

ARTICLE

Complementary effects of pollination and biocontrol services enable ecological intensification in macadamia orchards

Mina Anders¹  | Catrin Westphal^{1,2}  | Valerie M. G. Linden³  |
Sina Weier⁴  | Peter J. Taylor⁴  | Ingo Grass^{5,6} 

¹Functional Agrobiodiversity & Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Lower Saxony, Germany

²Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Lower Saxony, Germany

³School of Mathematical & Natural Sciences and Core Team Member of the Centre for Invasion Biology, University of Venda, Thohoyandou, Limpopo, South Africa

⁴Department of Zoology and Entomology, University of the Free State, Bloemfontein, Free State, South Africa

⁵Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Baden-Württemberg, Germany

⁶Center for Biodiversity and Integrative Taxonomy (KomBioTa), University of Hohenheim, Stuttgart, Germany

Correspondence

Mina Anders

Email: mina.anders@uni-goettingen.de

Funding information

Bundesministerium für Bildung und Forschung, Grant/Award Number: 01LL1802A; Deutsche

Forschungsgemeinschaft, Grant/Award Numbers: 405945293, 493487387

Handling Editor: Daniel S. Karp

Abstract

In many crops, both pollination and biocontrol determine crop yield, whereby the relative importance of the two ecosystem services can be moderated by the landscape context. However, additive and interactive effects of pollination and biocontrol in different landscape contexts are still poorly understood. We examined both ecosystem services in South African macadamia orchards. Combining observations and experiments, we disentangled their relative additive and interactive effects on crop production with variation in orchard design and landscape context (i.e., cover of natural habitat and altitude). Insect pollination increased the nut set on average by 280% (initial nut set) and 525% (final nut set), while biocontrol provided by bats and birds reduced the insect damage on average by 40%. Pollination services increased in orchards where macadamia tree rows were positioned perpendicular to orchard edges facing natural habitat. Biocontrol services decreased with elevation. Pest damage was reduced by higher cover of natural habitat at landscape scale but increased with elevation. Pollination and biocontrol are both important ecosystem services and complementary in providing high macadamia crop yield. Smart orchard design and the retention of natural habitat can simultaneously enhance both services. Conjoint management of ecosystem services can thus enable the ecological intensification of agricultural production.

KEYWORDS

Macadamia integrifolia, *Macadamia tetraphylla*, natural enemies, orchard design, South Africa, sustainable intensification

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

INTRODUCTION

New ways of agriculture must be implemented to sustain the global environment while also increasing crop production for a growing population (FAO, 2023). Conventional intensification is the most successful and widespread model for increasing agricultural yields to date, which usually involves the massive use of synthetic chemical pesticides and fertilizers for large-scale production in monocultures, but is often accompanied by high environmental impacts, such as soil degradation and loss of biodiversity (Garibaldi et al., 2017). More ecologically sustainable alternatives are urgently needed. One proposed approach is ecological intensification, that is, the substitution of conventional intensification practices with ecosystem services, such as pollination and biocontrol, in order to maintain (ecological replacement) or even enhance (ecological enhancement) agricultural yields (Bommarco et al., 2013).

Animal-mediated pollination increases yields of more than 75% of the globally most important crops, and about 35% of agricultural production depends at least partly on animal-mediated pollination (Klein et al., 2007). In many crops, such as almonds, cherries, or apples, managed honeybee colonies are used to forestall pollination deficits (Olhnuud et al., 2022; Reilly et al., 2020). However, several studies have shown that wild pollinators also play a critical role in agricultural pollination (Kremen et al., 2002) and, in fact, often outperform managed honeybees (Garibaldi et al., 2013; MacInnis & Forrest, 2019).

In addition, agricultural production benefits from biocontrol. Bats and birds are well-known providers of biocontrol services. They have been shown to reduce the density and damage of herbivorous insects, as well as increase crop yields, in a range of temperate and tropical agroecosystems (Boyles et al., 2011; Garcia et al., 2018; Johnson et al., 2010; Linden et al., 2019; Maas et al., 2016; Mols & Visser, 2002).

The landscape composition often moderates pollination and biocontrol services in agroecosystems. Natural habitat in farm surrounding can be an important source of pollinators and predators, and thus of pollination and biocontrol services (e.g., Castle et al., 2019; Gonthier et al., 2019). Spillover of pollinators from natural habitats to farms, as well as pollinator abundance and diversity, increase with the amount of natural habitat in the surrounding landscape (Kennedy et al., 2013; Kremen et al., 2007; Wu et al., 2021) and habitat patches in the crop vicinity (Carvalho et al., 2010; Klein, 2009; Klein et al., 2012). These spillover effects of pollinators can enhance crop yield, fruit set, and fruit quality (Bänsch et al., 2020; Holzschuh et al., 2012; Wu et al., 2021). Similarly, predators providing biocontrol services, such as bats and birds, often increase

in abundance and diversity on farms which are embedded in landscapes with a high amount of natural habitat (Boesing et al., 2017; Swartz et al., 2022; Weier et al., 2021; but see Karp et al., 2018). As a result, crop damage from pest species is often reduced in structurally complex agricultural landscapes (Bianchi et al., 2006; Weier et al., 2018).

In addition to the landscape composition, the design of agricultural fields and orchards influences the provisioning of ecosystem services. For example pest control is typically higher at field edges than at centers because of the higher density and activity of bat and bird species (Best et al., 1990; Jantzen & Fenton, 2013; Puckett et al., 2009). Further, a recent study has shown that the spatial arrangement within an orchard can positively affect pollinator spillover into orchards, allowing for greater pollinator densities also further from the orchard edge, for example, if the orientation of tree rows is perpendicular to the natural habitat, this eases pollinator movement into the orchard center (Anders et al., 2022).

Since both pollination and biocontrol are important ecosystem services in many agricultural production systems and the species that provide the two ecosystem services have similar underlying requirements (e.g., food resources and nesting sites inside and outside agroecosystems) it makes sense to manage them together (Lundin et al., 2021). Recent studies suggest that ecosystem services may interact with each other in contributing to crop yield and quality (Gagic et al., 2019; Garibaldi et al., 2018; Martínez-Salinas et al., 2022). When both ecosystem services affect the same parameter (i.e., fruit set), they can interact positively (synergistic), negatively (antagonistic) or do not interact, thus being additive. A synergistic interaction means that the increase of one service further enhances the other service, for example, the effect of pollination on crop yield is enhanced with higher biocontrol (Garibaldi et al., 2018). If one service is reduced at higher levels of the other service, this implies an antagonistic effect, though overall there is little evidence of antagonistic interactions between ecosystem services in the literature (but see Bartomeus et al., 2015). An additive effect would be the case, when both services independently affect the crop yield for instance (Gagic et al., 2019). The ecosystem services would be complementary, when they affect different yield parameters (e.g., fruit set and fruit quality), for instance when pollination service increases the fruit weight, but biocontrol increases the fruit set (Classen et al., 2014). So far, few experimental studies evaluated the additive and interactive effects of pollination and biocontrol in agroecosystems. These studies have examined effects in red clover, oilseed rape, or in coffee plantations (Classen et al., 2014; Lundin et al., 2012; Martínez-Salinas et al., 2022; Sutter & Albrecht, 2016). Martínez-

Salinas et al. (2022) showed that the combined positive effects of birds and bees on fruit set, fruit weight, and fruit weight uniformity were greater than their individual effects. In contrast, other studies found complementary effects, for example in melons or coffee (Classen et al., 2014; Strauss & Murch, 2004), or only pollinator but no biocontrol effects for cacao (Forbes & Northfield, 2017). None of these studies consider landscape effects on the interactions between the two ecosystem services. This is despite the fact that they depend on the landscape context (Landis, 2017; Tscharnke et al., 2005). For example, in agroecosystems with a low proportion of natural habitat, biocontrol and pollination services are often weak and therefore may only result in a small additive effect. In contrast, in landscapes with a higher proportion of natural habitat, the ecosystem services may increase in effect size allowing for potential synergistic effects. For example, enhanced pollination on farms with high amount of pollinator habitats can be a prerequisite for effective biocontrol of pests attacking fruits of pollinator-dependent crops. Moreover, the scales at which the individual ecosystem services are dependent on the landscape composition may differ (Martin et al., 2019). Thus, we are just beginning to understand how to manage the provisioning of multiple ecosystem services in real-world agroecosystems and different landscape contexts.

In this study, we experimentally examined the interaction of pollination and biocontrol services in 10 macadamia orchards in South Africa. The importance of pollination of macadamia flowers, the relevant species, pollinator behavior, and the role of landscape context and orchard management are largely understood and management options are being formulated (Anders et al., 2022; Evans et al., 2021; Grass et al., 2018; Howlett et al., 2015; Kämper et al., 2021). In contrast, the underlying mechanisms of macadamia pest species, their predators, and the potential moderating effects of the landscape context remain unclear. However, biocontrol is of high importance as macadamia farmers have a strong interest in minimizing insect damage to the nuts in order to sell their nuts at higher quality level and reduce the risk of insecticide resistances (Ellis et al., 2023). Previous studies show that bats and birds are important biocontrol agents in macadamia production, as their exclusion increases nut damage by up to 34% and reduces overall yield by up to 60% (Linden et al., 2019). Bats have also been identified as predators of the main macadamia pest species through fecal DNA analyses (Weier et al., 2019). In addition, bat foraging activity increases with bush cover, meaning that the landscape context can moderate biocontrol provided by bats (Swartz et al., 2022). To promote ecological intensification, we need to better understand the dynamics of biocontrol and the landscape effects. To do this, we set up exclusion experiments in

macadamia orchards, that varied in design and landscape context and investigated the following research questions: (1) Are there interacting or additive effects of pollination and biocontrol services on macadamia nut set and quality, respectively? (2) Are these effects moderated by the landscape context (i.e., share of natural habitats in the surrounding area and altitude) and orchard design? (3) Which landscape factors and orchard design factors can reduce insect damage?

METHODS

Study species

Macadamia (Proteacea) originated in Australia, but the commercially-important *M. integrifolia* and *M. tetraphylla* are nowadays cultivated worldwide with South Africa being the largest exporter (SAMAC, 2023). Macadamia is a mass-flowering crop that depends on insect pollination (Howlett et al., 2015). Pollinator exclusion reduced the final nut set by 19%–54% and pollination deficits have been reported to limit the yield strongly, as supplemental hand-pollination increased the final nut set by 44%–268% compared with open (insect-) pollination (Anders et al., 2022; Grass et al., 2018). An Australian study showed that macadamia is predominantly outcrossing, with 78%–90% of nuts being the result of cross-pollination, even when the parent varieties are up to 200 m apart (Richards et al., 2020). In addition, cross-pollination significantly increased nut size (kernel mass by 84%–96%) and kernel recovery (by 46%–50%) compared with self-pollinated nuts (Kämper et al., 2021). Hence, pollinators are important vectors to realize cross-pollination between macadamia varieties. A major problem for macadamia production in South Africa is nut damage by insect pests, such as stink bugs (Heteroptera) or moths (Lepidoptera) (De Villiers & Joubert, 2003). In 2022, the kernel damage caused an economic loss to the South African macadamia industry of over 6.8 million USD, which is 2.4% of the total export value (SAMAC, 2023). However, all bat species sampled within South African orchards forage on pest insects (Weier et al., 2019), making them important predators for reducing insect damage in macadamia production (Taylor et al., 2018; Weier et al., 2018).

A single mature *Macadamia* tree is capable of producing up to 2500 inflorescences—called racemes—during a growing season (Moncur et al., 1985). Each raceme contains between 100 and 300 individual flowers (Trueman, 2013) (Figure 1c). After successful fertilization, the flowers develop into initial nuts, which remain attached to the raceme while the unfertilized flowers drop. At this time, the initial nut set can be well recorded. In our study, this was three to

Nested exclusion treatment



Outcome



FIGURE 1 Nested exclusion experiment: (a) predator exclusion cages, the arrows indicate pollinator exclusion bags within the cage; (b) pollinator exclusion bags; (c) open pollination. As outcome, we assessed the (d) initial nut set (3–5 weeks after flowering), (e) final nut set (18–25 weeks after flowering), and nut quality: for example, (f) sound kernels, (g) nut borer damage, (h) early stink bug damage. Photographs by Mina Anders and Corrie Swanepoel.

five weeks after flowering, depending on the altitude. However, some nuts may drop during development and only those that remain on the raceme for about 18 to 20 weeks (final nut set) are likely to become mature and thus harvestable nuts. When the nuts are ripe, they fall from the raceme and are collected from the ground.

Study area and farms

This study was conducted in the Levuvhu Valley and at the southern foothills of the Soutpansberg mountain range, near Louis Trichardt, Limpopo Province, South Africa (23°3'0" S, 29°54'0" E). The region is characterized

by a subtropical, dry to moist climate, with a rainy season in summer from November to April. Daily temperatures range between 15 and 40°C in summer and 0 and 25°C in winter. The naturally occurring vegetation types in the Soutpansberg mountain range, which forms part of the Vhembe Biosphere Reserve, are Soutpansberg Bushveld and Tzaneen Sour Bushveld (Mostert et al., 2008). Habitat destruction and habitat degradation due to bush encroachment and plant invasions is a major threat to biodiversity in the Soutpansberg Mountains, for example, affecting endemic plant (Hahn, 2018; Moraswi et al., 2019), rodent (Taylor et al., 2016) and bat species (Weier et al., 2021). During our study, higher elevations were predominantly covered by natural bush with a few pine (*Pinus* spp.) and

gum tree (*Eucalyptus* spp.) plantations, while the native vegetation in the valley was largely replaced by intensive monocultures of macadamia (*M. integrifolia*, *M. tetraphylla* and hybrids), pecan nut (*Carya illinoensis* (Wangenh.) K. Koch), avocado (*Persea americana* Mill), bananas (*Musa* spp.), pine and gum trees. These crops were interspersed with remnants of natural habitats. We conducted fieldwork on private farms with the permission of the farmers.

In 2019, we selected 10 macadamia farms along an altitudinal gradient from 730 to 1330 m. This reflected an absolute difference of 4.2°C between the coolest and warmest farms considering the mean temperatures within the flowering period (July–September 2019). All selected farms were more than 5 km apart. The 10 farms were grouped into five farm pairs. The two farms of a pair were located at similar altitude, whereby one farm was located in a landscape with a high cover of natural habitats (mean: 60.7%, range: 35.1%–80.6%), and the other farm was located in a landscape dominated by orchards or agricultural fields (mean cover of natural habitats: 31.5%, range: 19.6%–45.4%). As natural habitats, we classified indigenous forest, bush, shrubland, and grassland, and calculated the combined relative cover within a 1 km radius of the center of each study site. The assessment was based on a land cover class map from 2018 (resolution: 20 × 20 m raster) (Department of Environmental Affairs SA, 2019). To also include land cover changes between 2018 and the observed season in 2019, we compared the land-cover class map with the latest Google Maps Satellite images (“Google Earth Pro,” 2020) (see Anders et al., 2022). Elevation of the study sites was extracted from Google Earth Pro (“Google Earth Pro,” 2020) and classified in two categories, that is, low and high elevation (730–900 m above sea level [asl], $n = 6$, and 1180–1330 m asl, $n = 4$, respectively).

The macadamia orchards of the farms were subdivided into several production units (i.e., blocks). On each farm, we chose a study block (mean: 5.6 ha; range: 1–28.5 ha) that bordered natural habitats as study site.

To minimize the effect of different macadamia varieties, we selected Pahala (788) for our study, a variety commonly grown in the region. However, Pahala (788) was not available in two out of 10 farms, which, instead, grew the following varieties in our study block: 814, 842, 849, Mauka (742), and Kau (344). In addition, on three of the other “Pahala farms,” individual Pahala (788) trees had occasionally been replaced by other varieties so that due to the design of the study and the spatial arrangement of the trees, we had to include individual trees of 814, Kau (344), and 741. The selected varieties had similar flower morphology, flowering periods (Vock et al., 1998), and harvesting techniques. All experimental trees were in

full production and of comparable age (mean: 15.6 years; range: 8–27 years). All of the macadamia farms were managed conventionally, following the recommendations of agricultural extension officers for pesticide and fertilizer use. However, the study trees were excluded from the usual pesticide applications in the orchards shortly before (ca. three weeks) and until the end of the study period (May 2019 to May 2020) in order to standardize and reduce the potential impact of pesticides on pollinators. This meant that whole blocks were excluded on farms where pesticides were applied by helicopter, and rows were not sprayed on farms where trailer sprayers were used.

Experimental design

We selected eight trees on each of the 10 study farms, resulting in a total of 80 study trees. Two adjacent trees always formed a sample unit (Appendix S1: Figure S2). To analyze the ecosystem services provided by predators (bats and birds) and (insect) pollinators, we applied an experimental nested exclusion approach (Figure 1a–c). The exclusion of bats and birds as predators versus no exclusion provides insight into their biocontrol services (Linden et al., 2019). Cages, made of a wooden frame (dimensions 5 × 10 × 5 m) and a large nylon mesh net (net eye size 2 × 2 cm) surrounding one sampling unit each, ensured their exclusion, but not of smaller predators (e.g., spiders). Half of the trees were covered by these cages, while the other half served as control. The net prevented diurnal as well as nocturnal predators from foraging in the trees. Pollinators, in contrast, could easily pass the net (Anders et al., 2022). In addition, we experimentally excluded pollinators at each tree, including trees within and outside of the cages. For this purpose, we selected six racemes per tree where all flowers were still closed but would open in the next few days. One or more racemes were enclosed in a net bag (Rewe Mehrweg-Frischenetz, 100% polyester, mesh size: 0.05 mm, bag size: 310 × 280 mm), which allowed wind pollination but not insect pollination (Figure 1b). We randomly chose three suitable racemes in the lower part of the tree (<2 m) and in the upper part of the tree (>2 m). When counting the initial nut set, we removed the bags to allow for comparable growing conditions of all marked racemes. As a control, we randomly marked 20 racemes per tree, again half in the lower and half in the upper part of the tree. In combination with the predator exclusion, we thus had four treatments: exclusion of both predators and pollinators (bagged racemes on caged trees), pollinator exclusion only (bagged racemes on open trees), predator exclusion only (open racemes on caged trees), and

no exclusion (open racemes on open trees). We analyzed the main effects and two-way interactions of biocontrol and pollination on nut set, as we assumed that both ecosystem services influence nut set. Pollination is a prerequisite for fruit set (Anders et al., 2022; Grass et al., 2018). Biocontrol is critical, as some of the macadamia pests in the study area can cause premature nut shedding (Jones, 2002; Van den Berg et al., 1999). Due to the developmental biology of macadamia nuts and our study design, we were unable to analyze the interaction between pollination and biocontrol on nut quality. The nuts fall to the ground when ripe, so it is not possible to trace which raceme the nuts were attached to before they fell and thus which pollinator treatment they received. Hence, we only analyzed the effects of pollinator exclusion on nut set, but not on nut quality.

To assess effects of the orchard design on pollination and biocontrol services, we applied the nested exclusion on four trees at the edge of the block adjacent to natural habitats and four trees in 50 m distance from the edge, that is, in the center of the study block at each study orchard. From here on, this will be referred to as “position in block.” Moreover, we recorded the orientation of the planted tree rows from the orchard edges to natural habitats (perpendicular $n = 5$, parallel $n = 5$). We also recorded whether the block was irrigated or not (yes $n = 6$, no $n = 4$).

Nut set and quality assessment

In September 2019, once the first nuts had developed (this took between 3 and 5 weeks after flowering, depending on the altitude and water management of the farms), the initial nut set was counted and in early December 2019, 18–20 weeks after flowering, the final nut set was recorded.

Macadamia nuts were collected weekly or biweekly between January and May 2020. Randomly, 1 kg of the yield that was collected from the caged and open sample units was analyzed. The samples were dried, cracked and inspected for quality defects. Total sample weight, shell and kernel weight were recorded. The total kernel weight was divided into sound (undamaged) and unsound (damaged) kernels. The unsound kernels were classified into the following seven types of damage: immature = immature nuts; fungi = damage caused by fungus, which is often a result of minor insect damage of the husk (Jones, 2002); nut borer = damage caused by nut borers (e.g., *Thaumatotibia batrachopa*, Meyrick, 1908); early stink bug (ESB) = damage caused by a stink bug at an early stage of nut development; late stink bug (LSB) = damage caused by a stink bug at a late stage of nut development; shell marks = indefinite light or dark marks on the shell and

germination = germinated seeds. As insect damage we considered the combined damage of nut borer, ESB and LSB. The insect damage was used as indicator for nut quality. See Appendix S1: Section S2 for a detailed description of the quality analyses.

Bat activity and arthropod assessment

To assess the bat activity in the orchards, we passively recorded the echolocation calls of the bats with SM4BAT recorders (Song Meter SM4BAT FS Ultrasonic Recorder, Wildlife Acoustics Inc., USA). Between June 2019 and March 2020, the calls were recorded every six weeks, resulting in five rounds. For each round, the recording time was between 5:00 p.m. and 6:00 p.m., and 11:00 p.m. and 12:00 a.m. for two consecutive nights. All call sequences were manually identified to the species level using AnalookW (version 3.8; Corben, 2006) after converting them to zero-crossing (ZC) files using Kaleidoscope (version 1.1.15; 2022).

To assess the availability of potential prey for bats and potential pest insects, we recorded the abundance of arthropods on and under the study trees in six rounds between June 2019 and May 2020. Each tree was surveyed for arthropods for 10 min. The trunk and lower hanging branches were observed for 5 min, while the canopy and higher branches were observed for another 5 min using a ladder. All arthropod individuals were identified in the field to order level.

Statistical analysis

Effects of pollination and biocontrol on nut set and quality

We used generalized linear mixed models (glmmTMB) fitted with R package “glmmTMB” (Brooks, 2017) in R (R Core Team, 2022) to analyze the effects of pollination and biocontrol exclusion on nut set and quality. For testing the sole effect of pollination on the nut set, we used the initial and final nut set as response and the pollinator exclusion treatment (pollinator exclusion vs. open racemes) as fixed effect. For testing the combined effect of pollination and biocontrol, we used the pollinator exclusion treatment, the biocontrol exclusion treatment (predator exclusion and open trees) and their interaction as fixed effects. For all models regarding the nut set, site, pair, and tree individual were included as nested random effects, and study block age as a crossed random effect. We accounted for the high number of zeros in the data (zero-inflation) by adding a general zero-inflation parameter

($z_{\text{formula}} \approx 1$). We chose a negative binomial distribution with linear parameterization (Hardin & Hilbe, 2007).

To analyze nut damage with and without biocontrol, we fitted a binomial glmmTMB for each type of damage and the combined insect damage. The exclusion treatment (predator exclusion vs. open trees) was included as fixed effect, the site and pair as nested random effects, and the age of the study block as crossed random effect. As the nuts for the quality analysis were pooled within a tree pair, we did not use the individual tree as random effect like we did for the nut set models.

Effects of landscape context and orchard design on nut set and nut quality

To test the effects of pollination and biocontrol services under different landscape and orchard design contexts, we applied a multi-model inference approach (Burnham & Anderson, 2002). For each analysis, we first fitted a global model including all explanatory variables and ecologically meaningful two-way interactions that were related to our research questions. We then used the “dredge” command (package “MuMIn”) (Bartoń, 2022) to generate candidate models with all possible combinations of the variables and interactions. To avoid over-parameterization, we limited the number of variables in each candidate model to four. The relative importance of each explanatory variable and two-way interaction was assessed by the sum of Akaike weights ($\sum w_i$) across all models including the variable or interaction. The AICc (Corrected Akaike Information Criterion) for each model was calculated. The derived models within a delta AICc < 2 compared with the best-fitting model from the top model set were considered as equally meaningful. When there was more than one model in the top model set, we selected the model from the set that included only variables with an importance value with $\sum w_i > 0.5$ for interpretation. To check the model fits, we compared all models in the top model set with the null model, which contained the same random effects but no fixed effects. If the difference in AICc between the null model and the model being evaluated was greater than 2, we considered it to be meaningful. In addition, we calculated the marginal and conditional R^2 values to check how well the model explained the variation in our response variables.

Considering the surrounding landscape and orchard design, the global models predicting the initial and final nut sets, respectively, included the following fixed effects: cover of natural habitats, row orientation, position in block, irrigation, and altitude and their two-way interaction with the exclusion treatment. Again, we set the pair, site, and individual tree as

nested effects, the orchard block age as crossed random effect, and included a general zero-inflation formula. A negative binomial distribution with linear parameterization was most appropriate to model the initial nut set (Hardin & Hilbe, 2007), while a Poisson distribution best fitted the data for the final nut set. Across the model set of candidate models, we always limited the number of model terms by model to four to avoid overparameterization.

To evaluate the effects on nut quality, we performed two analyses. First, we tested whether the effect of biocontrol (exclusion treatment) on nut quality was dependent on landscape and orchard design contexts. Therefore, we used a binomial as global model that included insect damage (damaged nuts/sound and damaged nuts in grams) as response, and contained cover of natural habitats, altitude, row orientation, position in block, number of arthropods in trees, bat activity and their two-way interaction with exclusion treatment of predators as fixed effects. Pair and site were included as nested random effects and block age as a crossed random effect. As the number of arthropods in trees was positively correlated with altitude, all models that included these two predictors were excluded from the model set.

Second, we tested which landscape and orchard design factors influence nut quality independent from bat and bird exclusion. To do this, we ran a binomial global model, in which insect damage was set as response, while bat activity, cover of natural habitats, altitude, row orientation, number of arthropods in trees and position in the block were included as fixed effects. Again, all models that contained the combination of altitude and number of arthropods were excluded. Also here, pair and site were included as nested random effects, and age and biocontrol exclusion treatment were included as crossed random effects.

RESULTS

Pollinators increase nut set and predators enhance nut quality

We counted the nut set of 2037 racemes (Appendix S1: Table S1). The initial as well as the final nut set were significantly increased by insect pollination (Table 1). The initial nut set of open racemes was almost four times higher compared to pollinator exclusion (mean = 2.69, SE = 0.57 vs. mean = 0.70, SE = 0.16, $p < 0.001$), and the final nut set was more than six times higher after insect pollination (mean = 0.46, SE = 0.18 vs. mean = 0.07, SE = 0.03, $p < 0.001$). Experimental exclusion of

bats and birds did not affect nut set, and there was neither a synergistic nor an antagonistic interaction between biocontrol and pollination on nut set (Figure 2, Table 1).

The quality analyses of in total 36.14 kg macadamia nuts in shell showed the following results. The harvested nuts had an average total kernel rate (TKR = dry nut weight/dry nut in shell weight) of 32%, consisting of 25% sound kernels and 7% unsound kernels. The largest proportion of unsound kernels were immature nuts (69.4%), followed by damage due to ESB damage (9.6%), nut borers (9.1%), fungi (6.5%), and LSB damage (1.7%). Unspecified shell damage and germination account for the remaining 3.7% of unsound kernels. However, the probability of immature nuts, germination, shell marks, and damage by fungi, nut borers and ESBs significantly increased in the exclusion cages (Figure 3). The probability of insect damage, that is, the combined damage from nut borers, ESBs and LSBs, was 70% higher when birds and bats were excluded compared with open trees (mean = 0.034, SE = 0.007 vs. mean = 0.020, SE = 0.012, $p < 0.001$) (Figure 3).

The biocontrol exclusion increased the abundance of hemipterans (including detrimental aphids and bugs) by 60% (mean = 3.00, SE = 0.92 vs. mean = 4.81, SE = 1.44, $p < 0.001$), but had no effect on the abundance of hymenopterans (including pollinating bees,

parasitoid wasps and ants; Appendix S1: Table S2, Figure S2).

Interaction of pollination and biocontrol with landscape context and orchard design

The analysis of the initial nut set including the interaction of orchard design and landscape factors with the nested exclusion of pollinators and predators yielded four models within delta AICc < 2 (Table 2). All four models in the set contained pollination exclusion treatment as predictor (Table 1). Additionally, the predator exclusion treatment, the position in block and the altitude, as well as the interaction between pollination and row or altitude were included in the models. We selected the fourth-ranked model for interpretation, because, here all included variables had an importance value $\Sigma w_i > 0.5$, which was not the case for the other models (Table 3). The interaction of row orientation and pollinator exclusion experiment was significant, but the general pattern of a considerable increase in initial nut set after open pollination remained the same with both row orientations. However, the increase in nut set was more pronounced in rows oriented perpendicular to the natural habitat edges (Figure 4a).

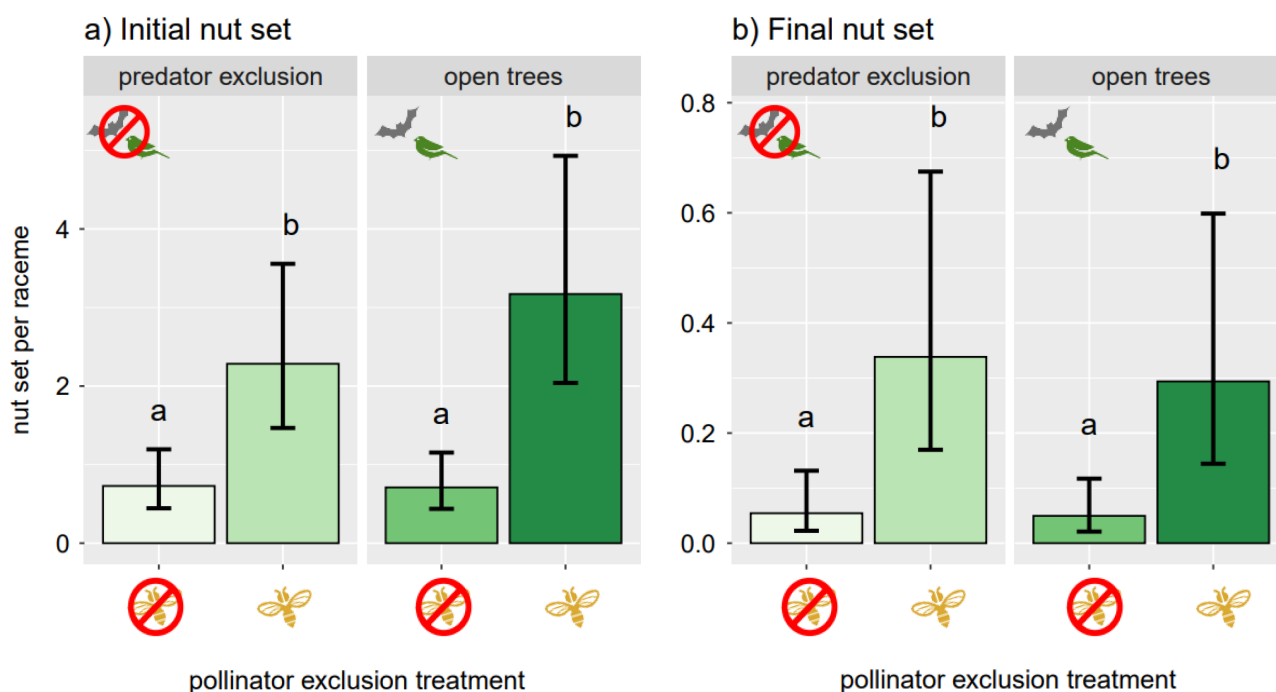


FIGURE 2 Initial and final nut set after the nested exclusion treatments: (a) initial nut set, (b) final nut set. Different letters indicate significant differences between all four groups ($p \leq 0.05$); error bars indicate the confidence levels (0.05 and 0.95).

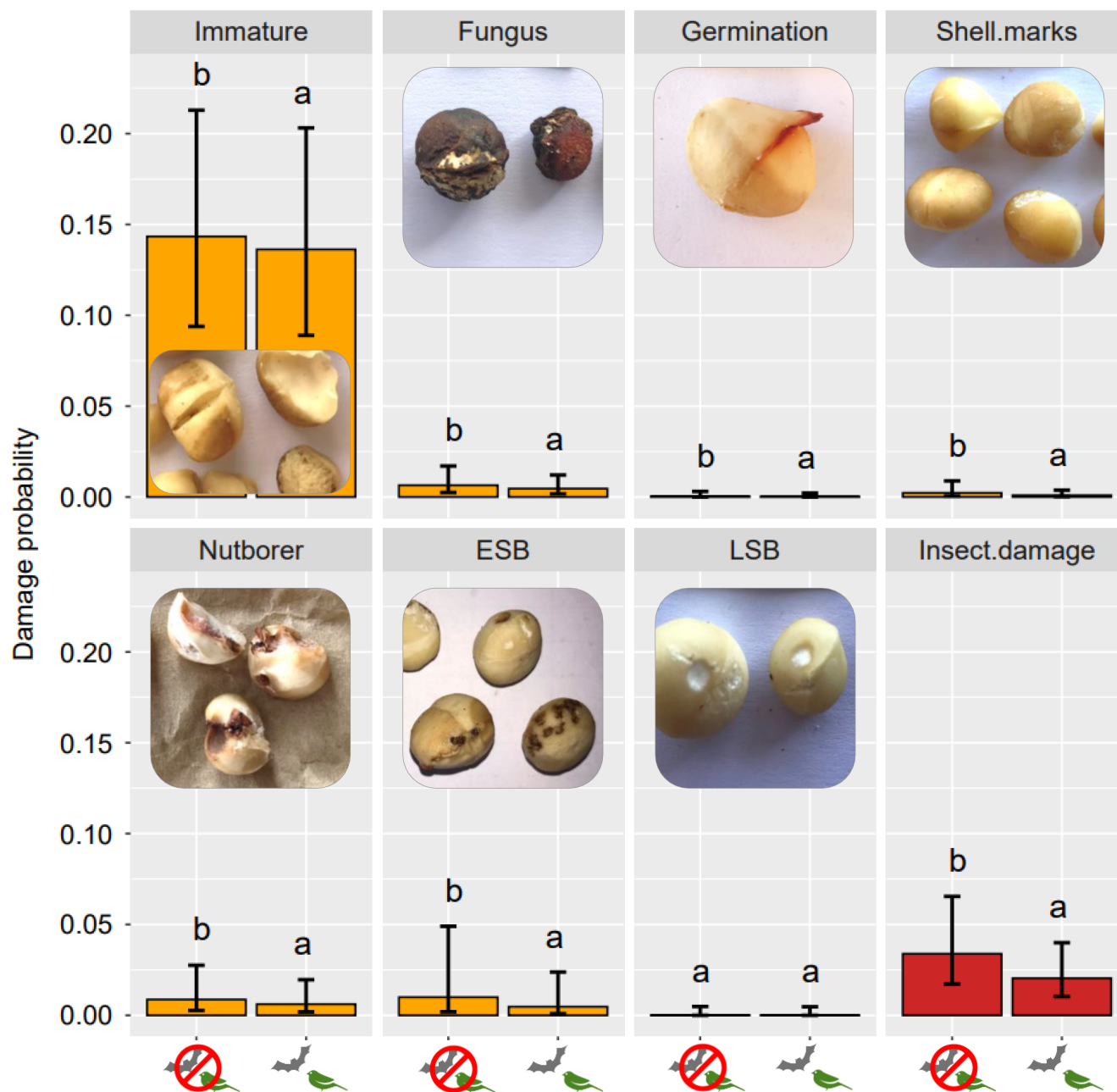


FIGURE 3 Probabilities of damage types in unsound kernel, with and without biocontrol exclusion (ESB, early stink bug; LSB, late stink bug). Letters indicate significant differences with and without biocontrol exclusion ($p \leq 0.05$). Photographs by Corrie Swanepoel.

The model selection of the best fitting models regarding the final nut set resulted in one model within delta AICc < 2. It included position in block and the interaction between altitude and the pollination exclusion experiment as fixed effects (Table 3). The final nut set was higher at higher altitudes, and the effect of pollination exclusion was stronger, meaning a lower final nut set after pollinator exclusion and a higher nut set after open pollination at higher altitudes (Figure 4b). In addition,

the final nut set is significantly reduced by 50% at the orchard edges.

Regarding the insect damage after biocontrol exclusion, model selection gave one most likely model within delta AICc < 2, including the predator exclusion treatment, position in block, altitude, and the interaction of altitude and predator exclusion. The probability of insect damage was significantly increased, that is, about three times, at the orchard edges to the natural habitats compared with the

TABLE 1 Interacting effect between pollination and biocontrol on the initial and final nut set.

Predictor	χ^2	df	<i>p</i>
Initial nut set			
Pollination exclusion	219.28	1	<0.001
Biocontrol exclusion	3.93	1	0.047
Pollination exclusion × biocontrol exclusion	3.97	1	0.046
Final nut set			
Pollination exclusion	99.70	1	<0.001
Biocontrol exclusion	0.35	1	0.554
Pollination exclusion × biocontrol exclusion	0.12	1	0.726

Note: Bold denotes statistical significance ($p \leq 0.05$).

center of the blocks. The probability of insect damage was enhanced at higher altitudes. However, where trees were accessible to bats and birds, there was a significant reduction in damage at both high and low altitudes (Figure 4c). Bat activity had no effect on insect damage.

Landscape and orchard design factors affect nut quality

The multi-model inference approach to test the effects of landscape context (i.e., altitude and cover of semi-natural habitat), bat activity, arthropod abundance, and orchard design on nut quality, independent from biocontrol exclusion, yielded one most likely model (Table 4). This model contained three predictors as

TABLE 2 Global models and model sets of the best-fitting models within delta AICc < 2 for the analyses of the interaction between ecosystem services (pollination and biocontrol) and landscape and orchard design factors.

Model	Response	Predictor variables	R^2_c	R^2_m	df	AICc	dAICc	Akaike weight
Global model initial nut set (ins) ^a								
ins1	Initial nut set	POL + row + BPC POL × row	0.245	0.106	11	5807.33	0.00	0.273
ins2		POL + row + PIB POL × row	0.247	0.108	11	5808.34	1.01	0.165
ins3		POL + altitude + BPC + POL × altitude	0.251	0.113	11	5808.94	1.61	0.122
ins4		POL + row + POL × row	0.246	0.109	10	5809.16	1.83	0.109
Global model final nut set (fns) ^b								
fns1	Final nut set	POL + altitude + PIB POL × altitude	0.759	0.283	10	2781.130	0.00	0.782
Global model insect damage (id) ^c								
id1	insect damage	BPC + altitude + PIB BPC × altitude	0.996	0.385	8	1353.614	0.00	1.000
Global model insect damage in landscape context (idL) ^d								
idL1	insect damage	PIB + habitat + altitude	0.996	0.393	8	1447.278	0.00	0.342
idL2		PIB + habitat + row + arthropods	0.999	0.368	9	1448.079	0.80	0.230

Note: The predictor variables are: POL = pollinator exclusion (open pollination/pollinator exclusion), BPC = biocontrol exclusion, habitat = cover of natural habitats in 1 km radius, altitude (low: 730–900 m asl/high: 1180–1330 m asl), row = row orientation (parallel/perpendicular), irrigation (yes/no), PIB = position in block (edge/center), arthropods = number of arthropods in trees, bat.activity = number of bat calls. As model evaluation, the conditional R -squared (R^2_c) and marginal R -squared (R^2_m), conditional Akaike information criterion (AICc), delta AICc = difference in AICc between a model and the top ranked model (dAICc) and Akaike weights are shown. The R^2 are calculated applying the trigamma-method, while for binomial models, the theoretical R^2 is shown. The underlined models are presented in Tables 3 and 4 and used for interpretation.

^aglmmTMB(initial_nut_set ~ POL × BPC × (habitat + altitude + row + PIB + irrigation) + (1|age) + (1|pair/Site_ID/Tree_ID), ziformula = ~1, family = "nbinom2").

^bglmmTMB(final_nut_set ~ POL × BPC × (habitat + altitude + row + PIB + irrigation) + (1|age) + (1|pair/Site_ID/Tree_ID), ziformula = ~1, family = "poisson").

^cglmmTMB(cbind(insect.damage, not.ins.dam) ~ BPC × (habitat + altitude + row + PIB + arthropods + bat.activity) + (1|age) + (1|pair/Site_ID), family = "binomial").

^dglmmTMB(cbind(insect.damage, not.ins.dam) ~ habitat + altitude + row + PIB + arthropods + bat.activity + (1|BPC) + (1|age) + (1|pair/Site_ID), family = "binomial").

TABLE 3 Best-fitting models showing the interaction of pollination and biocontrol with different landscape and orchard design contexts.

Predictor	χ^2	df	p
model ins4—Response: Initial nut set			
(Intercept)	0.12	1	0.732
Pollinator exclusion	29.90	1	0.306
Row orientation	1.05	1	<0.001
Pollinator exclusion $\times$ row orientation	39.65	1	<0.001
model fns1—Response: Final nut set			
(Intercept)	16.03	1	<0.001
Altitude	6.75	1	0.009
Position in block	6.09	1	0.014
Pollinator exclusion	30.68	1	<0.001
Pollinator exclusion $\times$ altitude	16.65	1	<0.001
model id1—Response: Insect damage			
(Intercept)	90.77	1	<0.001
Biocontrol	270.24	1	<0.001
Altitude	3.78	1	0.051
Position in block	1185.45	1	<0.001
Biocontrol exclusion $\times$ altitude	95.92	1	<0.001

Note: The model for insect damage includes only the exclusion of predators, but not of pollinators. Bold denotes statistical significance ($p \leq 0.05$).

fixed effects, altitude, cover of natural habitat, and position in the block. Bat activity, in contrast, was not included. The probability of insect damage increased with altitude and at orchard edges next to natural habitat. Furthermore, the cover of natural habitat (% in 1 km radius) significantly reduced the probability of insect damage (Figure 5). For example, the probability of damage was on average 0.04 (SE = 0.02) in landscapes with 30% natural habitats, while it was reduced to 0.02 (SE = 0.01) in landscapes with 60% natural habitats.

DISCUSSION

Combining exclusion treatments and orchard design with landscape context, our study shows that both pollination and biocontrol are complementary ecosystem services driving macadamia production. Animal pollination increased the initial and final nut set by 280% and 525%, respectively. Biocontrol by bats and birds reduced insect damage of nuts by 40%. Orchard design and landscape context moderated the ecosystem services: Pollination

services increased in orchards where macadamia tree rows were positioned perpendicular to orchard edges facing natural habitat. Insect damage decreased with greater cover of natural habitat at landscape scale and increased with elevation. Smart orchard design and the conservation of natural habitat can simultaneously enhance both services.

Interplay of pollination and biocontrol services

In this study, we tested the additive and interactive effects of insect pollination and biocontrol by bats and birds on macadamia production. In line with previous research that studied the two ecosystem services separately (Anders et al., 2022; Grass et al., 2018; Linden et al., 2019), our study confirmed the importance of both ecosystem services using a nested exclusion experiment.

Contrary to our expectation that biocontrol and pollination services additively increase macadamia nut set, as indicated by Linden et al. (2019), we found that the nut set primarily depended on pollination, but not on biocontrol. Here, insect pollination increased the initial nut set and therefore also indirectly the final nut. We assumed that the biocontrol service would further increase final nut set, because some of the macadamia pest insects in the study area can cause premature nut drop (Jones, 2002; Van den Berg et al., 1999). However, there are other causes of premature nut drop besides pest infestation, such as drought and even selective fruit abscission of self-pollinated immature fruits is hypothesized (Richards et al., 2020) or the macadamia pests relevant at our study sites do not usually lead to premature nut shedding. Nevertheless, biocontrol services were of relevance as services provided by bats and birds considerably reduced the insect damage of nuts and thus increased the nut quality. Also fungal damage, which can be an indirect insect damage (Jones, 2002), was significantly reduced in situations where trees were accessible to bats and birds compared with the exclusion treatment. While the relative insect damage was generally low (7% unsound kernel rate, of which 20% was insect damage), its reduction is still important considering high rates of chemical pesticide application in macadamia orchards, with farmers often aiming at very low levels of pest damage (1%–2% unsound kernel rate).

Analyzing the effects of the two services in combination, we could demonstrate that they affect different aspects of macadamia production. Pollination service is a prerequisite for high yield (Anders et al., 2022; Grass et al., 2018; Kämper et al., 2019), while biocontrol services significantly reduce pest damage (Linden et al., 2019; Maas et al., 2016; Taylor et al., 2018; Weier

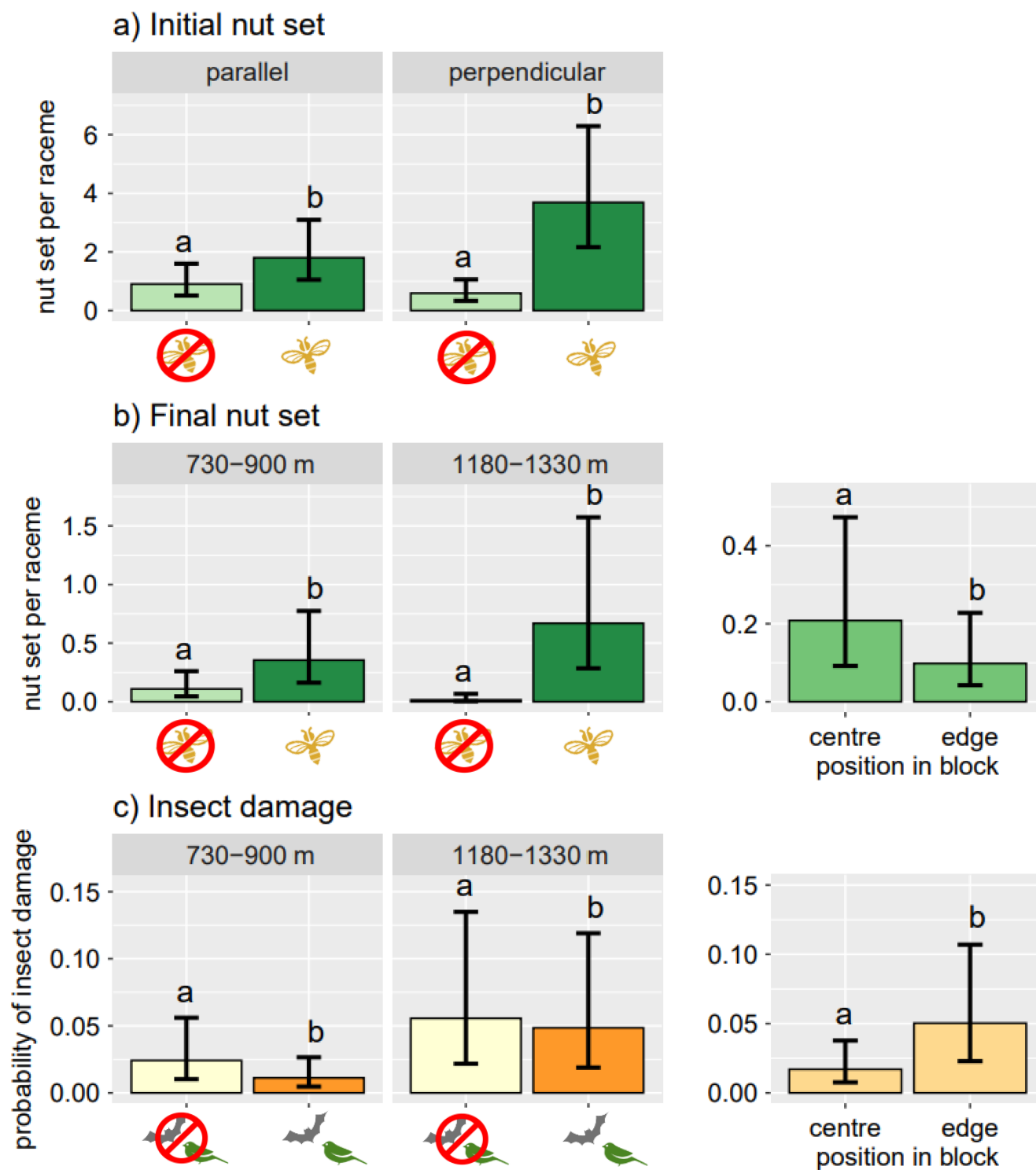


FIGURE 4 Interaction of exclusion treatments and landscape and orchard design factors. The best-fitting models are shown. (a) The pollination exclusion interacted with the row orientation (parallel/perpendicular) when predicting the initial nut set (model ins4). (b) The pollination exclusion interacted with the altitude (low: 720–900 m asl/ high: 1180–1330 m asl) and position in block was significant predicting the final nut set (model fns1). (c) When predicting the probability of insect damage (model id1), the exclusion of the predators interacted with the altitude, and the effect of the position in block was significant). Letters above the bars indicate statistical significance between the groups ($p \leq 0.05$) and the error bars indicate the confidence levels (0.05 and 0.95).

et al., 2019). Moreover, the foraging activity of bats and birds on arthropods significantly reduced the overall arthropod abundance in the trees, especially the

Hemiptera, which comprise major pest species for macadamia (e.g., *Aphis gossypii*, Glover 1877 and *Nezara viridula*, Linnaeus, 1758; see Appendix S1: Section S1,

Figure S1, Table S3). In contrast, the abundance of other arthropod groups, including Hymenoptera that include beneficial insects such as pollinating bees and parasitoid wasps, was not affected.

Orchard design and landscape context moderate pollination and biocontrol services

We found a significant interaction of pollination service and tree row orientation with respect to initial nut set. The difference between pollinator exclusion and no exclusion was more pronounced in orchards with perpendicular row orientation toward the natural habitats at the orchard edges, because this orchard design improves the pollination service by insects (Anders et al., 2022). In particular, by orienting the tree rows perpendicular toward the orchard edges, spillover of pollinators from natural habitats is enhanced and the nut set is increased sustainably. Thus, optimized orchard design is a viable approach for ecological intensification of macadamia production, in particular, the initial nut set.

TABLE 4 Best-fitting model of landscape and orchard design factors predicting insect damage.

Predictor	χ^2	df	<i>p</i>
model idL1—Response: Insect damage			
(Intercept)	113.36	1	<0.001
Altitude (high)	149.79	1	<0.001
Position in block (edge)	1200.42	1	<0.001
Natural habitats	63.35	1	<0.001

Note: Bold denotes statistical significance ($p \leq 0.05$).

The final nut set of open pollinated racemes was almost doubled at high altitudes compared with low altitudes. The final nut set of bagged, that is, wind- or self-pollinated, racemes was higher at low altitudes, which could be due to different wind and microclimate conditions in the valley. As previously shown, the higher altitudes generally had a positive effect on the final nut set in the study area (Anders et al., 2022). A possible reason is the cooler climate at higher altitudes, which may have mitigated the extremely hot and dry season in 2019/2020, which was a problem for macadamia cultivation (personal communication with farmers: G. Whyte, P. Thomas January 2020).

Biocontrol by predators significantly reduced insect damage regardless of orchard design, position in block and cover of natural habitat in the near landscape, making biocontrol an important ecosystem service in all contexts. We found a significant interaction of biocontrol service and altitude. While the biocontrol services by predators decreased insect damage in all locations, the magnitude varied depending on the altitude. Biocontrol service was stronger in lower altitudes reducing the probability of insect damage on average by 50% (from 0.024 to 0.012), than in higher elevations where the reduction was 13% (from 0.056 to 0.049). It has been shown that bat activity tends to be higher at lower altitudes in the Soutpansberg region, possibly providing higher levels of biocontrol service in the valley (Linden et al., 2014; Weier et al., 2017). It is possible that the abundance, diversity, and activity of predators change with altitude because of the different landscape characteristics. The availability of alternative food sources for predators may differ, which may influence their presence and effectiveness in controlling pests. The insect damage

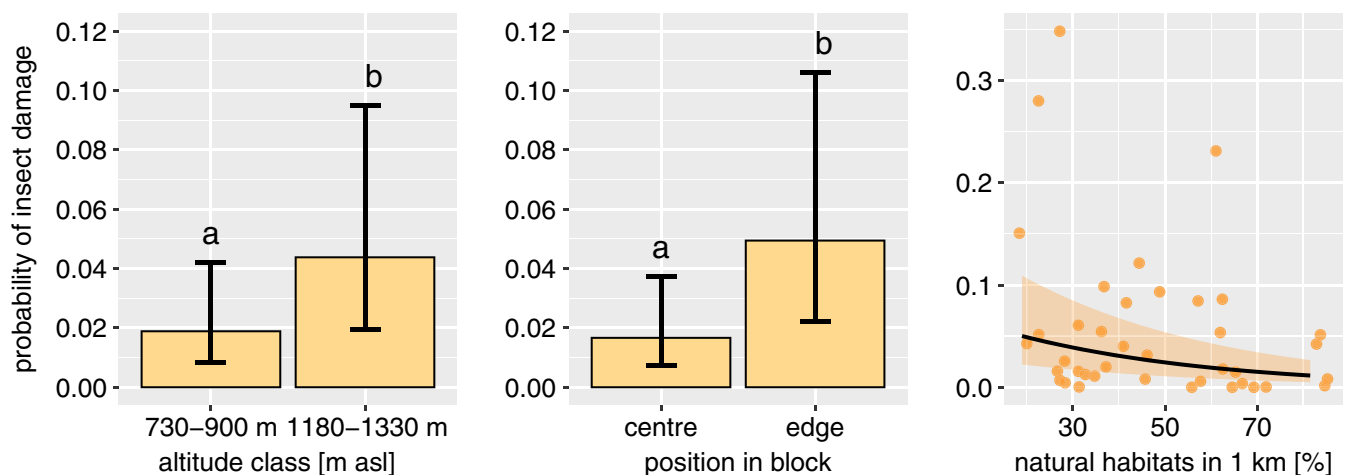


FIGURE 5 Additional analysis of landscape and orchard design effects on the insect damage without biocontrol exclusion as fixed effect. The best-fitting model (model idL1) contains altitude, position in block and cover of natural habitats as fixed effects. Letters indicate statistical significance between the groups ($p \leq 0.05$) and the error bars and the shade indicates the confidence levels (0.05 and 0.95).

was particularly high at higher altitudes. Pest pressure could be elevated at higher altitudes due to a different microclimate that favors insect populations. Interestingly, the pest pressure perceived by the farmers is the opposite, being much higher in the lower farms (personal communication with farmers and managers). This can be explained by the history of the landscape, as the macadamia orchards in the valley are on average much older (about 40–60 years) than those at higher altitudes so that the introduced pest species have had more time to establish. As a result, insecticide use in the lower region is generally more rigorous than in the higher located orchards (personal communication with farmers and managers), possibly resulting in less insect damage there. However, we point out that the 10 selected study farms were conventionally managed farms where pesticide use is comparable. To summarize, the altitude factor in our analysis is a mixture of many factors, including microclimate, landscape history and other unknown influences, thus should be interpreted with caution. Although altitude is ambiguous, it is important to include it in the analysis in order to separate its influence from the other effects analyzed.

We did not detect an interaction between the cover of natural habitat or orchard design with biocontrol exclusion. However, analyzing the effects on insect damage independently from the biocontrol exclusion, we found that greater cover of natural habitat in the surrounding landscape was negatively related to insect damage on farms. This is likely driven by the higher abundance of predating birds and bats, as shown by previous studies on the study farms (Weier et al., 2018). Moreover, natural vegetation is habitat for parasitoid insects. For example, the wasp *Trissolcus basalis* (Wollaston, 1858), but also the tachinid flies *Bogusia bequaerti* (Villeneuve, 1913) and *Bogusia antinorii* (Rondani, 1873) are natural enemies of two common stink bug pest species in Limpopo, that is, *Nezara viridula* (Linnaeus, 1758) and *Bathycoelia distincta* Distant (De Villiers & Joubert, 2003; Pal et al., 2022). Hymenopteran parasitoid abundance increased with altitude and natural habitat cover in macadamia orchards in Levuhu Valley (unpublished data). Contrary to our expectation we detected no direct effect of bat activity on insect damage. This could be explained by the fact that bat activity does not fully coincide with their predation activity, for example, if bats instead only traverse the plantation or forage exclusively locally in particularly suitable locations (Weier et al., 2021).

Despite the positive effects of natural habitat, the insect damage was, on average, more than doubled at the orchard edge to natural habitat as compared with 50 m distance from the edge, which is in line with studies

finding increased pest infestation at crop edges (Aigner et al., 2017; Minarro & Prida, 2013; Renkema et al., 2014; Venugopal et al., 2014). At the same time, increased predator activity and thus increased biocontrol services are proclaimed at field or orchard edges, including by birds and bats that often forage at field edges (Kolkert et al., 2021). Linden et al. (2019) suggest that biocontrol services still outweigh negative edge effects, including greater pest pressure, in macadamia orchards.

We point out that row orientation of macadamia trees to orchard edge did not affect insect damage. Anders et al. showed that a perpendicular orientation of macadamia tree rows next to natural habitat bordering orchard blocks promoted macadamia pollination (2022). This is likely because it facilitated pollinator spillover from natural habitat surroundings into orchards (Carvalho et al., 2010). With our study, we were able to disprove the concern that along with the desirable pollinators, undesirable insect pests could also more easily enter the orchard and cause increased insect damage.

CONCLUSION

Insect pollination and biocontrol by bats and birds are both crucial ecosystem services in macadamia production and complement each other to increase yields and reduce insect damage of macadamia nuts. By optimizing the orchard design, that is, implementing a perpendicular orientation of tree rows facing natural habitat, macadamia pollination can be substantially improved. In addition, to enhance nut quality, it is essential to restore and retain natural habitats in and around orchards. A smart combination of both measures can result in complementary effects, improving the overall nut production and quality in a sustainable way, and following the integrated approach of ecological intensification (Bommarco et al., 2013).

AUTHOR CONTRIBUTIONS

Ingo Grass, Catrin Westphal, and Peter J. Taylor conceived the study and supervised the project. Valerie M. G. Linden selected and oversaw the study sites. Valerie M. G. Linden, Sina Weier, and Mina Anders implemented the experiment and collected data. The bat calls were identified by Valerie M. G. Linden, Sina Weier, and Peter J. Taylor. Mina Anders performed the data analysis with advice from Ingo Grass and Catrin Westphal. Mina Anders wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

We thank all famers, landowners and managers, Alan Whyte, Phillip Potgieter, Marius Mostert, Murray Stewart, Pierre Thomas, Jacques Bouwer, Gertien Le Roux, Louis Jordaan, Dave Pope, Richardt Bouwer, Derrick Bouwer, Andy Tonks, and Greame Whyte, for their cordial cooperation and their permission to conduct our experiments on their land and are grateful for their assistance. We thank Colin Schoeman who helped with insect identification, Antonia Hammer who contributed to the bat call identification and the field assistants, and Fabian Osten, Vusani Mephethe, and Lorraine Ramotjiki for their support during fieldwork. Moreover, we also thank Dr. Daniel Karp and two anonymous reviewers for their constructive comments that helped to improve the manuscript. The study was conducted within the framework of the South African Limpopo Landscapes Network—SPACES2: SALLnet project (grant number: 01LL1802A) funded by the German Federal Ministry of Education and Research (<http://www.bmbf.de/bmbf/en/>). Catrin Westphal is grateful for being funded by the Deutsche Forschungsgemeinschaft (Deutsche Forsschungsgemeinschaft; Project numbers 405945293 and 493487387). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Anders et al., 2024a) are available in Dryad at <https://doi.org/10.5061/dryad.5dv41nsc6>. Code (Anders et al., 2024b) is available in Zenodo at <https://doi.org/10.5281/zenodo.8382838>.

ORCID

Mina Anders  <https://orcid.org/0000-0002-9302-1876>
 Catrin Westphal  <https://orcid.org/0000-0002-2615-1339>
 Valerie M. G. Linden  <https://orcid.org/0000-0001-8161-9689>
 Sina Weier  <https://orcid.org/0000-0003-3922-1495>
 Peter J. Taylor  <https://orcid.org/0000-0001-9048-7366>
 Ingo Grass  <https://orcid.org/0000-0001-7788-1940>

REFERENCES

- Aigner, B. L., T. P. Kuhar, D. A. Herbert, C. C. Brewster, J. W. Hogue, and J. D. Aigner. 2017. "Brown Marmorated Stink Bug (Hemiptera: Pentatomidae) Infestations in Tree Borders and Subsequent Patterns of Abundance in Soybean Fields." *Journal of Economic Entomology* 110(2): 487–490. <https://doi.org/10.1093/jee/tox047>.
- Anders, M., C. Westphal, V. M. G. Linden, S. Weier, P. Taylor, and I. Grass. 2024a. "Complementary Effects of Pollination and Biocontrol Services Enable Ecological Intensification in Macadamia Orchards [Dataset]." Dryad. <https://doi.org/10.5061/dryad.5dv41nsc6>.
- Anders, M., C. Westphal, V. M. G. Linden, S. Weier, P. Taylor, and I. Grass. 2024b. "Complementary Effects of Pollination and Biocontrol Services Enable Ecological Intensification in Macadamia Orchards." Zenodo. <https://doi.org/10.5281/zenodo.8382838>.
- Anders, M., I. Grass, V. M. G. Linden, P. J. Taylor, and C. Westphal. 2022. "Smart Orchard Design Improves Crop Pollination." *Journal of Applied Ecology* 60(4): 624–637. <https://doi.org/10.1111/1365-2664.14363>.
- Bänsch, S., T. Tscharnke, D. Gabriel, and C. Westphal. 2020. "Crop Pollination Services: Complementary Resource Use by Social vs Solitary Bees Facing Crops with Contrasting Flower Supply." *Journal of Applied Ecology* 58: 1365–2664. <https://doi.org/10.1111/1365-2664.13777>.
- Bartomeus, I., V. Gagic, and R. Bommarco. 2015. "Pollinators, Pests and Soil Properties Interactively Shape Oilseed Rape Yield." *Basic and Applied Ecology* 16(8): 737–745. <https://doi.org/10.1016/j.baae.2015.07.004>.
- Bartoń, K. 2022. "MuMin: Multi-Model Inference." <https://CRAN.R-project.org/package=MuMin>.
- Best, L. B., R. C. Whitmore, and G. M. Booth. 1990. "Use of Cornfields by Birds during the Breeding Season: The Importance of Edge Habitat." *American Midland Naturalist* 123(1): 84. <https://doi.org/10.2307/2425762>.
- Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharnke. 2006. "Sustainable Pest Regulation in Agricultural Landscapes: A Review on Landscape Composition, Biodiversity and Natural Pest Control." *Proceedings of the Royal Society B: Biological Sciences* 273(1595): 1715–27. <https://doi.org/10.1098/rspb.2006.3530>.
- Boesing, A. L., E. Nichols, and J. P. Metzger. 2017. "Effects of Landscape Structure on Avian-Mediated Insect Pest Control Services: A Review." *Landscape Ecology* 32(5): 931–944. <https://doi.org/10.1007/s10980-017-0503-1>.
- Bommarco, R., D. Kleijn, and S. G. Potts. 2013. "Ecological Intensification: Harnessing Ecosystem Services for Food Security." *Trends in Ecology & Evolution* 28(4): 230–38.
- Boyles, J. G., P. M. Cryan, G. F. McCracken, and T. H. Kunz. 2011. "Economic Importance of Bats in Agriculture." *Science* 332(6025): 41–42.
- Brooks, M. E. 2017. "{glmmTMB} Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling."
- Burnham, K. P., and D. R. Anderson. 2002. "A Practical Information-Theoretic Approach." *Model Selection and Multimodel Inference* 2: 70–71.
- Carvalho, L. G., C. L. Seymour, R. Veldtman, and S. W. Nicolson. 2010. "Pollination Services Decline with Distance from Natural Habitat Even in Biodiversity-Rich Areas." *Journal of Applied Ecology* 47(4): 810–820. <https://doi.org/10.1111/j.1365-2664.2010.01829.x>.
- Castle, D., I. Grass, and C. Westphal. 2019. "Fruit Quantity and Quality of Strawberries Benefit from Enhanced Pollinator Abundance at Hedgerows in Agricultural Landscapes." *Agriculture, Ecosystems & Environment* 275(April): 14–22. <https://doi.org/10.1016/j.agee.2019.01.003>.
- Classen, A., M. K. Peters, S. W. Ferger, M. Helbig-Bonitz, J. M. Schmack, G. Maassen, M. Schleuning, E. K. V. Kalko, K. Böhning-Gaese, and I. Steffan-Dewenter. 2014.

- “Complementary Ecosystem Services Provided by Pest Predators and Pollinators Increase Quantity and Quality of Coffee Yields.” *Proceedings of the Royal Society B: Biological Sciences* 281(1779): 20133148. <https://doi.org/10.1098/rspb.2013.3148>.
- Corben, C. 2006. *AnalookW for Bat Call Analysis using ZCA Titley Electronics*. Ballina: Titley Electronics. <https://users.lmi.net/corben/>.
- De Villiers, E. A., and P. H. Joubert. 2003. *The Cultivation of Macadamia*. Nelspruit, South Africa: ARC-Institute for Tropical and Subtropical Crops.
- Department of Environmental Affairs SA. 2019. “Environmental GIS.” <https://egis.environment.gov.za/>.
- Ellis, K. L., J. M. Anderson, T. Yonow, D. J. Kriticos, and N. R. Andrew. 2023. “Biology and Ecology of Insect Pests in Macadamia: A Review of the Current Status of IPM Strategies in Australia.” *Journal of Integrated Pest Management* 14(1): 26. <https://doi.org/10.1093/jipm/pmad024>.
- Evans, L. J., L. Jesson, S. F. J. Read, M. Jochym, B. T. Cutting, T. Gayrard, M. Jammes, R. Roumier, and B. G. Howlett. 2021. “Key Factors Influencing Forager Distribution across Macadamia Orchards Differ among Species of Managed Bees.” *Basic and Applied Ecology* 53: 74–85. <https://doi.org/10.1016/j.baae.2021.03.001>.
- FAO. 2023. *The State of Food Security and Nutrition in the World 2023*. Rome, Italy: FAO; IFAD; UNICEF; WFP; WHO. <https://openknowledge.fao.org/handle/20.500.14283/cc3017en>.
- Forbes, S. J., and T. D. Northfield. 2017. “Increased Pollinator Habitat Enhances Cacao Fruit Set and Predator Conservation.” *Ecological Applications* 27(3): 887–899. <https://doi.org/10.1002/eap.1491>.
- Gagic, V., A. Marcora, and L. Howie. 2019. “Additive and Interactive Effects of Pollination and Biological Pest Control on Crop Yield.” *Journal of Applied Ecology* 56(11): 2528–35. <https://doi.org/10.1111/1365-2664.13482>.
- Garcia, L., F. Celette, C. Gary, A. Ripoché, H. Valdes-Gomez, and A. Metay. 2018. “Management of Service Crops for the Provision of Ecosystem Services in Vineyards: A Review.” *Agriculture Ecosystems & Environment* 251(January): 158–170. <https://doi.org/10.1016/j.agee.2017.09.030>.
- Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, et al. 2013. “Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance.” *Science* 339(6127): 1608–11. <https://doi.org/10.1126/science.1230200>.
- Garibaldi, L. A., G. K. S. Andersson, F. Requier, T. P. M. Fijen, J. Hipólito, D. Kleijn, N. Pérez-Méndez, and O. Rollin. 2018. “Complementarity and Synergisms among Ecosystem Services Supporting Crop Yield.” *Global Food Security* 17(June): 38–47. <https://doi.org/10.1016/j.gfs.2018.03.006>.
- Garibaldi, L. A., B. Gemmill-Herren, R. D’Annolfo, B. E. Graeb, S. A. Cunningham, and T. D. Breeze. 2017. “Farming Approaches for Greater Biodiversity, Livelihoods, and Food Security.” *Trends in Ecology & Evolution* 32(1): 68–80. <https://doi.org/10.1016/j.tree.2016.10.001>.
- Gonthier, D. J., A. R. Sciligo, D. S. Karp, L. Adrian, K. Garcia, G. Juarez, T. Chiba, S. Gennet, and C. Kremen. 2019. “Bird Services and Disservices to Strawberry Farming in Californian Agricultural Landscapes.” *Journal of Applied Ecology* 56(8): 1948–59. <https://doi.org/10.1111/1365-2664.13422>.
- Google Earth Pro. 2020. “Google.” <https://www.google.com/intl/de/earth/about/versions/#earth-pro>.
- Grass, I., S. Meyer, P. J. Taylor, S. H. Foord, P. Hajek, and T. Tschardt. 2018. “Pollination Limitation despite Managed Honeybees in South African Macadamia Orchards.” *Agriculture, Ecosystems & Environment* 260(June): 11–18. <https://doi.org/10.1016/j.agee.2018.03.010>.
- Hahn, N. 2018. “An Historic Account of the Extinct High Rainfall Grasslands of the Soutpansberg, South Africa.” *Transactions of the Royal Society of South Africa* 73(1): 20–32. <https://doi.org/10.1080/0035919X.2017.1346528>.
- Hardin, J. W., and J. M. Hilbe. 2007. *Generalized Linear Models and Extensions*. College Station, TX: Stata Press.
- Holzschuh, A., J.-H. Dudenhoeffer, and T. Tschardt. 2012. “Landscapes with Wild Bee Habitats Enhance Pollination, Fruit Set and Yield of Sweet Cherry.” *Biological Conservation* 153(September): 101–7. <https://doi.org/10.1016/j.biocon.2012.04.032>.
- Howlett, B. G., W. R. Nelson, D. E. Pattemore, and M. Gee. 2015. “Pollination of Macadamia: Review and Opportunities for Improving Yields.” *Scientia Horticulturae* 197(December): 411–19. <https://doi.org/10.1016/j.scienta.2015.09.057>.
- Jantzen, M. K., and M. B. Fenton. 2013. “The Depth of Edge Influence among Insectivorous Bats at Forest–Field Interfaces.” *Canadian Journal of Zoology* 91(5): 287–292. <https://doi.org/10.1139/cjz-2012-0282>.
- Johnson, M. D., J. L. Kellermann, and A. M. Stercho. 2010. “Pest Reduction Services by Birds in Shade and Sun Coffee in Jamaica.” *Animal Conservation* 13(2): 140–47. <https://doi.org/10.1111/j.1469-1795.2009.00310.x>.
- Jones, V. P. 2002. *IPM of Insects and Mites Attacking Macadamia Nuts in Hawaii*. Honolulu: College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.
- Kaleidoscope Pro Analysis Software. 2022. “USA: Wildlife Acoustics.” <https://www.wildlifeacoustics.com/products/kaleidoscope-pro>.
- Kämper, W., S. J. Trueman, S. M. Ogbourne, and H. M. Wallace. 2021. “Pollination Services in a Macadamia Cultivar Depend on Across-Orchard Transport of Cross Pollen.” *Journal of Applied Ecology* 58: 2529–39. <https://doi.org/10.1111/1365-2664.14002>.
- Kämper, W., H. M. Wallace, S. M. Ogbourne, and S. J. Trueman. 2019. “Dependence on Cross-Pollination in Macadamia and Challenges for Orchard Management.” *Proceedings* 36(1): 76. <https://doi.org/10.3390/proceedings2019036076>.
- Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, et al. 2018. “Crop Pests and Predators Exhibit Inconsistent Responses to Surrounding Landscape Composition.” *Proceedings of the National Academy of Sciences of the United States of America* 115(33): E7863–E7870. <https://doi.org/10.1073/pnas.1800042115>.
- Kennedy, C. M., E. Lonsdorf, M. Neel, N. Williams, T. Ricketts, R. Winfree, R. Bommarco, et al. 2013. “A Global Quantitative Synthesis of Local and Landscape Effects on Wild Bee Pollinators in Agroecosystems.” *Ecology Letters* 16: 584–599. <https://doi.org/10.1111/ele.12082>.
- Klein, A.-M. 2009. “Nearby Rainforest Promotes Coffee Pollination by Increasing Spatio-Temporal Stability in Bee Species Richness.” *Forest Ecology and Management* 258(9): 1838–45. <https://doi.org/10.1016/j.foreco.2009.05.005>.
- Klein, A.-M., C. Brittain, S. D. Hendrix, R. Thorp, N. Williams, and C. Kremen. 2012. “Wild Pollination Services to California Almond Rely on Semi-Natural Habitat.” *Journal of Applied Ecology* 49(3): 723–732.

- Klein, A.-M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharnkte. 2007. "Importance of Pollinators in Changing Landscapes for World Crops." *Proceedings of the Royal Society B-Biological Sciences* 274(1608): 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kolkert, H. L., R. Smith, R. Rader, and N. Reid. 2021. "Prey Removal in Cotton Crops next to Woodland Reveals Periodic Diurnal and Nocturnal Invertebrate Predation Gradients from the Crop Edge by Birds and Bats." *Scientific Reports* 11(1): 5256. <https://doi.org/10.1038/s41598-021-84633-8>.
- Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, et al. 2007. "Pollination and Other Ecosystem Services Produced by Mobile Organisms: A Conceptual Framework for the Effects of Land-Use Change." *Ecology Letters* 10(4): 299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. "Crop Pollination from Native Bees at Risk from Agricultural Intensification." *Proceedings of the National Academy of Sciences of the United States of America* 99(26): 16812–16. <https://doi.org/10.1073/pnas.262413599>.
- Landis, D. A. 2017. "Designing Agricultural Landscapes for Biodiversity-Based Ecosystem Services." *Basic and Applied Ecology* 18(February): 1–12. <https://doi.org/10.1016/j.baae.2016.07.005>.
- Linden, V. M. G., I. Grass, E. Joubert, T. Tscharnkte, S. M. Weier, and P. J. Taylor. 2019. "Ecosystem Services and Disservices by Birds, Bats and Monkeys Change with Macadamia Landscape Heterogeneity." *Journal of Applied Ecology* 56: 2069–78. <https://doi.org/10.1111/1365-2664.13424>.
- Linden, V. M. G., S. M. Weier, I. Gaigher, H. J. Kuipers, M. J. A. Weterings, and P. J. Taylor. 2014. "Changes of Bat Activity, Species Richness, Diversity and Community Composition over an Altitudinal Gradient in the Soutpansberg Range, South Africa." *Acta Chiropterologica* 16(1): 27–40. <https://doi.org/10.3161/150811014X683246>.
- Lundin, O., M. Rundlöf, M. Jonsson, R. Bommarco, and N. M. Williams. 2021. "Integrated Pest and Pollinator Management – Expanding the Concept." *Frontiers in Ecology and the Environment* 19(5): 283–291. <https://doi.org/10.1002/fee.2325>.
- Lundin, O., H. G. Smith, M. Rundlof, and R. Bommarco. 2012. "When Ecosystem Services Interact: Crop Pollination Benefits Depend on the Level of Pest Control." *Proceedings of the Royal Society B-Biological Sciences* 280(1753): 20122243. <https://doi.org/10.1098/rspb.2012.2243>.
- Maas, B., D. S. Karp, S. Bumrungsri, K. Darras, D. Gonthier, J. C.-C. Huang, C. A. Lindell, et al. 2016. "Bird and Bat Predation Services in Tropical Forests and Agroforestry Landscapes." *Biological Reviews* 91(4): 1081–1101. <https://doi.org/10.1111/brv.12211>.
- MacInnis, G., and J. R. K. Forrest. 2019. "Pollination by Wild Bees Yields Larger Strawberries than Pollination by Honey Bees." *Journal of Applied Ecology* 56(4): 824–832. <https://doi.org/10.1111/1365-2664.13344>.
- Martin, E. A., M. Dainese, Y. Clough, A. Baldi, R. Bommarco, V. Gagic, M. P. D. Garratt, et al. 2019. "The Interplay of Landscape Composition and Configuration: New Pathways to Manage Functional Biodiversity and Agroecosystem Services across Europe." *Ecology Letters* 22(7): 1083–94. <https://doi.org/10.1111/ele.13265>.
- Martínez-Salinas, A., A. Chain-Guadarrama, N. Aristizábal, S. Vilchez-Mendoza, R. Cerda, and T. H. Ricketts. 2022. "Interacting Pest Control and Pollination Services in Coffee Systems." *Proceedings of the National Academy of Sciences of the United States of America* 119(15): e2119959119. <https://doi.org/10.1073/pnas.2119959119>.
- Minarro, M., and E. Prida. 2013. "Hedgerows Surrounding Organic Apple Orchards in North-West Spain: Potential to Conserve Beneficial Insects." *Agricultural and Forest Entomology* 15(4): 382–390. <https://doi.org/10.1111/afe.12025>.
- Mols, C. M. M., and M. E. Visser. 2002. "Great Tits Can Reduce Caterpillar Damage in Apple Orchards." *Journal of Applied Ecology* 39(6): 888–899. <https://doi.org/10.1046/j.1365-2664.2002.00761.x>.
- Moncur, M. W., R. A. Stephenson, and T. Trochoulias. 1985. "Floral Development of Macadamia Integrifolia Maiden & Betche under Australian Conditions." *Scientia Horticulturae* 27(1): 87–96. [https://doi.org/10.1016/0304-4238\(85\)90058-5](https://doi.org/10.1016/0304-4238(85)90058-5).
- Moraswi, I., S. O. Bamigboye, and M. P. Tshisikhawe. 2019. "Conservation Status and Threats to Vascular Plant Species Endemic to Soutpansberg Mountain Range in Limpopo Province, South Africa." *International Journal of Plant Biology* 10(1): 7978.
- Mostert, T. H. C., G. J. Bredenkamp, H. L. Klopper, C. Verwey, R. E. Mostert, and N. Hahn. 2008. "Major Vegetation Types of the Soutpansberg Conservancy and the Blouberg Nature Reserve, South Africa." *Koedoe* 50(1): 32–48. <https://doi.org/10.4102/koedoe.v50i1.125>.
- Olhnuud, A., Y. Liu, D. Makowski, T. Tscharnkte, C. Westphal, W. Panlong, M. Wang, and W. van der Werf. 2022. "Pollination Deficits and Contributions of Pollinators in Apple Production: A Global Meta-Analysis." *Journal of Applied Ecology* 59(12): 2911–21. <https://doi.org/10.1111/1365-2664.14279>.
- Pal, E., J. D. Allison, B. P. Hurley, B. Slippers, and G. Fourie. 2022. "Genetic Diversity of the Two-Spotted Stink Bug *Bathycorbia distincta* (Pentatomidae) Associated with Macadamia Orchards in South Africa." *PLoS One* 17(6): e0269373. <https://doi.org/10.1371/journal.pone.0269373>.
- Puckett, H. L., J. R. Brandle, R. J. Johnson, and E. E. Blankenship. 2009. "Avian Foraging Patterns in Crop Field Edges Adjacent to Woody Habitat." *Agriculture, Ecosystems & Environment* 131(1): 9–15. <https://doi.org/10.1016/j.agee.2008.08.015>.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Reilly, J. R., D. R. Artz, D. Biddinger, K. Bobiwash, N. K. Boyle, C. Brittain, J. Brokaw, et al. 2020. "Crop Production in the USA Is Frequently Limited by a Lack of Pollinators." *Proceedings of the Royal Society B: Biological Sciences* 287(1931): 20200922. <https://doi.org/10.1098/rspb.2020.0922>.
- Renkema, J. M., G. Christopher Cutler, and K. Rutherford. 2014. "Molecular Analysis Reveals Lowbush Blueberry Pest Predation Rates Depend on Ground Beetle (Coleoptera: Carabidae) Species and Pest Density." *BioControl* 59(6): 749–760. <https://doi.org/10.1007/s10526-014-9614-7>.
- Richards, T. E., W. Kämper, S. J. Trueman, H. M. Wallace, S. M. Ogbourne, P. R. Brooks, J. Nichols, and S. H. Bai. 2020. "Relationships between Nut Size, Kernel Quality, Nutritional

- Composition and Levels of Outcrossing in Three Macadamia Cultivars.” *Plants* 9(2): 228. <https://doi.org/10.3390/plants9020228>.
- SAMAC. 2023. “Macadamias Industry Statistics – SAMAC.” <https://samac.org.za/industry-statistics/>.
- Strauss, S. Y., and P. Murch. 2004. “Towards an Understanding of the Mechanisms of Tolerance: Compensating for Herbivore Damage by Enhancing a Mutualism.” *Ecological Entomology* 29(2): 234–39. <https://doi.org/10.1111/j.0307-6946.2004.00587.x>.
- Sutter, L., and M. Albrecht. 2016. “Synergistic Interactions of Ecosystem Services: Florivorous Pest Control Boosts Crop Yield Increase through Insect Pollination.” *Proceedings of the Royal Society B-Biological Sciences* 283(1824): 20152529. <https://doi.org/10.1098/rspb.2015.2529>.
- Swartz, E., S. M. Weier, M. E. Pretorius, and M. Keith. 2022. “Natural Vegetation Edges Promote Bat Activity in Macadamia Orchards in Northeastern South Africa.” *African Journal of Wildlife Research* 52(1): 155–171. <https://doi.org/10.3957/056.052.0155>.
- Taylor, P. J., I. Grass, A. J. Alberts, E. Joubert, and T. Tschardtke. 2018. “Economic Value of Bat Predation Services – A Review and New Estimates from Macadamia Orchards.” *Ecosystem Services* 30(April): 372–381. <https://doi.org/10.1016/j.ecoser.2017.11.015>.
- Taylor, P. J., A. Nengovhela, J. Linden, and R. M. Baxter. 2016. “Past, Present, and Future Distribution of Afromontane Rodents (Muridae: Otomys) Reflect Climate-Change Predicted Biome Changes.” *Mammalia* 80(4): 359–375. <https://doi.org/10.1515/mammalia-2015-0033>.
- Trueman, S. J. 2013. “The Reproductive Biology of Macadamia.” *Scientia Horticulturae* 150: 354–59.
- Tschardtke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. “Landscape Perspectives on Agricultural Intensification and Biodiversity – Ecosystem Service Management.” *Ecology Letters* 8(8): 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.
- Van den Berg, J., M. A. Steyn, and W. P. Greenland. 1999. “Hemiptera Occurring on Macadamia in the Mpumalanga Lowveld of South Africa.” *African Plant Protection* 5(2): 89–92.
- Venugopal, P. D., P. L. Coffey, G. P. Dively, and W. O. Lamp. 2014. “Adjacent Habitat Influence on Stink Bug (Hemiptera: Pentatomidae) Densities and the Associated Damage at Field Corn and Soybean Edges.” *PLoS One* 9(10): e109917. <https://doi.org/10.1371/journal.pone.0109917>.
- Vock, N., D. Bell, L. Bryen, D. Firth, K. Jones, E. Gallagher, I. McConachie, et al. 1998. “Macadamia Variety Identifier.” edited by G. Ayling. Nambour, Australia: Agrilink Series.
- Weier, S. M., I. Grass, V. M. G. Linden, T. Tschardtke, and P. J. Taylor. 2018. “Natural Vegetation and Bug Abundance Promote Insectivorous Bat Activity in Macadamia Orchards, South Africa.” *Biological Conservation* 226(October): 16–23. <https://doi.org/10.1016/j.biocon.2018.07.017>.
- Weier, S. M., V. M. G. Linden, I. Gaigher, P. J. C. White, and P. J. Taylor. 2017. “Changes of Bat Species Composition over Altitudinal Gradients on Northern and Southern Aspects of the Soutpansberg Mountain Range, South Africa.” *Mammalia* 81(1): 49–60. <https://doi.org/10.1515/mammalia-2015-0055>.
- Weier, S. M., V. M. G. Linden, A. Hammer, I. Grass, T. Tschardtke, and P. J. Taylor. 2021. “Bat Guilds Respond Differently to Habitat Loss and Fragmentation at Different Scales in Macadamia Orchards in South Africa.” *Agriculture, Ecosystems & Environment* 320(October): 107588. <https://doi.org/10.1016/j.agee.2021.107588>.
- Weier, S. M., Y. Moodley, M. F. Fraser, V. M. G. Linden, I. Grass, T. Tschardtke, and P. J. Taylor. 2019. “Insect Pest Consumption by Bats in Macadamia Orchards Established by Molecular Diet Analyses.” *Global Ecology and Conservation* 18(April): e00626. <https://doi.org/10.1016/j.gecco.2019.e00626>.
- Wu, P., P. Dai, M. Wang, S. Feng, A. Olhnuud, X. Huanli, X. Li, and Y. Liu. 2021. “Improving Habitat Quality at the Local and Landscape Scales Increases Wild Bee Assemblages and Associated Pollination Services in Apple Orchards in China.” *Frontiers in Ecology and Evolution* 9(March): 621469. <https://doi.org/10.3389/fevo.2021.621469>.

SUPPORTING INFORMATION

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

How to cite this article: Anders, Mina, Catrin Westphal, Valerie M. G. Linden, Sina Weier, Peter J. Taylor, and Ingo Grass. 2024. “Complementary Effects of Pollination and Biocontrol Services Enable Ecological Intensification in Macadamia Orchards.” *Ecological Applications* e3049. <https://doi.org/10.1002/eap.3049>