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Impact of Cropland Management on Invertebrate Richness and Abundance in Agroforestry Systems in Bali, Indonesia

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Abstract: The intensive management of cropland refers to a reduction in habitat complexity (i.e., shade tree cover, tree species richness, crop species richness) to gain more profits. This usually entails a decrease in biodiversity, but agroforestry systems have been shown to provide a solution to the need for profits while maintaining biodiversity and ecosystem services. Invertebrates are important bioindicators since they are not just affected by a decrease in habitat complexity; they are also key for the maintenance of ecosystems given their ecological roles. We aimed to understand how agricultural intensification impacted invertebrate abundance and richness in an agroforestry system in Bali, Indonesia. We set up 53×25 m^2 plots and collected data via pitfall and pan traps. We linked those data to vegetation data (canopy cover, tree species richness, crop species richness), habitat type (rustic vs. polyculture), and productivity. Overall, we found that the abundance and richness of invertebrate taxa were positively influenced by increasing canopy cover and crop and tree species richness. This supports the habitat heterogeneity hypothesis, which indicates that increased habitat complexity promotes higher invertebrate species richness and abundance. The abundance and richness of certain invertebrate taxa, including agents of biocontrol, were shown to increase in plots with higher yields, thus solidifying the important role of invertebrate communities in the provision of ecosystem services. Harvesting crops from complex agroforestry systems ensures a sustainable income for local communities as well as habitats for invertebrates.

Keywords: ecosystem services; agricultural intensification; sustainability; rustic systems; polyculture systems; habitat heterogeneity hypothesis; canopy cover

1. Introduction

Species are disappearing from our ecosystems at an alarming rate [1,2]. The value of conservation is typically measured by the richness and diversity of species inhabiting an area [3,4]. Given that the habitat shift from forest to agricultural land is the main factor threatening biodiversity in the tropics, there has been increasing focus on the measurement

of biodiversity loss across gradients of agricultural management [3–6]. Agricultural intensification, i.e., the reduction in the structural and taxonomic complexity of farms through the adoption of monoculture farming alongside the prophylactic use of broad-spectrum agrochemicals, was encouraged and subsidized by government authorities globally to increase crop productivity and, in turn, profits [7]. In the pursuit of high yields, biodiversity is inevitably jeopardized, not only through direct habitat loss but also through the use of agrochemicals, temperature increases due to a lack of shade, and decreased plant diversity, reducing potential resources for species [3,5]. Agroforestry systems, when natural forest and shade trees are present within agricultural environments, have been considered a solution to preserving biodiversity while also providing sustainable yields [8,9]. Traditional and rustic systems, examples of agroforestry systems, have been shown to harbor high levels of biodiversity, with the presence of shade trees directly influencing the richness of species [6,10,11].

When biodiversity is preserved in agroforestry systems, the associated ecosystem services (i.e., function of an ecosystem that provides benefits to humans [12]) provided by that system are enhanced [8,13]. The presence of shade trees can improve water filtration and water retention, carbon sequestration, provide natural solutions for weed and pest biological control, and improve soil fertility [8]. Additionally, smaller temperature fluctuations are observed in agroforestry systems, thus increasing the resilience of ecosystems to climate change and allowing for species to persist in the face of temperature increases more so than in systems that are exposed to the sun [14]. While traditional, rustic systems were abandoned in order to optimize yields, it is the presence of species such as invertebrates that creates productive and resilient agricultural landscapes [8,12,14].

Invertebrates play an important role within agricultural systems as agents of biological control, pollinators, bioturbators, and nutrient cyclers, and they are known to be sensitive to changes in land use [2,13]. Some of the ecological factors known to alter the diversity of invertebrate species are a lack of shade cover, the presence of invasive species, competition for resources due to reduced habitat availability, and the direct and indirect consequences of the application of agrochemicals [4,6,15–17]. Crop productivity and efficiency are also reliant on invertebrates, with yields reduced by up to 90% with the removal of *Apis mellifera*, indicating that a reduction in invertebrates can also lead to a decline in crop yields [18]. Furthermore, an invertebrate decline does not just negatively affect yields but reduces the suitability of agricultural habitats for vertebrates, such as birds, due to the reduction in food availability [19]. The monitoring of invertebrate assemblages is fundamental but remains to be an underdeveloped area of research, and the causes of insect decline are still not fully understood [20].

The diversity and abundance of invertebrates can be influenced by environmental variables linked with land management [13,14,17]. Increased land management with the consequent decrease in habitat complexity (i.e., reduction in shade cover, tree species richness, and crop richness) are expected to reduce invertebrate species diversity based on the habitat heterogeneity hypothesis (i.e., an increased complexity in habitats, with a consequent increase in niche dimensionality, results in increased species diversity [21]). This hypothesis has been tested mainly in response to variations in species richness and the diversity of several taxa (including invertebrates, e.g., [22,23]), but there is evidence of influence on the abundance of taxa as well (e.g., [24,25]).

Throughout the 20th century, agricultural intensification, amongst other factors, led to extensive deforestation in Indonesia, with coastal and lowland areas experiencing particularly severe logging and encroachment [26]. In an effort to discourage further encroachment on the island of Bali due to an increasing population and limited forest reserves, in 1977, forested areas were separated into four categories: (1) production forest; (2) conservation forest; (3) wildlife or nature preserve; and (4) tourist or recreational area [27]. In West Bali, areas of production forest (*hutan produksi*) act as a buffer between settlements and areas of protected forest (*hutan lindung*) and are allowed to be entered and cultivated by members of the local community. That said, production forests in Indonesia are often encroached

and replaced with low complexity croplands. In production forests, cultivation is regulated by local government authorities and is suggested to be limited to indigenous crop species. It is production forests such as these, agricultural landscapes that are embedded into primary forest, that have been found to boast high levels of biodiversity globally due to their proximity to conservation forests and the maintenance of connectivity [3,28–30]. Although the production forests of Bali have been maintained for almost 50 years, there has been little to no research as to the invertebrate (and other animal taxa) abundance and richness within them and how it compares to that of more disturbed, polyculture agroforest environments. We aimed to understand how agricultural intensification impacted invertebrate abundance and richness. Based on the habitat heterogeneity hypothesis [21], we predicted a decrease in abundance and richness of invertebrates as a consequence of a reduction in the habitat quality of the cropland (measured by richness of crops and native forest trees), a reduction in shade cover, and an increase in profits obtained from crops. We also predict that rustic systems (i.e., crops under natural forest tree cover) will have higher invertebrate richness and abundance than polyculture systems (i.e., multi-crop systems with no cover of natural forest trees). That said, we expect some taxa of invertebrates, especially the ones considered as pests, to increase with an increased level of agricultural intensification given the relationship between pests and reduced habitat complexity [13,31]. This is expected since farmers in the study area do not use/very rarely use agrochemicals.

2. Materials and Methods

2.1. Study Area

We collected data from May to August 2023 in polyculture systems and rustic systems neighboring a natural forest in Yeh Embang Kauh in the Jembrana Regency of Bali, Indonesia. The elevational range of the study area is from 220 to 480 m asl. The annual precipitation is 1010 mm with a wet season (average of >100 mm rain month^{-1} and 18–22 rainy days month^{-1}) from October until April and a drier season (20–100 mm month^{-1} and 2–13 rainy days month^{-1}) from May until September. Figure 1 shows the climatic diagram of the nearby weather station at Yeh Panas, situated close to sea level. Please note that we collected data over the dry period, thus excluding potential confounding effects of weather conditions (especially rainfall). The crops in the study area are grown and farmed by members of the local community under the farming cooperative Kelompok Tani Hutan (KTH). They harvest crops for local consumption and to sell for profit. Most of the polyculture croplands are adjacent to farmers' houses, and the rustic croplands, located in the area of the production forest, are situated at the foot of the protected forest. Kesatuan Pengelolaan Hutan Bali Barat (KPH), the provincial government forestry authority, gives members of KTH permission to grow and harvest crops within the production forest. The crops that are being grown in the rustic systems comprise coffee *Coffea* spp., cocoa *Theobroma cacao*, vanilla *Vanilla planifolia*, durian *Durio zibethinus*, banana *Musa* spp, Siaw nutmeg *Myristica fragrans*, and clove *Syzygium aromaticum*, while the polyculture farms harvest clove, coconut *Cocos nucifera*, cocoa, and coffee.

2.2. Data Collection

We set up 53 × 25 m^2 plots (32 in the rustic system, 21 in the polyculture system) selected based on the local farmers' knowledge of where the crops are grown within the systems (Figures 2 and 3). We classified the 53 plots as "rustic" or "polyculture" based on the presence or absence of native forest trees. In the rustic plots, multiple types of cropping trees were being grown alongside native tree species. In the polyculture plots, multiple types of cropping trees were being grown, but there were no native forest trees. We left at least 50 m distance between each plot based on recommendation from previous studies (e.g., [32,33]). Production forests are a political land zonation, which does not necessarily reflect into practice. In theory, production forests should be used sustainably without the removal of forest trees, but in practice, many production forests in Indonesia are converted into agricultural lands without forest trees, including monocultures. In our study area, the

production forest is well preserved, but there were some areas that were cleared in the past and no longer host native forest trees. Due to the clearance of native forest trees, five plots were classed as polyculture systems despite being located in the area of production forest. We identified invertebrate taxa up to species level. When it was not possible to identify taxa to species level, we identified them to family level and used morphospecies for the analysis. The resolution of taxonomic designation compromises a lack of keys for groups in the study area. Hence, morphospecies were used from order to family levels [34].
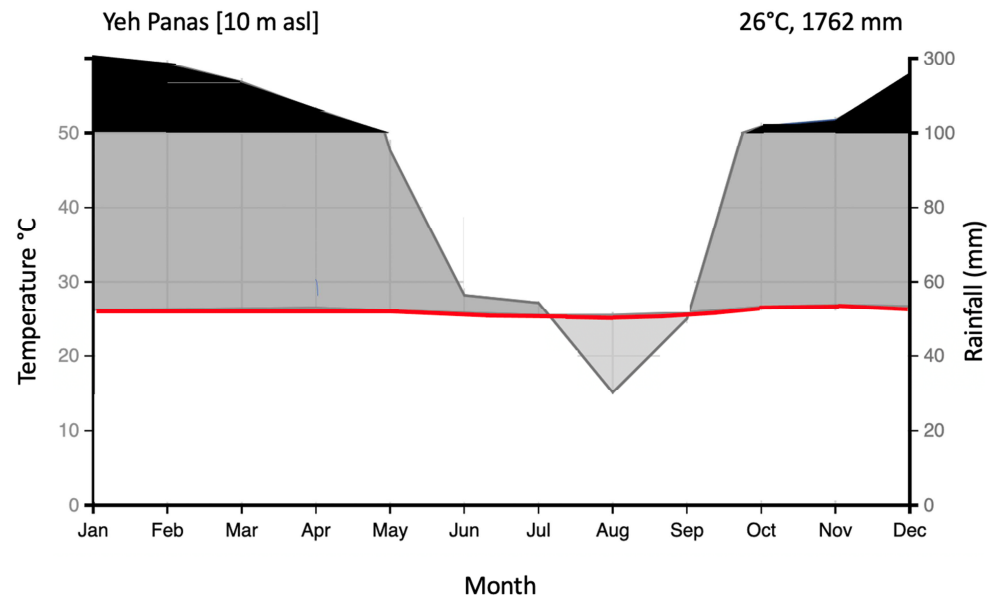
Figure 1. Climatic diagram of Yeh Panas, West Bali, showing a perhumid period in the austral summer and a drier period in the austral winter. Red line indicates mean temperatures.
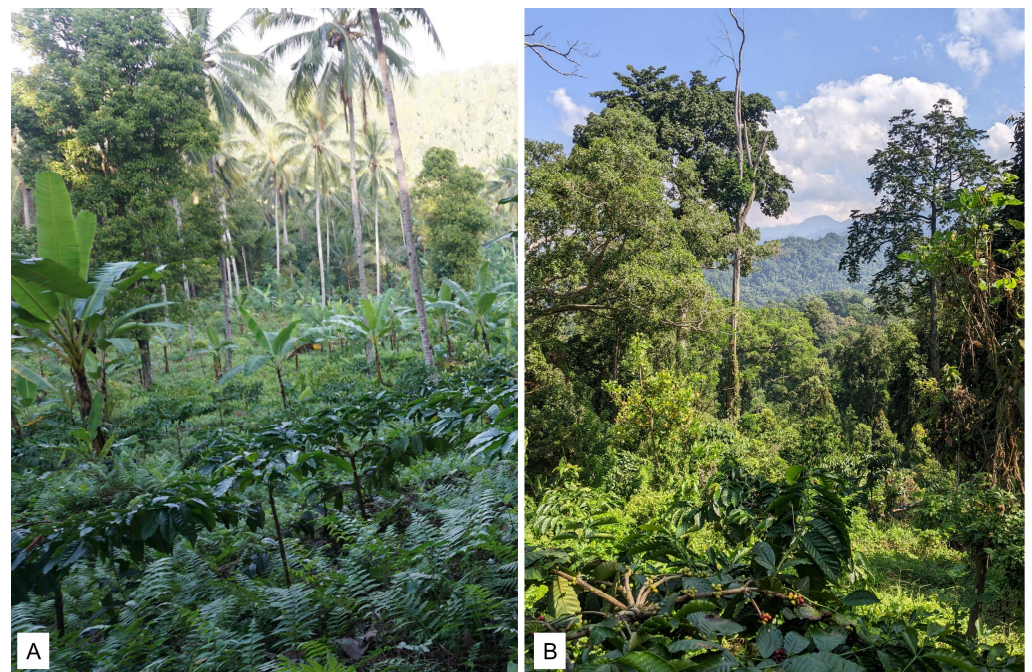

Figure 2. Examples of polyculture (**A**) and rustic (**B**) systems in the Yeh Embang Kauh study area in western Bali, Indonesia. Plots classed as rustic systems host native forest trees, while the tree cover in polyculture systems is only given by crop trees.
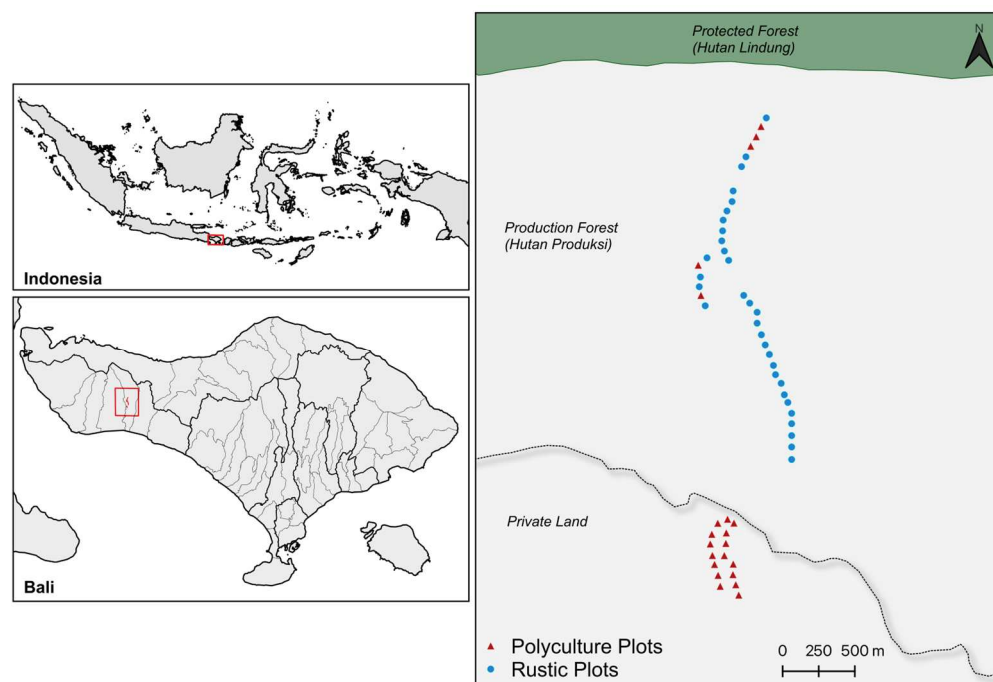
Figure 3. Map of the study area and geographical position of plots. Red frames indicate the position within Indonesia and Bali. Note that five plots in the production forest area were classified as polyculture plots as they had no cover from forest tree species due to past forest clearance.

To determine shade cover of each plot, we used the Canopea application, which calculates the proportion of area shaded from photographs [35]. Within the plots, we took four random and independent photographs and calculated the mean value for each plot [35]. We kept a minimum distance of 5 m between the points of where photos were captured and a 5 m minimum distance from the edge of the field [36]. We made sure that the calculations did not bias the calculation of the tree shade cover by not including understory canopy, such as banana leaves [36]. We then collected the number of crop species richness ("crop richness" hereafter) and tree species richness ("tree richness" hereafter) for each plot. We then estimated (1) productivity of each crop plant/year based on local knowledge; (2) overall yields/year for each crop in each plot; and (3) the overall productivity of each plot.

Once in each plot, we installed invertebrate traps between 0800 and 0900 h in a single line at 12.25 m at the middle of each plot [13]. The traps used were pitfall traps (clear cups) and pan traps (colored pans orange and blue, as there can be a preference of color in some pollinators [37]). We set six pitfall traps (diameter: 11 cm) in a diagonal line at the 12.25 m, kept a space of 1 m between each trap, and then positioned the pan traps (inner dimensions: $37 \times 27 \times 2$ cm) in opposite corners of the pitfall traps. The arrangement of the traps is visualized in Campera et al. [13]. A solution of clean water and 5 mL of liquid detergent was used to fill the pitfalls to one-third, and the pan traps were filled to half [13]. We returned to retrieve traps after six hours. The samples were then put into a plastic jar with 70% ethanol solution and kept in a freezer to preserve individuals for subsequent counting and identification of species [13]. We used an Olympus SZ61 microscope to perform the identification and a taxonomic key [13].

2.3. Ethics and Permission

The research was part of a collaborative project between Oxford Brookes University in the UK, Universitas Warmadewa in Bali, and Bumi Lestari Conservana, a for-profit social enterprise that processes non-timber forest products from Indonesia forests. The research part of the project, where it concerns non-Indonesian researchers, was conducted with approval from Indonesia's National Research and Innovation Agency in Jakarta (BRIN);

this also entailed an animal care and use ethical approval from BRIN. For the collection of invertebrates, we followed the guidelines from the Animal Behavior Society [38].

2.4. Data Analysis

We used generalized linear models to determine the differences in terms of vegetation structure and yields between rustic and polyculture systems. We presented the estimated marginal means calculated via the "emmeans" package. For invertebrates, we considered morphospecies at order level for our analysis. When the order included taxa with different ecological roles, we further separated them into functional groups within the same order (when the sample size was enough to allow for statistical comparisons). We did not have enough sample size to run analysis on the pollinator Hymenoptera and other under-sampled taxa (i.e., Lepidoptera, Opiliones, Phasmatodea, and Thysanoptera). We further separated the family Formicidae from the Hymenoptera, although we included the tribe Oecophyllini in Hymenoptera with biological control function and not with Formicidae, as they are tree ants and do not have the ecological function of ground-dwelling ants [39]. We calculated profits from yields, asking an average selling price for each crop from farmers (in IDR) and then converting that to USD using a conversion rate of 1 IDR = 0.000064 USD. We ran generalized linear models to assess the impact of habitat (rustic vs. polyculture), canopy cover, crop richness, tree richness, and yields (fixed effects) on invertebrate assemblages (abundance and richness) (response variables). We ran generalized linear models via the "glmmTMB" function in the "glmmTMB" package for R v 4.3.1, as this function includes several fit families that are suitable to deal with count data [40]. We tested poisson, compois, genpois, nbinom1, nbinom2, and tweedie families for the abundance and richness. We selected the fit family and included or excluded a zero-inflation term based on the QQ plot residuals and residual vs. predicted plot from the package "DHARMa" [41]. We used $p = 0.05$ as threshold for significance and $p = 0.1$ as threshold to define trends towards significance.

3. Results

Rustic systems were characterized by a higher richness of native trees (polyculture plots by definition had no native trees present), higher canopy cover, and a lower richness of crops than polyculture systems (Table 1). The yields did not differ significantly between rustic and polyculture systems. We recorded 17 crops that provide profits in the area. These comprise lower canopy trees (teak *Tectona grandis*, durian, jackfruit *Artocarpus heterophyllus*, nutmeg, mangosteen *Garcinia mangostana*, rambutan *Nephelium lappaceum*, guava *Psidium guajava*, avocado *Persea americana*, coconut), understory trees (clove, banana, coffee, cocoa), epiphytes (vanilla), and other herbaceous strata (cardamom *Elettaria cardamomum*, konjac *Amorphophallus konjac*, galangal *Alpinia galanga*) (Figure 4). Clove, teak, and coconut made most of the profits from polyculture systems, while vanilla, jackfruit, and nutmeg were important in the rustic systems. Durian, coffee, and cacao were important in providing alternative profits in both systems (Figure 4).

Table 1. Estimated marginal means (SE) and model outputs based on generalized linear models to understand the difference between rustic and polyculture systems in terms of vegetation and yields in 53 agroforestry plots in Bali, Indonesia.

Variable [a]	Rustic (N = 32)	Polyculture (N = 21)	Z Value	*p*-Value
Canopy cover (%)	34.60 (2.98)	21.10 (3.68)	2.86 **	0.004
Crop richness	3.99 (0.21)	5.49 (0.30)	−4.31 **	<0.001
Tree richness	3.56 (0.32)	0.00 (0.00)	NA	NA
Yields (USD)	234.0 (38.3)	347.0 (67.6)	1.55	0.120

[a] family fit: Gaussian for canopy cover, genpois for crop and tree richness, Gamma for yields. ** $p < 0.01$. NA: Not Available.
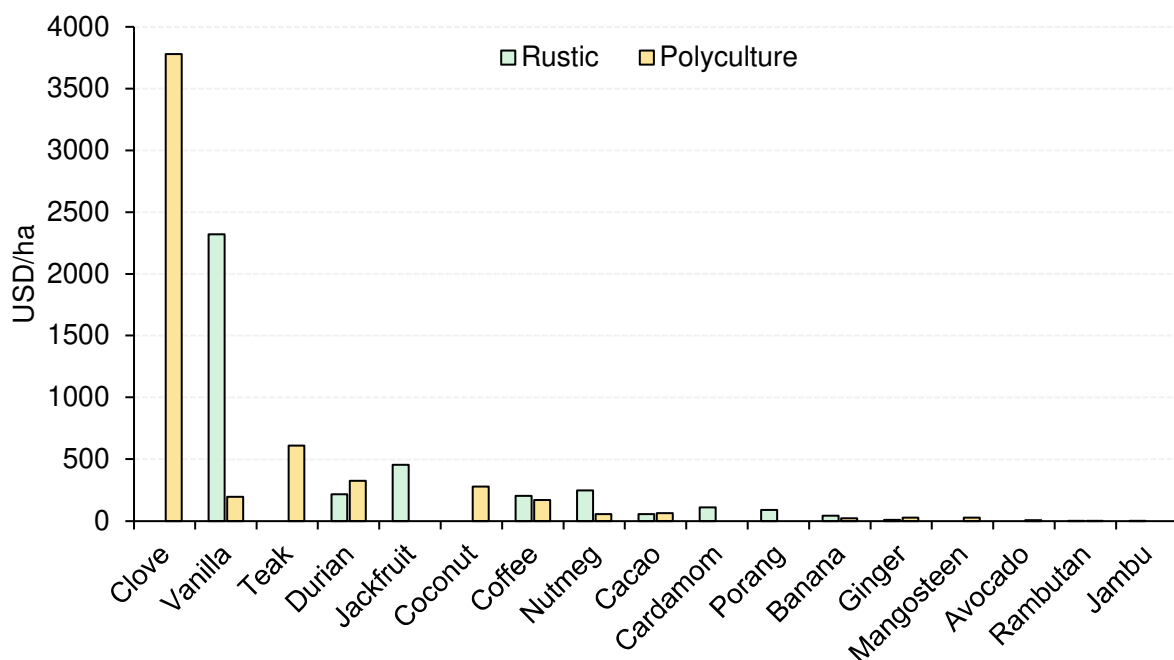
Figure 4. Total yields (USD/ha) provided by crops in the Yeh Embang Kauh village, Bali, Indonesia, separated by rustic and polyculture systems. Data are based on 53 agroforestry plots (32 in the rustic system, 21 in the polyculture system).

We found a total of 133 morphospecies of invertebrates (105 in rustic; 71 in polyculture systems). The total number of individuals recorded was 2603, with 2016 in rustic and 587 in polyculture systems (Table 2).

Table 2. Richness and abundance of invertebrates found in 53 agroforestry plots in Bali, Indonesia.

Taxa	Rustic (N = 32)		Polyculture (N = 21)		Total (N = 53)	
	Richness	**Abundance**	**Richness**	**Abundance**	**Richness**	**Abundance**
Araneae	11	95	10	42	16	137
Blattodea	4	25	2	4	4	29
Coleoptera	10	13	7	8	15	21
Dermaptera	4	7	1	6	4	13
Diptera (pest)	8	113	8	71	10	184
Diptera (other)	8	128	3	79	8	207
Hemiptera	13	74	8	33	16	107
Hymenoptera (biological control)	15	82	11	46	20	128
Hymenoptera (pollinator)	2	4	5	5	7	9
Hymenoptera (Formicidae) [a]	17	1321	8	214	17	1535
Isopoda	2	86	1	50	2	136
Lepidoptera	4	4	2	2	6	6
Opiliones	1	1	0	0	1	1
Orthoptera	3	71	2	44	3	115
Phasmatodea	0	0	1	1	1	1
Talitridae	1	42	1	8	1	50
Thysanoptera	1	1	0	0	1	1
Zygentoma	1	26	1	14	1	40
Total	**105**	**2027**	**71**	**576**	**133**	**2603**

[a] Oecophyllini are included in the Hymenoptera (biological control).

Canopy cover had a significant positive impact on the abundance of non-pest Diptera ($Z = 2.30$, $p = 0.021$) and overall abundance of invertebrates ($Z = 2.02$, $p = 0.044$) and

the abundance and richness of Coleoptera (Z = 2.07, *p* = 0.038 and Z = 2.02, *p* = 0.043, respectively) and Formicidae (Z = 2.13, *p* = 0.033 and Z = 2.37, *p* = 0.018, respectively). Canopy cover had a significant negative impact on the abundance of Hymenoptera, with the function of biological control (Z = −1.99, *p* = 0.046) (Tables 3 and A1).

Table 3. Significant results and trends towards significance of the generalized linear models to explain the factors influencing abundance and richness of invertebrates in 53 agroforestry plots in Bali, Indonesia.

Response	Predictor	Coefficient	Std Error	Z Value	*p*-Value
Araneae (richness)	Crop richness	−0.169	0.099	−1.69	0.090
Blattodea (richness)	Yields (USD)	7.0×10^{-4}	4.2×10^{-4}	1.65	0.099
Coleoptera (abundance)	Canopy cover	0.027	0.013	2.07 *	0.038
	Habitat [a]	−2.136	1.103	−1.94	0.053
	Tree richness	0.415	0.210	1.98 *	0.048
Coleoptera (richness)	Canopy cover	0.029	0.014	2.02 *	0.043
	Habitat [a]	−2.114	1.152	−1.84	0.067
Diptera-non pest (abundance)	Canopy cover	0.020	0.009	2.30 *	0.021
Hemiptera (abundance)	Habitat [a]	−1.312	0.752	−1.75	0.081
	Tree richness	0.485	0.165	2.93 **	0.003
	Yields (USD)	10.5×10^{-4}	5.5×10^{-4}	1.92	0.055
Hemiptera (richness)	Tree richness	0.329	0.126	2.62 **	0.009
Hymenoptera-biological control (abundance)	Canopy cover	−0.023	0.011	−1.99 *	0.046
	Crop richness	0.281	0.146	1.92	0.055
	Habitat [a]	−1.376	0.793	−1.74	0.083
	Tree richness	0.533	0.163	3.26 **	0.001
	Yields (USD)	8.7×10^{-4}	5.1×10^{-4}	1.69	0.091
Hymenoptera-biological control (richness)	Yields (USD)	6.8×10^{-4}	2.8×10^{-4}	2.41 *	0.016
Hymenoptera-Formicidae [b] (abundance)	Canopy cover	0.017	0.008	2.13 *	0.033
	Habitat [a]	0.887	0.546	1.67	0.095
	Yields (USD)	8.0×10^{-4}	3.1×10^{-4}	2.56 *	0.011
Hymenoptera-Formicidae [b] (richness)	Canopy cover	0.008	0.003	2.37 *	0.018
Orthoptera (abundance)	Tree richness	0.208	0.094	2.22 *	0.026
Talitridae (abundance)	Habitat [a]	1.911	0.880	2.17	0.030
	Yields (USD)	8.7×10^{-4}	4.0×10^{-4}	2.17 *	0.030
Talitridae (richness)	Habitat [a]	2.415	1.221	1.98 *	0.048
Zygentoma (abundance)	Crop richness	0.306	0.152	2.02 *	0.044
Total abundance	Canopy cover	0.011	0.006	2.02 *	0.044
	Yields (USD)	6.3×10^{-4}	2.2×10^{-4}	2.80 **	0.005
Total richness	Tree richness	0.095	0.042	2.28 *	0.023

[a] reference category: rustic; [b] Oecophyllini are included in the biological control category; * *p* < 0.05; ** *p* < 0.01.

Tree richness had a significant positive impact on the abundance and richness of Hemiptera (Z = 2.93, *p* = 0.003 and Z = 2.62, *p* = 0.009, respectively); on the abundance of Coleoptera (Z = 1.98, *p* = 0.048), Hymenoptera with the function of biological control (Z = 3.26, *p* = 0.001), and Orthoptera (Z = 2.22, *p* = 0.026); and on the overall richness of invertebrates (Z = 2.28, *p* = 0.023).

Crop richness had a significant positive impact on the abundance of Zygentoma (Z = 2.02, *p* = 0.044), a trend towards a positive significance on the abundance of Hymenoptera with the function of biological control (Z = 1.92, *p* = 0.055), and a trend towards a negative significance on the abundance of Araneae (Z = −1.69, *p* = 0.090).

Yields, i.e., the overall profits gained from crops within each plot, had a significant positive impact on the abundance of Formicidae (Z = 2.56, *p* = 0.011) and Talitridae (Z = 2.17, *p* = 0.030), on the total abundance of invertebrates (Z = 2.80, *p* = 0.005), and on the richness of Hymenoptera with the function of biological control (Z = 2.41, *p* = 0.016). Yields had a positive impact that trended towards significant regarding the abundance of Hemiptera (Z = 1.92, *p* = 0.055) and Hymenoptera with the function of biological control (Z = 1.69, *p* = 0.091), and on the richness of Blattodea (Z = 1.65, *p* = 0.099).

Finally, the abundance and richness of Talitridae (Z = 2.17, *p* = 0.030 and Z = 1.98, *p* = 0.048, respectively), were higher in rustic systems than in polyculture systems. We also found a trend towards a higher abundance of Formicidae (Z = 1.67, *p* = 0.095) in rustic systems than in polyculture systems. Polyculture systems tended to have a higher abundance of Coleoptera (Z = −1.94, *p* = 0.053), Hemiptera (Z = −1.75, *p* = 0.081), and Hymenoptera with the function of biological control (Z = −1.74, *p* = 0.083) and a higher richness of Coleoptera (Z = −1.84, *p* = 0.067) than rustic systems.

4. Discussion

4.1. The Effect of Cropland Management

Overall, we found that the abundance and richness of invertebrate taxa were positively influenced by increasing canopy cover, crop and tree richness, and/or yields. This supports the habitat heterogeneity hypothesis that indicates that increased habitat complexity promotes higher invertebrate species richness and abundance. This finding, explored in more detail below, indicates the importance of habitat complexity and diversity when aiming to achieve a biodiverse landscape and preserve the provision of ecosystem services by invertebrate species.

Increased canopy cover had a significant impact on the abundance and richness of several invertebrate taxa. First, the total abundance of invertebrates increased with increased canopy cover, and within invertebrates, Coleoptera, non-pest Diptera, and Formicidae abundance significantly increased. Furthermore, alongside increased abundance, we found an increased richness in Coleoptera and Formicidae. The observed increase in invertebrate abundance with increased canopy cover is well documented within the literature (e.g., [6]), yet the response of Dipteran populations within high canopy cover systems remains contested, as Dipterans have been found to either be unaffected or negatively affected by increasing shade [42–44]. The optimization of non-pest Dipteran populations is beneficial for agroforestry environments through their emerging roles as important pollinators of crops, such as cacao [45]. Increased canopy cover not only indicates increased strata and floristic diversity within this context, but high canopy cover also bolsters ecosystems against climate change due to the creation of microclimates [46]. This in turn helps to preserve phenological synchronies between invertebrate species and crop/non-crop species. Additionally, tropical ectotherms are particularly sensitive to temperature changes, and temperature extremes can significantly affect ant assemblages and herbivore–parasitoid interactions [47–49]. Although the impact of canopy cover on crop productivity is debated within the literature and within general farming rhetoric, there seems to be a general consensus on intermediate levels of canopy cover (~30%) optimizing crop productivity in agroforestry systems while also providing a sufficient habitat for preserving biodiversity [6,50,51].

We found that tree richness was a significant factor in determining the abundance of Coleoptera, Hemiptera, Orthoptera, and species of Hymenoptera important in the provision of biological control; with increased tree richness, the abundance of these taxa increased. Similarly, the abundance of Hymenopterans important for biological control also increased with crop richness. This is in line with Sperber et al. [52], who found that parasitoid family numbers increased with increasing tree richness and remarked that parasitoid numbers found in a cacao-agroforestry system were equal to those of the associated forest biome. This is likely due to increased access to floristic resources and nest sites associated with increased tree and crop richness but also due to the high abundance of other invertebrate species [53]. Our finding is further bolstered by Kök et al. [54], who explains that the

use of non-crop plant species within agricultural environments can support conservation biological control. The preservation of the abundance of Hymenopterans contributing to biological control, many of which are parasitoids, is essential within complex polyculture and rustic systems, as by promoting invertebrate abundance and richness through agroecological practices, populations of crop pest species can also increase, as we found with the populations of Coleoptera (which included potential pests such as individuals from the families Chrysomelidae, Ptinidae, and Scarabaeidae), Hemiptera (in the study area, we found individuals from families that are considered pests, such as Dictyopharidae, Fulgoridae, Pentatomidae, and the subfamily Triatominae), and Orthoptera [53,55,56]. Therefore, ensuring the presence of agents of biological control is key to maintain productivity and safeguard farmers' incomes, particularly as tree productivity has been found to increase with the increased abundance of parasitoids [57,58].

In addition to the increased abundance of Hymenopterans important for biological control with increased crop richness, Zygentoma abundance and Hemiptera richness was also significantly higher. These taxa are important in the digestion of organic matter, and as a result, they play a key role in nutrient cycling. Additionally, in a recent study by Kurniawan et al. [59], when comparing conventional and agroforest systems, they found that Zygentoma were entirely absent in conventional croplands, indicating a sensitivity to agrochemicals. It is unsurprising to see significantly higher Hemiptera richness with increasing crop richness, as Hemiptera are significant crop pests. However, it is diverse polycultures that are most resistant to pests, and with increased complexity comes increased populations of natural predators [52,53]. It is no coincidence that Hymenoptera with the function of biological control (mainly predator wasps) were co-aligned with Hemiptera in a predator–prey scenario. Furthermore, we expected to see an increase in soil-dwelling detritivore abundance with increased crop richness, as there would be greater access to shelter and food through the abundance of plant debris found in complex polyculture and rustic systems and potentially higher soil quality due to diverse root systems allowing for greater sources of belowground C and ambient oxygen, enhancing resource availability [60–62].

We found that the abundance and richness of several taxa of invertebrates and invertebrates as a whole increased with yields. Within the context of this study site, yields are a measure of how complex the plot is (in terms of variety and the number of plants of different crops) rather than the intensity of management. Therefore, the increased invertebrate abundance observed in plots with high yields is likely to be due to the mixed strata created by the presence of a diverse array of crops, both in terms of above-soil and below-soil. This is in line with Stenchly et al.'s [63] finding that in cocoa-agroforest farms, across three levels of management, spider abundance was positively influenced by the presence of understory and herbaceous crops, indicating the importance of multi-strata systems. This is further backed up by Staton et al.'s [58] finding that natural enemy abundance was higher when farming systems contained flowering understory, represented by herbaceous crops and understory trees within our field site. Concurrent to this finding, they reported reduced aphid colonies and aphid-damaged fruits, indicating the importance of multi-strata agroforestry systems in maintaining the provision of vital ecosystem services [58]. Increases in invertebrate abundance and richness are unsurprising when considering increased yields, particularly with regards to Blattodea, Hemiptera, and Hymenoptera richness, all of which have been found to be significant crop pests due to them feeding on leaves and the eggs of other insects. However, these species have also been found to occasionally pollinate economically important plants and contribute to the decomposition of organic matter [13]. Preserving farmer income is essential in promoting agroecological practices, and this is a clear example of how increased biodiversity and increased vegetation does not threaten productivity but in fact bolsters it.

An important factor shaping our results is the presence of extensive, protected forest in close proximity to the field site and the controlled and regulated use of the primary forest to produce commodity crops, as echoed by Philpott et al. [64]. Not only does this contribute to Indonesia's sustainable development goals, but the preservation of its

biodiversity helps to safeguard Indonesia's rich cultural heritage, of which wildlife and the environment contribute significantly [65]. Though we were investigating the effect of management on invertebrate taxa abundance and richness, the presence of these taxa will inevitably be contributing to the preservation of the rich and diverse rustic systems in which they also depend through pollination and nutrient cycling. Furthermore, as mentioned previously, agroforestry systems are capable of increasing the resilience of ecosystems against climate change through carbon sequestration; the creation of microclimates for temperature-sensitive crops, such as coffee; and physically bolstering environments against the increased likelihood of extreme weather events [66,67]. It is also important to note that some taxa (mainly considered as pests or biocontrol agents, i.e., Coleoptera, Hemiptera, and Hymenoptera with the function of biological control) were more prevalent in polyculture systems than in rustic systems, supporting the idea that complex agriculture systems without natural shade tree cover can sustain similar levels of biodiversity than rustic systems and forested areas [68,69] and that more complex habitats (i.e., rustic systems) host less pests [13,31].

4.2. Study Limitations

While we are confident that the design of our study gave us the opportunity to effectively assess the impact of management intensity on invertebrate biodiversity, we would like to highlight the following potential shortfalls of our investigation. First, the data collection methods could have led us to underestimating flying invertebrate richness and abundance, especially pollinators, due to the exclusive use of pitfall and pan traps. In addition to pan traps, other methods (e.g., net sampling, pollard transects, etc.) would have been complementary [70]. Furthermore, different taxa have different color preferences, and using a higher variety of colors for pan traps may have increased the breadth of the invertebrate richness we sampled [37,71]. Second, the time of the re-collection of pitfall traps is usually longer (e.g., 24 h [72]); thus, our method might have underestimated species richness and abundance if compared to other sites. Nevertheless, the aim of our study was to compare different management conditions, not to provide an exhaustive assessment of invertebrate assemblages. Third, we are missing contrasting conditions, such as intensive monocultures and non-productive areas. Taking this into account, we plan to expand our investigation to nearby sites around the West Bali National Park. The fact that all plots were taken from a healthy environment meant that we controlled for potential environmental and site-specific confounding factors.

5. Conclusions

From this study and the extensive associated literature, it is clear that agroforestry systems, such as the polyculture croplands and production forest of Yeh Embang Kauh, can positively influence the abundance and richness of invertebrates through increasing habitat complexity, i.e., increased planted (tree/crop) diversity and canopy cover, thus helping to conserve biodiversity. Through our research, we can also conclude that the abundance and richness of certain invertebrate taxa, including agents of biocontrol, were shown to increase in plots with higher yields, thus solidifying the important role of invertebrate communities in the provision of ecosystem services. Through close regulations and support from the provincial government forestry authority (KPH) and other government organizations, harvesting crops from these systems ensures a sustainable income for the local community, which encourages them to continue these practices while also engaging farmers with local conservation, of which they can be the champions.

Appendix A

Table A1. Full results of the generalized linear models to explain the factors influencing the abundance and richness of invertebrates in 53 agroforestry plots in Bali, Indonesia.

Response	Predictor	Coefficient	Std Error	Z Value	*p*-Value
Araneae (abundance)	Intercept	0.582	0.498	1.17	0.242
	Canopy cover	-0.005	0.007	-0.71	0.478
	Crop richness	0.010	0.085	0.11	0.909
	Habitat [a]	0.361	0.397	0.91	0.363
	Tree richness	0.042	0.085	0.49	0.623
	Yields (USD)	4.3×10^{-4}	3.3×10^{-4}	1.29	0.196
Araneae (richness)	Intercept	0.795	0.528	1.51	0.132
	Canopy cover	0.000	0.007	0.01	0.989
	Crop richness	-0.169	0.099	-1.69	0.090
	Habitat [a]	0.000	0.419	0.00	0.999
	Tree richness	-0.009	0.010	-0.09	0.929
	Yields (USD)	4.7×10^{-4}	3.0×10^{-4}	1.56	0.120
Blattodea (abundance)	Intercept	-0.198	1.446	-0.14	0.891
	Canopy cover	0.004	0.015	0.26	0.794
	Crop richness	-0.305	0.268	-1.14	0.255
	Habitat [a]	0.989	0.915	1.08	0.279
	Tree richness	-0.057	0.192	-0.30	0.768
	Yields (USD)	6.5×10^{-4}	4.3×10^{-4}	1.53	0.125
Blattodea (richness)	Intercept	-1.149	1.296	-0.89	0.375
	Canopy cover	0.006	0.014	0.43	0.668
	Crop richness	-0.234	0.235	-1.00	0.319
	Habitat [a]	0.939	0.896	1.05	0.295
	Tree richness	-0.004	0.177	-0.02	0.983
	Yields (USD)	7.0×10^{-4}	4.2×10^{-4}	1.65	0.099
Coleoptera (abundance)	Intercept	-1.454	1.056	-1.37	0.169
	Canopy cover	0.027	0.013	2.07 *	0.038
	Crop richness	0.006	0.161	0.04	0.971
	Habitat [a]	-2.136	1.103	-1.94	0.053
	Tree richness	0.415	0.210	1.98 *	0.048
	Yields (USD)	-5.8×10^{-4}	9.9×10^{-4}	-0.58	0.562

Table A1. *Cont.*

Response	Predictor	Coefficient	Std Error	Z Value	*p*-Value
Coleoptera (richness)	Intercept	−1.590	1.083	−1.47	0.142
	Canopy cover	0.029	0.014	2.02 *	0.043
	Crop richness	0.019	0.165	0.12	0.907
	Habitat [a]	−2.113	1.152	−1.84	0.066
	Tree richness	0.358	0.227	1.58	0.114
	Yields (USD)	-5.0×10^{-4}	10.0×10^{-4}	−0.50	0.619
Dermaptera (abundance)	Intercept	−2.954	1.627	−1.82	0.070
	Canopy cover	0.028	0.020	1.42	0.154
	Crop richness	0.165	0.238	0.69	0.488
	Habitat [a]	−0.090	1.246	−0.07	0.942
	Tree richness	0.067	0.306	−0.22	0.827
	Yields (USD)	-0.1×10^{-4}	10.8×10^{-4}	−0.01	0.990
Dermaptera (richness)	Intercept	−3.809	1.674	−2.28 *	0.023
	Canopy cover	0.015	0.019	0.82	0.413
	Crop richness	0.308	0.237	1.30	0.193
	Habitat [a]	−0.191	1.341	−0.14	0.887
	Tree richness	0.131	0.273	0.48	0.631
	Yields (USD)	-1.3×10^{-4}	11.1×10^{-4}	−0.12	0.907
Diptera-pest (abundance)	Intercept	1.162	0.593	1.96	0.050
	Canopy cover	−0.002	0.008	−0.29	0.772
	Crop richness	0.039	0.102	0.39	0.700
	Habitat [a]	0.037	0.555	0.07	0.947
	Tree richness	0.025	0.118	0.21	0.830
	Yields (USD)	-4.4×10^{-4}	4.3×10^{-4}	−1.03	0.305
Diptera-pest (richness)	Intercept	0.019	0.573	0.03	0.973
	Canopy cover	0.001	0.007	0.10	0.923
	Crop richness	0.051	0.096	0.53	0.594
	Habitat [a]	−0.163	0.484	−0.34	0.737
	Tree richness	0.060	0.104	0.58	0.565
	Yields (USD)	-4.1×10^{-4}	4.3×10^{-4}	−0.94	0.349
Diptera-non pest (abundance)	Intercept	1.974	0.811	2.43 *	0.015
	Canopy cover	0.020	0.009	2.30 *	0.021
	Crop richness	−0.160	0.143	−1.11	0.265
	Habitat [a]	−0.723	0.645	−1.12	0.262
	Tree richness	0.042	0.142	0.30	0.767
	Yields (USD)	-7.6×10^{-4}	7.9×10^{-4}	−0.97	0.334
Diptera-non pest (richness)	Intercept	−0.256	0.672	−0.38	0.704
	Canopy cover	0.012	0.008	1.42	0.128
	Crop richness	−0.011	0.111	−0.10	0.922
	Habitat [a]	−0.169	0.544	−0.31	0.757
	Tree richness	0.040	0.116	0.35	0.729
	Yields (USD)	-5.1×10^{-4}	5.3×10^{-4}	−0.95	0.342
Hemiptera (abundance)	Intercept	−0.640	0.908	−0.71	0.481
	Canopy cover	0.008	0.011	0.69	0.491
	Crop richness	0.084	0.152	0.55	0.580
	Habitat [a]	−1.312	0.752	−1.75	0.081
	Tree richness	0.485	0.165	2.93 **	0.003
	Yields (USD)	10.5×10^{-4}	5.5×10^{-4}	1.92	0.055
Hemiptera (richness)	Intercept	−1.641	0.777	−2.11 *	0.035
	Canopy cover	0.009	0.009	1.03	0.305
	Crop richness	0.160	0.115	1.39	0.165
	Habitat [a]	−0.743	0.644	−1.15	0.249
	Tree richness	0.329	0.126	2.62 **	0.009
	Yields (USD)	3.5×10^{-4}	4.0×10^{-4}	0.86	0.389
Hymenoptera-biological control (abundance)	Intercept	−0.593	0.910	−0.65	0.515
	Canopy cover	−0.023	0.011	−1.99 *	0.046
	Crop richness	0.281	0.146	1.92	0.055
	Habitat [a]	−1.376	0.793	−1.74	0.083
	Tree richness	0.533	0.163	3.26 **	0.001
	Yields (USD)	8.7×10^{-4}	5.1×10^{-4}	1.69	0.091

Table A1. *Cont.*

Response	Predictor	Coefficient	Std Error	Z Value	*p*-Value
Hymenoptera-biological control (richness)	Intercept	−0.028	0.662	−0.04	0.966
	Canopy cover	−0.009	0.009	−0.98	0.327
	Crop richness	−0.016	0.117	−0.14	0.892
	Habitat [a]	−0.519	0.582	−0.89	0.373
	Tree richness	0.159	0.127	1.25	0.213
	Yields (USD)	6.8×10^{-4}	2.8×10^{-4}	2.41 *	0.016
Hymenoptera-Formicidae [b] (abundance)	Intercept	1.354	0.606	2.23 *	0.026
	Canopy cover	0.017	0.008	2.13 *	0.033
	Crop richness	0.070	0.109	0.64	0.519
	Habitat [a]	0.887	0.546	1.67	0.095
	Tree richness	0.074	0.118	0.63	0.530
	Yields (USD)	8.0×10^{-4}	3.1×10^{-4}	2.56 *	0.011
Hymenoptera-Formicidae [b] (richness)	Intercept	0.493	0.260	1.90	0.058
	Canopy cover	0.008	0.003	2.37 *	0.018
	Crop richness	0.011	0.043	0.26	0.792
	Habitat [a]	−0.117	0.222	−0.53	0.598
	Tree richness	0.071	0.050	1.43	0.153
	Yields (USD)	2.1×10^{-4}	1.9×10^{-4}	1.12	0.263
Isopoda (abundance)	Intercept	−1.286	1.931	−0.67	0.506
	Canopy cover	0.008	0.018	0.43	0.667
	Crop richness	−0.217	0.312	−0.69	0.487
	Habitat [a]	0.417	1.454	0.29	0.774
	Tree richness	0.233	0.232	1.00	0.317
	Yields (USD)	-7.7×10^{-4}	14.7×10^{-4}	−0.53	0.598
Isopoda (richness)	Intercept	−1.340	1.823	−0.74	0.462
	Canopy cover	0.010	0.019	0.56	0.578
	Crop richness	−0.330	0.319	−1.04	0.300
	Habitat [a]	0.271	1.483	0.18	0.855
	Tree richness	0.195	0.241	0.81	0.418
	Yields (USD)	-9.4×10^{-4}	16.7×10^{-4}	−0.56	0.575
Orthoptera (abundance)	Intercept	0.862	0.525	1.64	0.101
	Canopy cover	−0.006	0.007	−0.81	0.417
	Crop richness	−0.003	0.090	−0.03	0.974
	Habitat [a]	−0.662	0.451	−1.47	0.142
	Tree richness	0.208	0.094	2.22 *	0.026
	Yields (USD)	1.4×10^{-4}	4.2×10^{-4}	0.03	0.973
Orthoptera (richness)	Intercept	0.198	0.630	0.31	0.753
	Canopy cover	0.008	0.008	1.04	0.298
	Crop richness	−0.090	0.109	−0.82	0.410
	Habitat [a]	−0.745	0.549	−1.36	0.175
	Tree richness	0.163	0.116	1.40	0.162
	Yields (USD)	1.2×10^{-4}	3.9×10^{-4}	0.31	0.755
Talitridae (abundance)	Intercept	−1.559	1.498	−1.04	0.298
	Canopy cover	−0.011	0.016	−0.71	0.478
	Crop richness	0.164	0.241	0.68	0.495
	Habitat [a]	1.911	0.880	2.17	0.030
	Tree richness	−0.243	0.193	−1.26	0.208
	Yields (USD)	8.7×10^{-4}	4.0×10^{-4}	2.17 *	0.030
Talitridae (richness)	Intercept	−2.015	1.638	−1.23	0.219
	Canopy cover	−0.017	0.020	−0.85	0.397
	Crop richness	0.131	0.279	0.47	0.639
	Habitat [a]	2.415	1.221	1.98 *	0.048
	Tree richness	−0.386	0.282	−1.37	0.171
	Yields (USD)	6.2×10^{-4}	11.1×10^{-4}	0.56	0.578
Zygentoma (abundance)	Intercept	−2.372	0.987	−2.40 *	0.016
	Canopy cover	0.003	0.012	0.27	0.790
	Crop richness	0.306	0.152	2.02 *	0.044
	Habitat [a]	0.267	0.791	0.34	0.736
	Tree richness	0.124	0.163	0.76	0.446
	Yields (USD)	1.8×10^{-4}	7.1×10^{-4}	0.26	0.799

Table A1. *Cont.*

Response	Predictor	Coefficient	Std Error	Z Value	*p*-Value
Zygentoma (richness)	Intercept	−1.720	1.360	−1.26	0.206
	Canopy cover	0.000	0.017	0.00	0.998
	Crop richness	0.196	0.227	0.86	0.387
	Habitat [a]	0.227	1.057	0.21	0.830
	Tree richness	0.125	0.237	0.53	0.597
	Yields (USD)	5.0×10^{-4}	10.3×10^{-4}	0.48	0.629
Total abundance	Intercept	2.682	0.409	6.56 **	<0.001
	Canopy cover	0.011	0.006	2.02 *	0.044
	Crop richness	0.036	0.075	0.48	0.634
	Habitat [a]	0.334	0.387	0.86	0.389
	Tree richness	0.101	0.085	1.19	0.233
	Yields (USD)	6.3×10^{-4}	2.2×10^{-4}	2.80 **	0.005
Total richness	Intercept	2.098	0.236	8.89 **	<0.001
	Canopy cover	0.004	0.003	1.48	0.139
	Crop richness	0.003	0.040	0.07	0.942
	Habitat [a]	−0.221	0.192	−1.16	0.248
	Tree richness	0.095	0.042	2.28 *	0.023
	Yields (USD)	2.0×10^{-4}	1.9×10^{-4}	1.04	0.298

[a] reference category: rustic; [b] Oecophyllini are included in the biological control category; * $p < 0.05$; ** $p < 0.01$.

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