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Plant Diversity Increased Arthropod Diversity and Crop Yield in Traditional Agroforestry Systems but Has No Effect on Herbivory

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Abstract: Improving agricultural production in response to the increasing food demand remains a major challenge in agroecology. The world has made significant efforts to meet this issue by developing several cultivation techniques, such as the use of chemical fertilizers and arable land conversion into agricultural land. However, most of these techniques have caused a significant loss of biodiversity and ecosystems services. Recent data suggest that biological conservation within and around agroforestry systems are potential solutions that can both reduce biodiversity loss and guarantee crop production. This logic is based on the hypothesis that increasing plant diversity in and around agricultural systems can limit the pest attack rate and increase crop yield. We tested this hypothesis using structural equation modeling on empirical data collected in agroforestry systems around the Pendjari biosphere reserve in West Africa. We measured crop diversity, crop yield, arthropod pest diversity, abundance, the rate of crop herbivory, and the diversity of plants in surrounding natural vegetation in 32 permanent plots. We estimated arthropod diversity and abundance using pitfall traps. We found a direct positive effect for plant diversity and a direct negative effect of arthropod herbivory on crop yield. The diversity of plants in surrounding natural vegetation had a direct positive effect on arthropod pest diversity but a marginal negative direct effect on the rate of crop herbivory. We found no significant direct or indirect effect for crop diversity. Our findings underline the important role of biodiversity conservation in agricultural production improvement. We suggest that the conservation of plant diversity around agroforestry systems may be an effective option to control herbivory damage. Its combination with other pest control techniques may further limit crop depredation and ensure the long-term conservation of wildlife.

Keywords: diversity in human modified landscape; agrobiodiversity; pest control; crop yield; theory of biotic resistance; agroecology



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1. Introduction

Improving global agricultural productivity is a major concern in the current context of increasing food demand [1–3]. In recent decades, advanced agricultural practices focusing on increased crop productivity rather than increasing arable land led to the improvement of world food production. For example, the development of effective cropping techniques, including soil fertility management, agricultural intensification, crop rotation, and genetic selection contributed to increased world food production [4–7]. World production of cereals, oilseeds, fruits and vegetables has increased by 47% [8], with an overall yield increase of 25% on only a 7% increase in crop land [2]. However, the increase in world food production seems to overlap with non-food production.

Globally, 62% of the world crop production is used for human food, 35% for livestock, and 3% for bioenergy, seeds, and other industrial products, with a remarkable disparity

between regions [9,10]. Because most of the increase in world food production requires increasing land conversion and deforestation instead of agricultural intensification [11,12], the gain that is made on ensuring food security is accompanied with a significant loss of biodiversity [13–18]. An important sustainability debate has focused on how to mitigate the increasing demand of land for agricultural purposes and the opportunity to share vs. spare land to achieve both biodiversity conservation and sustainable use of these lands [19–24]. The rationale behind land-sparing is centered around the urgency to conserve biological diversity in the current context of increased extinction of species and rapid biodiversity loss. Thus, sparing lands to provide habitat refuge for vulnerable and endangered species is considered a valuable land-use form, as converting these lands into pasture or crop thereby erodes the fundamental basis for sustainable agriculture [24]. Land-sharing promotes ecosystem services by integrating several land-use forms on limited land with the goal of liberating other lands for biodiversity conservation [22]. Such intensification of agricultural land use focuses on promoting agrobiodiversity as a mitigating strategy.

Consequently, the role of remnant natural vegetation and plant diversity in agricultural systems in improving crop yield with limited chemical inputs has received increasing attention [25]. Plant diversity in agricultural systems provides functional diversity that can limit the spread of pathogens and pests and promote beneficial insects for efficient biological control and pollination services [26–30]. Sustainable production of food in poor or developing countries therefore requires diversified agro-ecosystems to control crop herbivory [25,26,31]. Despite the increasing human-mediated environmental filtering and loss of biodiversity, our understanding of the role of diversity in agroecological systems on human nutrition and health [32,33] and on ecosystem services is still limited but increasing [34,35]. In addition, our understanding of how mixed farming affects crop yield is limited. However, previous studies have shown that plant diversity in natural ecosystems or agricultural systems can improve agricultural production [3,36–38] due to niche complementarity [39–41].

In this study, we tested the biotic resistance hypothesis that biodiversity mitigates damage caused by pests and increases productivity [33]. Specifically, we used structural equation modeling (SEM) to examine the relative roles of plant diversity in natural vegetation and in agroforestry systems on crop yield and how such effects are mediated by reduced crop herbivory. Structural equation modelling [42] is a powerful statistical tool that combines in a single causal network several predictor and response variables [43]. We hypothesized that plant diversity would increase the diversity of arthropod pests and indirectly decrease crop yield by increasing pest herbivory rates due to diverse arthropod communities. We hypothesized a stronger indirect effect of plant diversity than a direct effect on crop yield. We highlighted how the degree of connectivity between natural landscapes, which house a rich diversity and abundant insect community, and agricultural landscapes during the growing season can influence the productivity of agroforestry systems [44,45].

2. Materials and Methods

2.1. Study Area

The Pendjari Biosphere Reserve covers 4661.4 km² and is located in the northwest of Benin between 10°30' N–11°30' N and 0°50'–2°00' E. The annual rainfall ranges from 1000 to 1100 mm, with an average annual temperature of 27 °C (21–40 °C) [46]. The rainy season lasts nearly five months, from mid-May to October, followed by a dry season from November to February. The Biosphere reserve is organized into three main zones: a core area or protected zone (The Pendjari National Park), a buffer zone, and a transition zone, where sustainable agriculture is permitted. The Pendjari Biosphere Reserve is dominated by woodland, tree, shrub, and grassy savannas. The most abundant plant species include *Anogeissus leiocarpa*, *Combretum* spp., *Pterocarpus erinaceus*, *Acacia gourmaensis*, *Crossopteryx febrifuga*, *Detarium microcarpa*, *Burkea africana*, and *Terminalia macroptera* in the savanna. *Pari-nari congensis* and *Pterocarpus santalinoides* are the main plant species in riparian forests and

Khaya senegalensis and *Vitex chrysocarpa* in gallery forests [47]. Wildlife is mainly dominated by Kob, *Kobus kob* (9.65 individuals/km²), and western buffaloes (5.91 individuals/km²), with species such as the cheetah and the waterbuck rare in the reserve [48]. In the transition zone of the Biosphere reserve, farmers practice traditional agroforestry systems established on poorly developed tropical ferruginous and hydromorphic soils [49]. Plant communities in the transition zone are increasingly degraded by a rapidly growing population [50]. A population growth rate of 36.79% was recorded from 2000 to 2013.

The Pendjari hunting zone is bordered by two main roads (Tanguieta–Batia road, and the Tanguieta–Porga road), which serve as a clear border for the Biosphere reserve. Along the two main roads and inside the Pendjari hunting zone, local populations establish traditional agroforestry systems and are authorized to gather non-timber forest products within the first 5 km perpendicular to the roads [51]. Along the two roads, three main ethnic groups are established: the Berba, which accounts for 65% of the population along the northwestern side, and the Wama and Gourmantche, which account for 30% and are established along the northeastern side [52]. Farm extensions in the area occupied by the Wama–Gourmantche are constrained by the Atacora chain of mountains, which have unsuitable soil for agriculture. Traditional agroforestry systems in the region occupied by the Berba are more diversified than that of the Wama–Gourmantche [50].

2.2. Measuring Plant, Arthropod Diversity, and Crop Yield

To test the effects of wild (non-crop) plant and crop diversity on arthropod diversity, crop herbivory rate, and yield, we randomly sampled 32 traditional agroforestry systems and 8 surrounding natural habitats within 100 m from the edge of agroforestry systems. Within each agroforestry system or adjacent natural vegetation, we established a 30 × 30 m plot to survey and record every plant species in the plot. Adult tree species with a diameter at breast height (dbh) ≥ 5 cm were counted within each plot, and the species in lower vegetation layers (dbh < 5 cm), including herbs, were counted within five 5 m × 5 m quadrats (one quadrat in the center and four in the corners of the plot). Plant diversity in agroforestry systems and adjacent vegetation was simply estimated as species richness.

Arthropods are both pests and beneficial components of agricultural systems [29,53–55]. As such, they can cause crop damage through herbivory but also serve as predators of insect herbivores, thereby providing beneficial services that can increase crop yield. It is estimated that 30–40% of crop yield is lost to pests [22]. Arthropod diversity and abundance can be influenced by neighboring vegetation [55,56]. We measured arthropod diversity and abundance, particularly the differences between functional groups, to investigate how arthropods can affect crop herbivory in traditional agroforestry systems. To measure arthropod abundance and diversity in soil and litter, we installed in each plot 36 pitfall traps, each filled with soapy water. These traps were spaced 5 m apart, and arthropods were collected 72 h after the traps were set in the morning and conserved in alcohol prior to species identification. A total of 1152 pitfall traps were used for the 32 30 × 30 m plots. Arthropod species were identified (Table 1) by the entomology laboratory at the University of Parakou (Parakou, Benin), and the number of individuals of each species was counted. For species that were not directly identified, a morphotype was attributed to each individual arthropod, according to their morphological aspects, for an in-depth species determination [57].

The rate of crop herbivory was measured as the percentage of crop leaves damaged by pests 8 weeks after the period of seed sowing in these farms. To estimate crop yield, we selected maize and sorghum because they represent the main food source for local population in the study area [58]. For each of the 32 agroforestry parklands, we visited the farmers at the end of the farming season during the crop harvesting period to estimate the quantity of maize and sorghum harvested. To estimate crop yield for maize and sorghum, farmers harvest corn cobs and sorghum panicle when they are dry. The corns were then shelled after 14 days and the grain removed from the cob. Because this process is performed using traditional machines, and each farmer paid CFA 500 (~USD 1) per 100 kg, we were

able to confirm the production based on the money that they paid. The sorghum panicle was also sun dried and winnowed to obtain the grains. The grains were put in a container and then weighed. We estimated the size of each of the 32 farms in hectares and used this to estimate the total weight for both corn and sorghum in kilogram per unit of hectare. This was used as our estimate of crop yield [59,60].

Table 1. List of arthropods collected in pitfall traps in the agroforestry systems around the Pendjari Biosphere Reserve.

Scientific Name	Family	Order	Trophic Group
<i>Oplostomus fuliginus</i>	Scarabaeidae	Coleoptera	Omnivore
<i>Ctenicera destructor</i>	Elateridae	Coleoptera	Herbivore
<i>Gryllus</i> sp.	Grillidae	Orthoptera	Herbivore
<i>Smicronyx fulvus</i>	Curculionidae	Coleoptera	Herbivore
<i>Zonocerus variegatus</i>	Pyrgomorphidae	Orthoptera	Herbivore
<i>Toxoptera citricida</i>	Aphididae	Hemiptera	Herbivore
<i>Blaniulus guttulatus</i>	Blaniulidae	Diplopoda	Herbivore (roots)
<i>Locusta migratoria</i>	Acrididae	Orthoptera	Herbivore
<i>Cerotoma arcuata</i>	Chrysomelidae	Coleoptera	Herbivore
<i>Stenaptinus insignis</i>	Carabidae	Coleoptera	Herbivore
<i>Tachyura parvula</i>	Carabidae	Coleoptera	Necrophage
<i>Polydesmus</i> spp.	Polydesmidae	Diplopoda	Herbivore (roots)
Caterpillar	Papilionidae	Lepidoptera	Herbivore
<i>Trichopluchia ni</i>	Noctuidae	Lepidoptera	Herbivore
<i>Schistocerca gregaria</i>	Acrididae	Orthoptera	Herbivore
<i>Ichneumonide</i>	Ichneumonidae	Hymenoptera	Carnivore
<i>Dysdercus</i> sp.	Pyrrhocoridae	Heteroptera	Nectarivore
<i>Vanessa cardui</i>	Nymphalidae	Lepidoptera	Nectarivore
<i>Diabrotica virgifera</i>	Chrysomelidae	Lepidoptera	Herbivore
<i>Blaniulus</i> sp.	Blaniulidae	Myriapoda	Detritivore
<i>Schistocerca</i> sp.	Acrididae	Orthoptera	Herbivore
<i>Helicoverpa armigera</i>	Noctuidae	Lepidoptera	Herbivore
<i>Nymphalis polychloros</i> (larvae)	Nymphalinae	Lepidoptera	Herbivore
<i>Geotrupes stercorarius</i>	Geotrupidae	Coleoptera	Coprophage

2.3. Statistical Analysis

To test the effect of plant species richness (agroforestry systems and adjacent vegetation) on arthropod abundance, we used a generalized linear model with a negative binomial error structure, given the overdispersion of the arthropod abundance. We used the package *boot* [61] to conduct a bootstrap regression to test the effects of plant species richness on arthropod diversity (number of arthropods species). We used a simple linear model to test the effect of plant species richness (agroforestry system and adjacent vegetation) on crop yield. The central goal of this study was to elucidate the mechanistic role that plant diversity mediated by the effect on arthropods diversity and abundance and the resulting changes in crop herbivory rate in driving crop yield. For this purpose, we used the R package *lavaan* [62] to develop a structural equation model [43] to test the direct or indirect effects of plant diversity in agroforestry systems and adjacent vegetation on arthropod diversity and how this affected crop herbivory rate and crop yield. Structural equation models (SEM) are probabilistic models used to fit a single network of hypotheses to data that include several predictors and response variables [43]. SEM relies on causal assumptions between variables [63,64]. All statistical tests were performed in R 3.5.1.

3. Results

In the agroforestry systems, we identified 24 arthropod species, which belong to 16 families and 8 orders (Table 1). The arthropod community was dominated by coleoptera (29%), lepidoptera (25%), and orthoptera (21%). Herbivores represented 71% of the species. Nearly 75% of these arthropods were plant pests and were mostly adults. The arthropods that were pests for crops represented 25% of the total richness and were either at the larval or adult stages (Table 1). The crops mainly included maize, sorghum, and in some villages, millet, and cowpea. The minimum crop yield was 0.5 kg/ha, and the maximum was 6235 kg/ha (Table 2). In the agroforestry systems, we identified a total of eight species with *Vittelaria paradoxa* (70%) as the most dominant species, followed by *Parkia biglobosa* (20.8%) and *Lannea acida* (5%). Other plant species in the agroforestry system included

Anarcadium occidentale, *Sterculia setigera*, *Acacia polyacantha*, *Prosopis africana*, and *Monotes kerstingii*. In adjacent natural habitats, we identified 31 species, dominated similarly by *Vittelaria paradoxa* (30.5%) and *Parkia biglobosa* (8.5%), also including *Combretum fragrans* (7.6%), *Terminalia avicennioides* (6.8%), *Burkea africana* (5.9%), and *Sterculia setigera* (3.4%).

Table 2. Main variables for the structural equation model, including mean, median, and standard deviation (SD) for arthropod number and diversity, crop yield, richness, total plant diversity, and herbivory rates. The number of sites sampled to estimate these variables is also indicated.

	Arthropod Abundance	Arthropod Richness	Crop Yield (kg/ha)	Total Plant Richness	Crop Richness	Herbivory Rate (%)
Minimum	1	1	0.5	6	2	1.34
Median	9.5	4	550	11.5	3.5	2.96
Mean	13.2	4.7	828.9	10.8	3.7	3.02
Maximum	47	13	6250	14.0	6	4.52
SD	11.2	3.4	1155.9	2.5	1.03	0.97
Sample size	32	32	32	32	32	14

Total plant diversity had significant effect on crop yield and arthropod diversity (Figure 1). Arthropod diversity increased non-linearly with arthropod abundance ($\beta = 0.04 \pm 0.75$; Figure 2A) but slightly decreased with plant diversity in the surrounding natural vegetation ($\beta = 0.36 \pm 0.12$; $p = 0.01$; Figure 2B). We found no significant effect of crop diversity in agroforestry systems on the rate of herbivory ($\beta = -0.06 \pm 0.16$, $p = 0.71$; Figure 2C) and on crop yield (Figure 1, Table 3), but total surrounding plant diversity tended to increase crop yield ($\beta = 4.21 \pm 1.78$; $p = 0.02$, Figure 1) without a direct effect on herbivory rates (Figure 1). Similarly, arthropod diversity did not affect herbivory rates (Figure 1) or crop yield ($\beta = -0.64 \pm 3.09$, $p = 0.84$, Table 3). Surprisingly, crop diversity had no significant effect on arthropods diversity ($\beta = 0.06 \pm 0.28$; $p = 0.82$, Table 2), crop herbivory rate ($\beta = -0.04 \pm 0.21$, $p = 0.85$), or yield ($\beta = -1.06 \pm 2.35$, $p = 0.65$; Table 3, Figure 1). However, crop herbivory tended to significantly decrease crop yield ($\beta = -0.2 \pm 0.61$; Figures 1 and 2D).

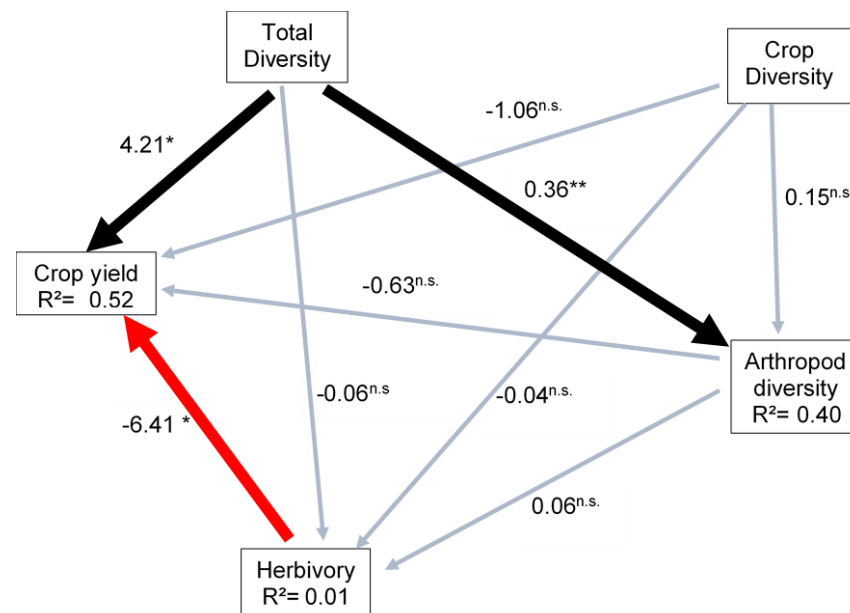


Figure 1. Structural equation model of the effects of plant diversity on crop yield, arthropod diversity and the negative effect of herbivory on crop yield in agroforestry systems. The thick black lines indicate positive relationships, the red line indicates negative relationships, and the gray lines non-significant relationships (n.s). * $p < 0.05$, ** $p < 0.01$. R^2 is the proportion of variance explained.

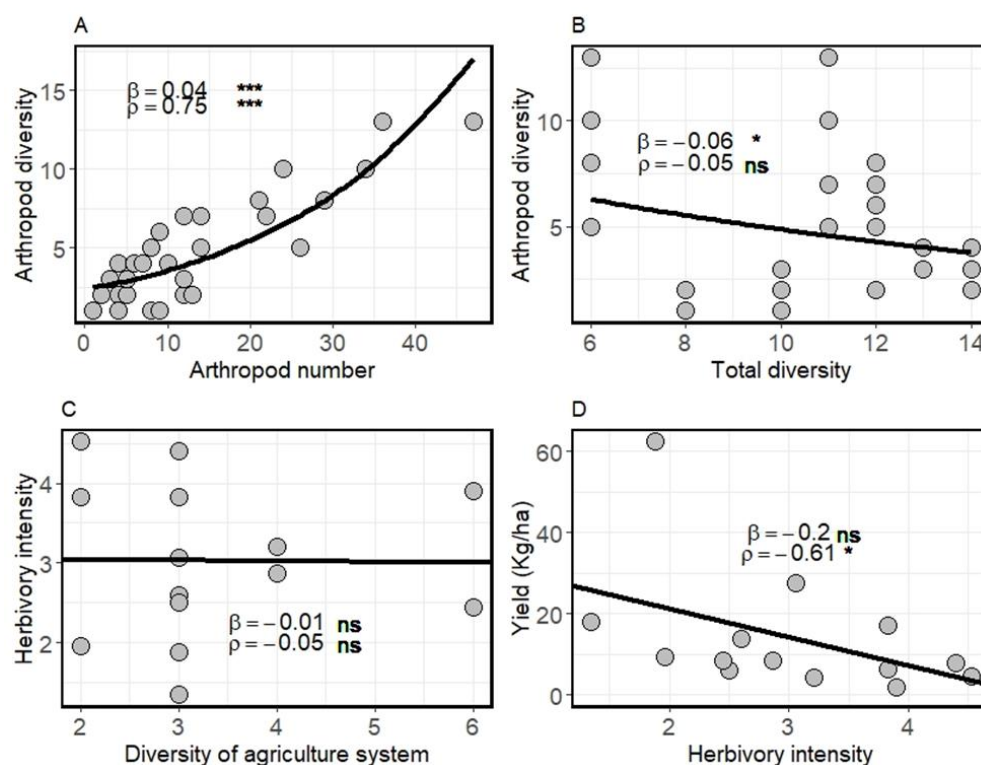


Figure 2. Effects of (A) arthropod abundance, (B) total diversity on arthropod diversity, effect of (C) crop diversity on crop herbivory intensity, and (D) the effect of herbivory intensity on crop yield. β is the slope of the regression and ρ is the Pearson correlation coefficient. Asterisks indicate * $p < 0.05$, *** $p < 0.001$ and ns: non-significant.

Table 3. Path coefficients of structural equation model (SEM) between response and explanatory variables of the functional diversity of natural systems and agroforestry systems and agricultural yield. The column “Std.all” shows the standardized all-path coefficients, and “Std.lv” shows path coefficients with only latent variables coefficients standardized.

Causal Relationships in the SEM	Estimate	SE	z	p	Std.lv	Std.all
Herbivory~Arthropod diversity	0.064	0.281	0.228	0.820	0.064	0.078
Herbivory~Crop diversity	−0.039	0.213	−0.184	0.854	−0.039	−0.052
Herbivory~Total diversity	−0.059	0.162	−0.366	0.714	−0.059	−0.130
Crop yield~Herbivory	−6.407	2.937	−2.181	0.029	−6.407	−0.402
Crop yield~Arthropod diversity	−0.635	3.099	−0.205	0.838	−0.635	−0.049
Crop yield~Crop diversity	−1.063	2.348	−0.453	0.651	−1.063	−0.088
Crop yield~Total diversity	4.210	1.784	2.360	0.018	4.210	0.540
Arthropod diversity~Total diversity	0.363	0.119	3.062	0.002	0.363	0.654
Arthropod diversity~Crop diversity	0.148	0.199	0.747	0.455	0.148	0.160

4. Discussion

We documented how plant and crop diversity can mediate the impact of arthropod diversity, abundance, and subsequent herbivory on crop yield in traditional agroforestry systems in a West African biosphere reserve. We hypothesized that crop yield will be positively associated with plant diversity in natural vegetation surrounding the agroforestry systems. We found no significant effect of crop diversity, but we found a significant positive influence of plant diversity around agroforestry systems on crop yield. These results add to the growing evidence that crop yield can benefit from the conservation of a range of different tree and shrub species within and around farms [32,65]. Consistent with the theory of biotic resistance, which suggests that increasing plant diversity will reduce crop damage caused by pests, one can expect an increase in the productivity and crop yield of agroforestry systems with higher diversity [33]. The increase in crop yield observed here can also be explained by the border spillover effect, where farms benefit

from the surrounding vegetation in terms of organic matter intake [60,66,67]. It may also result from the positive effects of microbial activity or ecosystem services efficiency. Our results revealed the presence of many decomposers belonging to Geotrupid family such as *Geotrupes stercorarius*, which are normally found in fresh dung, horse dung, and the droppings of different animals and beetles such as *Oplostomus fuliginus* (Table 1). Our results also highlight the importance of ecosystem services on agroecological systems.

One of the consequences of biological diversity is to maintain ecosystem services, including soil quality, pollination services, and pest control in agricultural systems [25]. We hypothesized that the positive effects of plant diversity on crop yield will be mediated by a negative direct effect on pest diversity and abundance, which is expected to cause increased crop herbivory rates. We found that plant diversity increased crop yield without reducing herbivory rate. However, arthropod pest diversity increased with diversity in surrounding natural vegetation, particularly with the predominance of Coleoptera and Lepidoptera larvae (Table 1). This contrasts with the prediction from the biotic resistance hypothesis [33] that plant diversity mitigates damage caused by pests. This result may be explained by the positive effect of plant diversity in surrounding habitats on positive ecological interactions such as crop pollination services due to pollinators' diversity and abundance in adjacent agroforestry systems [68,69]. Consistent with the associated resistance hypothesis, such diversity of neighbouring species could have mitigated herbivory damage by reducing the effect of specialized pests [70,71]. In addition, previous studies show that regional and agricultural biodiversity can decrease plant diseases and the proportion of grain-eating or fruit-eating animals in farms [44,72,73], which altogether can positively affect crop yield. The positive effect of plant diversity in surrounding habitats on arthropod diversity is perhaps due to the mitigating effect of a diverse surrounding habitat, which acts as a windbreak to limit agricultural pesticide spillover into agroforestry parklands and its negative effect on arthropod species [74,75]. In addition, arthropods encompass a wide range of species, including flying insect species, which can have positive and antagonistic interactions with crops. We did not record any flying arthropod species during our fieldwork, and this may explain the positive correlation between arthropod diversity or abundance and plant diversity in surrounding habitats [76,77].

Pest diversity can increase herbivory rate and reduce crop yield. However, in our study system, we found no significant direct or indirect effect of arthropod diversity on herbivory rate and on crop yield. Previous studies suggest that such lack of arthropod diversity effect may be due to pest specialization, environmental conditions, pest specificity, or the indirect effects of herbicide use in neighbouring fields [78–81]. The traditional agroforestry systems we studied in northern Benin were mixed systems composed of cereal crops, yam fields, cassava, sweet potato, and trees such as *Vitellaria paradoxa* and *Parkia biglobosa* [82]. These crop systems also coexist with large cotton farms that require heavy use of pesticides, which may affect the arthropod communities. This area was subjected to long-term agricultural activities that caused massive losses of forest land and modified forest management [50,52]. Crop pests can be affected by forest management and plant diversity around agricultural systems [83].

Our results show that pest diversity was not associated with herbivory rate. However, we found that herbivory rate had a significant negative direct effect on crop yield. This result adds to similar evidence provided by previous studies [84]. Cereals are annual crops that allocate more resources to growth and reproduction rather than to their survival [85]. Herbivory, by reducing crop growth, directly negatively impacts crop productivity [86] due to increasing biomass replacement costs and shifting biomass allocation away from reproduction [87]. The loss of leaves or the reduction in the leaf biomass due to pests could increase crop sensitivity to water stress that might reduce stomatal conductance necessary for photosynthesis [88].

5. Conclusions

In this study, we found that the diversity of natural vegetation surrounding agroforestry systems played a major role in crop yield improvement by directly increasing yield or by reducing the effect of herbivory. Fragments of natural habitats surrounding traditional agroforestry systems may be sufficient to provide essential ecosystems services for increasing agricultural yield. Our results suggest that plant species around and within traditional agroforestry systems need to be safeguarded to improve crop yield. Maintaining biodiversity around agroforestry systems must be prioritized in areas with strong demographic growth, limited by agricultural land availability, and a subsequently weak economy.

Author Contributions: D.K.N. and O.G.G. conceived the ideas of this study and designed the methodology. D.K.N. collected the data. O.G.G. and D.K.N. led the data analysis. D.K.N. wrote the draft of the paper with critical editorial contribution from O.G.G. All authors have read and agreed to the published version of the manuscript.

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