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Smart orchard design improves crop pollination

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Abstract

1. More sustainable and environmentally friendly agricultural practices, including ecological intensification, are needed to reduce biodiversity loss and environmental degradation.

2. We evaluated the potential of ecological intensification through the enhancement of pollination services in an intensively managed and insect-pollinated crop, *Macadamia integrifolia*. We compared the effects and importance of agronomic practices that include agronomic input (i.e. irrigation and managed honeybees), orchard design requiring no external inputs (i.e. spatial orchard structure) and landscape factors in 10 South African macadamia orchards.

3. In comparison to experimental pollinator exclusion, insect pollination increased the initial and final nut set by 304% and 23%, respectively. However, nut set was pollination limited as hand pollination further improved nut set.

4. Flower visitation rates increased with the cover of semi-natural habitats in the surrounding landscape (1 km radius). This effect was outperforming the effect of the number of managed honeybee colonies, as agronomic practice.

5. Initial nut set increased with orchard design and flower visitation rates. Perpendicular orientation of the planted macadamia rows towards the semi-natural habitats increased initial nut set more than threefold compared to parallel row orientation. The initial nut set was 80% higher at the edge to semi-natural habitats than in the orchard centre. In contrast, agronomic practices, such as irrigation, did not increase initial nut set. Final nut set depended on the preconditions of the initial nut set, additionally, high altitudes and the position in the centre of the orchard had positive effects.

6. *Synthesis and applications*: Pollination services were prerequisites for high yields in macadamia and could be improved without further agronomic input. Especially, the orchard design, that is, spatial arrangement of tree rows and semi-natural habitats at local and landscape scales, was more important to boost insect pollination and the initial development of macadamia nuts than agronomic practices, such as high levels of irrigation. Considering the urgency to reduce the environmental impacts of agricultural production, we highlight the high potential of ecological

intensification by a smart orchard design and the restoration and conservation of semi-natural habitats in the orchards and their surrounding landscape.

1 | INTRODUCTION

We face a global necessity for improvement of agricultural efficiency, because on the one hand, the demand for food is rising and on the other hand, land degradation and climate change impede agricultural production (Webb et al., 2017). To meet the growing food and energy demands, the area under agricultural production is expanded and management is intensified. Conventional intensification of agriculture comprises increasing inputs of artificial fertilisers and pesticides (FAO, 2021) as well as land degradation in the long term (Smith et al., 2016). Further, the resulting transformation of semi-natural habitats into agricultural land is a major driver of global biodiversity loss (IPBES, 2019). Conventional intensification of agriculture is promoted to close yield gaps (Tscharntke et al., 2012). However, the current focus on conventional agronomic practices and their intensification creates high burdens on the environment (Garibaldi et al., 2017). In semiarid cropping systems, irrigation is a major input that can result in water scarcity (Rosa et al., 2020). Current modes of conventional intensification are therefore likely not sustainable in the long-term (Cassman & Grassini, 2020).

In contrast to conventional intensification of agriculture, ecological intensification is based on supporting regulating ecosystem services in agricultural systems, such as pollination or biological pest control (Bommarco et al., 2013). By managing specific components of biodiversity, the delivery of ecosystem services is enhanced, which can be used to complement or replace artificial inputs and to increase agricultural productivity. This results in reduced environmental costs without negative impacts on crop productivity (Kleijn et al., 2019). While the concept is well studied for arable crops, especially in the northern hemisphere, there are only a few studies that explore the potential of ecological intensification practices in orchards or agroforestry systems such as almonds, apples or macadamia (Proteaceae; commercially most important species: *Macadamia integrifolia* Maiden & Betche and *M. tetraphylla* L.A.S. Johnson; but see De Leijster et al., 2019; Wu et al., 2021).

Further, more knowledge is needed about the effectiveness of different ecological intensification practices, alone and in combination with other practices (Kleijn et al., 2019). Moreover, practices that increase ecosystem services without artificial inputs such as irrigation or chemicals must be investigated. These practices are for instance the spatial arrangement and design of orchards and fields.

In entomophilous crops, insect pollination services can improve fruit set, yields and fruit quality (Klatt et al., 2014; Wu et al., 2021). While limited crop pollination services are commonly mitigated by managed honeybees, wild insect pollinators can even be much more efficient than honeybees (Garibaldi et al., 2013). Ecological intensification through pollination does not mean an increase of managed honeybee colonies but rather the promotion of wild pollinators (Garibaldi et al., 2014). Pollination by wild insects is often related to spill-over processes from natural habitats, where the pollinators find resources such as food and nesting sites (Kremen et al., 2007).

Several studies have highlighted the role of natural habitats in the surrounding landscape for the provisioning of pollination services (Klein et al., 2012) and their stability (Garibaldi et al., 2011). For example, pollination in coffee decreases with increasing distance to natural forest (Klein, 2009). Likewise, pollination services by wild bees in mango orchards strongly depends on adjacency to natural habitat (Carvalheiro et al., 2010).

Hence, distance to semi-natural habitats can modify pollinator diversity and pollination services on farms and so do spillover effects at orchard borders to semi-natural habitats. Further, the layout of tree rows can have an impact on the movement patterns of foraging insect pollinators (Brittain, Williams, et al., 2013). This means that the design of an orchard, like edge structures or row arrangement, might be important factors to enhance pollination service. The same applies for the planting of different varieties, as the availability of genetically different pollen is important for effective cross pollination enhancing nut set and quality (Kämper et al., 2021).

Moreover, the effect of insect pollination can interact with management factors, e.g. irrigation or nutrient availability. Tamburini et al. (2019) found mostly positive-synergistic relationships between pollination and other factors in their review on pollination under different environmental conditions. For instance, soil properties and crop pests are expected to affect the contribution of pollination to yield by altering the amount of resources a plant can allocate to reproduction, independently of the amount of pollen provided (Tamburini et al., 2019). Further, if the supplementation with managed honeybees is considered as a management factor, this can affect pollination service, by simply increasing the number of pollinators, for instance, in apple (Olhnuud et al., 2022) or almond orchards (Brittain, Williams, et al., 2013).

The benefits of improved pollination can be obscured by the reproductive strategy of plants and potential responses to environmental conditions including management factors or abiotic or biotic stressors, such as pests or drought that cause fruit abscission (Bos et al., 2007;

Olhnuud et al., 2022). To evaluate the pollination success, that is, whether a flower received sufficient pollen for the fruit set, it is, therefore, important to assess the initial fruit set while the final fruit set is a meaningful indicator of yield outcomes (Olhnuud et al., 2022).

In addition to the mentioned environmental and management factors, different climatic conditions along altitudinal gradients may further influence pollination services. Changing climatic conditions cause shifts in pollinator communities resulting in lower species richness at high altitudes (Classen et al., 2015).

Pollinator dependence and pollination deficits are well known in macadamia, and several studies have been conducted to study the effects of pollination services on crop yields (Grass et al., 2018; Kämper et al., 2021). However, despite the great economic importance of macadamia crops (SAMAC, 2021), the interactive effects of climatic, environmental and agronomic factors have not been studied. In the past years, South Africa has developed into the world's largest macadamia producer (SAMAC, 2021) and the expansion of macadamia orchards has led to the loss of natural forests and savannah habitats (Department of Environmental Affairs SA, 2019). One centre of macadamia production is the province Limpopo in northern South Africa that is currently undergoing rapid agricultural expansion and intensification since it is a major mainstay of South Africa's tropical fruit industry. Most crops (e.g. tomatoes, mangos, macadamia and avocados) are irrigated, and high volumes of chemical applications are used for fertilisation and pest control, in order to increase yields (Sikora et al., 2020). At the same time, Limpopo is a hotspot of biodiversity (Perera et al., 2018) that is strongly threatened by climate change and increasing water scarcity (Masih et al., 2014).

To study whether ecological intensification is a viable option for sustainably increasing macadamia production, we selected 10 macadamia orchards that differed in agronomic practices, orchard design as well as landscape factors. In each study orchard, we established a pollination experiment and recorded flower-visitation. Along an altitudinal gradient, we analysed how landscape composition (cover of semi-natural habitats) and orchard design that did not include agronomic inputs (i.e. orientation of tree rows towards semi-natural habitats, adjacency to semi-natural habitats, number of different varieties) affect pollination success and nut set and can outweigh the importance of agronomic practices of conventional intensification (i.e. irrigation, managed honeybees). We addressed the following questions: (1) How important are insect pollination services for the initial and final nut set of macadamia and how do different agronomic practices (i.e. irrigation and managed honeybee colonies), and orchard design (i.e. number of varieties, orientation of tree rows and tree position in the block), as well as landscape composition and altitude interact and affect the initial and final nut set under different pollination treatments (hand, open and self/wind pollination)? (2) Which are the main drivers of flower visitation rates by pollinators in the macadamia orchards? (3) How do flower visitation rates in combination with agronomic practices, orchard design, landscape composition and altitude ultimately affect the initial and final nut set?

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted the study 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 characterised by a sub-tropical, dry to moist climate, with a rainy season in summer from November to April. Daily temperatures range between 15 and 40°C and 0 and 25°C in summer and winter, respectively. The Soutpansberg mountain range forms part of the Vhembe Biosphere Reserve. The naturally occurring vegetation types are Soutpansberg Bushveld and Tzaneen Sour Bushveld (Mostert et al., 2008). Habitat destruction is considered as one of the most prominent threats for biodiversity in the Soutpansberg Mountain range, for example, for endemic plant (Moraswi et al., 2019) and bat (Weier et al., 2021) species. During our study, the areas at higher altitudes were mostly covered by natural bush with few pine (*Pinus* spp.) and gum tree (*Eucalyptus* spp.) plantations while the native vegetation in the valley was largely replaced by intensive monocultures of macadamias (*M. integrifolia*, *M. tetraphylla* and hybrids), pecan nuts (*Carya illinoinensis* (Wangenh.) K.Koch), avocados (*Persea americana* Mill), bananas (*Musa* spp.), pines and gum trees that were interspersed with remnants of natural or seminatural habitats. Fieldwork was carried out on private farms and all farmers gave their permission.

2.2 | Study sites and experimental design

In March 2019, we selected five pairs of macadamia farms along an altitudinal gradient from 600 to 1300 m, while the farms of each pair were located at similar altitudes (Figure S1). 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). This year was characterised by an extremely hot and dry season (personal communication with the farmers: G. Whyte, D. Bouwer, P. Potgieter, September 2019). One farm of each pair was located in a landscape with high agricultural land use intensity, where the landscape composition was dominated by orchards or agricultural fields (mean cover of semi-natural habitats: 31.5%, range: 19.6%–45.4%). The other farm was located in a landscape with a high cover of natural and semi-natural habitats (mean: 60.7%, range: 35.1%–80.6%.).

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) as study site that abutted semi-natural habitats. Here, we selected four trees at the edge of the block adjacent to semi-natural habitats and four trees 50 m to the edge, that is, in the centre of the study block. This resulted in a total number of 80 study trees. Half of the trees were surrounded by cages made out of a large mesh net (mesh size: 1.5 cm) for a different study focussing on bats and birds. The net did not prevent

pollinators from accessing the trees and cage was included as a random effect (yes/no).

One mature tree can bear up to 2500 inflorescences, called racemes, in one season (Moncur et al., 1985) and each of them has 100 to 300 flowers (Trueman, 2013; Figure S3a). When withered, all flowers were very delicate and fell off at light touch. Some weeks after pollination, the fertilised flowers developed into initial nuts that adhere firmly to the raceme (while the rest has dropped off) and thus could be well recorded. In our study, this time was 3–5 weeks after flowering depending on the altitude. Still, some of the nuts commonly drop during development (fruit abortion) and only those that remained for around 18 to 20 weeks on the raceme (final nut set) were likely to evolve into mature nuts.

To reduce confounding effects due to different varieties, we aimed to standardise the studied macadamia varieties and selected Pahala (788) as it was one of the most common varieties in the region. In 2 out of the 10 farms, Pahala (788) was not available, so we used the following varieties there instead: 814, 842, 849, Mauka (742) and Kau (344). In three farms, we further had to include individual trees of 814, Kau (344) and 741 in addition to Pahala (788) due to the spatial arrangement of the trees and the study design. The selected varieties were similar in terms of floral morphology, flowering period (Bell et al., 1998) and harvesting technique. All macadamia farms were managed conventionally and followed recommendations for pesticide and fertiliser use made by their consultants. However, the study trees were excluded from usual pesticide applications in the orchards to reduce and standardise potential effects of plant protection measures on pollinators, that is, in farms where pesticides were applied by helicopter entire blocks were excluded, while in farms with trailer sprayers the respective rows were not sprayed.

2.3 | Landscape composition, orchard design and agronomic practices

We recorded the landscape composition, orchard design and agronomic practices in order to examine their effects on different aspects of macadamia cultivation (research questions (1)–(3)).

To characterise landscape composition, we quantified the cover of natural and semi-natural habitats (comprising indigenous forest, bush, shrubland and grassland) in 1 km radius around the centre of the study site, based on a land-cover class map (from 2018 provided by the Department of Environmental Affairs of the Republic of South Africa, resolution: 20×20 m raster; Department of Environmental Affairs SA, 2019; see Supporting Information). The altitude values were extracted from Google Earth Pro (2020).

As orchard design, we considered three aspects. Firstly, we assessed the number of different macadamia varieties per study block to account for cross pollination. We distinguished between one single variety (cross pollination by wind unlikely), two varieties (cross pollination possible) and several varieties, that is, three to five, (cross pollination with different pollen donors likely). This grouping also ensured a balanced number of samples per group. The benefit of cultivating

different macadamia varieties at close distance to each other, enhancing cross pollination and thus yield, is well studied (Herbert et al., 2019; Howlett et al., 2019; Trueman & Turnbull, 1994). However, in these studies, the performance of cross pollination is explored experimentally, by applying hand-pollination, but not empirically. Secondly, our experimental design allowed us to determine the effect of adjacent semi-natural habitats at the edge compared to the centre of the block. Thirdly, we recorded the orientation of the planted rows of macadamia trees towards the orchard edges to semi-natural habitats (perpendicular $n = 5$, parallel $n = 5$; Figure S2).

We additionally recorded different agronomic practices: the number of managed honeybee colonies within a 1 km radius around study sites (mean: 10.9, range: 0–42) and whether the block was irrigated or not (yes $n = 6$, no $n = 4$; Figure S1).

2.4 | Pollination experiment

To analyse the relevance of insect mediated pollination services, potential pollination limitation and the interacting effects of agronomic practices, orchard design and landscape composition on the initial and final nut set along an altitudinal gradient (research question (1)), we conducted a pollination experiment. Per study tree, we selected 32 racemes and applied three pollination treatments: (i) pollinator exclusion with mesh bag, (self and wind pollination possible but no insect pollination, six racemes), (ii) open pollination by wind and insects (20 racemes) and (iii) supplemental hand pollination (six racemes; see Figure S3). The difference between the resulting initial nut set after pollinator exclusion and open pollination indicates the pollination services provided by insects, while the difference between the initial nut set after open pollination and hand pollination indicates potential pollination limitation. The open pollinated racemes only were additionally used to analyse how the initial and final nut set is affected by flower visitation rates in combination with agronomic practices, orchard design, landscape composition and altitude (research question (3)).

For the pollinator exclusion, we randomly selected three racemes in the lower (<2 m) and upper (>2 m) parts of the tree, respectively, of which the flowers were still closed but would open in the next few days. We enclosed one or more racemes with one mesh bag (mesh size: 0.05 mm, bag size: 310×280 mm, Rewe Mehrweg-Frischenetz, 100% polyester, see Figure S3a). As the racemes often grew very close together, we had to envelop two or three racemes together instead of one.

In each tree, we further selected 20 racemes for open pollination, again, half of them in the upper and in the lower part of the tree. For the hand pollination, we selected racemes with flowers that opened shortly before the application of the treatment. We collected pollen from a different variety (e.g. 816, 842 or 849) to achieve the highest possible nut set by cross pollination with a plastic tube (⌀ 40 mm). The tube was placed over a raceme and then gently shaken so that the pollen was deposited at the inner walls (Grass et al., 2018; Trueman & Turnbull, 1994). The pollen was then transferred to the open flowers

by carefully placing the tube over the target raceme and rotating it so that the collected pollen was deposited on the stigmata. To ensure proper hand pollination, we repeated this procedure at three to four consecutive days.

The macadamia nuts of our study trees developed after three to 5 weeks depending on the altitude, which we call the initial nut set (Figure S4a). We quantified both the initial and final nut sets of the racemes assigned to the three pollination treatments. The initial nut set can be used as an indicator of pollination success. In contrast, the final nut set (18–20 weeks after flowering; Figure S4b) indicates the yield outcomes. It is related to the plant's reproductive strategy and potential responses to environmental conditions including management factors or abiotic or biotic stressors, such as pests or drought (Bos et al., 2007).

2.5 | Flower visitation rates

We recorded the flower visitation rates and pollinator species richness of flower-visiting insects by observing the racemes of the study trees (research question (2)). On each tree, we selected a subset of open racemes that were close together and thus feasible to observe simultaneously. Due to the varying number of flowering racemes on the trees, we observed three to 20 racemes for 5 min, alternating the upper or lower part of the tree. Each individual insect that visited a raceme was counted once, even if it visited a raceme several times. The flower visitors were identified in the field, or if unknown were caught and identified to family or morphospecies level. We repeated the observations three times at different days and daytimes (morning: 8 AM–11 AM, midday: 11 AM–2 PM, afternoon: 2 PM–5 PM). The observations were conducted only in good weather conditions (no rain, weak breeze at a maximum of 3 Bft) during the main flowering season between July and September 2019. For better comparability with other studies, we calculated the flower visitation rates in visits per raceme and h. In addition to the visual assessments of the flower visitors, we estimated the total number of flowering racemes per tree by counting a subset, that is, all flowering racemes in a quarter of the tree, and extrapolating this number to the entire tree.

2.6 | Statistical analyses

2.6.1 | General approach

To test the effects of agronomic practices, orchard design, landscape composition and altitude on flower visitation and nut set, we used generalised linear mixed models (glmmTMB) from the R package 'glmmTMB' (Brooks et al., 2017) in R (R Core Team, 2022). Applying a multimodel inference approach (Burnham & Anderson, 2002), we first fitted a global model including all explanatory variables and ecologically meaningful two-way interactions that were related to our research questions. Then, we

used the 'dredge' command (package 'MuMIn'; Bartoń, 2020) to generate candidate models with all possible combinations of the variables and interactions. To prevent overfitting, we limited the number of variables in each candidate model to a maximum of six. While we used different explanatory variables according to the question as fixed effects, we consistently included the farm pair, site, cage and individual trees as nested random effects and the age of the study block as crossed random effect. All derived models with a delta AICc < 2 compared to the best-fitting model were selected and used for interpretation. We report the Akaike weights (w_i) as a measure of the relative likelihood of individual models. The relative importance of each explanatory variable and two-way interaction was assessed by the sum of Akaike weights ($\sum w_i$) over all models including the variable or interaction. Only variables with $\Sigma w_i > 0.5$ were considered for interpretation.

We included an unspecified zero-inflation term to account for an excess of zeros in the two global models predicting the initial nut set (pollination experiment and only open pollinated) and flower visitation rates, while we specified the initial nut set in the zero-inflation term to model the zeros in the two global models for the final nut set (pollination experiment and only open pollinated). When modelling the final nut set, the initial nut set was included as a covariate in the models. In doing so, we could analyse the effects of agronomic practices, orchard design, altitude and landscape composition on the final nut set by controlling their effects on the initial nut set.

All variables were scaled to a mean of zero and a standard deviation of one prior to modelling. We validated each model using the R package 'DHARMa' (Hartig, 2020) and tested for collinearity using the R package 'performance' (Lüdecke et al., 2021). We did not detect collinearity between explanatory variables (variance inflation factors were <5 for each variable, James et al., 2013).

The presented effects were predicted with the R packages 'effects' (Fox, 2003) and 'emmeans' (Lenth et al., 2022). The predictions of one variable were based on the means of the other continuous variables and the averages over categorical variables in both packages. We further performed multiple comparisons with 'emmeans'.

2.6.2 | Pollination experiment

We tested the effects of the pollination treatment, irrigation, flower visitation rates, position in block, row orientation, number of varieties per block and altitude on the initial and final nut set, respectively, allowing all two-way interactions of the pollination treatment with the other variables (research question (1)). For both global models, we chose a negative binomial distribution with linear parameterization (Hardin & Hilbe, 2007).

2.6.3 | Flower visitation rates

To analyse the effects of landscape composition, local floral resources, orchard design and agronomic practices on flower visitation

rates (research question (2)), we applied a square root transformation to the response variable (observed flower visits per raceme in 1 h) to achieve a Gaussian distribution. The global model included the following explanatory variables as fixed effects: cover of semi-natural habitats, estimated number of flowering racemes per tree, altitude, number of managed honeybee colonies, row orientation and position in block. Additionally, the two-way interactions between cover of semi-natural habitats and respectively number of flowering racemes, the position in block and the altitude were included, as well as a two-way interaction of row orientation and the position in block. We further accounted for the wind speed as crossed random effect, because wind can have a negative influence on the flying flower visitors, resulting in reduced visitation rates (e.g. Brittain, Kremen, et al., 2013).

2.6.4 | Nut set of open pollinated racemes

Finally, we tested the effects of flower visitation rates and their two-way interactions with agronomic practices, that is, irrigation, and orchard design, that is, number of varieties per block, row orientation and position in the block, as well as with altitude on only the open pollinated racemes addressing research question (3). In both global models (initial and final nut set) a negative binomial distribution with quadratic parameterization was most appropriate (Hardin & Hilbe, 2007).

3 | RESULTS

3.1 | Pollination experiment

We counted the initial and final nut set on 2608 racemes (pollinator exclusion: $n = 563$, open pollination: $n = 1580$, hand pollination: $n = 463$). The sum of all nuts was initially 14,045 and dropped by the time of the final count to 1394.

Regarding the interacting effects of agronomic practices and orchard design along the altitudinal gradient (research question (1)), we found two best-fitting models for the initial nut set and one best-fitting model for the final nut set within a delta AICc < 2 (see Table S1). The explanatory variables that were included in both sets of best-fitting models were: pollination treatment ($\sum w_i$ initial = 1.00; $\sum w_i$ final = 1.00), row orientation ($\sum w_i$ initial = 1.00; $\sum w_i$ final = 1.00) and their interaction treatment: row orientation ($\sum w_i$ initial = 1.00; $\sum w_i$ final = 1.00; Table 1). For the initial nut set, the number of varieties ($\sum w_i$ initial = 1.00; $\sum w_i$ final = 0.01), the interaction treatment: varieties ($\sum w_i$ initial = 1.00; $\sum w_i$ final = 0.00) were included, all other variables had lower importance values ($\sum w_i < 0.5$). Only for the final nut set, position in block ($\sum w_i$ initial = 0.15; $\sum w_i$ final = 0.99) and altitude ($\sum w_i$ initial = 0.15; $\sum w_i$ final = 0.74) occurred additionally in the model set. Moreover, the initial nut set was a meaningful predictor for the zeros observed for the final nut set, indicating high levels of fruit abortion, too.

TABLE 1 The relative importance of explanatory variables expressed by $\sum w_i$ (sum of Akaike weights) for models predicting initial and final nut set of racemes in relation to different pollination treatments. All variable and their two-way interactions that were included in the global models are shown, variables that were considered for interpretation are highlighted in bold.

Variables	Initial nut set	Final nut set
Zero-inflation formula = ~initial nut set	—	**1.00**
Pollination treatment	**1.00**	**1.00**
Row orientation	**1.00**	**1.00**
Pollination treatment: row orientation	**1.00**	**1.00**
Number of varieties	**1.00**	0.03
Pollination treatment: number of varieties	**1.00**	0.00
Position in block	0.14	**0.99**
Altitude	0.15	**0.74**
Flower visitation rates	0.44	0.01
Initial nut set	—	0.20
Irrigation	0.19	0.01
Pollination treatment: altitude	0.00	0.05
Pollination treatment: position in block	0.00	0.01
Pollination treatment: irrigation	0.00	0.00
Pollination treatment: flower visitation rates	0.00	0.00

Hereafter, we present the directions of the effects with high importance values ($\sum w_i > 0.5$). In general, the pollination treatments showed a strong effect on both, the initial and final nut set (Table 2; Figure 1). After pollinator exclusion, in most cases, not a single nut developed per raceme (initial nuts per raceme = 0.63, SE = 0.17, final nuts per raceme = 0.66, SE = 0.15). As compared to pollinator exclusion, the open pollinated racemes produced considerably more nuts: the initial nut set was increased by 404% (predicted mean = 2.55, SE = 0.63) and the final nut set by 23% (predicted mean = 0.81, SE = 0.08). The comparison between open pollination and supplementary hand pollination indicated a further increase of the initial and final nut set on average by 737% (predicted mean = 16.24, SE = 4.00) and 367% (predicted mean = 2.17, SE = 0.22), respectively.

The treatment further interacts with the row orientation. While a perpendicular row orientation towards the edge of semi-natural habitats has no or rather a negative effect on the initial nut set after pollinator exclusion or hand pollination, the initial nut set of open pollinated racemes shows an increasing trend (Figure 1). Regarding the final nut set, the pattern is similar, only the negative effect of perpendicular row orientation on hand pollinated racemes is pronounced.

Likewise, the number of varieties per block interacts with the pollination treatment, but only for the initial nut set (Figure 2). A high

number of varieties per block shows generally an increase of the initial nut set. After pollinator exclusion, the nut set in blocks with three to five varieties is highest as compared to one or two varieties, being as high as after open pollination in single-variety blocks. Also, hand pollination, which results in increased nut sets as compared to pollinator exclusion or open pollination, reveals higher nut sets in blocks with two or more varieties.
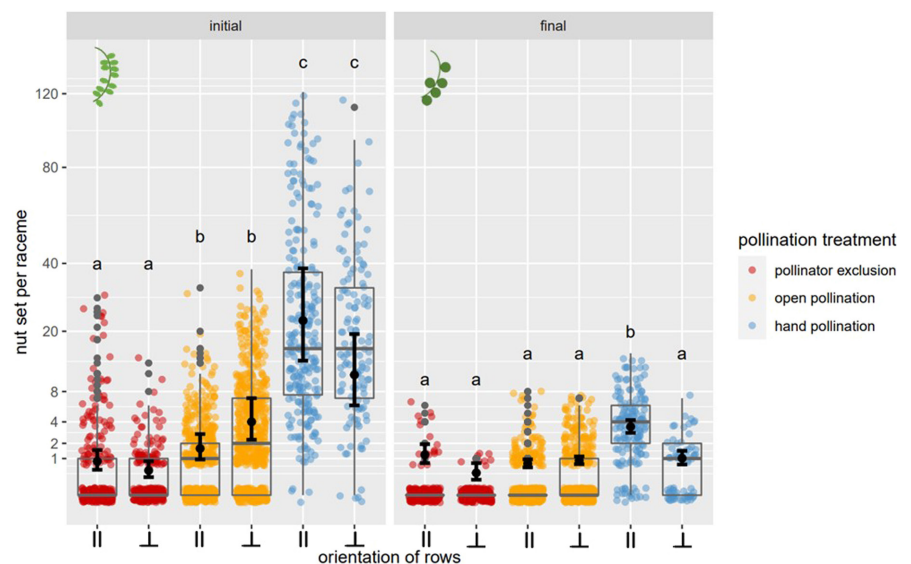
3.2 | Flower visitation rates

To assess the main drivers of flower visitation rates by pollinators in the macadamia orchards (research question (2)), we conducted 56 h of pollinator observations and counted 2395 flower visitors that belonged to 28 different morphospecies of the following orders (number of morphospecies per order is given in brackets): Hymenoptera (11), Coleoptera (8), Diptera (5), Lepidoptera (1), Thysanoptera (1), Hemiptera (1) and Psocoptera (1). According to Howlett et al. (2015), we considered 11 morphospecies as potential pollinators ($n = 442$). 95% of the pollinators were honeybees (*Apis mellifera*).

TABLE 2 Predicted nut set per treatment. Mean values and 95% confidence intervals for the initial and final nut set predicted with the selected best models Tins1 and Tfns1.
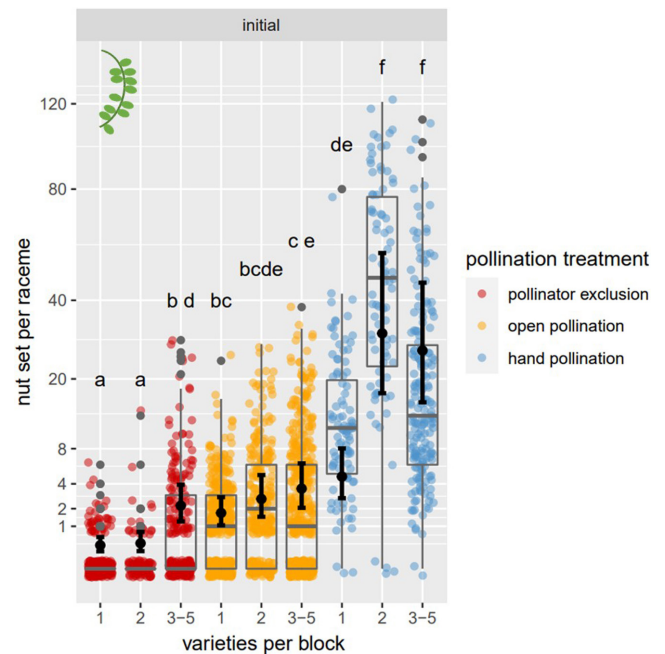
Pollination treatment	Nut set	Predicted nuts per raceme (confidence interval)
Pollinator exclusion	Initial	0.63 (0.37; 1.07)
Open pollination	Initial	2.55 (1.57; 4.15)
Hand pollination	Initial	16.24 (10.02; 26.33)
Pollinator exclusion	Final	0.66 (0.42; 1.03)
Open pollination	Final	0.81 (0.67; 0.99)
Hand pollination	Final	2.17 (1.78; 2.64)

We found six best-fitting models (Table S2). All of them included cover of semi-natural habitats ($\Sigma w_i = 0.94$), row orientation ($\Sigma w_i = 0.79$) and number of honeybee colonies in a 1 km radius around the sites ($\Sigma w_i = 0.78$). Several of the best-fitting models included additionally the position in block ($\Sigma w_i = 0.81$). All other variables and interactions had $\Sigma w_i > 0.5$ (Table 3).

The flower visitation rates increased with the cover of semi-natural habitats, for example, the mean number of pollinators was

FIGURE 2 Interacting effects between the pollination treatments and the number of varieties per block on the initial nut set. The black points and error bars show the predicted means and 95% confidence intervals. Different letters indicate significant differences between the groups. Predictions are based on the best-fitting models Tins1 (Table S1).

FIGURE 1 Interacting effects between the pollination treatments (pollinator exclusion allowing only self and wind pollination, open pollination by wind an insects and hand pollination by pollen collected from one to two different varieties) and orientation of the rows towards the edge to semi-natural habitats (∥=parallel/⊥=perpendicular). The black points and error bars show the predicted means and 95% confidence intervals. Different letters indicate significant differences between the groups. Predictions are based on the best-fitting models Tins1 and Tfns1 (Table S1).

TABLE 3 The relative importance of explanatory variables expressed by $\sum w_i$ (sum of Akaike weights) predicting flower visitation rate. Variables that were considered for interpretation are highlighted in bold.

Variables	Flower visitation rate
Semi-natural habitats	**0.94**
Position in block	**0.81**
Row orientation	**0.79**
Managed honeybee colonies	**0.78**
Flowering racemes per tree	0.48
Altitude	0.37
Semi-natural habitat: flowering racemes per tree	0.28
Semi-natural habitat: position in block	0.23
Position in block: row orientation	0.15
Semi-natural habitat: altitude	0.10

twice as high (3.0 individuals per raceme/h) in orchards with 60% semi-natural habitat cover, as compared to orchards with 40% semi-natural habitat cover (mean = 1.4; Figure 3a). Likewise, in orchards with 30 honeybee colonies, the flower visitation rate was on average about twice as high (3.3) as in orchards with 10 honeybee colonies (1.7; Figure 3b). Moreover, the flower visitation rates were on average 25% higher in the centre of the block as compared to the edge, while they were reduced on average by 44% in blocks with parallel rows towards the edge of semi-natural habitats as compared to blocks with perpendicular rows (Figure 3c,d).

3.3 | Nut set of open pollinated racemes

To analyse how flower visitation rates in combination with agronomic practices, orchard design, landscape composition and altitude ultimately affect the initial and final nut set (research question (3)) we only observed the open pollinated racemes. The multimodel inference approach revealed 10 models for the initial nut set and seven models for the final nut set (Table S3). The explanatory variables with $\sum w_i > 0.5$ that were included in the sets of models for both growth stages were: position in block ($\sum w_i$ initial = 0.99; $\sum w_i$ final = 0.93), flower visitation rates ($\sum w_i$ initial = 0.72; $\sum w_i$ final = 0.43), row orientation ($\sum w_i$ initial = 0.72; $\sum w_i$ final = 0.37), altitude ($\sum w_i$ initial = 0.28; $\sum w_i$ final = 0.70; Table 4). The model set for the final nut set contained the variable initial nut set ($\sum w_i$ final = 1.00). Again, the initial nut set was a meaningful predictor for the zeros observed for the final nut set (Table 4).

In the following, only the effects of variables with high importance values ($\sum w_i > 0.5$) are presented. The effect of the position in the block was opposed for the initial and final nut sets (Figure 4a,d). The nut set was initially about 80% higher at the edge to semi-natural habitats compared to the centre of the block, in contrast, the final nut set at the edge was reduced by 47% relative to the

centre. The initial nut set was more than tripled in blocks with rows that were oriented perpendicular towards the semi-natural habitats (mean = 1.06, SE = 0.36) compared to parallel rows (mean = 3.49, SE = 1.27; Figure 4b). Moreover, the initial nut set increased with raising flower visitation rates, for example, while racemes with a flower visitation rate of 2.0 pollinators/h develop on average 1.9 initial nuts, racemes with flower visitation rates of 8.0 pollinators/h hour develop about 3.0 initial nuts (Figure 4c).

4 | DISCUSSION

The provisioning of pollination services in macadamia along an altitudinal gradient was determined by multiple and partly interacting effects of landscape composition, orchard design and agronomic practices. Our pollination experiment corroborated the high reliance of macadamia on cross pollination for nut production as shown by enhanced nut set in the open (23%) and hand pollination treatments (367%). Moreover, the flower visitation rate of insect pollinators was one of the most important variables explaining the initial nut set of open pollinated racemes. Interestingly, flower visitation rates were mainly driven by landscape composition (i.e. the cover of semi-natural habitats) and orchard design (row orientation) and less related to agronomic practices (supplementary honeybee colonies). These findings indicate that ecological intensification by promotion of pollination services based on landscape and orchard design could represent one element for sustainable macadamia production, despite farmers' high investments in conventional intensification practices, such as irrigation or managed honeybee colonies.

4.1 | Importance of pollination for initial and final nut set

Our pollination experiment confirmed previous results that macadamia crops are largely pollination limited, that nut set could be increased by insect pollination and most effectively by supplementary hand pollination (Grass et al., 2018; Trueman et al., 2022). However, we found different effects of orchard design, agronomic practices, landscape composition and altitude on the initial and final nut sets, which have not been reported so far. In addition to the pollination treatments, row orientation and higher numbers of varieties per block were explaining the initial nut set. Focusing on the open pollinated racemes, we found a positive effect of the position at the edge of the block, perpendicular row orientation and flower visitation rates. This means that orchard design variables that enhanced flower visitation rates had a direct effect on the initial nut set. In contrast, the final nut set was mainly determined by the initial nut set and thus indirectly affected by these orchard design variables and flower visitation rates. Moreover, the final nut set was determined by the altitude and the position in the block.
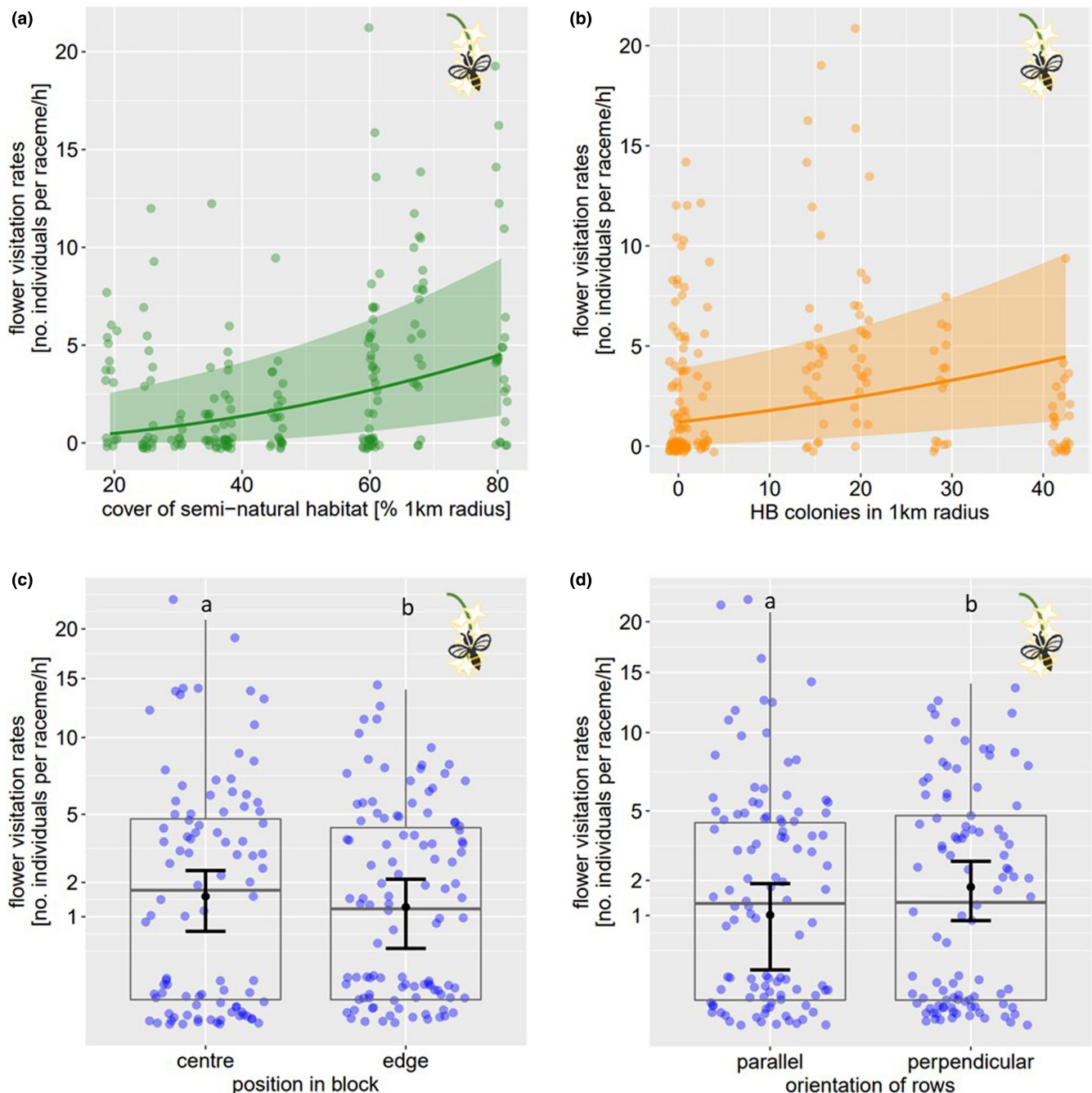
FIGURE 3 Most important effects ($\sum w_i > 0.5$) on the flower visitation rates: (a) cover of semi-natural habitats, (b) number of managed honeybee colonies, (c) position in the block and (d) orientation of the planted rows. The predicted means and 95% confidence intervals are shown and predictions are based on the best-fitting model pol1 (Table S2).

4.2 | Ecological intensification measures to enhance pollination services and nut set

4.2.1 | Orchard design

In general, orchard design variables (i.e. the number of varieties, row orientation and position in block) were included in a high number of models explaining either the initial or final nut set. Based on the pollination experiment, we could demonstrate that both initial and final nut set increased with the numbers of varieties per block.

Two or more varieties per block resulted in tendency in a higher initial nut set, even across all pollination treatments (3.1). A high number of varieties per block increased initial nut sets of open pollinated racemes by promoting cross pollination (Kämper et al., 2021). This applied also to racemes with pollinator exclusion, which could be explained by wind pollination (Urata, 1954). The number of varieties per block was not meaningful for hand pollinated racemes, as we increased the nut set by explicitly collecting pollen from different varieties, even in other blocks. Many studies have already demonstrated the increase of nut

TABLE 4 The relative importance of explanatory variables expressed by Σw_i (sum of Akaike weights) predicting initial and final nut set of open pollinated racemes. Variables that were considered for interpretation are highlighted in bold.

Variables	Initial nut set	Final nut set
Zero-inflation formula = ~initial nut set	—	**1**
Initial nut set	—	**1**
Position in block	**0.99**	**0.93**
Flower visitation rates	**0.72**	0.43
Row orientation	**0.72**	0.37
Altitude	0.28	**0.70**
Irrigation	0.42	0.43
Number of varieties	0.22	0.28
Flower visitation rates: position in block	0.19	0.18
Flower visitation rates: row orientation	0.18	0.00
Flower visitation rates: altitude	0.03	0.09
Flower visitation rates: irrigation	0.08	0.00
Flower visitation rates: number of varieties	0.02	0.00

set by cross pollination experimentally by hand pollination for macadamia (Herbert et al., 2019; Howlett et al., 2019; Trueman & Turnbull, 1994). Here, we empirically reinforce the success of cross pollination in blocks with multiple cross-pollen donors that is provided by insect pollinators and marginally by wind pollination. In blocks with only one or two varieties, pollinators function as vectors to provide cross pollination between trees of different varieties in other blocks of the farm.

With respect to the row orientation, we found that rows that were planted perpendicular to semi-natural habitats had a positive effect on the flower visitation rates (3.2). This positive effect apparently translated into improved pollination services as we found three times higher initial nut set in open pollinated racemes of trees grown in rows with a perpendicular orientation to the semi-natural habitats (3.3). The effect of the row orientation in orchards has been well studied focussing on plant physiological aspects, such as solar radiation and water consumption (Olesen et al., 2007; Trentacoste et al., 2015), but not regarding pollination services. The pollinators, which presumable spill over from the semi-natural habitats, forage presumably along the orchard rows rather than crossing them (Brittain, Williams, et al., 2013). Therefore, planting macadamia trees in rows with a perpendicular orientation towards the semi-natural habitat could be one ecological intensification measure promoting pollination services in macadamia orchards.

The position in the block did prominently affect the nut set. The racemes at the orchard edge to semi-natural habitats developed higher initial nut sets (3.3). The reason could be not only the quantity but also the quality of the pollination services. While the flower visitation rates were higher in the centre than at the edge of the orchard block (3.2), the movement of the pollinators might be restricted to the inner block due to the rich flower supply in between the macadamia trees. In contrast, pollinators that visit the trees at the edge are more likely to come from a different block and thus have collected pollen from flowers of a different variety producing cross pollination (Kämper et al., 2021). It is also possible that the ratio of wild non-honeybee pollinators, which are potentially more effective pollinators than honeybees (Garibaldi et al., 2013), is higher at the edge of the orchard due to spillover from the semi-natural habitats (Blitzer et al., 2012). The presence of non-honeybee pollinators at the edge increased the effectiveness of honeybees, as they changed their foraging pattern and increased cross row movements (Brittain, Williams, et al., 2013). Hence, a higher amount of orchard edges with neighbouring semi-natural habitats could be a measure to increase pollination services. On the other hand, the final nut set was higher in the centre, indicating lower abscission rates in the interior of the orchard. The reasons could be a higher pest pressure at the orchard edges as compared to the centre or other unknown processes after pollination.

4.2.2 | Agronomic practices

Interestingly, we did not find an effect of irrigation on nut production (3.1 and 3.3). Unfortunately, irrigation recommendations are scarce due to a lack of comprehensive studies and the varying water demand of macadamia among varieties and even individual trees, additionally, water supply is anyhow dependent on climate conditions (Carr, 2013).

It stands out that the number of managed honeybee hives was less relevant for the flower visitation rates than semi-natural habitats (3.2). The density of managed honeybee colonies at the sites was generally low (mean: 0.03 colonies per hectare) compared to the vague recommendation of 1–3 colonies per hectare (de Villiers & Joubert, 2003). Furthermore, at half of the sites, there were even no managed colonies within a 1 km radius.

4.2.3 | Landscape composition and altitude

The cover of semi-natural habitats in the surrounding landscape was the most important and positive effect for flower visitation rates (3.2), which in turn increased the initial and final nut set (3.3), supporting previous results of enhanced pollination services by natural habitat (Carvalheiro et al., 2010; Klein et al., 2012). At the same time, almost all observed pollinators were honeybees, although at half of the sites no managed honeybee colonies were placed. Hence, we assume that a great proportion of the pollinators were wild honeybees living in semi-natural habitats in the surrounding area.

The altitude, in contrast, played a minor role for flower visitation rates and initial nut set but had a significant positive effect
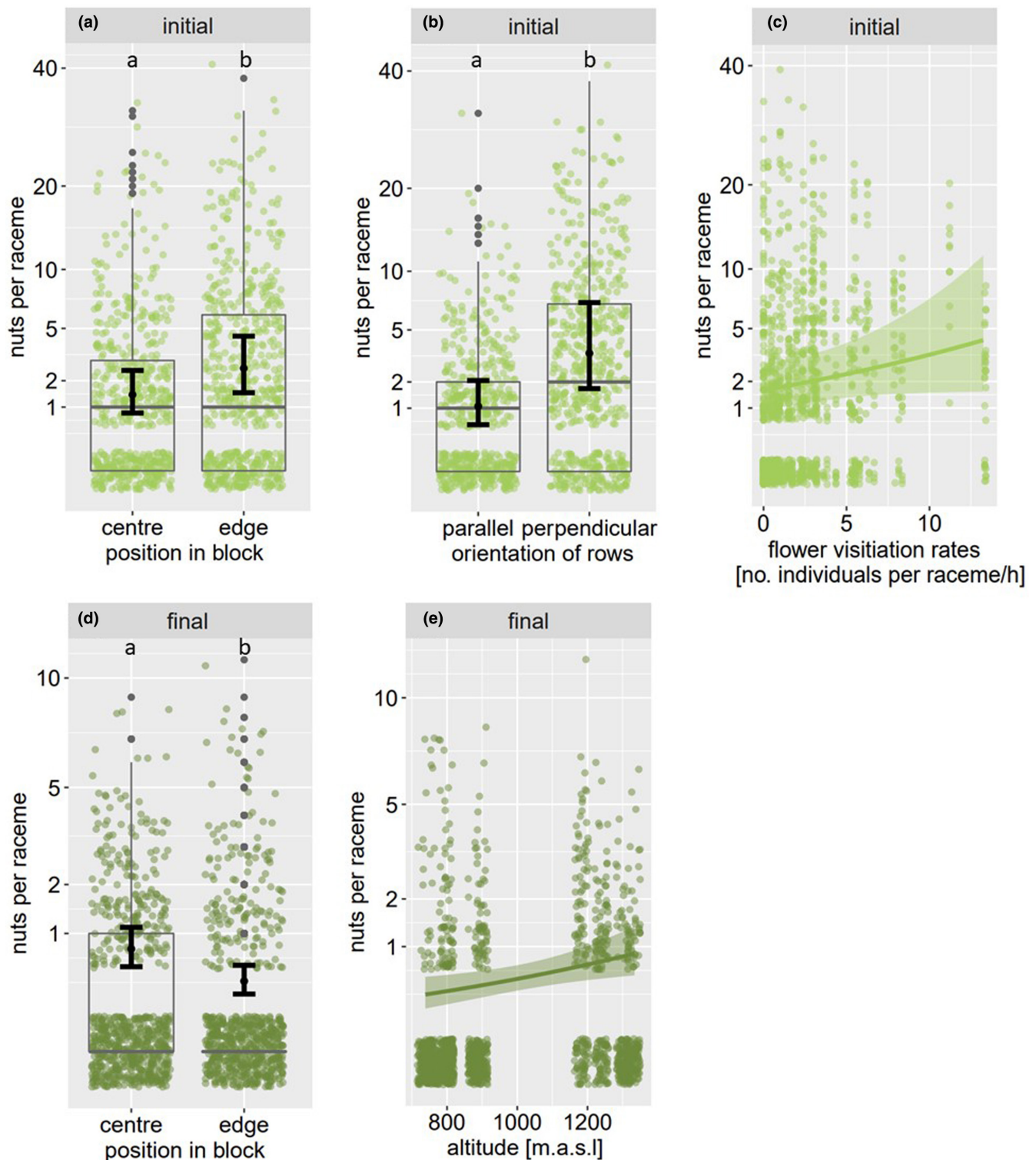
(a)
initial
a
b
40
20
10
5
2
1
nuts per raceme
centre
edge
position in block
(b)
initial
a
b
parallel
perpendicular
orientation of rows
(c)
initial
0
5
10
flower visitiation rates
[no. individuals per raceme/h]
(d)
final
a
b
10
5
2
1
centre
edge
position in block
(e)
final
800
1000
1200
altitude [m.a.s.l]

FIGURE 4 Most important effects ($\sum w_i > 0.5$) on initial and final nut set: (a) position in the block, (b) orientation of rows and (c) flower visitation rates, and on final nut set: (D) position in block and (E) altitude. The black points and error bars or rather lines and ribbons indicate the predictions and 95% confidence intervals. Predictions are based on models ins1 and fns2 (Table S3).

on the final nut set (3.3). Possible reasons are on the one hand the cooler climate at higher altitudes, which could have affected pest pressure (Poggetti et al., 2019) or could have mitigated the extremely hot and dry season in 2019/2020, which was a problem for macadamia cultivation (personal communication with the farmers: G. Whyte, P. Thomas January 2020). On the other hand, the landscape history differed in the lower and higher locations of the Levuvhu Valley. At higher altitudes, cultivation of macadamia started later than in the valley and the cover of macadamia orchards is lower, instead, there were often eucalyptus or pine

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plantations. Consequently, macadamia pest species were not as long and well established as in the valley and pest pressure was lower (personal communications with D. Bouwer), which resulted in higher a final nut set.

5 | CONCLUSIONS

Our study demonstrated that crop pollination services and initial nut set could be enhanced through smart orchard design (i.e. spatial arrangement of trees and rows, plantings of multiple varieties per block) and higher amounts of semi-natural habitats adjacent to the production blocks and in the surrounding landscape rather than through agronomic practices. Many studies investigated the orchard design in terms of the spatial distribution of varieties for different crops (e.g. Kämper et al., 2021), but to date, the effect of orchard design on pollination services by insect pollinators remains understudied. Here, our study makes an important contribution by showing ways for ecological intensification. Considering the urgency to reduce the environmental impacts of agricultural production under climate change (IPBES, 2019), we demonstrate the high potential of ecological intensification measures (orchard design, landscape management) in an intensively managed, economically important crop, which is grown in regions with high biodiversity that are vulnerable to climate change (Costello et al., 2022) and land degradation (Roetter et al., 2021). The enhancement of pollination services through ecological intensification can reduce pollination deficits and help to reduce external inputs while sustaining or even increasing the productivity of macadamia orchards. Further, the recommended ecological intensification measures contribute to pollinator conservation and, importantly, might buffer against climate change through increasing stability of pollination services (Senapathi et al., 2021).

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data available via the *Dryad Digital Repository* 10.5061/dryad.c866t1gb6 (Anders et al., 2022).

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SUPPORTING INFORMATION

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