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The potential of diversification in coffee systems to enhance coffee productivity, biological pest control services and pollination services: a systematic review

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Abstract

Although agricultural productivity of coffee farms has increased, the accompanying biodiversity decline increases reliance on external inputs. The addition of trees, shrubs and other plants in farms can contribute to biodiversity conservation by creating a viable habitat for wildlife. Yet, there is still limited understanding of the effect of plant diversity in coffee systems, when taking into account the possible trade-offs, synergies and additive effects between coffee productivity, biological pest control and pollination services associated with diversification. This study reviews the strength and type of interactions between the beforementioned clusters also considering the effect of the altitudinal gradient. A systematic review was conducted to quantify these interactions between selected indicators for each cluster (n = 77 studies). The study level data was summarized and used to make path diagram giving insight on the strength of the interactions. Linear mixed-effect models were used to analyse plot data on the effect of plant diversity on coffee productivity as well as biological pest control and pollination services.

The strongest positive correlations found in the path diagram are between the biodiversity-mediated ecosystem services and coffee productivity. Furthermore, findings indicate that a positive correlation of medium strength exists between biodiversity-mediated ecosystem services and plant diversity. Coffee productivity has a weak negative correlation with plant diversity and altitude is not found to impact pest control services nor productivity from study level data.

In addition, plant diversity, coffee productivity and biodiversity-mediated ecosystem services are interconnected through multiple additive effects and through a trade-off between coffee productivity and biological pest control services. Both study and plot data indicates that increased plant diversity in coffee systems have an additive positive effect on biological pest control and pollination services. Plot data indicates that these services are enhanced respectively through an increase in taxonomical and structural diversity. A trade-off exists, however, between the positive response of the abundance of natural enemies and the negative response of coffee productivity to increased taxonomical diversity. Moreover, a negative additive effect was found for altitude on biological pest control and pollination services through the analysis of plot data.

The findings can be used to inform the sustainable management of coffee systems; increased plant diversity in farms is found to increase biodiversity and the ecosystem services they provide. However, taxonomical diversity is demonstrated to have a direct negative impact on coffee productivity.

Keywords: agroforestry, coffee, pollination services, pest control services, productivity

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1. Introduction

Conventional agriculture – consisting mostly of monocultures – has been largely successful in increasing agricultural production, yet has also become a principal cause of many environmental and social problems including biodiversity loss, land degradation, climate change, water insecurity and disruption of social systems (Waldron et al., 2017). Expansion in agricultural land has become the leading cause of deforestation and native habitat loss, with roughly 38% of the land surface of the earth being used to grow food (Wilson & Lovell, 2016). Therefore, there is a societal need to move away from the narrow focus on monocultures and move towards the design of sustainable farming systems that respect and enhances broader environmental and societal goals (Waldron et al., 2017). Integrating trees and other perennials into the agricultural landscape, also known as agroforestry, is increasingly being recognized as a viable option for sustainable farming (Wilson & Lovell, 2016; Jose, 2009).

The addition of trees, shrubs and other perennials in agricultural systems contributes to biodiversity conservation by creating a viable habitat for wildlife (Jose, 2009). Increased biodiversity can provide useful services; predatory insects and birds can suppress the population density of pests (Wilson & Lovell, 2016). Furthermore, pollinator activity can increase yield, fruit weight and fruit set, thereby positively affecting coffee productivity (Imbach et al., 2017). Yet, agroforestry systems are commonly perceived to have a considerably lower productivity compared to monoculture coffee systems (Jezeer et al., 2018), although previous studies on agroforestry systems have documented differing effects of the presence of shade trees on the productivity of the coffee crop (Campanha et al., 2004; Soto et al., 2000). Therefore, this study aims to understand how plant diversity is interconnected with coffee productivity and these biodiversity-mediated ecosystem services.

Numerous studies have argued that agroforestry can contribute to up to nine out of the 17 SDG's including climate action (SDG 13), poverty reduction (SDG 1), responsible agricultural production (SDG 12) and sustainable land management (SDG 15) (FAO, 2018; Farelly, 2016 & van Noordwijk, 2020). Despite the potential benefits of diversification practices for sustainable coffee systems, agroforestry practices have not been widely adopted by farmers. Sustainable practices are increasingly used by farmers, yet still less than a third of farms worldwide use a sustainable intensification method on their farmland (Pretty, 2018). Yet, there is currently a growing need for the sustainable production of coffee, such as agroforestry, because of increasing demand and climatic pressures (Pham et al., 2019). Coffee is a climate-sensitive perennial crop, and climate variability is projected to put increasing pressure on the cultivation of coffee through a decline in coffee productivity and an increasing incidence of pests (Pham et al., 2019). Agroforestry systems can increase resilience to climate change by providing a moderate microclimate enhancing water infiltration and storage while reducing temperature extremes and evaporation (Gomes et al., 2020; Waldron et al., 2017). At the same time, the global demand for coffee is increasing. Although the global coffee area

decreased to 10.2 million ha from 11.1 million ha between 1990 and 2010, production still increased with 36% providing evidence that there was an overall intensification in multiple key countries in coffee production such as Brazil and Colombia (FAO, 2014). While agricultural productivity has increased on a global scale, the biodiversity decline disrupts ecological interactions, thereby increasing the reliance of coffee production on external inputs (de Souza et al., 2012). The potential of diversification for biodiversity conservation and thereby biodiversity-mediated ecosystem services should thus be studied to gain further insight into whether more diverse coffee systems can conserve biodiversity without causing a significant decline in coffee productivity.

A long-standing debate remains regarding conservation goals: should they be met by conserving biodiversity within agricultural systems, known as land sharing, or through maximizing the land area available for conservation by maximizing agricultural production on the land that is devoted to it, known as land sparing (Chandler et al., 2013). Proponents of agroecological approaches challenge the assumptions that underly this dichotomy. One of the assumptions that is challenged is whether conservation-friendly agricultural practices are inevitably low-yielding (HLPE, 2019). Agroforestry systems are often associated with a decline in coffee productivity (Gomes et al., 2020; Jezeer et al., 2018). Although this has been heavily debated, empirical studies are lacking (Chandler et al., 2013).

Whilst there is a growing number of studies that focuses on ecosystem service provision in coffee systems, there are still few studies focused on the trade-offs, additive effects and synergies between ecosystem services which are critical for sustainable coffee production (Chain-Guadarrama et al., 2019). Pollination and pest control services are the principal ecosystem services provided by biodiversity; still whether these services affect production in synergistic, additive or antagonistic ways is identified as a research gap as well as the strength and type of relationships between them (Chain-Guadarrama et al., 2019). Therefore, the aim of this study is to analyse the manner in which plant diversity, coffee productivity and the beforementioned biodiversity-mediated ecosystem services are interrelated to inform sustainable farm management.

A systematic review is conducted to quantify the impact of plant diversity on coffee productivity, biological pest control and pollination services in coffee systems. The impact of altitude will also be analyzed as the climate gradient associated with altitude can considerably influence the incidence of pest (Jonsson et al., 2015) and coffee productivity (Sarmiento-Soler et al., 2020).

The central research question of this paper is: what is the effect of plant diversity in coffee systems, when taking into account the possible trade-offs, synergies and additive effects between coffee productivity, biological pest control and pollination services associated with diversification?

The following sub-questions need to be answered in order to answer the central research question:

(1) What is the direct impact of plant diversity on coffee productivity, and indirectly through biological pest control and pollination services?

(2) What are the trade-offs, synergies and additive effects among coffee productivity, biological pest control and pollination services associated with diversification?

2. Theory

2.1 A conceptual framework to quantify diversification

A conceptual framework has been developed to quantitatively assess the direct and indirect impact of plant diversity on (i) pollination services, (ii) pest control services and (iii) coffee productivity (fig.1). The extent to which a coffee field is diversified is identified by considering both structural diversity and taxonomical diversity. Borges Silva et al. (2022) identifies tree density and canopy cover as indicative for the structural diversity of an ecosystem. Therefore, these indicators signify structural diversity in this study. Taxonomical diversity concerns the richness and diversity of plant species (Hanif et al., 2019) and has been assessed through the use of plant species richness as an indicator (Tribot et al., 2016). Moreover, Borges Silva (2022) and Tribot et al. (2016) identify the Shannon index as being indicative for taxonomical diversity. The Shannon-Wiener diversity index quantitatively measures the abundance and richness of woody species in order to quantify the tree diversity of that site (Moutsambote et al., 2016). Consequently, the Shannon-Wiener index is often used as a measurement for the total plot diversity of shade trees in studies characterizing the diversification of different coffee systems (Teodoro et al., 2009; Nesper et al., 2017), especially when only one or few individuals of one tree species are present at a certain site (Veddeler et al., 2006). The Shannon index and plant species richness are thus both representative of taxonomical diversity in this study.

Biological pest control is defined in this study as the use of organisms to suppress the population density of pests (Bale et al., 2008). Predators that have mainly been reported to act as natural enemies against pests and diseases are birds, bats and ants (Gras et al., 2016), although other animals such as predatory wasps have also been reported to suppress pest populations on coffee farms (Scalon et al., 2011). Vertebrate pest regulation services, chiefly birds and bats, have been shown in numerous studies to reduce insect pests on the coffee crop (Lindell et al., 2018; Chain-Guadarrama et al., 2019). In addition to vertebrates, ants are reported as effective biocontrol agents in coffee agroforestry systems. Coffee arboreal ants, e.g., protect coffee plantations from colonization by important pests such as the coffee berry borer (CBB) (Gras et al., 2016). Eumenid wasp species also provide pest caterpillars to its larvae which feed on the leaves of the coffee plant (Klein et al., 2004). Coffee is cultivated within many biodiverse habitats, however the intensification of coffee cultivation is threatening biodiversity and thereby also the ecosystem services that they provide (Chain-Guadarrama et al., 2019). Mobile organisms are especially vulnerable to changes in farm management and landscape changes (Chain-Guadarrama et al., 2019., Kremen et al., 2007). The diversity and abundance of natural enemies of pests is strongly influenced by the configuration and amount of anthropogenic and native habitats within a landscape (Boesing et al., 2017). Consequently, coffee farmers can considerably benefit from reduced pest losses by providing a suitable habitat for key predator species on coffee pests (Chain-Guadarrama et al., 2019). The degree to which these organisms provide pest control services in coffee farms is measured using the indicator

abundance of natural enemies. This indicator was chosen as it has been reported to have a considerable impact on coffee productivity through suppressing pests (Classen et al., 2014). Any species that acted as a natural enemy to pests on coffee farms were included.

Pollination services are services for crop production provided by bees and other pollinators

(Liss et al., 2013). Most often bees are assumed to be the most important pollinators, however other insects such as butterflies, flies, beetles, wasps and moths can also contribute to global pollinator-dependent crops (Rader et al., 2015). Coffee productivity can be significantly improved by pollination services, enhancing fruit weight, fruit set and yield of the coffee crop (Imbach et al., 2017; Classen et al., 2014; Boreux et al., 2013). Pollinators are also substantially affected by the loss and fragmentation of natural habitat, often leading to lower re-colonization rates. Although differing effects have been reported by studies (Kremen et al., 2007). Multiple studies have established that more diversified agroforestry coffee systems also can play a critical role in the conservation of pollinators and its accompanying services populations (De Beenhouwer et al., 2013; Jha et al., 2014).

The degree in which pollination occurs at coffee field is measured in this study with the indicators: abundance of pollinators, pollinator species richness and visitation frequency of pollinators. These indicators were chosen as measurement for pollination as (i) they were found to have strong influence on coffee production through fruit set, fruit weight and yield (Chain-Guadarrama et al. 2019), (ii) Liss et al. (2013) found that these were some of the most common measurements of pollination services. Measurements for any pollinator species were reported in this study.

The framework (fig. 1) provides an overview of the relationships that are tested and the indicators selected for each cluster. Altitude is the only biophysical landscape indicator measured therefore it is not classified as a cluster.

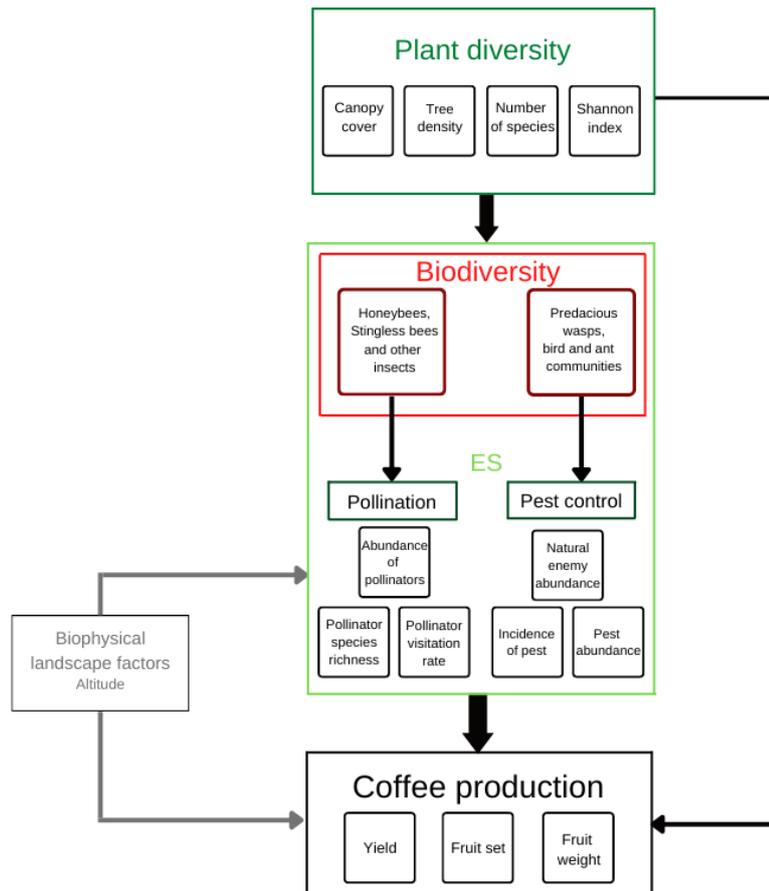


Figure 1. Conceptual framework assessing the impact of diversification on coffee farms on biodiversity-mediated ecosystem services and coffee production. Altitude is a biophysical landscape factor that can also influence ecosystem services and production through changes in climate along an altitudinal gradient.

2.2 Hypotheses

Based on previous research conducted on diversification and its biodiversity-mediated benefits as well as on coffee productivity, this study has several hypotheses on the interconnectedness of these clusters which are summarized in the table below.

Table 1. The expected relationships between plant diversity, coffee productivity and the biodiversity-mediated ecosystem services. The expected direction of the effect is given along with a short explanation and its references.

Predictor	Response	Direction of the effect	Explanation	References
Plant diversity	Biological pest control services	Increase	Intensification of coffee cultivation is threatening biodiversity	Chain-Guadarrama et al., 2019; Kremen et al., 2007
	Pollination	Increase	Intensification of coffee cultivation is threatening biodiversity	Chain-Guadarrama et al., 2019; Kremen et al., 2007
	Coffee productivity	Decline	Coffee monocultures maximize the efficient use of the farmland	Hames, 1983; Jezeer et al., 2018
Pollination services	Coffee productivity	Increase	Movement of pollen by pollinators between coffee plants increases productivity	Imbach et al., 2017; Classen et al., 2014
Biological pest control services	Coffee productivity	Increase	Pest control services cause a decline in pests on coffee plants	Lindell et al., 2018; Chain-Guadarrama et al., 2019
Altitude	Biological pest control services	Increase	Favourable climate at lower altitudes for pests	Jaramillo et al., 2011, Lomelí-Flores et al. 2010
	Pollination	Decline	Favourable climate at lower altitudes	Samnegård et al. 2016
	Coffee productivity	Increase	More likely to exceed the temperature thresholds for coffee cultivation at a higher altitude	Sarmiento-Soler et al., 2020

3. Materials and Methods

A systematic review was conducted in order to synthesize the state of knowledge on the direct effect of diversification in coffee plantations on coffee productivity and indirectly through biodiversity-mediated ecosystem services; biological pest control and pollination services. PRISMA, the preferred reporting items for systematic reviews and meta-analyses statement, was used as a guideline to accurately and transparently report how studies are identified, selected, appraised and synthesized in the systematic review (Page et al., 2021).

3.1 Search strategy

In order to review and compile literature on the direct and indirect effects of more diverse coffee systems, a search was conducted using the search engine Web of Science. In addition, reports were sought for retrieval from meta-analyses that came up through the search and reference lists from studies yielded from the search were examined. The search was performed in the period from February 2022 till June 2022, without restriction on the publication year. The search was restricted to peer-reviewed scientific journals in English. The term used to search for papers was ((coffee*) AND (agroforest*) AND (pollinat OR yield* OR product* OR pest control* OR natural enem* OR pesticide*)). The search yielded 627 studies. Each study was numbered and saved in a pdf format. Then the studies went through a first screening by assessing the 'article title', 'abstract' and 'keywords'. The first screening was done following two criteria: i) papers were excluded if unrelated to the impact of diversification strategies in coffee systems on coffee productivity, biological pest control or pollination services, ii) lab experiments or studies evaluating models are excluded as this study is interested in field data. Meta-analyses that the search yielded were screened for relevant studies.

Then, a full-text screening was conducted in order to select relevant articles according to further eligibility criteria: i) papers are excluded if the study does not include quantitative measures of the selected indicators for tree diversity and either yield or associated ecosystem services, pollination and biological pest control for the same observation sites, ii) review papers or meta-analyses are excluded to avoid duplicates. The selected indicators for tree diversity were tree density, canopy cover, plant species richness and the Shannon-Wiener index as this study is interested in both structural and taxonomical diversity and therefore functioned as part of the first eligibility criteria mentioned above when conducting the full-text screening. When data from relevant studies could not be directly collected from online sources, the corresponding author of the study was directly contacted to ask for the data.

Figure 2. shows a flow diagram of the selection process for the systematic review so that readers of this study can fully understand the selection steps that are taken from identification of studies to final selection. No automation tools were used to collect the data. The assessment of each record was done by one reviewer. Single screening is more efficient in time and resources than if it's done by multiple reviewers however it is relevant to note that there is a higher risk that relevant studies may be missed (Page et al., 2021).

Selection process for studies included in the systematic review

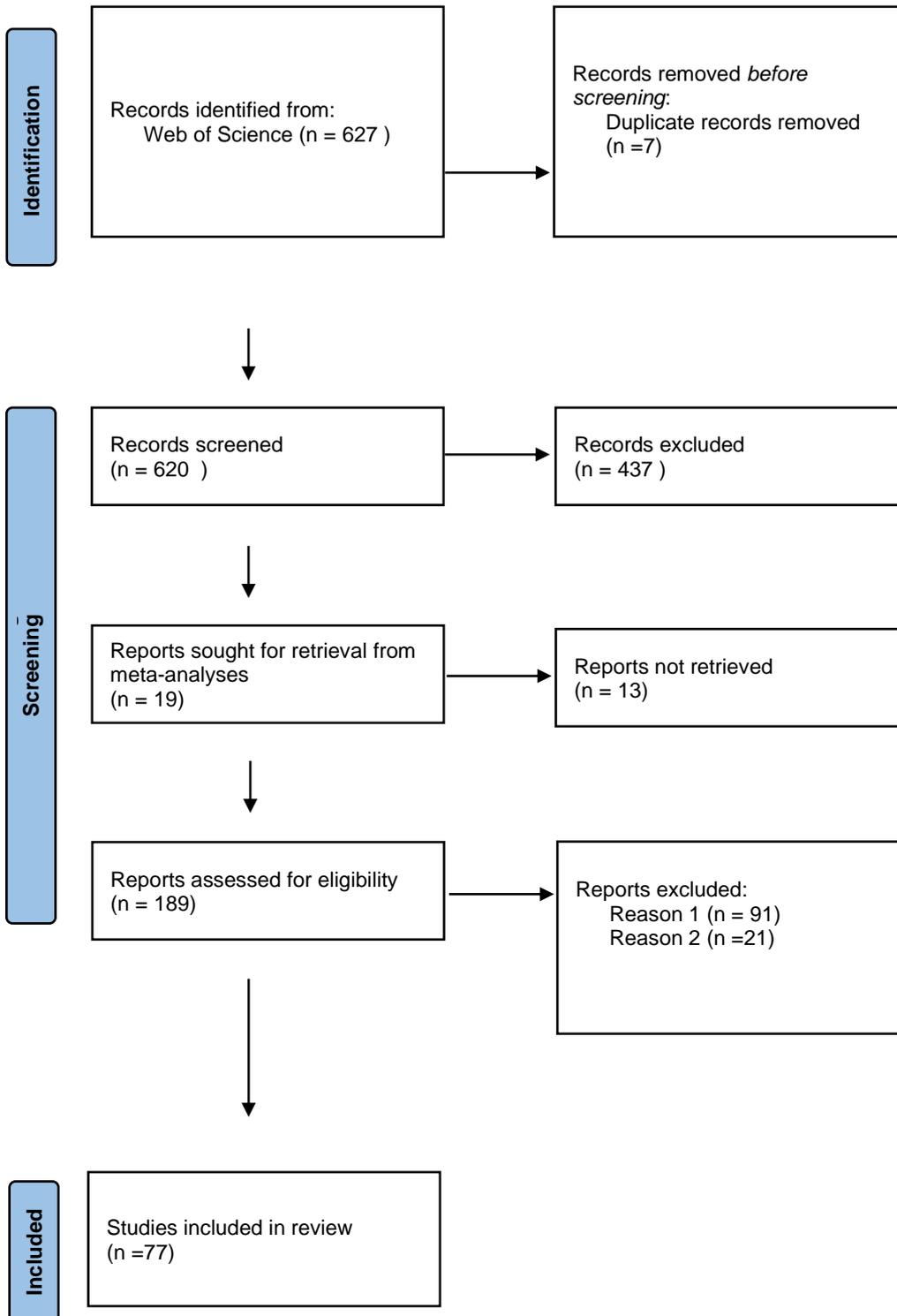


Figure 2. Flow diagram for the selection process of the systematic review adapted from Page et al., (2021). Reason 1: papers are excluded if the study does not include quantitative measures of tree diversity and either yield or associated ecosystem services, pollination and biological pest control for the same observation sites; reason 2: review papers or meta-analyses are excluded to avoid duplicates.

3.2 Characterization of the selected papers

3.2.1 General information

For each study of relevance included in the systematic review, general information was documented, such as: year of publication, first author and the country the study was conducted, see appendix C. The explanatory and response variable that were measured in each study were documented and prescribed to the cluster (i.e. plant diversity) that they relate to. The indicators that are measured for each cluster are summarized in the table below (table 2).

Furthermore, the type of statistical analysis that the study ran was documented along with the statistical results. The predictor coefficient, the Pearson's r , z -value and the p -value, also known as statistical significance, were documented when provided by the study, see appendix D. The p -value was considered significant when $p \leq 0.5$.

Table 2. The variables included for each clusters for which data is collected. Altitude is not a cluster and is therefore only measured by the indicator altitude.

Cluster	Indicators
Plant diversity	Canopy cover
	Tree density
	Plant species richness
	Shannon index
Coffee productivity	Yield
	Fruit weight
	Fruit set
Pollination services	Pollinator species richness
	Pollinator visitation rate
	Abundance of pollinators
Biological pest control services	Abundance of natural enemies
	Pest abundance
	Incidence of pest
Altitude	Altitude

3.2.2 Study level data

The response of each indicator was classified from the perspective of sustainability as positive, negative or neutral (see Appendix D). Sustainability is defined in this study as the maintenance of ecosystems including diversity of animal and plant communities as well as maintain its productive capacity (USDA, 2008).

A sustainable system is defined for the clusters pollination, biological pest control and coffee productivity respectively as: an increase in pollination services, an increase in pest control services and a maintained or increased coffee productivity. The relationship was classified as neutral when the relationship was not statistically significant. If the relationship was classified as statistically significant, it was determined whether the relationship is negative or positive through the predictor coefficient or correlation coefficient provided by the paper. If neither was given, the direction of the relationship was determined through statements from the author about the relationship.

3.2.3 Plot level data

To determine whether trade-offs, synergies or additive effects exist, studies were also selected if plot data was provided for relationships between indicators that fall under the cluster of plant diversity and either coffee productivity, pollination and biological pest control. General information was also documented for these studies as well plot data (see appendix E). The altitude for each plot was recorded when provided by the study. If data was given for subplots or i.e. fruit weight was given per shrub, it was converted to data per plot. For yield, the unit was converted to data ha⁻¹ if it was given in data plot⁻¹. In addition, tree density was converted to trees ha⁻¹ if given as trees plot⁻¹.

3.3. Data analysis

3.3.1 Path diagram

The interest of the first sub-question of this study was to understand how plant diversity directly impacts coffee productivity, and indirectly through biological pest control and pollination services. Therefore, as the objective was to further understand the interconnectedness between the beforementioned clusters, a path diagram was chosen to visualize the strength and directionality of the relationships. Path diagrams are flowcharts that show the interconnectedness with lines used to indicate a causal flow (Steiger, 2009). Each path is connected by arrows, wires (lines) or slings (line with two arrowheads) and involves two variables (Steiger, 2009).

Limited studies provided the standardized predictor coefficient, while a greater number of studies provided the correlation coefficient, Pearson's *r*, for the documented relationships. Thus, the Pearson's *r* was chosen as a parameter of effect size to determine the strength of the relationship between indicators, summarizing the correlation of the bivariate relationships (Kelley & Preacher, 2012). As the Pearson's *r* does not determine the directionality of the relationship between variables, each path is

connected by wires. Wires and slings are most often used to represent relationships that are 'undirected' or do not show causality (Steiger, 2009).

Cohen (1988) defines effect size as the degree to which the phenomenon is present in the population. The value of the effect size for the correlation coefficient r can vary between -1, a perfect negative correlation, and a +1, a perfect positive correlation.

Cohen (1992) states that the effect size is large if the value of the Pearson's r lies around more than 0.5, medium if the effect size varies around 0.3 and low if it varies around 0.1. Following Cohen (1992), the strength of the relationships between the clusters could be determined. The Pearson's r was inverted when a negative correlation indicated a positive contribution to that ecosystem service (i.e. incidence of pest). The effect size was finally derived for the relationships between two clusters (i.e. plant diversity and pollination) by summing and taking the average of the correlation coefficient's for the bivariate relationships.

3.3.2 Data standardization

Before the analyses were performed, the response variables for pollination services and pest control services were standardized using z scores for each study. In addition, plant species richness was standardized as the level of measurement differed considerably between studies and a linear increase in species richness cannot be assumed. Standardization allowed for comparisons between studies with different methodologies and differences in measurement level (i.e. plant level or plot level) (Gelman & Hill, 2006). Furthermore, it allowed for i.e. the effect of plant diversity on pollination services to compare between different pollinators. Each measure was also z-transformed to remove the influence of measurement scale differences between indices. The predictor coefficient from the output of the linear mixed-effect models was standardized using the ratio of the standard deviations of the independent variable and the dependent variable and multiplying this ratio by the unstandardized coefficient .

Canopy cover was given in percentage, making it comparable between studies without the need to standardize the data. The Shannon index is measured between studies using the same method, hence the index could also directly be used for comparison. In addition, the yield data could all be converted to kg ha^{-1} , thereby also allowing the analysis of the effect of diversification of coffee systems on unstandardized yield data.

3.3.3 Statistical analysis

As this study also aims to analyse field data, mixed effect linear models were used (lmer function in R package lme4). The study was included as a random effect to account for the lack of independence between studies. The p-values were derived using the Satterthwaite approximation, often used to assess statistical significance for mixed-effect models (Luke, 2016) and the marginal and conditional coefficient of determination (R^2_m and R^2_C) were used to determine the explained variance of the model. The marginal R^2 is the variance explained by the fixed effects and the conditional R^2 is the

variance explained by both the fixed effects and random effects (Sotirchos et al., 2019).

Models were selected using the Akaike information criterion (AIC) which estimates the relative quality of statistical models for a given dataset (Cavanaugh, 2019). Linear responses of each variable were tested to the different explanatory variables as well as for a linear model using polynomial curve fitting using AIC. The model with the lowest AIC was selected, offering the best fit (Cavanaugh, 2019).

The models were run for plant diversity indicators as a fixed effect and for plant diversity and altitude as fixed effects. The model was run with only plant diversity indicators as a fixed effect even when altitude was available for some plots to ensure that each study included in the systematic review providing field data for the relevant clusters was included in the final analysis, giving more reliable results due to the larger sample (Faber & Fonseca, 2014).

Field data also allowed for the visualisations of the relationships between the response and predictor variables using the package ggplot2 and the package tidyverse. The average and standard deviation of the response variable were also determined and included in the graphs. The strength of causal relationships between predictor and response variables were assessed using the standardized estimate coefficient calculated from the estimate coefficient. Relationships between variables were considered to be significant when the p-value was ≤ 0.05 . The packages lme4, lmerTest, AICcmodavg and MuMIn were used to perform the statistical analysis in R4.1.2.

4. Results.

4.1 General results

4.1.1 The geographical location of the studies

There were 77 studies yielded from the search that met the criteria. From the 77 selected studies most were conducted in Central America (n=20), mainly Costa Rica (n=10), as well as Mexico (n=16) and Indonesia (n=10; fig. 3). Africa (n=13), Asia (n=14) and South America (n=14) yielded the least studies (appendix B). However, most studies within the beforementioned continents were conducted in the largest coffee producing countries (FAO, 2020), Brazil (n=5), Colombia (n=5) and Indonesia (n=10) except for Vietnam (appendix A). There could be a geographical bias in the results due to the fact that a large number of studies are conducted within the same region, i.e. 15 of the 16 studies conducted in Mexico were done in the highlands of Chiapas, a coffee-growing region (Jha & Vandermeer, 2009).

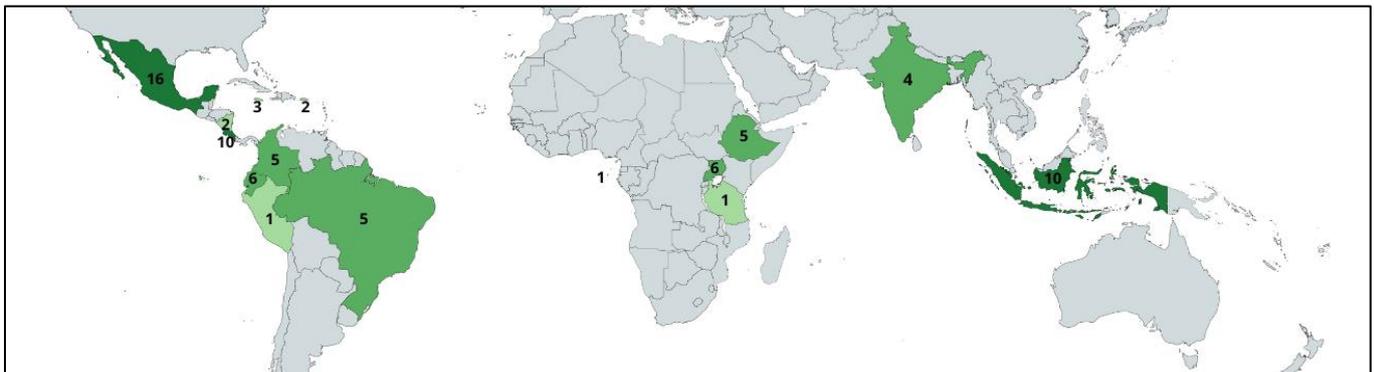


Figure 3. Map indicating how many studies were found in each country. Countries with no studies are displayed in grey.

4.1.2 The general characteristics and methods of the studies

Most studies contained data on at study level between indicators related to one or more of the clusters (67.7%) while a limited number of the studies contained data on indicators per plot related to one or more of the clusters (30.7%; Appendix C).

Furthermore, most studies that assessed and quantified only one of the clusters provided data on biological pest control services (51.2%), followed by coffee productivity (26.8%) and pollination services (21.4%) in coffee systems (fig. 4). Several studies also reported on more than one cluster (fig. 4), most jointly assessed the clusters coffee productivity and pollination services (52.4%), followed by the clusters coffee productivity and biological pest control services (33.3%) and studies assessing all clusters (14.3%). None of the studies reported on the two clusters biological pest control services and pollination services.

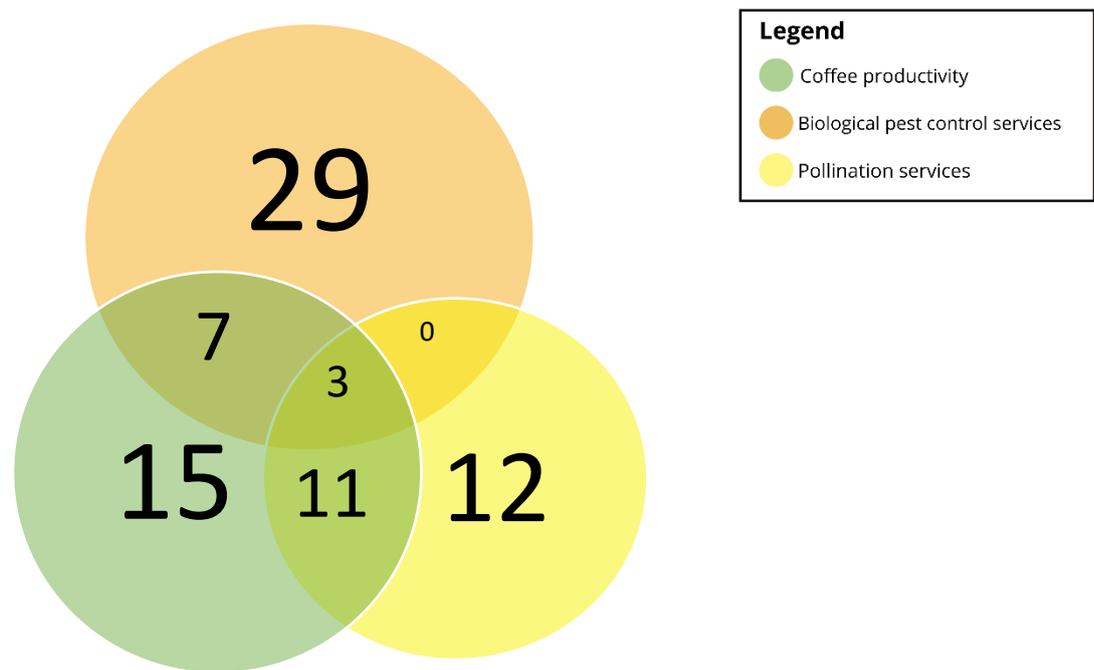


Figure 4. Venn diagram showing the number of studies that contain indicators related to one or more of the clusters. Three clusters are displayed: coffee productivity, pollination services and biological pest control services. Studies may have used multiple indicators from different clusters.

Most studies that provided study level data on the severity of pests measured incidence of pest (n=25), while a limited number of studies reported on pest abundance (n=5). For field data, studies reported exclusively on the incidence of pest while none reported pest abundance. Moreover, coffee productivity was most often addressed with the indicator yield (n=16), yet the influence of pollination services on coffee productivity was measured mostly through the impact of pollination services on the indicator fruit set (n=9). Lastly, a statistical analysis of the effect of plant diversity was most often done through respectively the assessment of canopy cover (n=23), plant species richness (n=16) and tree density (n=13), while most studies provided field data for tree density (n=18).

4.2. What is the direct impact of plant diversity on coffee productivity, and indirectly through biological pest control and pollination services?

4.2.1 Plant diversity

Studies mostly reported a positive response of pollination services and biological pest control services to plant diversity in coffee systems. Unexpectedly, coffee productivity was reported to mostly be positively impacted by plant diversity (see table 3).

The general impact of plant diversity on coffee productivity is mostly positive (n=8), followed by the same amount of neutral (n=5) and negative responses (n=5) (table 3). For the variable yield, responses were variable; mostly positive (n=6), followed by neutral (n=5) and negative responses (n=5). For the variables fruit weight (n=2) and fruit set (n=1), only positive responses were found.

Table 3. The effect of plant diversity on indicators of coffee productivity (n =19 of 15 studies), pollination services (=33 of 15 studies) and pest control services (n=39 of 17 studies). The number of positive, neutral and negative responses are indicated. Responses are deemed neutral when $p \geq 0.5$.

Production	Positive	Neutral	Negative
Total	8	5	5
Yield	5	5	5
Fruit weight	2	0	0
Fruit set	1	0	0
Pollination	Positive	Neutral	Negative
Total	17	11	5
Pollinator visitation rate	2	2	0
Pollinator species richness	9	7	2
Abundance of pollinators	6	2	3
Biological pest control	Positive	Neutral	Negative
Total	18	15	6
Incidence of pest	3	12	2
Pest abundance	10	1	1
Abundance of natural enemies	5	2	3

The general impact of plant diversity on pollination services is mostly positive (n=17), followed by neutral (n=11) and negative responses (n=5) (table 3). For the variables pollinator species richness and pollinator visitation rate, responses were mostly positive (n=9, 2; respectively), and neutral (n=7, 2; respectively). For the variable abundance of pollinators, responses were mostly positive (n=5), followed by negative (n=3) and neutral (n=2) responses. Thus, the response of abundance on pollinators to plant diversity in coffee systems was most varied.

Pollinators that were reported on included representatives from the orders Hymenoptera, Diptera, Lepidoptera and Coleoptera. Bees (Hymenoptera: Apoidea) were most commonly observed and included bees from the Apidae family (honey bees, stingless bees, bumble bees and carpenter bees), sweat bees (Halictidae), leafcutter bees (Megachilidae), butterflies (Lepidoptera), mason wasps (Eumenidae), beetles (Coleoptera: Macroductylus), Syrphid flies (Diptera: Syrphidae) and other flies (Diptera: Drosophilidae) (see fig. 5). These pollinator species were classified by studies in groups as either: butterflies, bees, wasps, all pollinators or pollinators except bees (fig. 5). For studies on butterflies and studies on all pollinators, responses were mostly positive (n=4, 4; respectively), and neutral (n=4, 4; respectively). For studies on bees, response were mostly positive (n=7), followed by neutral (n=3) and negative (n=3). Limited studies focused on the response of wasps and pollinators except bees to plant diversity. Wasps were reported to have a neutral response (n=1) and pollinators except bees were reported to have a positive (n=1) and negative (n=1) response to plant diversity.

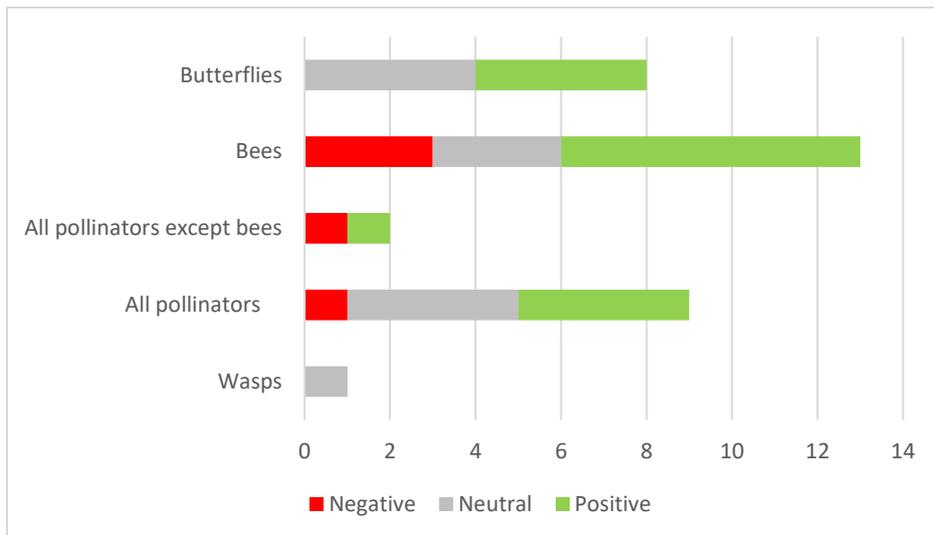


Figure 5. The response of different pollinator species to plant diversity in coffee systems (n=33 of 15 studies). Multiple observations can be from the same study. Positive responses are indicated by green bars, neutral responses by grey bars and negative responses by red bars.

The general impact of plant diversity on biological pest control services is mostly positive (n=18), followed by neutral (n=15) and negative responses (n=6). For the variables abundance of natural enemies and pest abundance, responses were mostly positive (n=5, 10; respectively), while responses were mostly neutral for incidence of pest (n=12).

The abundance and incidence of multiple pests were studied: coffee berry borer (*Hypothenemus hampei*), white stem borer (*Xylotrechus quadripes*), black twig borer (*Xylosandrus compactus*), brown eye spot (*Cercospora coffeicola*), red spider mite (*Tetranychus urticae*), coffee leaf miner (*Leucoptera coffeina*) and leaf rust (*Hemileia vastatrix*) (fig. 6).

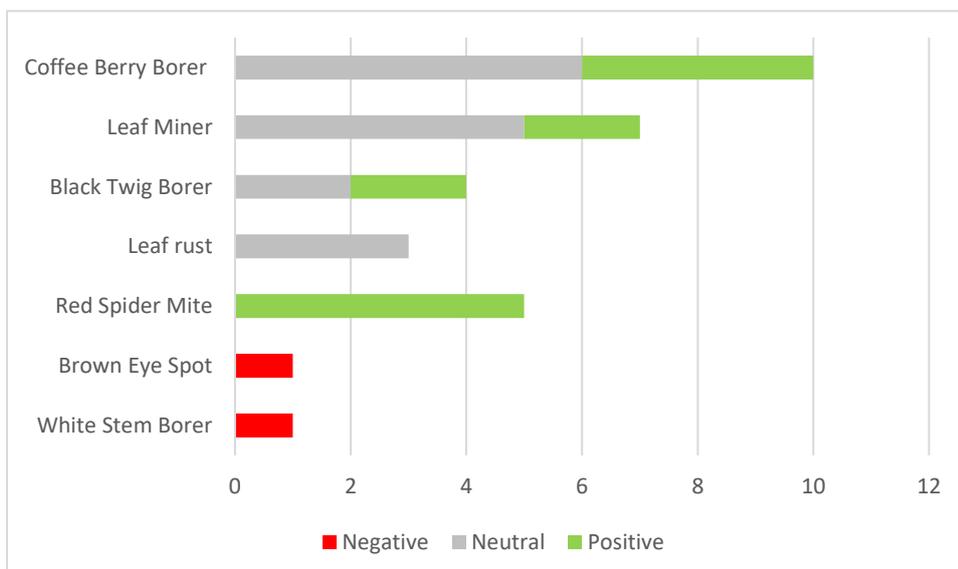


Figure 6. The response of different pests to plant diversity in coffee systems (n=29). Multiple observations can be from the same study. Positive responses are indicated by green bars, neutral responses by grey bars and negative responses by red bars.

For studies on the red spider mite, only positive responses were reported (n=5). For the coffee berry borer, the leaf miner, and the black twig borer, responses were mostly neutral (n=5, 4, 2; respectively), followed by positive responses (n =4, 2, 2). Leaf rust had a neutral response to plant diversity (n=3). Limited studies focused on the response of the white stem borer and brown eye spot to plant diversity. These pests only responded negatively to plant diversity (n=1, 1; respectively). Natural enemies that were observed are ants (Hymenoptera:Formicidae), predatory wasps (Eumenidae) and birds. Most studies reported an increase in the abundance of natural enemies with increased plant diversity (n=5), mostly increasing bird populations (n=3).

The effect of plant diversity on coffee productivity, biological pest control and pollination services also differs between the diversity indicators (table 4).

The impact of canopy cover on coffee productivity is mostly positive (n=3), followed by neutral responses (n=2) (table 4). Furthermore, the response of coffee productivity variables was mostly positive to tree density (n=4), followed by negative (n=2) and neutral responses (n=1). The response of coffee productivity to plant species richness and the Shannon index was not often reported. The Shannon index was found to have a positive impact on productivity (n=1), while plant species richness had a neutral (n=1) and negative (n=1) impact.

The response of pollination services to canopy cover and cluster variables was mostly positive (n=6, 4; respectively), followed by neutral responses (n=4, 1; respectively). The response of tree density was mostly negative (n=2), followed by both neutral (n=1) and positive (n=1) effects. The impact of the Shannon index on pollination services was not often reported on, with one study reporting a positive impact on pollination services.

The response of biological pest control services to the Shannon index and canopy cover was mostly positive (n=5,8; respectively), while the response to plant species richness, tree density and cluster variables was mostly neutral (n=5, 3, 2; respectively).

Table 4. The effect of the plant diversity indicators on coffee productivity, pollination services and pest control services. The number of positive, neutral and negative responses are indicated. Responses are deemed neutral when $p \geq 0.5$.

Effect on coffee productivity	Positive	Neutral	Negative
Shannon index	1	0	0
Canopy cover	3	2	1
Plant species richness	0	1	1
Tree density	4	1	2
Cluster	0	1	1
Effect on pollination services	Positive	Neutral	Negative
Shannon index	1	0	0
Canopy cover	6	4	0
Plant species richness	4	5	2
Tree density	1	2	2
Cluster	4	1	1
Effect on pest control services	Positive	Neutral	Negative
Shannon index	5	0	0
Canopy cover	8	5	2
Plant species richness	2	5	1
Tree density	1	3	1
Cluster	2	2	1

4.2.2. Pollination and biological pest control services

As expected, pollination services mostly increased coffee productivity (table 5). The general impact of pollination services on coffee productivity is mostly positive ($n=15$), followed by neutral ($n=2$) and negative ($n=1$) responses. For the variable fruit weight and yield, responses were solely positive ($n=2$, 2; respectively). For the variable fruit set, most responses were positive ($n=8$), followed by neutral ($n=2$) and negative responses ($n=1$).

Table 5. The impact of pollination services on indicators of coffee productivity; fruit set, fruit weight and yield. The number of positive, neutral and negative responses are indicated. Responses are deemed neutral when $p \geq 0.5$.

	Positive	Neutral	Negative
Fruit set	11	2	1
Fruit weight	2	0	0
Yield	2	0	0

Each report of the incidence of pest in response to abundance of natural enemies was positive (n=10). Multiple studies focused on vertebrate pest regulation services; the impact of bird populations (n=5) was measured for the incidence of the coffee berry borer (n=3), insect-caused leaf damage and pest infestations in general. No studies focused on the pest regulation services provided by bats.

Several studies measured the effectiveness of ant populations (n=5) as biocontrol agents in coffee systems. The ant species *A. instabilis* was shown to suppress CBB populations (n=3) as well as lepidoptera larvae (known as caterpillars) (n=1). Moreover, twig-nesting ants were found to decrease the incidence of the leaf miner (n=1).

Limited studies (n=2) measured the direct impact of abundance of natural enemies on productivity indicators; fruit set in response to incidence of pest was positive (n=1) and neutral (n=1). In addition, fruit weight in response to incidence of pest was neutral (n=1).

Table 6. The impact of abundance of natural enemies on the incidence of pest, fruit set and fruit weight. The number of positive, neutral and negative responses are indicated. Responses are deemed neutral when $p \geq 0.5$.

	Positive	Neutral	Negative
Incidence of pest	10	0	0
	Positive	Neutral	Negative
Fruit set	1	1	0
Fruit weight	0	1	0

4.2.3. Altitude

The general impact of altitude on coffee productivity is mostly positive, supporting the hypothesis that productivity increases in response to altitude only to some extent (see table 7)

The response of yield to altitude is mostly positive (n=4), followed by negative (n=2) and neutral responses (n=1). Moreover, fruit weight responded positively to altitude (n=1).

The incidence of pest in response to altitude was mostly negative (n=5) and neutral (n=5), followed by positive responses (n=3).

Table 7. The impact of altitude on indicators of coffee productivity and on incidence of pest. The number of positive, neutral and negative responses are indicated. Responses are deemed neutral when $p \geq 0.5$.

	Positive	Neutral	Negative
Yield	4	1	2
Fruit weight	1	0	0
	Positive	Neutral	Negative
Incidence of pest	3	5	5

The response of the coffee berry borer to altitude was variable with mostly neutral responses (n=3), followed by negative (n=2) and positive (n=2) responses (see figure 7). For leaf rust, the response to

altitude was reported as positive (n=1) and neutral (n=1). Furthermore, the responses of leaf spot (n=1) and the leaf miner (n=1) to altitude were negative and the white stem borer was reported to have a neutral response to altitude (n=1).

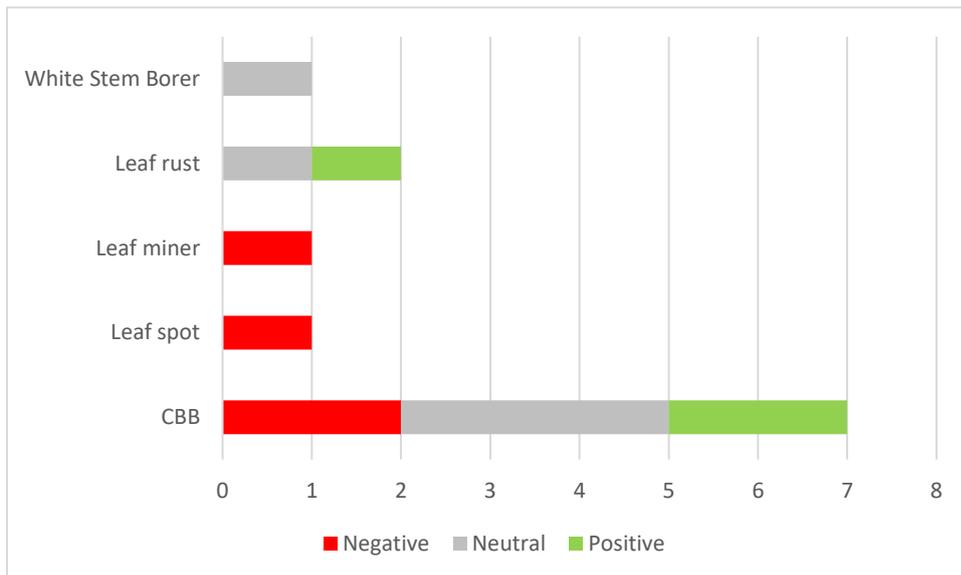


Figure 7. The response of different pests to altitude in coffee systems (n=13). Multiple observations can be from the same study. Positive responses are indicated by green bars, neutral responses by grey bars and negative responses by red bars.

4.2.4. Direct and indirect effects of diversification

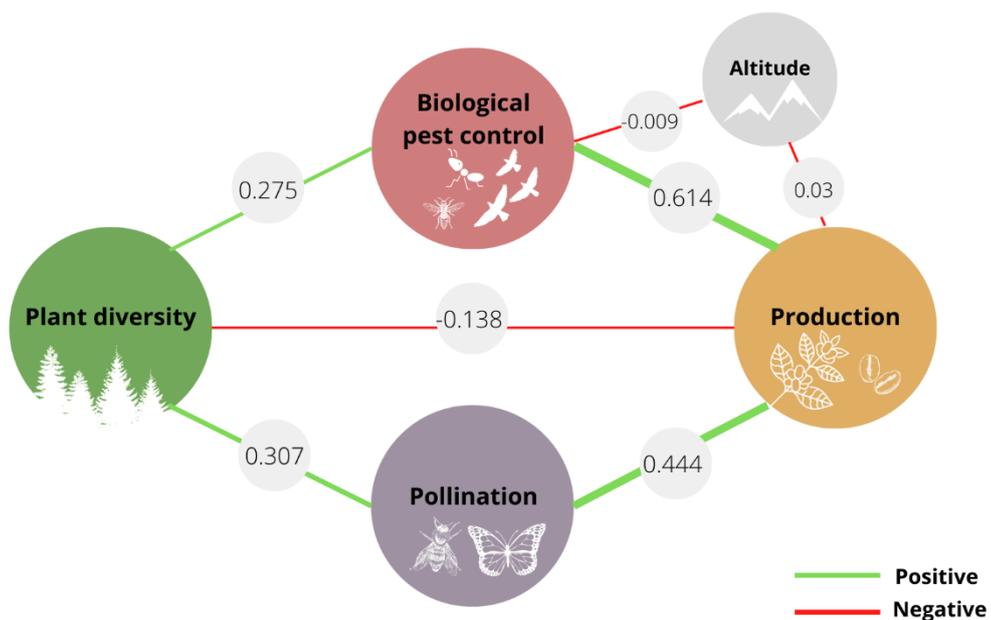


Figure 8. The correlation of plant diversity to coffee production directly and indirectly through the correlation of plant diversity with pollination services and biological pest control. The correlation of the biophysical landscape

factor altitude with coffee production and biological pest control is also reported. Green wires indicate a positive correlation and red wires indicate a negative correlation. The size of the wire indicates the strength of the relationship. Correlation between production and pollination is not reported due to a lack of studies analysing how these variable clusters are correlated.

The strongest relationship was found for biological pest control services and coffee productivity (fig. 8) The Pearson's r is 0.614, indicating a strong positive relationship ($n = 70$ plots of 4 studies) (Cohen, 1992). The second strongest relationship is between pollination and production ($r = 0.444$), indicating a strong positive relationship ($n = 201$ plots of 6 studies).

Correlations of medium strength can be found for the relationship between plant diversity and both pollination and biological pest control. Plant diversity and pollination are positively correlated ($n = 260$ plots of 6 studies) with the Pearson's r varying around 0.3, indicating that the effect size is medium (Cohen, 1992). Biological pest control also has a positive correlation with plant diversity ($n = 251$ plots of 8 studies) with a Pearson's r varying around 0.3. The effect size of the correlation between plant diversity and coffee production is low ($r = 0.1$), indicating a weak relationship (Cohen, 1992). Plant diversity and coffee production ($n = 697$ plots of 5 studies) thus have a weak negative relationship. Furthermore, biological pest control almost has no correlation with altitude ($n = 305$ plots of 3 studies) ($r = -0.009$). The low correlation was found due to strong variations between the individual studies that were clustered. The same type of variation is found for the relationship between production and altitude ($n=235$ plots of 3 studies). The strength of the correlation between production and altitude is low ($r = 0.03$).

4.3 What are the trade-offs, synergies and additive effects among coffee productivity, biological pest control and pollination services associated with diversification?

4.3.1 Coffee productivity

The model output indicates that coffee production only declines with increased plant species richness ($p < 0.001$), thus only partly supports the hypothesis that coffee production declines with increased diversity (fig. 9d). Yield was not significantly affected by the other plant diversity variables (fig. 9) nor altitude (fig. 10). The response of yield to plant diversity variables demonstrates that taxonomical diversity has a significant negative effect on production while structural diversity does not. Furthermore, model output showed that fruit weight was not significantly affected by canopy cover.

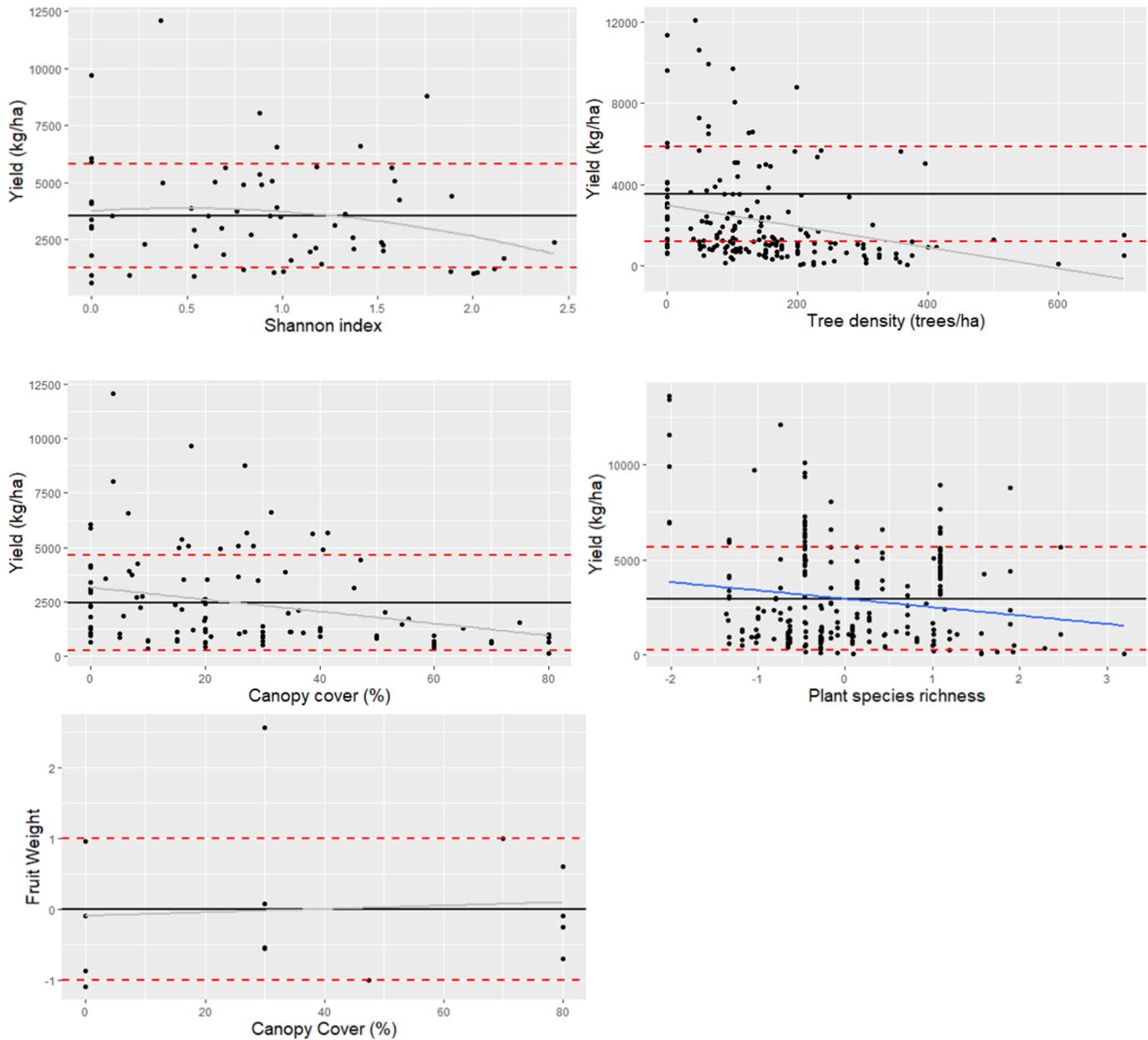


Figure 9. Yield (fig. a, b, c, d) in response to tree density ($n = 185$ plots of 9 studies), plant species richness ($n = 233$ of 7 studies) the Shannon index ($n = 65$ plots of 3 studies) and canopy cover ($n = 111$ plots of 4 studies) and fruit weight (fig. e) in response to canopy cover ($n = 14$ plots of 2 studies). A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot.

The strongest predictor of yield is plant species richness ($\beta = -0.166$, $R^2_{adj} = 0.03$), the other plant diversity variables did not have a significant effect. Tree density ($\beta = 0.004$, $R^2_{adj} = -0.075$) and altitude ($\beta = 0.009$, $R^2_{adj} = -0.093$) have very limited explaining power, with both variables explaining less than 1% of the variance in yield. In addition, results indicate that the Shannon index and altitude together explain only about 1.4% of the variance in yield. A polynomial regression was performed for the

response of yield to the Shannon index. Based on model selection using AIC, a quadratic term was added to the linear model. Canopy cover ($\beta = -0.033$) and altitude ($\beta = -0.088$) jointly explained around 1.1% of the variance in yield.

Although yield experiences a significant decline in response to plant species richness, the explained variance by the fixed effect is only 3%. Plant species richness is therefore not a strong explanatory variable for the change in yield found in the data. Moreover, the conditional R_2 for the response of yield to plant diversity variables and altitude is considerably larger than the marginal R_2 , indicating that much of the variance can be explained by the variation between studies additional to the fixed effects.

Studies reporting on fruit weight in response to plant diversity indicators were almost absent. Percentage canopy cover and fruit weight were measured by only 2 studies for the same plots. Hence, fruit weight in response to canopy cover is the only relationship reported for fruit weight in the results (fig. 9e). The fixed effect explains barely any variance of fruit weight ($\beta = 0.079$, $R_2m = 0.006$) and the random effect variable did not explain additional variance in the model.

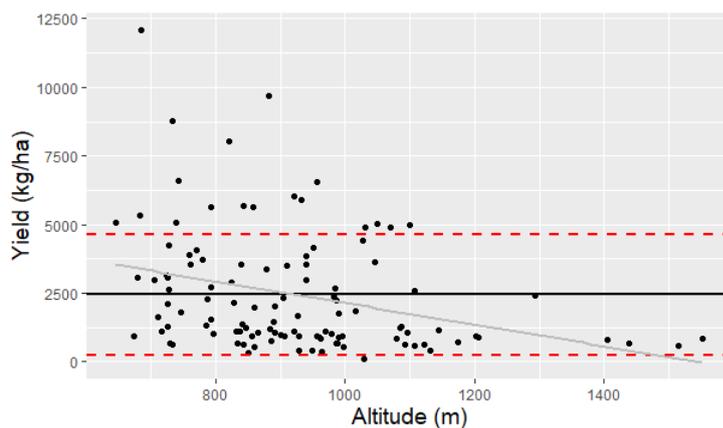


Figure 10. Yield in response to altitude ($n = 111$ of 4 studies). A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot.

Overall, little of the variance in yield and fruit weight is explained by plant diversity and altitude (fig. 9 & fig. 10). A strong increase nor decline in coffee productivity due to plant diversity can be found from these results. In addition, coffee productivity was not found to be significantly affected by altitude, thereby opposing the hypothesis that production increases with altitude.

Table 8. Outcomes from the mixed-effect linear models of yield and fruit weight in response to plant diversity and altitude. The fixed effect explanatory variables are plant diversity attributes and altitude and the response variables are yield and fruit weight. The study was added to the models as a random effect variable. The marginal (R_{2m}) and conditional (R_{2c}) coefficients of determination give the explained variance of the fixed effects and of the fixed and random effects of each model, respectively. P-values of <0.05 are marked in bold.

Model	Type	Fixed effects	R_{2m}	R_{2c}	β coefficient	P-value	SIG
Yield ~ Shannon index + Shannon index ² + Altitude + (1 study)	Polynomial	Shannon index			-0.179	0.620	
		Shannon index ²	0.0136	0.292	0.0779	0.667	
		Altitude			-0.122	0.311	
Yield ~ Canopy cover + Altitude + (1 study)	Linear	Canopy cover	0.011	0.414	-0.033	0.679	
		Altitude			-0.088	0.255	
Yield ~ Plant species richness + (1 study)	Linear	Plant species richness	0.03	0.58	-0.166	<0.001	***
Yield ~ Tree density + (1 study)	Linear	Tree density	0.004	0.757	-0.075	0.119	
Fruit weight ~ Canopy cover + (1 study)	Linear	Canopy cover	0.006	0.006	0.079	0.787	
Yield ~ Altitude + (1 study)	Linear	Altitude	0.009	0.419	-0.093	0.224	

4.3.2 Biological pest control services

Biological pest control increasing with plant diversity is supported to some extent. Abundance of natural enemies increased significantly with plant species richness ($p < 0.001$) (fig. 11a), while incidence of pest was not significantly affected by any of the environmental variables (fig. 12). The response of abundance of natural enemies to plant diversity also indicated that taxonomical diversity has a significant positive effect on abundance of natural enemies whilst structural diversity does not. Furthermore, abundance of natural enemies was significantly negatively affected by altitude (fig. 13). The variability of the effect of plant diversity and altitude on the incidence of pest can, to a great extent, be explained by the differing behaviour between pests.

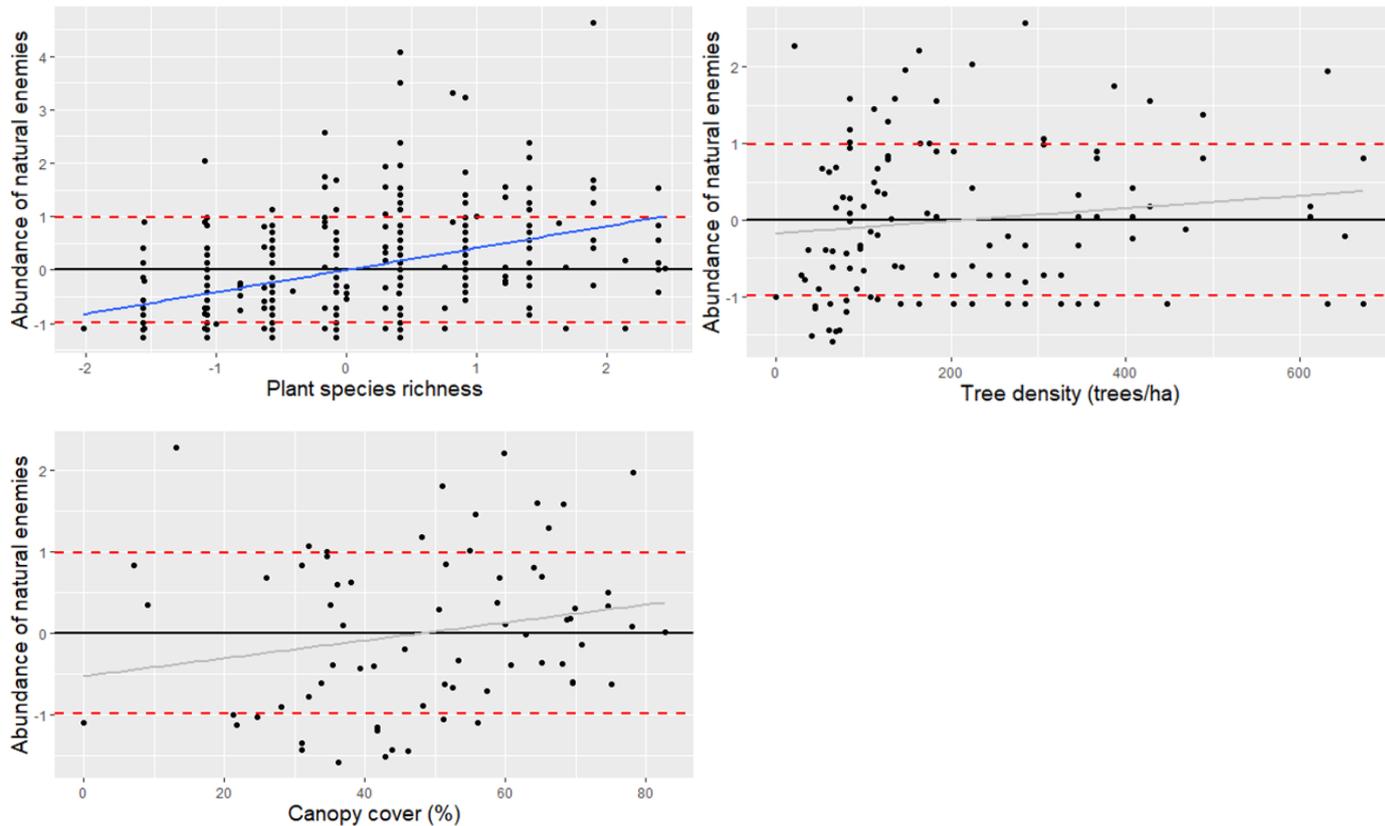


Figure 11. The abundance of natural enemies in response to canopy cover ($n = 70$ plots of 3 studies), tree density ($n = 117$ plots of 4 studies) and plant species richness ($n = 297$ of 4 studies). A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot. The abundance of natural enemies in response to tree density had one outlier that significantly influenced the model, therefore it was excluded.

Plant species richness is the strongest predictor of abundance of natural enemies ($\beta = 0.350$, $R_{2m} = 0.12$), followed by altitude ($\beta = -0.192$, $R_{2m} = 0.036$) which negatively affects natural enemies of pests (table 9). The response of natural enemies to tree density ($\beta = 0.244$, $R_{2m} = 0.054$) and canopy cover ($\beta = 0.260$, $R_{2m} = 0.042$) is variable, although more often studies have reported an above average abundance at a higher level of canopy cover and tree density as seen in figure 11. Taxonomical diversity is thus found to have a stronger explanatory power for the abundance of natural enemies than structural diversity.

No additional variance in abundance of natural enemies was explained by variance between studies, except for abundance in natural enemies in response to tree density ($R_{2m} = 0.054$, $R_{2c} = 0.102$).

Moreover, the abundance of natural enemies in response to the Shannon index was not measured by studies yielded by the systematic review. As a result, the abundance of natural enemies in response to the Shannon index could not be included in the results.

Table 9. Outcomes from the mixed-effect linear models of incidence of pest and abundance of natural enemies in response to plant diversity and altitude. The fixed effect explanatory variables are plant diversity attributes and altitude and the response variables are incidence of pest and abundance of natural enemies. Plot was added to the models as a random effect variable. The marginal (R_{2m}) and conditional (R_{2c}) coefficients of determination give the explained variance of the fixed effects and of the fixed and random effects of each model, respectively. P-values of <0.05 are marked in bold.

Model	Model	Fixed effects	R_{2m}	R_{2c}	β coefficient	P- value	SI G
Abundance of natural enemies ~Plant species richness + (1 plot)	Linear	Plant species richness	0.121	0.121	0.350	<0.001	***
Abundance of natural enemies ~ Canopy cover + (1 plot)	Linear	Canopy cover	0.042	0.042	0.260	0.085	.
Abundance of natural enemies ~ Tree density + (1 plot)	Linear	Tree density	0.054	0.102	0.244	0.069	.
Abundance of natural enemies ~ Altitude + (1 plot)	Linear	Altitude	0.036	0.036	-0.192	<0.001	***
Incidence of pest ~ Plant species richness + (1 plot)	Linear	Plant species richness	0.005	0.005	0.070	0.352	
Incidence of pest ~ Canopy cover + (1 plot)	Linear	Canopy cover	0.003	0.003	0.057	0.337	
Incidence of pest ~Tree density + (1 plot)	Linear	Tree density	0.006	0.006	0.077	0.218	
Incidence of pest ~ Shannon index + altitude + (1 plot)	Linear	Shannon index	0.036	0.036	0.166	0.091	.
Incidence of pest ~Altitude + (1 plot)	Linear	Altitude	0.002	0.002	-0.046	0.362	
						0.471	

Incidence of pests in response to tree density ($\beta = 0.077$, $R_{2m} = 0.006$), canopy cover ($\beta = 0.057$, $R_{2m} = 0.003$) and plant species richness ($\beta = 0.070$, $R_{2m} = 0.005$) is highly variable and can explain almost none of the variance in the incidence of pests. In addition, the Shannon index ($\beta = 0.166$) and altitude ($\beta = -0.089$) jointly explain just 3.6% in the variance of the incidence of pests.

There is large variability in the incidence of pests depending on the type of pest (fig. 12), i.e. the incidence of the white stem borer is more often higher than average when plant species richness is higher while the opposite is found for the incidence of the leaf miner. A similar relationship exists between incidence of pest and altitude ($\beta = -0.046$, $R_{2m} = 0.002$) with almost none of the variance in the incidence of pest being explained by altitude. For none of the models, additional variance is explained by variance between studies.

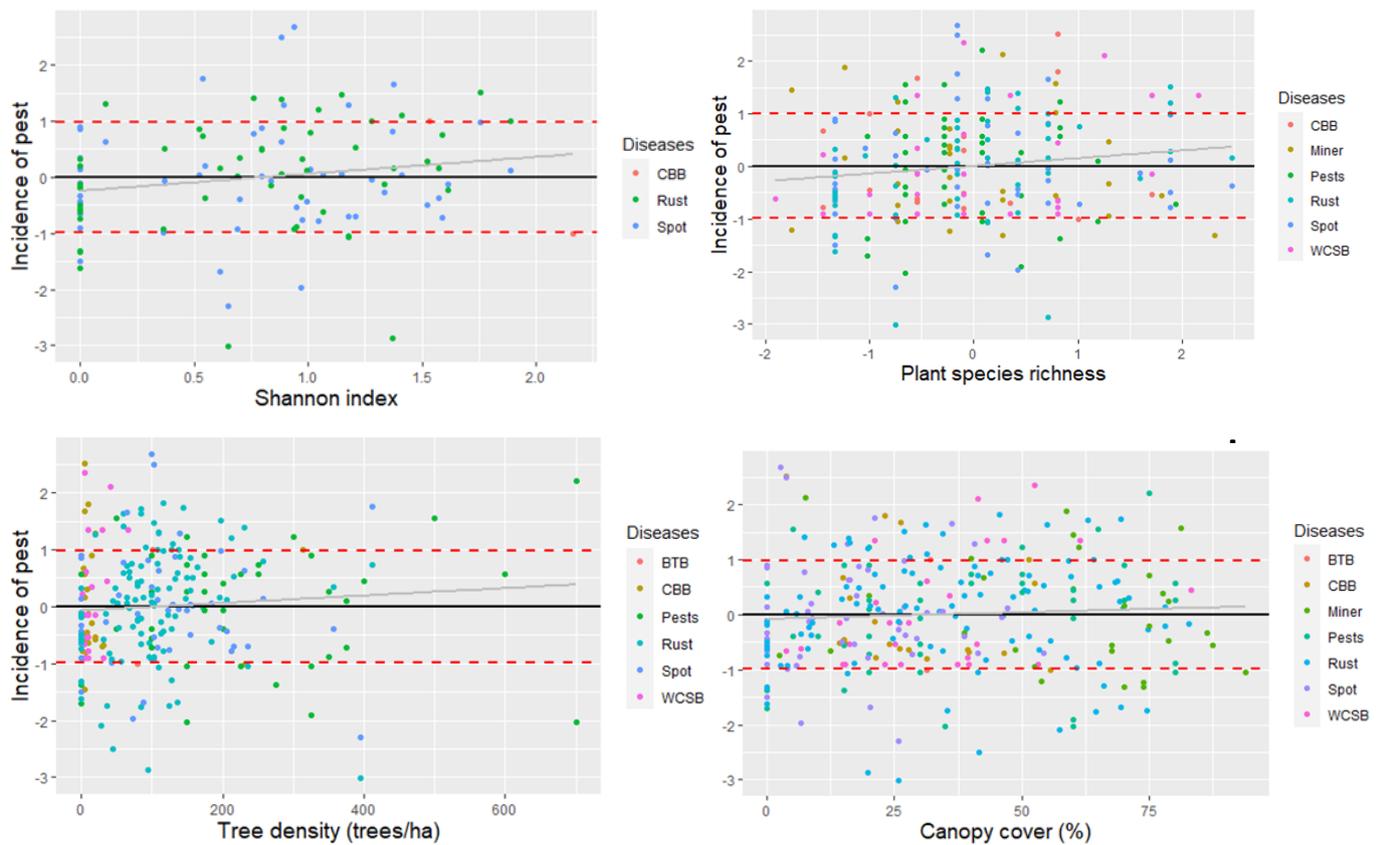


Figure 12. Incidence of pest in response to plant species richness ($n = 226$ plots of 5 studies), tree density ($n = 259$ plots of 7 studies), canopy cover ($n = 282$ plots of 7 studies) and the Shannon index ($n = 105$ plots of 2 studies). The diseases for which the studies have measured the incidence of the pest are indicated by colour. Diseases that were included in the field data are the Coffee Berry Borer (CBB), the Black Twig Borer (BTB), the leaf miner (Miner), the White Coffee Stem Borer (WCSB), leaf spot (Spot), leaf rust (Rust). Field data provided by Jezeer et al. (2019) measured Rust, Broca, Ojo, Ara, Sec, Pota and other which is indicated by 'Pests' in the legend. A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot.

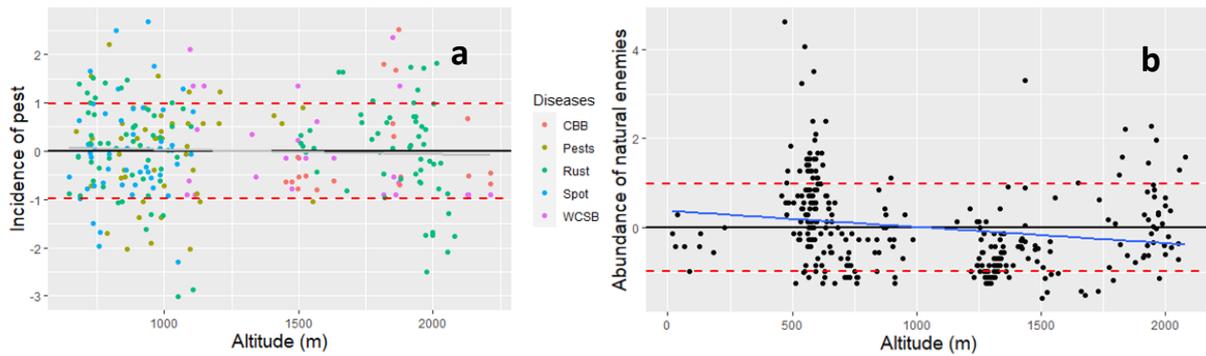


Figure 13. Incidence of pest ($n = 248$ plots of 4 studies) and abundance of natural enemies ($n = 292$ plots of 4 studies) in response to altitude, respectively. A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot.

4.3.3 Pollination services

Pollination services are found to be positively affected by structural diversity, supporting the hypothesis that pollination services are positively impacted by increased plant diversity to a certain extent. Pollinator species richness increased significantly with tree density ($p=0.012$) and was not significantly affected by the other plant diversity variables (fig. 14). Thus, taxonomical diversity does not significantly affect pollination services. In addition, pollinator species richness declined significantly with altitude ($p = 0.004$). The abundance of pollinators was not significantly affected by the plant diversity variables nor altitude.

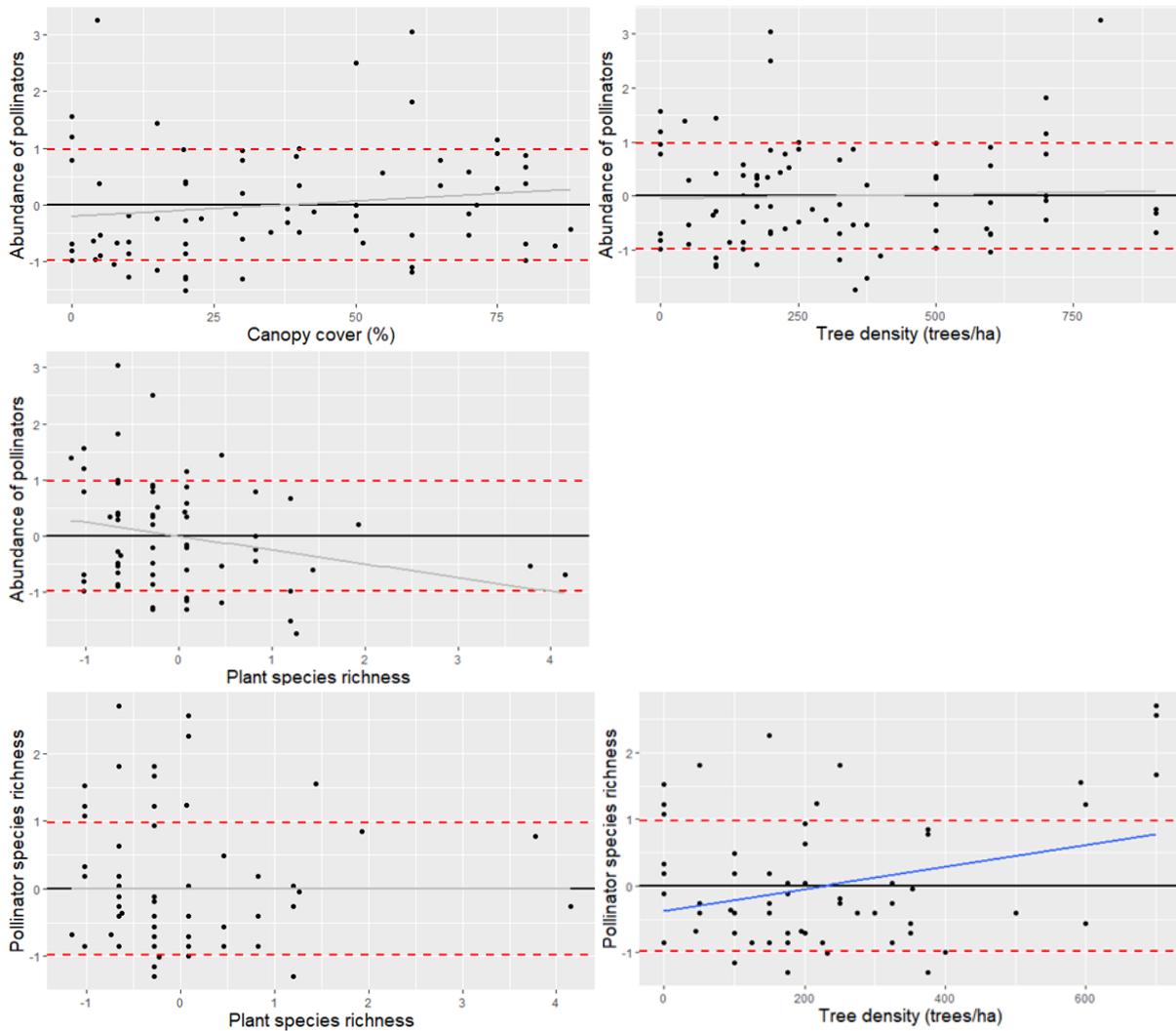


Figure 14. The abundance of pollinators (fig. a, b, c) in response to canopy cover ($n = 75$ from 2 studies), tree density ($n = 82$ plots of 3 studies) and plant species richness ($n=64$ of 2 studies) and the pollinator species richness (fig. d, e) in response to tree density ($n = 65$ of 2 studies) and pollinator species richness ($n = 65$ of 2 studies). A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot.

The strongest predictor of pollinator species richness is altitude ($\beta = -0.346$), followed by tree density ($\beta = 0.297$). Altitude and tree density together explain about 20.2% of the variance in pollinator species richness (table 10). Plant species richness explains almost none of the variance in pollinator species richness ($\beta = -0.001$, $R_2m = 0.000$). Subsequently, it can be concluded from the models that structural diversity has a stronger impact on pollinator species richness than plant species richness.

Neither structural or taxonomical diversity has an impact on abundance of pollinators. Abundance of pollinators in response to tree density ($\beta = 0.037$, $R_2m = 0.001$), canopy cover ($\beta = 0.148$, $R_2m =$

0.022) and plant species richness ($\beta = -0.066$, $R_2m = 0.004$) does not show a clear pattern and can explain almost none of the variance in the incidence of pests. Furthermore, abundance of pollinators is not significantly impacted by altitude ($\beta = -0.09$, $R_2m = 0.01$) (fig. 15).

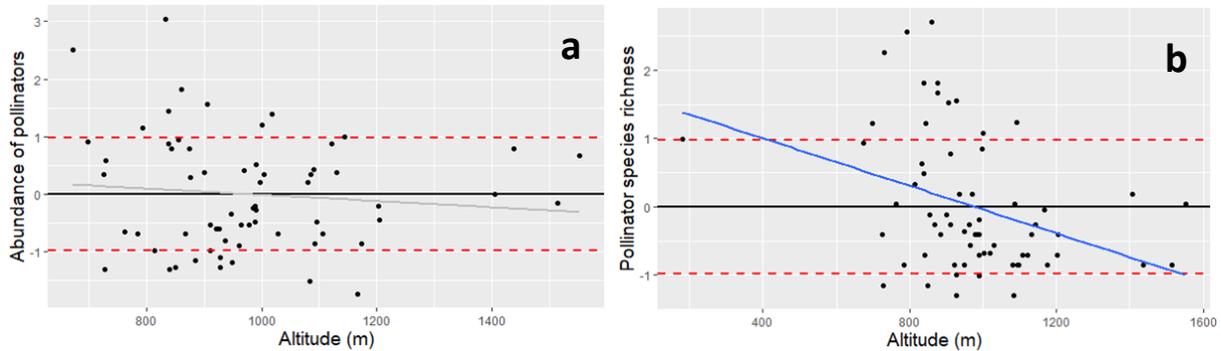


Figure 15. The abundance ($n = 65$ plots of 2 studies) and species richness of pollinators ($n = 65$ plots of 2 studies) in response to altitude, respectively. A grey regression line indicated a non-significant relationship and a blue regression line a significant relationship. Average and standard deviation of the response variable are displayed as reference values with the horizontal black line, average of the response variable, and dotted red lines, the standard deviation. Each dot represents one plot.

For none of the models, additional variance in pollinator species richness nor abundance of pollinators is explained by variance between studies. Neither abundance and species richness of pollinators in response to the Shannon index were measured by studies that the search yielded. Thus, the analysis of pollination services in response to plant diversity is limited to the variables tree density, plant species richness and canopy cover.

Table 10. Outcomes from the mixed-effect linear models of abundance and species richness of pollinators in response to plant diversity and altitude. The fixed effect explanatory variables are plant diversity attributes and altitude and the response variables are abundance and species richness of pollinators. Plot was added to the models as a random effect variable. The marginal (R_2m) and conditional (R_2c) coefficients of determination give the explained variance of the fixed effects and of the fixed and random effects of each model, respectively. P-values of <0.05 are marked in bold.

Model	Type	Fixed effects	R_2m	R_2c	β coefficient	P-value	SIG
Abundance of pollinators ~ Canopy cover + (1 plot)	Linear	Canopy cover	0.022	0.022	0.148	0.205	
Abundance of pollinators ~ Tree density + (1 plot)	Linear	Tree density	0.001	0.001	0.037	0.740	
Abundance of pollinators ~ Plant species richness + (1 plot)	Linear	Plant species richness	0.059	0.059	-0.245	0.0507	.
Abundance of pollinators ~ Altitude + (1 plot)	Linear	Altitude	0.010	0.010	-0.090	0.437	
Pollinator species richness ~ Tree density + altitude + (1 plot)	Linear	Tree density			0.297	0.012	*
	Linear	Altitude	0.202	0.202	-0.346	0.004	**
Pollinator species richness ~ Plant species richness + (1 plot)	Linear	Plant species richness	0.000	0.000	-0.001	0.995	

4.3.4 Trade-offs, synergies and additive effects

The results from the linear mixed-effect models indicate that plant diversity, coffee productivity and biodiversity-mediated ecosystem services are interconnected, consisting of both additive effects and trade-offs. Synergistic effects between the clusters were however not identified. The findings indicated that increased plant diversity has an additive positive effect for biological pest control and pollination services. Structural diversity is found to significantly increase species richness of pollinators, while taxonomical diversity is found to significantly enhance the abundance of natural enemies. Thus, when taking the type of diversification of coffee systems into account, it can be concluded that structural diversity solely enhances the species richness of pollinators without causing a decline in coffee productivity nor affecting pest control services. Increasing taxonomical diversity, however, causes a trade-off between biological pest control services and coffee productivity. Model results show that abundance of natural enemies significantly increases with taxonomical diversity, while yield significantly declines. Therefore, if type of diversity is also specified, there are no trade-offs due to increasing the structural diversity of a coffee farm. Lastly, an additive effect of altitude exists on biological pest control and pollination services. Both abundance of natural enemies and pollinator species richness significantly declined with altitude. Thus, results demonstrate that at a higher altitude, both biodiversity-mediated ecosystem services will decline.

5. Discussion

In the present paper, it was discussed what the effect of plant diversity in coffee agroforestry systems is, when taking into account the possible trade-offs, synergies and additive effects between coffee productivity, biological pest control and pollination services associated with diversification.

The path diagram gave evidence that plant diversity, through biodiversity-mediated ecosystem services, has a relatively strong positive correlation with coffee productivity, while diversity directly has a negative correlation with productivity. The positive correlations between plant diversity and biodiversity-mediated ecosystem services were of medium strength and the strongest positive correlation was found between these ecosystem services and coffee productivity.

Furthermore, the results from the linear-mixed effect models indicated that increased plant diversity has additive effects for biodiversity-mediated ecosystem services. Structural diversity significantly enhances pollinator species richness and taxonomical diversity significantly increases the abundance of natural enemies. Altitude also has an additive effect on biodiversity-mediated ecosystem services as both abundance of natural enemies and pollinator species richness significantly declined. However, the results also indicate that an increase in taxonomical diversity causes a significant decline in yield, thus a trade-off between increased abundance of natural enemies and yield is found.

It was hypothesized that the direct effect of plant diversity on coffee productivity is negative. The results contradicted the hypothesis that coffee productivity would decline with increased plant diversity to an extent: the path diagram showed only a weak negative relationship of diversification

with coffee productivity. Furthermore, there was a contradiction in the results as a larger number of studies reported a positive effect of plant diversity on coffee productivity. However, these studies did not provide either field data nor the Pearson's r for the relationship they found. Thus, coffee productivity was found to have both a positive and negative response to increased plant diversity in coffee systems through different analyses.

The mixed-effect linear models only showed a significant negative effect on yield for plant species richness, subsequently it is not concluded that a strong negative relationship exists between diversification and coffee productivity in coffee systems. While other plant diversity variables did not significantly influence coffee productivity, figure 9 does show up until what extent of diversification, an above average has been reported. Soto-Pinto et al. (2000) and Sarmiento-Soler (2020) indicated a range exists in canopy cover when coffee yield is maintained. The highest percentage within the range for both studies is respectively 48% and 30%. Although this relationship did not become clear with the current dataset, figure 9c does show an above average yield is reported up until about 40% canopy cover. Figure 9a also displays that up until about a Shannon index of 1.8, an above average yield ha^{-1} has been measured. Furthermore, an above average yield is found to mostly occur at a tree density below 200 trees ha^{-1} (fig. 9b).

Additionally, it needs to be taken into account that agroforestry coffee systems can reduce risks for small growers by diversifying the system with production of fruits, wood and other products (Campanha et al., 2004) for which the benefits are not taken into account in this study. A considerable amount of studies included in the review (Cerdeira et al., 2020; Peeters et al., 2003; Campanha et al., 2004) diversified the farms with plants and trees such as: timber trees, fruit trees and musaceae plants,

The hypothesis that pollination services and biological pest control services would be positively impacted by increased plant diversity was largely supported. The path diagram demonstrated that a positive relationship of medium strength exists between plant diversity and the beforementioned ecosystem services. Field data also presented a significant positive response of pollinator species richness to tree density and for abundance of natural enemies to plant species richness. Field data thereby indicates that both structural and taxonomical diversity should be increased to enhance both pollination and biological pest control services in coffee farms. Still, it also needs to be considered that increased taxonomical diversity was also found to cause a decline in coffee productivity. Still, other plant diversity indicator did not significantly affect biological pest control and pollination services thus the hypothesis is only partly supported by field data.

Although abundance of natural enemies increased with more diverse coffee systems, incidence of pests and pest abundance differed considerably between pests. The abundance and incidence of several pests were shown to decline in more diverse coffee systems: the abundance of the red spider mite (Teodoro et al. 2008; Teodoro et al. 2009), the incidence of the black twig borer (Bukomeko et al., 2017) and the coffee berry borer were reported to decline (Nesper et al., 2017). Only the white stem borer (Liebig et al. 2016) and brown-eye spot (Johnson et al., 2009) were reported to increase in more diverse coffee systems. Thus, in order to effectively inform coffee farmers whether a more diverse coffee farm is beneficial, it needs to be considered which pests are prevalent to

understand whether abundance and incidence of pests will increase or decline. This is because countries in which insect pests and mites are reported differs between pests (Barrera, 2008).

Furthermore, for pollination services a larger sample size would be beneficial to increase the reliability of current results (Faber & Fonseca, 2014) as only 2 studies provided data on pollinator species richness in this study. It would be valuable of this result upholds as well in a larger sample size of plot data. In addition, a larger study could be beneficial in order to be able to make a distinction between pollinator species. Kennedy et al. (2013) finds, for example, that while monocultures cause a decline in bumblebees, this type of farming does benefit wild pollinator abundances. Furthermore, the study by Klein et al. (2002), included in the systematic review, reported that the abundance of social bees increased with declining land-use intensity, while solitary bee abundance declined. Coffee fruit set was also almost exclusively found to be positively impacted by pollination services (n=8), except one study by Bravo-Monroy & Potts (2015) that reported a negative correlation between coffee fruit set and the visitation frequency of stingless bees. Thus, both the manner in which pollination services are interconnected with plant diversity and coffee productivity can differ between pollinator species.

Pollination and biological pest control services were found to have a positive effect on coffee productivity as expected. The path diagram indicated that a strong positive relationship exists between coffee productivity and these ecosystem services. Each report of the incidence of pest in response to abundance of natural enemies was positive (n=10) and 83.3% of responses of coffee productivity to pollination were positive (n=18). Moreover, as mentioned before, a positive correlation of medium strength exists between plant diversity and biodiversity-mediated ecosystem services, biological pest control and pollination services as well as a strong positive correlation between the ecosystem services and coffee productivity. The combined results from the path diagram and study responses summarized in table 3 thus demonstrate that increased diversity increases biodiversity-mediated ecosystem services and thereby increased diversity indirectly positively correlates with coffee productivity.

The hypothesis that pollination services decline with altitude was supported by the results, while the hypothesis that biological pest control would increase with altitude was not. The impact of altitude on the incidence of pests was assessed by multiple studies, yet no studies reported on the relationship between altitude and pollination services nor about its impact on natural enemies of pests. Thus, the effect of altitude reported by studies could just be summarized for incidence of pest and coffee productivity. The impact of altitude was reported as being variable with around 38,5% negative responses, 38.5% neutral responses and 23% positive responses (n=13). Testing the relationship of altitude with incidence of pest using the linear-mixed effect models showed a similar result with variable responses of pests to altitude. This can be explained by the climate gradient that is associated with altitude which can partially determine the infestation levels of pests. Multiple studies have reported that this gradient can have contrasting effects on different pests ((Jonsson et al., 2015; Liebig et al., 2016). Altitude had a variable effect on CBB infestations in coffee systems (n=7). Furthermore, leaf spot (n=1) and the coffee leaf miner (n=1) were both found to increase at higher

altitudes while coffee leaf rust was reported to decline at higher altitudes ($n=1$). It is surprising that the effect of altitude on CBB occurrence is variable. CBB infestations in coffee plantations above 1500 meters were not reported until 2001, which is the altitude range in which *C. arabica* is preferably cultivated (Jaramillo et al., 2011). Only due to recent increasing temperatures, CBB infestations also occur at higher altitudes. This suggests that altitude should have a positive effect on the suppression of CBB, yet studies reported variable effects of altitude on the coffee berry borer. Following these results, not only the region but also the altitude of a coffee farm is decisive on the prevalence of different pests. Again, a larger sample size would give a more reliable indication of the effect of altitude on different pests (Faber & Fonseca, 2014).

In addition, the findings from the linear mixed-effect models supported the hypothesis that pollination services would decline with altitude but opposed the hypothesis that biological pest control services increased with altitude. Altitude has an additive negative effect on biodiversity-mediated ecosystem services as both abundance of natural enemies and pollinator species richness significantly declined with altitude. Although altitude has a variable impact on the incidence of pest, the abundance of natural enemies does decline at higher altitudes. This may be explained by abiotic factors such as temperature can lead to lower foraging rates or restricted energy consumption and biotic factors such as a decline in forest cover (Classen et al., 2015; Šálek et al., 2018).

Lastly, altitude was found to have a variable effect on coffee productivity, therefore the hypothesis that productivity would increase was not confirmed. Sarmiento-Soler et al. (2020) also reported that altitude had a variable impact on coffee yield depending on the whether the coffee system is conventional or organic. This could explain some of the variability in the effects of altitude found in the results.

An important limitation of this study to note is that the amount of studies that could be analysed are limited. The Pearson's r nor standardized predictor coefficient was given for most studies included in the systematic review, thereby the reliability of the path diagram could be improved. This is also showcased by the differing results on the response of coffee productivity to increased plant diversity in coffee systems. The same issue arose for field data as little studies provided its data in the supplementary materials nor through personal contact.

For further research, I thus suggest to expand the dataset and include more relevant studies to increase the reliability of the assessment of the interconnectedness of plant diversity with coffee productivity, pollination and biological pest control services. Principally, it is recommended to expand the field dataset for pollination services as the sample size was relatively low. A larger dataset would also be able to create a better overview of the impact of plant diversity and altitude on the incidence of pests as well as a distinction between effects of altitude on conventional and organic farms.

In addition, research should include distance from the forest as an indicator to assess the potential of diversification for increasing biodiversity-mediated benefits. The indicator was measured in multiple studies for both natural enemy and pollinator populations, often having a significant effect on these populations (Campera et al., 2021; Gras et al., 2016; Boreux et al., 2013). Thus, to give a more comprehensive analysis of the effect of diversification of coffee systems, distance to forest should also

be included.

Moreover, a distinction should be made for the pest control services of natural enemies on conventional and organic farms. Insecticides can mask the impact of diversification on coffee productivity, but pesticide use can also reduce ecosystem services such as pollination by causing harm to pollinator species (Lindell et al., 2018). Thus, studying the effect of plant diversity on organic or conventional farms may give considerably different results. Comparing the effect on both farms can also inform integrated pest management (IPM), which has been put forward to shift the reliance on pesticides to also include other pest management strategies. Among which increasing the populations of natural enemies of, among others crops, coffee pests is an important aspect of IPM (Lindell et al., 2018).

Based on these findings, it is recommended for coffee farmers to increase the plant diversity in their coffee system. Increased diversification contributes not only to biodiversity conservation, but also increases biodiversity-mediated ecosystem services that increase coffee productivity. Principally, increasing structural diversity on coffee farms is recommended as the results of this study indicate an increase in pollination services while coffee productivity remains unaffected.

6. Conclusion

Plant diversity, coffee productivity and biodiversity-mediated ecosystem services are interconnected through both additive effects and through a trade-off. Both study and plot data demonstrated that more diverse coffee systems have an additive positive effect on biological pest control and pollination services. These services are enhanced respectively through an increase in taxonomical and structural diversity. Moreover, altitude has a negative additive effect on biological pest control and pollination services through the analysis of plot data. A trade-off exists, however, between the positive response of the abundance of natural enemies and the negative response of coffee productivity to increased taxonomical diversity. These findings have implications for biodiversity conservation in coffee systems; increased plant diversity in farms is found to increase biodiversity and the ecosystem services they provide. Still, in order to accurately inform the sustainable management of coffee farms, the direct negative effect of taxonomical diversity should be considered as well as the diverse effects of diversification on coffee pests.

7. Appendices

Appendix A – Number of studies per country

Country	Number of studies found in the review
Mexico	16
Indonesia	10
Costa Rica	10
Uganda	6
Ecuador	6
Brazil	5
Colombia	5
Ethiopia	5
India	4
Jamaica	3
Nicaragua	2
Puerto Rico	2
Peru	1
Tanzania	1
São Tomé	1

Number of studies yielded through the systematic review per country.

Appendix B – Number of studies per continent

Continent	Number of studies found in the review
Central America	20
North America	16
Asia	14
South America	14
Africa	13

Number of studies yielded through the systematic review per continent

Appendix C – Description of the documentation of general data

Number	Number that the study was assigned in the review
Title	Title of the study
Year	Year of study

First author	Provide citation for the first author
Journal	Provide the name of the journal
Main aim	Summarized aim taken from the abstract
Main conclusion	Summarized conclusions taken from abstract/conclusion
Country	Country in which the assessment was based
Continent	Continent where the study was conducted (Asia, Africa, South America, North America, Europe or Oceania)
Treatment	The types of treatments included in the study (e.g. shaded coffee systems and full sun coffee systems)
Individual data	1 indicates that the study provides data for individual observation sites on at least one of the explanatory and response variables or two response variables for the same observation site
Statistical data	1 indicates that the study provides statistical data to describe the relationship between explanatory and response variables of relevance to this study
Categories of indicators	The study assesses the impact of diversification on indicators that are assigned under the categories below:
Production	1 indicates that the study measures yield as an indicator of production
Pollination	1 indicates that the study measures rate of pollination or abundance of pollinators and 2 indicates that the study measures both indicators of pollination
Biological pest control	1 indicates that the study measures incidence of pest or abundance of natural enemy and 2 indicates that the study measures both indicators of biological pest control

Description of the variables included in the documentation of the general information on the studies included in the systematic review.

Appendix D - Description of the documentation of study level data

Number	Number that the study was assigned in the review
Model	When several relationships are described in the same study, it is indicated by number whether the same model was used for analysis
Explanatory variable	The explanatory variable that is measured in the study; if a cluster variable is used, the name given to the cluster variable is stated (individual variables included in the cluster variable are stated in the observation)
Unit	The unit of the explanatory variable

Response variable	The response variable measured
Unit	The unit of the response variable
General group resp var	The general group the response variable is in, either production, pollination or biological pest control
Observation	Observation of the response variable (e.g. type of pest or whether a compound variable was used)
Number of fields	Number of fields that the study measured
Number of plots	Number of plots that the study measured
Statistical method	The statistical method used in the study (e.g. linear regression, path model)
Predictor coefficient (estimate)	The estimate describes how much the response variable is expected to increase or decrease when the explanatory variable increases by one.
Coefficient standardized	The estimates resulting from a regression analysis where the underlying data have been standardized so that the variances of dependent and independent variables are equal to 1 (allows for the comparison of the relative magnitude of the effect of different explanatory variables on the response variable)
Correlation coefficient	The correlation between the response and explanatory variable
Z-statistic	The z-statistic (also called a z-score or standard score) provides information on how far from the mean a data point is
Significance	Indicate the significance of the relationship between the explanatory and response variable ('not stated' is noted if the significance of the relationship is not mentioned in the study)
Effect	From a sustainability perspective, indicate if the effect of diversification in coffee systems has a positive, neutral or negative effect on production, pollination and pest control
Coffee variety	The main coffee variety that is grown in the studied farms is noted; either arabica or robusta. When a specific variety of arabica or robusta is used, this is also noted.

Description of the characterization of the statistical data provided by the studies included in the systematic review.

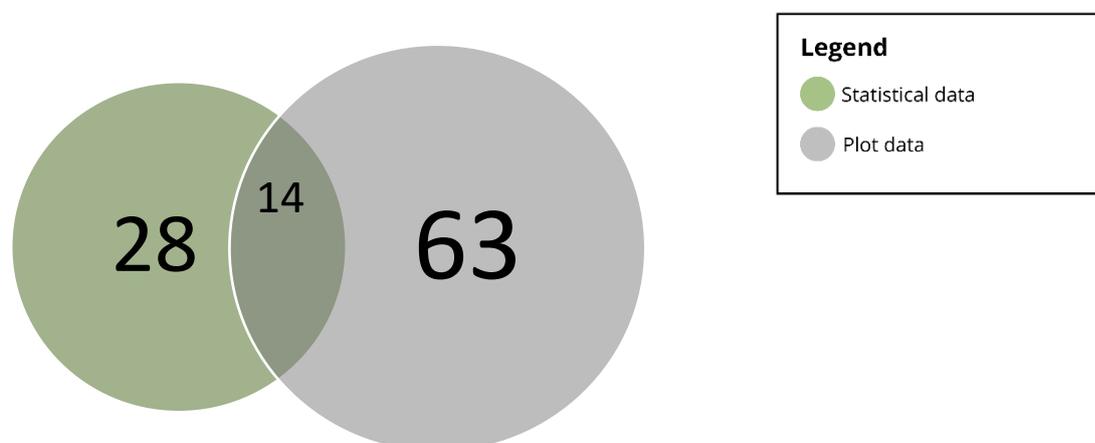
Appendix E - Description of the documentation of plot level data

Number	Number that the study was assigned in the review
Number of field	Number of the field
Number of plot	Number of the plot

Coffee variety	The main coffee variety that is grown in the studied farms is noted; either arabica or robusta. When a specific variety of arabica or robusta is used, this is also reported. ('not stated' is noted if the coffee variety is not mentioned in the study)
Altitude	The altitude measured at each plot or the altitudinal range is noted when the data is provided by the study ('not stated' is noted if the altitude is not mentioned in the study)
Observation	Observation of note (mostly used to describe in what form the data was provided)
Unit	Unit in which the indicator was measured
Standardized	The data is standardized using z-scores.
Number of species	A quantitative measure of the number of tree species present in an observed area
Tree density	A quantitative measure of tree cover in an observed area
Canopy cover	A quantitative measure of the proportion of the forest floor covered by a vertical projection of the tree crowns
Shannon index	A diversity index that quantitatively measures the abundance and richness of woody species in order to quantify the tree diversity of that site
Yield	A quantitative measure of the amount of agricultural production harvested—yield of the coffee crop—in the sample
Fruit weight	A quantitative measure of the fruit weight measured in the sample
Pollinator visitation rate	The number of visits of pollinators per observation period
Pollinator species richness	Diversity of pollinator species measured in the sample
Abundance of pollinators	Total pollinator abundance measured in the sample
Abundance of natural enemies	Total abundance of natural enemies of pests in the sample
Incidence of pest	Proportion or number of coffee plants that is affected by a pest in the sample
Pest abundance	Total abundance of pests measured in the sample

Description of the characterization of the plot data provided by the studies included in the systematic review

Appendix F – Number of studies providing statistical and plot data



Venn diagram showing the number of studies that contain data on indicators related to one or more of the thematic clusters per plot and the number of studies that contain data on the statistical relationship between indicators related to one or more of the thematic clusters.

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