them have omnivorous diets in our study area (Ocampo-Ariza et al., 2023). Finally, beetles represented 11.54% of all collected arthropods ($n=1183$; see Appendix S3 for a summary table of total abundances of all arthropod families collected).

Arthropod abundance increased with graft age, and was significantly higher in non-grafted trees (52.56 ± 3.49 arthropods) than in either young (25% lower = 39.27 ± 3.06 arthropods) or old grafted cacao (12% lower = 46.31 ± 3.58 arthropods; Figure 1A; Table 1). Our model predicted an arthropod richness decrease of ca. 22% (4.8 less species) in 3-month-old grafted cacao in comparison to non-grafted cacao trees. When grafted cacao reached 6 months old, that is old grafted cacao, the difference to non-grafted trees was predicted by the model to decrease by only 12% (2.8 species), pointing to a rapid recovery in the arthropod community (Figure 1B). The same patterns were observed for the diversity of the arthropod community, that is the Hill–Shannon Diversity index, for which young grafted cacao had on average 18% fewer effective species (2.6 effective species) than non-grafted trees, whereas old grafted cacao only had 13% fewer effective species (1.9 effective species). Notably, the dominance of arthropod communities (i.e. the Hill-Simpson index) remained comparable (between 8.9 and 10.6 effective species on average) among graft ages (Figure 1B), pointing to comparable community structures among all grafted cacao trees.

3.2 | Grafting and cacao yield

Cacao yield was predicted to be on average 47% higher (an increase of ca. 272 kg/ha) in plantations with grafted trees than on non-grafted areas in our study in 2021/2022 (Figure 1C; Appendix S4).

3.3 | Effects of grafting, shade-tree cover and distance to forest on selected arthropod groups

We found that arthropods were significantly more abundant and diverse in the rainy season than in the dry season, and this effect did not significantly differ among graft ages. Similarly, we found more arthropods, morphospecies and diverse communities at night than during the day, without significant differences among graft ages. Distance to forest did not impact the abundance of arthropods,

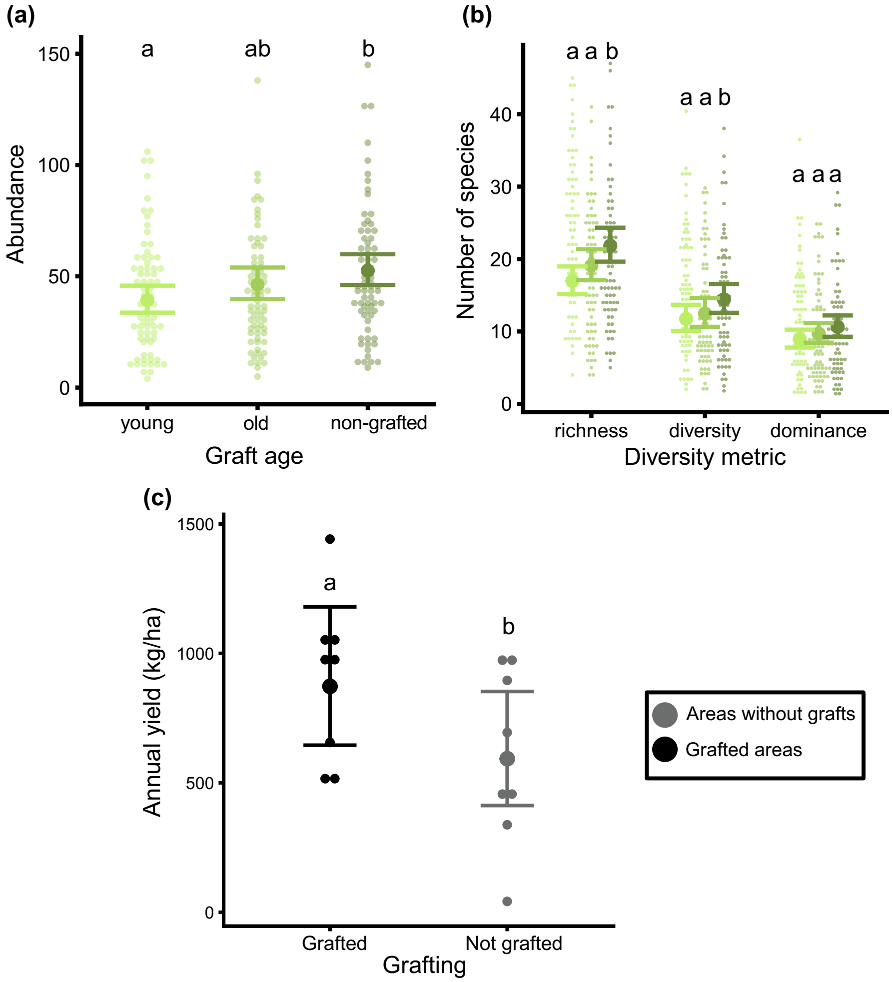

FIGURE 1 Arthropod abundance and diversity, and cacao yield on grafted and non-grafted cacao trees in agroforests from Piura, Peru. (A) and (B) display differences (with significance indicated by different letters above scatterplots) in overall arthropod abundance and diversity on cacao trees of two graft ages: Young grafted cacao (light green, grafting performed 3 months before first sampling); old grafted cacao (medium green, grafted 6 months before first sampling) and non-grafted control trees (dark green, grown cacao never grafted before). (B) displays patterns in multiple diversity metrics assessed through Hill numbers: Richness (the number of species per tree); diversity (the number of functional species using the Hill–Shannon diversity index) and dominance (the number of functional species using the Hill-Simpson dominance index). (C) displays difference in annual yield per hectare between non-grafted agroforests and grafted plots of ca. 0.14 ha within them during 2021 and 2022. For the graft age category, non-grafted trees were used as the intercept in the model. Significant effects are indicated by different letters (a, b) on top of dotplots.

but it increased arthropod species richness and diversity, and it decreased community dominance, expressed in a higher number of effective species (estimated by the Hill-Simpson index) far from the forest (Appendix S5). At high shade-tree covers, the diversity of arthropod communities on non-grafted trees and old grafted cacao decreased. The opposite pattern was observed for young grafted cacao, on which arthropod diversity increased by 50% between unshaded cacao trees and cacao trees covered by 80% canopy of shade-trees (Table 1; Appendices S2 and S5).

We found that graft age affected the abundance of spiders, natural enemies and beetles, which were significantly less abundant in young grafted cacao than in non-grafted cacao trees (Figure 2A–C). However, 6 months after grafting, that is in old grafted cacao, the abundances of all arthropod groups were not significantly different to those in non-grafted trees (Figure 2A–F). The abundance of aphids, phytophagous insects and ants showed no significant change due to grafting.

Similar to the entire arthropod community, we found that time of the day and season significantly impacted the abundance of the six arthropod groups that we assessed. However, distance to forest only had a significant positive effect on the abundance of predatory arthropods (both spiders and other natural enemies); whereas we could not find a significant effect of shade-tree cover on the abundance of any of the arthropod groups we assessed (Table 2; Appendix S5).

4 | DISCUSSION

Developing management strategies that minimize trade-offs between biodiversity and crop yield in tropical agriculture is essential

TABLE 1 Averaged effects of graft age, distance to forest and shade-tree cover above cacao trees in best model solutions with ΔAIC ≤ 2 on the abundance, morphospecies richness and two diversity metrics (diversity and dominance) of arthropods found on cacao trees in Piura, Peru.

	Arthropod abundance		Richness		Diversity		Dominance	
Predictors	**IRR**	***p***	**IRR**	***p***	**Estimates**	***p***	**Estimates**	***p***
Intercept	**46.01 (38.51–54.98)**	**<0.001**	**14.86 (13.12–16.83)**	**<0.001**	**8.86 (7.47–10.49)**	**<0.001**	**6.22 (5.22–7.41)**	**<0.001**
Graft age (young)	**0.75 (0.64–0.89)**	**0.001**	**0.78 (0.71–0.86)**	**<0.001**	**0.81 (0.71–0.93)**	**0.002**	0.84 (0.70–1.00)	0.053
Graft age (old)	**0.86 (0.73–1.01)**	**0.074**	**0.88 (0.80–0.97)**	**0.008**	0.87 (0.76–1.01)	0.065	0.91 (0.76–1.09)	0.310
Season (rainy)	**1.57 (1.37–1.81)**	**<0.001**	**1.81 (1.67–1.97)**	**<0.001**	**1.85 (1.66–2.06)**	**<0.001**	**1.74 (1.51–2.01)**	**<0.001**
Time (night)	**0.83 (0.72–0.95)**	**0.007**	**1.18 (1.09–1.28)**	**<0.001**	**1.44 (1.31–1.59)**	**<0.001**	**1.52 (1.31–1.76)**	**<0.001**
Distance to forest (m)	1.07 (0.97–1.18)	0.153	**1.13 (1.04–1.24)**	**0.005**	1.03 (0.86–1.22)	0.774	**1.18 (1.08–1.30)**	**<0.001**
Shade-tree cover (%)	1.03 (0.95–1.12)	0.443	1.01 (0.96–1.07)	0.638	**1.18 (1.05–1.33)**	**0.007**		
Graft age (young) × distance to forest					**1.19 (1.05–1.34)**	**0.005**		
Graft age (old) × distance to forest					**1.23 (1.08–1.40)**	**0.002**		
Graft age (young) × shade-tree cover					**0.81 (0.69–0.95)**	**0.009**		
Graft age (old) × shade-tree cover					**0.78 (0.66–0.92)**	**0.003**		

Note: Bold numbers highlight predictors with significant effects, and grey cells indicate predictors which were excluded in the averaged model.

Abbreviation: IRR, incidence rate ratios.

to increase the sustainability of agricultural practices. Here, we show that cacao grafting has high benefits for smallholders farmers in restoring and increasing agroforest yields, while maintaining arthropod biodiversity in agroforests. Therefore, grafting offers a socio-ecologically sustainable alternative to mitigate threats to smallholder incomes associated to yield loss, and to reduce the risk of old cacao agroforest abandonment and further forest encroachment in tropical areas. Based on this evidence, we suggest prioritizing the rehabilitation of old and abandoned cacao agroforests through grafting.

In contrast to our expectations, grafting was not related to a severe decline of arthropod diversity and abundance. Young grafted cacao trees had significantly fewer arthropods than non-grafted cacao trees, but only 3 months later, arthropod abundance was not statistically different from that in non-grafted trees, pointing towards a quick recovery of arthropod communities after grafting. Moreover, the number of effective species calculated through the Hill-Simpson dominance index was not significantly different across graft ages or in comparison to non-grafted trees, which likely indicates that the species composition and community structure on young grafted cacao was only slightly affected (Jost, 2006). The initial decrease in arthropods on young grafted cacao may be expected as a result of the simplified architecture of these trees, with an open canopy and reduced feeding, resting and refuge resources available for arthropods (Lawton, 1983). Being surrounded by other large trees, including older cacao trees and shade-trees, likely promoted a quick recolonization of grafted trees (Cromartie, 1975; Klein et al., 2002). Recolonization may take longer if grafted cacao were dominating the agroforest or were isolated from older trees. However, our experimental design fits the typical reality for smallholders, as progressive grafting is locally believed to be the best way to rejuvenate cacao without sacrificing income before grafted cacao become productive, which may take ca. 2 years.

The decreased arthropod diversity on young grafted cacao was due to a lower abundance of beetles, spiders and other predatory and parasitic arthropods. Beetles are known to be sensitive to land-use change and shade thinning in cacao agroforestry systems (Bos et al., 2007; Clough et al., 2010), and this insect order includes several taxa specialized in exploiting resources from lignified plant tissue (e.g. Heyborne et al., 2003), which is greatly reduced in young grafted cacao. Spiders, which partly rely on specific plant structures and shaded environments to attach their webs or hide during hunting (Gonçalves-Souza et al., 2011; Lopes Rodrigues et al., 2014), as well as other natural enemies were significantly less abundant in young grafted cacao, compared to non-grafted trees. This finding supports results of studies showing the vulnerability of predatory groups to disturbances such as land-use change or a decrease in shade cover (e.g. Klein et al., 2002; Perfecto et al., 1996). Moreover, it supports the theory of trophic island biogeography (Holt, 2009), according to which predators

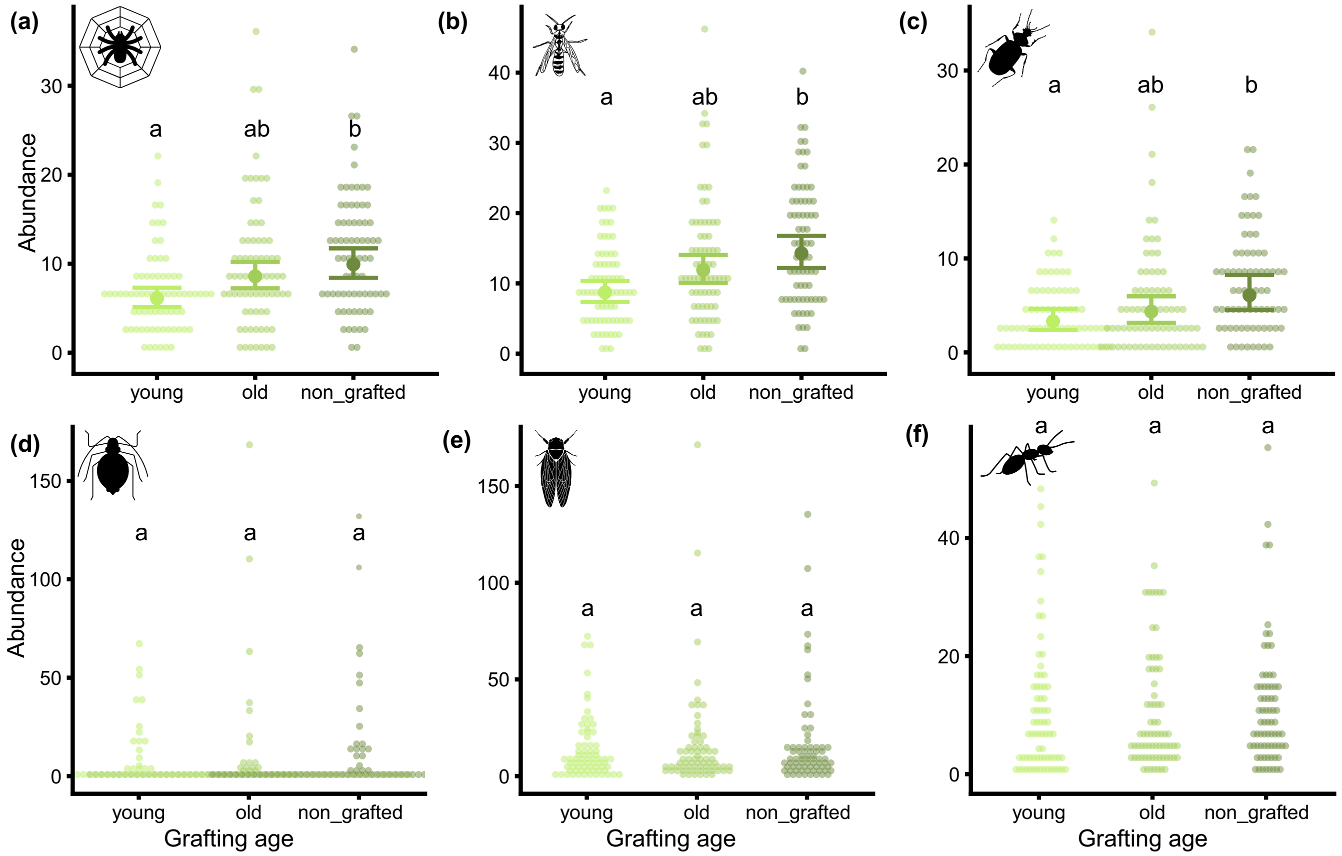

FIGURE 2 Differences across graft ages (young = grafted cacao performed 3–6 months ago; old = grafted cacao performed 6–9 months ago; and non-grafted = trees without grafting) in the abundance of selected arthropod groups: (A) spiders; (B) natural enemies; (C) beetles; (D) aphids; (E) other phytophagous insects; and (F) ants. For the graft age category, non-grafted trees were used as the intercept in the model. Differing letters above scatterplots indicate significant differences between graft ages ($p < 0.001$).

are more prone than their herbivorous prey to disappear due to landscape-level changes in habitat availability and isolation, considering their high trophic position and their often lower abundances. Nevertheless, this decrease was only temporary and the abundance of both spiders and other natural enemies became comparable to non-grafted cacao with increasing age of the grafted trees.

In contrast to natural enemies, phytophagous insects were just as abundant on young grafted cacao as on old grafted cacao or non-grafted trees. This is probably due to the increased amount of meristematic tissue on cacao grafts, which provides an easy source of food for many herbivorous species (e.g. Espírito-Santo et al., 2007). At the same time, the stable populations of herbivorous sap-sucking insects such as aphids and scale bugs may explain why ants, known for their mutualism with these insects (Carroll & Janzen, 1973; Clough et al., 2017), were just as abundant on old and young grafted cacao, and on non-grafted trees. Nevertheless, since grafted trees retained large portions of the original trunk of the non-grafted tree, it is also likely that mostly sessile insects such as aphids, as well as social insects such as ants simply remained on the tree and moved towards the new grafted tissue. Moreover, since the largest proportion of ants are ground nesters (Borror & Delong, 1955), changes in vegetation structure may have little effect on the number of foraging workers that reach cacao trees searching for food.

Beyond the effects of grafting, we found that distance to forest had a positive impact on arthropod species richness and diversity. This might be due to the lower abundance and predatory activity of insectivorous birds with increasing forest distance (as shown by Ocampo-Ariza et al., 2022), coinciding in with the peak of abundance of arthropods in the rainy season found in our study. High shade-tree cover resulted in a decrease in arthropod diversity on grafted trees. This supports findings from Indonesian cacao agroforestry (Steffan-Dewenter et al., 2007), as high temperatures and low humidity enhance the activity of most of the ectothermic insects, and the availability of resources such as flowers and fresh plant material (Ferreira da Costa & Gonçalves, 2023; Horák & Rébl, 2013).

As expected, cacao grafting significantly improved crop yield by ca. 47% already less than 2 years after grafting in comparison to adjacent non-grafted agroforest plots. Most likely, the large yield gap between the controls and the grafted trees is derived from the use of higher-yielding and compatible genetic materials for the grafts (Vansynghel et al., 2023; Zavaleta et al., 2022) and the increased vitality of the young tissue, supported by a grown and developed root system in the rootstock (Rivard & Louws, 2008). Our yield estimates for grafted trees may be slightly higher than the final harvest,

TABLE 2 Effects of graft age, distance to forest and shade-tree cover above cacao trees in best model solutions with ΔAIC ≤ 2 on the abundance of selected arthropod groups found on cacao trees in Piura, Peru.

	Ants (Formicidae)		Aphids (Aphididae)		Phytophagous insects		Beetles (Coleoptera)		Spiders (Araneae)		Natural enemies	
Predictors	**IRR**	***p***	**IRR**	***p***	**IRR**	***p***	**IRR**	***p***	**IRR**	***p***	**IRR**	***p***
Intercept	14.37 (11.77–17.53)	**<0.001**	8.05 (2.89–22.42)	**<0.001**	3.70 (2.84–4.80)	**<0.001**	3.72 (2.61–5.31)	**<0.001**	9.95 (8.17–12.12)	**<0.001**	12.59 (10.49–15.10)	**<0.001**
Shade-tree cover (%)	1.14 (0.99–1.31)	0.072	1.74 (0.87–3.49)	0.120	0.90 (0.81–1.01)	0.079	0.94 (0.83–1.08)	0.384	1.04 (0.95–1.14)	0.394	1.02 (0.94–1.11)	0.642
Time (night)	**0.40 (0.31–0.51)**	**<0.001**	**0.20 (0.08–0.49)**	**<0.001**	**1.53 (1.27–1.85)**	**<0.001**	**1.24 (0.97–1.58)**	**0.088**	**0.57 (0.47–0.70)**	**<0.001**	**0.72 (0.63–0.82)**	**<0.001**
Season (rainy)	**1.15 (0.89–1.47)**	**0.281**	**0.36 (0.14–0.93)**	**0.035**	**2.13 (1.75–2.59)**	**<0.001**	**2.16 (1.81–2.59)**	**<0.001**	**1.78 (1.55–2.03)**	**<0.001**	**1.79 (1.57–2.04)**	**<0.001**
Distance to forest (m)	1.04 (0.90–1.19)	0.625	0.52 (0.23–1.14)	0.103	1.13 (0.93–1.35)	0.212	1.10 (0.84–1.44)	0.479	**1.21 (1.04–1.41)**	**0.012**	**1.21 (1.05–1.38)**	**0.006**
Graft age (young)							**0.62 (0.43–0.89)**	**0.010**	**0.59 (0.48–0.73)**	**<0.001**	**0.61 (0.52–0.72)**	**<0.001**
Graft age (old)							**0.71 (0.52–0.96)**	**0.027**	**0.82 (0.69–0.99)**	**0.040**	**0.83 (0.71–0.97)**	**0.016**
Time (night) × graft age (young)							0.66 (0.43–1.01)	0.055	1.36 (0.98–1.89)	0.067		
Time (night) × graft age (old)							1.08 (0.74–1.60)	0.684	1.18 (0.86–1.62)	0.304		
Dist. forest × graft age (young)									1.11 (0.95–1.29)	0.184		
Dist. forest × graft age (old)									1.11 (0.96–1.29)	0.156		

Note: Bold numbers highlight predictors for which we identified significant effects, and grey cells indicate predictors which were excluded from the final model, after selection using MuMIn::dredge.

because of fruit losses due to pests (e.g. squirrels, ants, and other insects) and fungal diseases. But these losses are very low in our region (≤10%; Vansynghel et al., 2022).

Cacao yield is especially dependent on the compatibility of genetic materials, which directly influences pollination and fruit-set success (Vansynghel et al., 2023). Hence, the selection of compatible genotypes is an essential element for success. In our case, grafting material was carefully selected to guarantee an increase in fruit-set and quality through the use of native genotypes of *Gran Blanco de Piura*, known for their unique sensorial characteristics and premium prices for national and international markets (Thomas et al., 2023; Tscharntke et al., 2023). However, proper plantation management is crucial both to guarantee the survival and tending of grafts, which maximizes associated yield gains. Here, we report exclusively on yield gains in grafted compared to non-grafted trees in well-managed cacao agroforests. It remains to be tested how different management intensities may affect these benefits. Moreover, more work is needed to determine whether the additional income derived from high-yielding grafts compensates for the monetary investments related to grafting (selection and acquisition of grafting material, technical assistance for grafting and management, etc.). But it is likely more cost-effective than establishing a new plantation and acquiring new land and thinning forest for such purpose.

Our study showcases the value of grafting as a biodiversity-friendly measure for improving crop yield and quality of old cacao plantations with dwindling yields and/or suboptimal sensorial quality traits. The establishment of new cacao plantations and agroforests in encroached forests is known to be a main driver of forest loss and further degradation of forest patches (e.g. Kalischek et al., 2023). Given the continuous increase in cacao demand worldwide, and the resulting growth in cacao crop area in the last 20 years (FAO, 2023), it is increasingly urgent to develop strategies that allow smallholder farmers to meet income needs and demand without compromising tropical forest area. Grafting provides an easily implemented strategy to rejuvenate cacao trees, with success rates of over 90% (Suryani, 2021). In our study area, grafting is carried out by trained persons who provide the service across the Norandino Ltda. cooperative (E. Espinoza, 2024, pers. comm.). This may limit accessibility due to associated costs. However, grafting can also be performed directly by farmers after short trainings, or even following available manuals (Zavaleta et al., 2022). Likely, the most limiting factor for the success of large-scale grafting approaches is the availability of grafting material from genotypes desired by producers. Addressing this will require a special focus on the development and maintenance of working collections which may serve as sources for such initiatives (Ceccarelli et al., 2022; Lavoie et al., 2023; Tscharntke et al., 2023).

Since we found that cacao grafting appears to have no long-term negative effects on arthropod biodiversity, it may be considered an agroecological intensification management strategy that increases crop yield without compromising ecological functions (Tscharntke et al., 2012). As such, it adds up to and may be combined with other recently proposed strategies to ecologically intensify cacao production, such as hand pollination (Vansynghel et al., 2023; Wanger et al., 2021). Moreover, grafting may promote a significant improvement and diversification of the genetic materials used in smallholding cacao crops around the world, which may in turn support both the conservation of native genetic diversity from the species, and the resilience of the crops to future disturbances such as climate change (Ceccarelli et al., 2021, 2022; Tscharntke et al., 2023).

In conclusion, our study highlights the innovative application of cacao grafting as an effective and sustainable method to rejuvenate old, unproductive cacao trees. This technique not only significantly boosts crop yield, but also enables the use of genetic diversity from native cacao and supports rapid recovery of arthropod biodiversity, demonstrating its dual benefits for agricultural productivity and ecological resilience. This approach offers valuable insights and actionable strategies for policymakers and practitioners aiming to enhance the sustainability of tropical agriculture. Upscaling this management strategy will rely on more detailed studies building on our approach to quantify the benefits of cacao grafting at different spatial and temporal scales.

AUTHOR CONTRIBUTIONS

The idea for this study was conceived by Carolina Ocampo-Ariza, Sophie Müller, Teja Tscharntke and Evert Thomas. The grafting experiment was conceived by Evert Thomas, Teja Tscharntke, Ingolf Steffan-Dewenter and Bea Maas, and was executed by Fredy Yovera, Carolina Ocampo-Ariza, and Justine Vansynghel. Sophie Müller and Carolina Ocampo-Ariza led insect-related fieldwork, and Fredy Yovera monitored plant yield. Sophie Müller developed all arthropod identification with help from Carolina Ocampo-Ariza and invaluable help from the iNaturalist platform. Carolina Ocampo-Ariza and Sophie Müller analysed the data and prepared the manuscript. Evert Thomas, Bea Maas, Teja Tscharnke, and Ingolf Steffan-Dewenter applied to DFG funding, and Sophie Müller acquired additional funding from the CBL. All co-authors commented and contributed to the final version of the manuscript.

ACKNOWLEDGEMENTS

We are grateful to all the farmers that allowed us to work on their farms during this experiment, and to the Norandino Ltda. Cooperative, which supported us throughout the development of our project. We are especially thankful to Rosa Santos and Brenda Reyes for their immense help in sampling the arthropods during the dry season, and to Denise Bertleff for her help during the rainy season. Samuel Guerrero and Angélica Cordova provided essential help with logistics during our fieldwork. Dr. Rachel Atkinson, Dr. Edgar Turner and an anonymous reviewer provided valuable feedback on this manuscript. This project and the grafting of plants were supported by the German Federal Ministry for Economic Cooperation and Development (BMZ), commissioned and administered through the Fund for International Agricultural Research (FIA) from the German Development Cooperation (GIZ), through the grant number 81219430. Further support came from the Deutsche Forschungsgemeinschaft DFG (TS 45/42-1, STE 957/27-1). SM received additional funding for her field visit from the Center of

Biodiversity and Sustainable Land Use (CBL) at the University of Göttingen. None of the authors have any conflict of interest that may have impacted the revision process of this manuscript.

CONFLICT OF INTEREST STATEMENT

All authors declare not to have any known competing financial or personal interest that could influence their work reported in this paper.

DATA AVAILABILITY STATEMENT

All code and data for this manuscript is available from the GRO.Data institutional repository from the University of Göttingen at: https://doi.org/10.25625/CVUEPO (Ocampo-Ariza et al., 2024).

STATEMENT ON INCLUSION

Our study brings together authors from a number of different nationalities, including authors based in Peru, and originally from this country. We gather a group of scientists in academic and non-academic institutions, as well as practitioners from the cacao sector. All authors were involved from early stages in the research process and their feedback was included to adapt methodologies and data analysis. Whenever relevant, we have cited published literature by scientists from Latin America and Peru, including efforts to seek information originally in Spanish. We acknowledge that more could have been done to seek the participation of national academic institutions, which we are hoping to address in future projects.

ORCID

Carolina Ocampo-Ariza https://orcid.org/0000-0002-4106-5586
Sophie Müller https://orcid.org/0009-0005-7923-1489
Justine Vansynghel https://orcid.org/0000-0002-4250-7016
Bea Maas https://orcid.org/0000-0001-9461-3243
Ingolf Steffan-Dewenter https://orcid.org/0000-0003-1359-3944
Teja Tscharntke https://orcid.org/0000-0002-4482-3178

REFERENCES

Aguilera, M. A., & Casanueva, M. E. (2005). Arañas chilenas: Estado actual del conocimiento y clave para las familias de araneomorphae. *Gayana (Concepción)*, *69*(2), 201–224. https://doi.org/10.4067/S0717-65382005000200001

Arnett, R. H., Jr., & Thomas, M. C. (2000). *American beetles, volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press.

Barton, K. (2015). Package 'mumin'. *Version*, *1*(18), 439.

Basset, Y. (2001). Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia*, *129*(2), 253–260. https://doi.org/10.1007/s004420100724

Borror, D. J., & Delong, D. M. (1955). *An introduction to the study of insects*. Rinehart & Co.

Bos, M. M., Steffan-Dewenter, I., & Tscharntke, T. (2007). The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. *Biodiversity and Conservation*, *16*(8), 2429–2444. https://doi.org/10.1007/s10531-007-9196-0

Carroll, C. R., & Janzen, D. H. (1973). Ecology of foraging by ants. *Annual Review of Ecology and Systematics*, *4*(1), 231–257. https://doi.org/10.1146/annurev.es.04.110173.001311

Ceccarelli, V., Fremout, T., Zavaleta, D., Lastra, S., Imán Correa, S., Arévalo-Gardini, E., Rodriguez, C. A., Cruz Hilacondo, W., & Thomas, E. (2021). Climate change impact on cultivated and wild cacao in Peru and the search of climate change-tolerant genotypes. *Diversity and Distributions*, *27*(8), 1462–1476. https://doi.org/10.1111/ddi.13294

Ceccarelli, V., Lastra, S., Loor Solórzano, R. G., Chacón, W. W., Nolasco, M., Sotomayor Cantos, I. A., Plaza Avellán, L. F., López, D. A., Fernández Anchundia, F. M., Dessauw, D., Orozco-Aguilar, L., & Thomas, E. (2022). Conservation and use of genetic resources of cacao (*Theobroma cacao* L.) by gene banks and nurseries in six Latin American countries. *Genetic Resources and Crop Evolution*, *69*(3), 1283–1302. https://doi.org/10.1007/s10722-021-01304-3

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Choate, P., & Choate, P. (1999). *Dichotomus keys to some families of Florida coleoptera* (pp. 23–33). Introduction to the Identification of Beetles (Coleoptera).

Clough, Y., Abrahamczyk, S., Adams, M.-O., Anshary, A., Ariyanti, N., Betz, L., Buchori, D., Cicuzza, D., Darras, K., Putra, D. D., Fiala, B., Gradstein, S. R., Kessler, M., Klein, A.-M., Pitopang, R., Sahari, B., Scherber, C., Schulze, C. H., Shahabuddin, … Tscharntke, T. (2010). Biodiversity patterns and trophic interactions in human-dominated tropical landscapes in Sulawesi (Indonesia): Plants, arthropods and vertebrates. In T. Tscharntke, C. Leuschner, E. Veldkamp, H. Faust, E. Guhardja, & A. Bidin (Eds.), *Tropical rainforests and agroforests under global change: Ecological and socio-economic valuations* (pp. 15–71). Springer. https://doi.org/10.1007/978-3-642-00493-3_2

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T. C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D. D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C. H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., … Tscharntke, T. (2011). Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(20), 8311–8316. https://doi.org/10.1073/pnas.1016799108

Clough, Y., Philpott, S. M., & Tscharntke, T. (2017). Services and disservices of ant communities in tropical cacao and coffee agroforestry systems. In *Ant-plant interactions: Impacts of humans on terrestrial ecosystems* (pp. 333–355). Cambridge University Press.

Clough, Y., Putra, D. D., Pitopang, R., & Tscharntke, T. (2009). Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biological Conservation*, *142*(5), 1032–1041. https://doi.org/10.1016/j.biocon.2008.12.027

Conceição, E. S. d., Lucia, T. M. C. D., Neto, A. d. O. C., Araújo, É. d. S., Koch, E. B. d. A., & Delabie, J. H. C. (2019). Ant community evolution according to aging in Brazilian cocoa tree plantations. *Sociobiology*, *66*(1), Article 1. https://doi.org/10.13102/sociobiology.v66i1.2705

Costa, J. T., & Crossley, D. A., Jr. (1991). Diel patterns of canopy arthropods associated with three tree species. *Environmental Entomology*, *20*(6), 1542–1548. https://doi.org/10.1093/ee/20.6.1542

Cromartie, W. J. (1975). The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology*, *12*(2), 517–533. https://doi.org/10.2307/2402172

Cuevas-Reyes, P., Quesada, M., Hanson, P., Dirzo, R., & Oyama, K. (2004). Diversity of gall-inducing insects in a Mexican tropical dry Forest: The importance of plant species richness, life-forms, host plant age and plant density. *Journal of Ecology*, *92*(4), 707–716.

Espírito-Santo, M. M., Neves, F. d. S., Andrade-Neto, F. R., & Fernandes, G. W. (2007). Plant architecture and meristem dynamics as the mechanisms determining the diversity of gall-inducing insects. *Oecologia*, *153*(2), 353–364. https://doi.org/10.1007/s00442-007-0737-8

FAO. (2023). *FAOSTAT, Food and agriculture data*. https://www.fao.org/faostat/en/#data/QCL/visualize

Ferreira da Costa, C. C., & Gonçalves, R. B. (2023). Living in the sunlight: Micro-environments with higher exposure of sunlight have more abundance and diversity of Hymenoptera in a Brazilian Atlantic Forest fragment. *Revista Brasileira de Entomologia*, *67*, e20220111. https://doi.org/10.1590/1806-9665-RBENT-2022-0111

Frank, E. F. (2010). *Crown volume estimates*. Eastern Native Tree Society. http://www.nativetreesociety.org/measure/volume/Crown+Volume+Estimates.pdf

Fremout, T., Thomas, E., Gaisberger, H., Meerbeek, K. V., Muenchow, J., Briers, S., Gutierrez-Miranda, C. E., Marcelo-Peña, J. L., Kindt, R., Atkinson, R., Cabrera, O., Espinosa, C. I., Aguirre-Mendoza, Z., & Muys, B. (2020). Mapping tree species vulnerability to multiple threats as a guide to restoration and conservation of tropical dry forests. *Global Change Biology*, *26*(6), 3552–3568. https://doi.org/10.1111/gcb.15028

Gibb, T. J., & Oseto, C. Y. (2006). *Arthropod collection and identification: Laboratory and field techniques*. Academic Press.

Gonçalves-Souza, T., Almeida-Neto, M., & Romero, G. Q. (2011). Bromeliad architectural complexity and vertical distribution predict spider abundance and richness. *Austral Ecology*, *36*(4), 476–484. https://doi.org/10.1111/j.1442-9993.2010.02177.x

Guerrero, J., Vasconcelos da Fonseca, C. R., Hammond, P., & Stork, N. (2003). Seasonal variation of canopy arthropods in Central Amazon. In Y. Basset, S. Novotny, E. Müller, & R. L. Kitching (Eds.), *Arthropods of tropical forests: Spatio-temporal dynamics and resource use on the canopy* (pp. 170–175). Cambridge University Press.

Hartig, F. (2017). *Package 'DHARMa'*. R Package.

Heyborne, W. H., Miller, J. C., & Parsons, G. L. (2003). Ground dwelling beetles and forest vegetation change over a 17-year-period, in western Oregon, USA. *Forest Ecology and Management*, *179*(1), 123–134. https://doi.org/10.1016/S0378-1127(02)00490-5

Hoehn, P., Tscharntke, T., Tylianakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 2283–2291. https://doi.org/10.1098/rspb.2008.0405

Holt, R. D. (2009). Toward a trophic Island biogeography. In J. B. Losos & R. E. Ricklefs (Eds.), *The theory of Island biogeography revisited* (pp. 143–185). Princeton University Press.

Horák, J., & Rébl, K. (2013). The species richness of click beetles in ancient pasture woodland benefits from a high level of sun exposure. *Journal of Insect Conservation*, *17*(2), 307–318. https://doi.org/10.1007/s10841-012-9511-2

Ivanova, Y., Tristán Febres, M. C., Romero, M., Charry, A., Lema, S., Choy, J. S., Vélez Betancourt, A. F., Castro Nuñez, A., & Quintero, M. (2020). *Moving towards a deforestation-free cacao and chocolate value chain with low greenhouse gas emissions* [Report]. International Center for Tropical Agriculture. https://cgspace.cgiar.org/handle/10568/110541

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kalischek, N., Lang, N., Renier, C., Daudt, R. C., Addoah, T., Thompson, W., Blaser-Hart, W. J., Garrett, R., Schindler, K., & Wegner, J. D. (2023). Cocoa plantations are associated with deforestation in Côte D'ivoire and Ghana. *Nature Food*, *4*(5), 384–393. https://doi.org/10.1038/s43016-023-00751-8

Klein, A.-M., Steffan-Dewenter, I., & Tscharntke, T. (2002). Predator–prey ratios on cocoa along a land-use gradient in Indonesia. *Biodiversity and Conservation*, *11*(4), 683–693. https://doi.org/10.1023/A:1015548426672

Klein, A.-M., Steffan-Dewenter, I., & Tscharntke, T. (2006). Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. *Journal of Animal Ecology*, *75*(2), 315–323. https://doi.org/10.1111/j.1365-2656.2006.01042.x

Kyriacou, M. C., Colla, G., & Rouphael, Y. (2020). Grafting as a sustainable means for securing yield stability and quality in vegetable crops. *Agronomy*, *10*(12), Article 12. https://doi.org/10.3390/agronomy10121945

Lavoie, A., Thomas, E., & Olivier, A. (2023). Local working collections as the foundation for an integrated conservation of *Theobroma cacao* L. in Latin America. *Frontiers in Ecology and Evolution*, *10*, 1063266. https://doi.org/10.3389/fevo.2022.1063266

Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, *28*(1), 23–39. https://doi.org/10.1146/annurev.en.28.010183.000323

Li, D. (2018). hillR: Taxonomic, functional, and phylogenetic diversity and similarity through hill Numbers. *Journal of Open Source Software*, *3*(31), 1041. https://doi.org/10.21105/joss.01041

Linares-Palomino, R., & Alvarez, S. I. P. (2005). Tree community patterns in seasonally dry tropical forests in the Cerros de Amotape Cordillera, Tumbes, Peru. *Forest Ecology and Management*, *209*(3), 261–272. https://doi.org/10.1016/j.foreco.2005.02.003

Lopes Rodrigues, E. N., Mendonça, M. D. S., & Costa-Schmidt, L. E. (2014). Spider diversity responds strongly to edge effects but weakly to vegetation structure in riparian forests of southern Brazil. *Arthropod-Plant Interactions*, *8*(2), 123–133. https://doi.org/10.1007/s11829-014-9294-3

Lüdecke, D. (2017). *sjPlot: Data visualization for statistics in social science*. R Package Version 2.4.0.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Brooks, M., & Brooks, M. M. (2017). *Package 'glmmtmb'*. R Package Version 0.2.0.

Marattukalam, J. G., & Saraswathyamma, C. K. (1992). Chapter 8—Propagation and planting. In M. R. Sethuraj & N. M. Mathew (Eds.), *Developments in crop science* (Vol. *23*, pp. 164–199). Elsevier. https://doi.org/10.1016/B978-0-444-88329-2.50014-3

Nawaz, M. A., Imtiaz, M., Kong, Q., Cheng, F., Ahmed, W., Huang, Y., & Bie, Z. (2016). Grafting: A technique to modify ion accumulation in horticultural crops. *Frontiers in Plant Science*, *7*, 1457. https://doi.org/10.3389/fpls.2016.01457

Nieves-Aldrey, J. L., Fontal-Cazalla, F., & Fernández, F. (2006). *Introducción a los Hymenoptera de la Región Neotropical*. Universidad Nacional de Colombia.

Nirosha, K., Kumar, B. A., Mamatha, A., & Sreenivas, M. (2023). Vegetable grafting: An emerging approach in vegetable production: A brief review. *The Pharma Innovation Journal*, *12*(7), 133–138.

N'zi, J.-C., Koné, I., M'bo, K. A. A., Koné, S., & Kouamé, C. (2023). Successful grafting elite cocoa clones (*Theobroma cacao* L.) as a function of the age of rootstock. *Heliyon*, *9*(8), e18732. https://doi.org/10.1016/j.heliyon.2023.e18732

Ocampo-Ariza, C., Maas, B., Castro-Namuche, J. P., Thomas, E., Vansynghel, J., Steffan-Dewenter, I., & Tscharntke, T. (2022). Trait-dependent responses of birds and bats to season and dry forest distance in tropical agroforestry. *Agriculture, Ecosystems & Environment*, *325*, 107751. https://doi.org/10.1016/J.AGEE.2021.107751

Ocampo-Ariza, C., Müller, S., Yovera, F. F., Thomas, E., Vansynghel, J., Maas, B., Steffan-Dewenter, I., & Tscharntke, T. (2024). Data and R code for: Cacao grafting increases crop yield without compromising biodiversity. *GRO.Data Repository*, https://doi.org/10.25625/CVUEPO

Ocampo-Ariza, C., Vansynghel, J., Bertleff, D., Maas, B., Schumacher, N., Ulloque-Samatelo, C., Yovera, F. F., Thomas, E., Steffan-Dewenter, I., & Tscharntke, T. (2023). Birds and bats enhance cacao yield despite suppressing arthropod mesopredation. *Ecological Applications*, *33*(5), e2886. https://doi.org/10.1002/eap.2886

Perfecto, I., Rice, R. A., Greenberg, R., & Van Der Voort, M. E. (1996). Shade coffee: A disappearing refuge for biodiversity. *BioScience*, *46*(8), 598–608. https://doi.org/10.2307/1312989

Posit Team. (2023). *RStudio: Integrated development environment for R* [Computer software]. Posit Software PBC. http://www.posit.co/

R Core Team. (2022). *R version 4.2. 2 (2022-10-31 ucrt)—'innocent and trusting': A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.r-project.org

Rakotomalala, A. A. N. A., Ocampo-Ariza, C., Arimond, I., Toledo-Hernández, M., Raveloaritiana, E., & Wurz, A. (2023). The importance of diversified farming for biodiversity: A synthesis based on studies by Teja Tscharntke. In C. F. Dormann, P. Batáry, I. Grass, A.-M. Klein, J. Loos, C. Scherber, I. Steffan-Dewenter, & T. C. Wanger (Eds.), *Defining agroecology: A festschrift for Teja Tscharntke*. Tredition. https://zenodo.org/records/10008730

Rice, R. A., & Greenberg, R. (2000). Cacao cultivation and the conservation of biological diversity. *AMBIO: A Journal of the Human Environment*, *29*(3), 167–173. https://doi.org/10.1579/0044-7447-29.3.167

Rivard, C. L., & Louws, F. J. (2008). Grafting to manage soilborne diseases in heirloom tomato production. *HortScience*, *43*(7), 2104–2111. https://doi.org/10.21273/HORTSCI.43.7.2104

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338. https://doi.org/10.1111/oik.07202

Ruf, F., Schroth, G., & Doffangui, K. (2015). Climate change, cocoa migrations and deforestation in West Africa: What does the past tell us about the future? *Sustainability Science*, *10*(1), 101–111. https://doi.org/10.1007/s11625-014-0282-4

Schaefer, M. (2018). *Brohmer—Fauna von Deutschland: Ein Bestimmungsbuch unserer heimischen Tierwelt*. Quelle & Meyer Verlag GmbH & Co.

Schroth, G., & Harvey, C. A. (2007). Biodiversity conservation in cocoa production landscapes: An overview. *Biodiversity and Conservation*, *16*(8), 2237–2244. https://doi.org/10.1007/s10531-007-9195-1

SENAMHI. (2020). *Piura y Lambayeque registraron records de temperatura en lo que va de Enero*. SENAMHI.

Somarriba, E., Peguero, F., Cerda, R., Orozco-Aguilar, L., López-Sampson, A., Leandro-Muñoz, M. E., Jagoret, P., & Sinclair, F. L. (2021). Rehabilitation and renovation of cocoa (*Theobroma cacao* L.) agroforestry systems. A review. *Agronomy for Sustainable Development*, *41*(5), 64. https://doi.org/10.1007/s13593-021-00717-9

Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M. M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S. R., Guhardja, E., Harteveld, M., Hertel, D., Hohn, P., Kappas, M., Kohler, S., Leuschner, C., Maertens, M., Marggraf, R., … Tscharntke, T. (2007). Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(12), 4973–4978. https://doi.org/10.1073/pnas.0608409104

Suryani, I. (2021). The development technique of side and budwood grafting improving production of cocoa in Mamuju Regency West Sulawesi, Indonesia. *OnLine Journal of Biological Sciences*, *21*(2), 199–206. https://doi.org/10.3844/ojbsci.2021.199.206

Tarmadja, S. (2015). The cacao flower visitor insects diversity and their potential as pollinators. In *KnE Life Sciences*, *ICBS-2013*, pp. 540–543. https://doi.org/10.18502/kls.v2i1.212

Thomas, E., Lastra, S., & Zavaleta, D. (2023). *Catalogo de cacaos de Perú*. Bioversity International y MOCCA.

Toledo-Hernández, M., Tscharntke, T., Giannini, T. C., Solé, M., & Wanger, T. C. (2023). Hand pollination under shade trees triples cocoa yield in Brazil's agroforests. *Agriculture*, *Ecosystems & Environment*, *355*, 108612. https://doi.org/10.1016/j.agee.2023.108612

Tscharntke, T., Clough, Y., Bhagwat, S. A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., & Wanger, T. C. (2011). Multifunctional shade-tree management in tropical agroforestry landscapes—A review. *Journal of Applied Ecology*, *48*(3), 619–629. https://doi.org/10.1111/J.1365-2664.2010.01939.X

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, *151*(1), 53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Tscharntke, T., Ocampo-Ariza, C., Vansynghel, J., Ivañez-Ballesteros, B., Aycart, P., Rodriguez, L., Ramirez, M., Steffan-Dewenter, I., Maas, B., & Thomas, E. (2023). Socio-ecological benefits of fine-flavor cacao in its center of origin. *Conservation Letters*, *16*(1), e12936. https://doi.org/10.1111/conl.12936

USAID. (2017). *Renovation & Rehabilitation for resilient coffee farms: A guidebook for roasters*, *traders and supply chain partners*. USAID. https://pdf.usaid.gov/pdf_docs/PA00TK8B.pdf

Vansynghel, J., Ocampo-Ariza, C., Maas, B., Martin, E. A., Thomas, E., Hanf-Dressler, T., Schumacher, N.-C., Ulloque-Samatelo, C., Yovera, F. F., Tscharntke, T., & Steffan-Dewenter, I. (2022). Quantifying services and disservices provided by insects and vertebrates in cacao agroforestry landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1982), 20221309. https://doi.org/10.1098/rspb.2022.1309

Vansynghel, J., Thomas, E., Ocampo-Ariza, C., Maas, B., Ulloque-Samatelo, C., Zhang, D., Tscharntke, T., & Steffan-Dewenter, I. (2023). Cross-pollination with native genotypes improves fruit set and yield quality of Peruvian cacao. *Agriculture*, *Ecosystems & Environment*, *357*, 108671. https://doi.org/10.1016/j.agee.2023.108671

Villalobos Rodríguez, M., & Orozco Estrada, S. (2012). *Calidad de cacao en centroamérica: Un vistazo a la situación en 2009*. CATIE, Centro Agronómico Tropical de Investigación y Enseñanza.

Voora, V., Bermúdez, S., & Larrea, C. (2019). *Global market report: Cocoa*. International Institute for Sustainable Development. http://www.jstor.com/stable/resrep22025

Wagner, T. (2001). Seasonal changes in the canopy arthropod fauna in Rinorea beniensis in Budongo Forest, Uganda. *Plant Ecology*, *153*(1), 169–178. https://doi.org/10.1023/A:1017514417913

Wanger, T. C., Dennig, F., Toledo-Hernández, M., Tscharntke, T., & Lambin, E. F. (2021). Cocoa pollination, biodiversity-friendly production, and the global market. *arXiv*, arXiv:2112.02877. https://doi.org/10.48550/arXiv.2112.02877

Wessel, M., & Quist-Wessel, P. M. F. (2015). Cocoa production in West Africa, a review and analysis of recent developments. *NJAS: Wageningen Journal of Life Sciences*, *74–75*(1), 1–7. https://doi.org/10.1016/j.njas.2015.09.001

Wickham, H. (2011). Ggplot2. *Wiley Interdisciplinary Reviews: Computational Statistics*, *3*(2), 180–185.

Wiegel, J. R., Rio, M. d., Gutiérrez, J. F., Claros Trujillo, L. M., Sánchez, D., Gómez, L., González, C., & Reyes, B. A. (2020). *Coffee and cacao market systems in the Americas: Opportunities for supporting renovation and rehabilitation*. International Center for Tropical Agriculture (CIAT). https://hdl.handle.net/10568/108108

Wurz, A., Tscharntke, T., Martin, D. A., Osen, K., Rakotomalala, A. A. N. A., Raveloaritiana, E., Andrianisaina, F., Dröge, S., Fulgence, T. R., Soazafy, M. R., Andriafanomezantsoa, R., Andrianarimisa, A., Babarezoto, F. S., Barkmann, J., Hänke, H., Hölscher, D., Kreft, H., Rakouth, B., Guerrero-Ramírez, N. R., … Grass, I. (2022). Win-win opportunities combining high yields with high multi-taxa biodiversity in tropical agroforestry. *Nature Communications*, *13*(1), Article 1. https://doi.org/10.1038/s41467-022-30866-8

Young, A. M. (1986). Distribution and abundance of Diptera in flypaper traps at *Theobroma cacao* L. (Sterculiaceae) flowers in Costa Rican cacao plantations. *Journal of the Kansas Entomological Society*, *59*(4), 580–587.

Zavaleta, D., Yovera, F. F., Conza, J., Rodríguez, C., Cruz Neira, A., Atkinson, R. J., & Thomas, E. (2022). *Manual de renovación de copa de cacao. Lecciones aprendidas del cacao Blanco de Piura y Chuncho* *de Cusco*. Bioversity International and CIAT. https://cgspace.cgiar.org/handle/10568/125646

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (Vol. *574*). Springer.

SUPPORTING INFORMATION

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

Appendix S1: Study area.

Appendix S2: Best models selected for model averaging for each response variable, and the predictor variables included in them.

Appendix S3: Summary of total abundances of each arthropod family collected during our sampling on cacao trees of three ages since grafting in agroforests in the region of Piura, Peru.

Appendix S4: Summary table of generalized linear mixed effect model evaluating the effect of grafting on the yield of cacao trees.

Appendix S5: Effects of environmental and management variables on diversity and abundance of arthropods on grafted cacao plants.

Appendix S6: Full manuscript translated to Spanish.

How to cite this article: Ocampo-Ariza, C., Müller, S., Yovera, F., Thomas, E., Vansynghel, J., Maas, B., Steffan-Dewenter, I., & Tscharntke, T. (2025). Cacao grafting increases crop yield without compromising biodiversity. *Journal of Applied Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2664.14851