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Effect of shade on biodiversity within coffee farms: a meta-analysis

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Keywords

conservation, agroecology, shade-grown, land use, sustainable agriculture

Abstract

Aligning crop production with conservation initiatives has long been a topic of debate, with agricultural intensification threatening biodiversity across the globe. Shade-grown coffee allows farmers to preserve biodiversity by providing viable habitat, but its conservation value remains unclear. In this meta-analysis, we screened existing literature using the PRISMA protocol to compare the effect of three shade intensities on species diversity and individual abundance: sun, low shade (LS) and high shade (HS). Furthermore, we examine differences between taxa, within taxa and between regions to establish which species benefit most from shade and whether these benefits vary dependent on geographical location. Out of 1889 studies, we included 69 studies in the analysis, and performed random-effects meta-analyses and meta-regressions. Overall, we found that species diversity was significantly higher in HS when compared to sun and LS, and species diversity in LS tended to be higher than in sun. In each treatment, the species diversity of birds was higher in the higher shade treatment, i.e., HS and LS. In addition, mammal and epiphyte species diversity was higher in HS when compared to LS. Similarly, studies from Latin America showed significantly higher species diversity and abundance in shaded farms when compared to sun farms. Studies conducted in Africa detailed the opposite relationship, with abundance being significantly higher in less shaded

systems, highlighting that land-use strategies must be region-specific. Moving forward, strategies to conserve biodiversity within coffee farms should: 1) account for region-specific variables; 2) end further encroachment; 3) maintain connectivity; and 4) optimise yield through prioritising faunal and floral diversity.

1. Introduction

The sustainable cultivation of commodity crops has become a global priority. Throughout the 21st century, governments have been eager to align increasing demand for consumables with the urgent need for our impact on biodiversity to be reduced through the establishment of global initiatives (CBD, 2011; IPBES, 2022; Larigauderie & Mooney, 2010; Navarro et al., 2017; Xu et al., 2021). Whilst agriculture and conservation in much of the twentieth century was perceived to exist in largely separate spheres, particularly in Western society, multi- and interdisciplinary approaches to sustainable agriculture have become increasingly familiar, with terms such as "regenerative", "organic" and "wildlife-friendly" commonplace amongst conservation biologists and agronomists alike (Abraham & Pingali, 2020). Shade-grown coffee is a perfect example of this. Shade coffee is the practice of growing coffee under varying levels of canopy cover to produce optimal climatic conditions for coffee growth, whilst also providing habitats for a diverse array of species (Philpott et al., 2008). As coffee (*Coffea* spp.) was first documented growing under the dense canopy cover of Ethiopia's lowland forests in the 16th century, the concept of shade-grown coffee is not novel (Aregay, 1988). Shade is rather a traditional practice abandoned for the sake of demand (Jha et al., 2014; O'Connell, 2003). Therefore, it is the goal of agronomists and ecologists alike to examine how shade can be utilised to fill demand, whilst preserving biodiversity and ecosystem services.

Providing shade cover for crops, especially when in close proximity to natural forest, is an effective way of providing habitat for wildlife within and around farms. Shade cover is one aspect of a strategy for conserving species *within* farms referred to as land-sharing (Campera et al., 2021a; Fischer et al., 2013). Land-sharing comprises the integration of farmland and native, diverse vegetation within the same landscape. Thus, biodiversity conservation is attempted through the provision of habitat for wildlife. Trees at varying strata provide connectivity within fragmented agricultural landscapes, reducing the deleterious impact of agriculture on both arboreal species and species with relatively large home ranges (Haggar et al., 2019). Additionally, when this shade is provided in close proximity to natural forest, farms can act as buffer zones between human-dominated landscapes and protected areas, bolstering ecosystems and species against the effects of human encroachment, otherwise known as edge effects (Kerr, 2013; Santos-Barrera & Urbina-Cardona, 2011). Shade-grown crop farmers, particularly with relation to coffee, can also access increased income via certifications and the possibility of conservation payments (Castro et al., 2015; Mas & Dietsch, 2004). Finally, shade bolsters ecosystem service provision through the presence of wildlife within and around coffee farms, including natural pest control, pollination and soil fertility, assisting farmers with yield and, in turn, income (De Beenhouwer et al., 2013; Jha et al., 2011). However, the ability of shaded farms to provide viable habitat is contested, with researchers debating the quality of this habitat, and whether or not this habitat replicates natural forest to the extent required for species, particularly those of conservation importance (Bedoya-Durán et al., 2023; Ong'ondo et al., 2022).

Another strategy for preserving biodiversity within farms is land-sparing; farms are maximally intensified, and other areas of land are set aside for conservation purposes (i.e., protected areas) (Campera et al., 2021a; Fischer et al., 2013; Pratzer et al., 2023). In this way, the goal is not for species to be able to persist in agricultural land, but rather that land is spared for conservation purposes so that biodiversity can be preserved. When sparing significant areas of untouched natural forest, land-sparing initiatives can sustain higher levels of biodiversity than in shaded coffee plantations, allowing farmers to maintain/optimise yield in intensified farmland (Cannon et al., 2019). Ensuring the intactness of spared forest poses its own challenges, and often land-sparing initiatives do not discourage further deforestation (Pratzer et al., 2023). Land-sparing and land-sharing have frequently been discussed as one versus the other, yet it is becoming clear that they are not opposing strategies (Valente et al., 2022). We will continue to discuss the dichotomy between land-sparing and land-sharing in this meta-analysis, whether this dichotomy should exist, and the delicateness with which one should approach “silver bullet” strategies.

Coffee has experienced a 67.9% surge in demand in the last 26 years alone, and is now considered one of the world’s most economically important traded commodities, with the global coffee industry worth around US$60 billion as of 2022 (Pancsira, 2022; Torga & Spers, 2020). In order to keep up with increasing demand, the shade cover often provided in traditional, smallholder coffee farms has been sacrificed to allow for agricultural intensification, such as mechanisation and yield optimisation (Jha et al., 2014; O’Connell, 2003). The shift from traditional, often organic, methods of farming to what are now considered conventional methods, such as prophylactic synthetic chemical use and monocultures, was ubiquitous within commodity crop agriculture, beyond coffee alone (Armengot et al., 2016; Jha et al., 2014). Such practices led to habitat degradation, pest resistance, issues concerning human health and biodiversity loss on a global scale (Abdi et al., 2013; Dregne, 2020; Dudley and Alexander, 2017; IPBES, 2022, Mahmood et al., 2016; Niering, 1968; Syafrudin et al., 2021; Zhou and Li, 2021). Whilst there have been strategies put forward to tackle such matters, such as Integrated Pest Management (IPM) in the 1970s that experienced varying levels of success between countries, there has been difficulty in promoting a move away from conventional farming and, instead, prioritising biodiversity. At the 2022 UN Biodiversity Conference of the Parties (CoP 15), the committee resolved that they had not achieved any of the expected outcomes decided upon at the previous conference. This is a common reality that is in line with the lack of consensus experienced at other intergovernmental conferences when discussing biodiversity within agriculture (Tiller et al., 2023).

Preserving biodiversity within farms is not only important in terms of conservation, but for farmers also. The presence of wildlife is vital in order for smallholder farmers to receive essential ecosystem services, such as pest control, pollination and soil quality improvement (De Beenhouwer et al., 2013; Jha et al., 2011). Increased soil macrofauna populations, such as nematodes, can lead to better nutrient distribution; increased bird, ant and nematode populations can increase natural predation of coffee berry borers (CBB; *Hypothanemus hampei*; Coleoptera: Curculionidae), the coffee industry's most expensive pest (at the cost of US$500 million per year); and increased shade has been found to increase pollinator diversity and visitation time (unit used universally to quantify pollination efficiency) (Manson et al., 2022a). In addition, initiatives to preserve biodiversity both directly and indirectly bolster ecosystems against climate change and actively promote synergistic benefits to mitigate climate change (Shin et al., 2022). Furthermore, the quality of coffee, i.e., taste, actively improves with increased shade (Muschler, 2001). According to the International Coffee Organisation, 70% of coffee farmers worldwide are smallholders, meaning that ecosystem service provision, climate change mitigation and sustainable incomes become particularly important. Coffee is almost exclusively grown in biodiversity hotspots, i.e. Southeast Asia, East Africa and Latin America, burdening smallholder farmers with the responsibility to produce a high-demand commodity crop whilst also preserving habitat for threatened species, including Critically Endangered mammals and birds (Bakermans et al., 2012; Etana et al., 2021; Nekaris et al., 2022).

Biodiversity preservation, and the ability of shade-coffee to supply this, is currently a priority of many researchers. There is often conflict as to the extent shade can preserve biodiversity. In addition to a lack of consensus, it is often the case that shade is presented as a binary variable: full sun vs shade; or moderate shade vs complex shade. It is rare that within- and between-species abundance and diversity are taken into account at multiple levels of shade. In this meta-analysis, we aim to compare the effects of different levels of shade on biodiversity to elucidate which shade level is the most beneficial. We do this by examining the effect of three shade intensities on species diversity and individual abundance: full sun (0-5% shade), low shade (6-30% shade) and high shade (>30% shade). In addition, we examine how these three shade intensities impact biodiversity between taxa, within taxa, between and between regions in order to gauge which species and which regions benefit most from shade, and how they benefit. We will then be able to provide taxa and region-specific conservation strategies and identify gaps in the literature with regards to how shade facilitates, or does not facilitate, biodiversity conservation.

2. Methods

This meta-analysis followed the *Preferred Reporting Items for Systematic Reviews and Meta-Analyses* (PRISMA) protocol (Page et al., 2021). Overall, the procedure consisted of four steps: 1) a literature search using relevant keywords; 2) screening all literature found in the initial search; 3) retrieval of data from sources deemed to be in line with chosen criteria; and 4) analysis of data extracted from these sources. We have outlined the first three stages in Figure 1.

2.1. *Literature search*

The first stage of the procedure was to use online databases to compile all relevant peer-reviewed literature. Using the Web of Science and SOLO databases, we collated a total of 3405 and 5539 papers, respectively, published until October 2023. We used the following key words to search for papers: coffee shade *conservation* (n=595;919); coffee shade *abundance* (n=269;343); coffee shade *density* (n=254;366); coffee shade *biodiversity* (n=632;862); coffee shade *species diversity* (n=454;715); coffee shade *species density* (n=162;223); coffee shade *species richness* (n=297;729); coffee shade *ecosystem services* (n=226;399); coffee shade *pest* (n=170;324); coffee shade *pollination* (n=58;86); coffee shade *productivity* (n=123;216); coffee shade *soil quality* (n=91;163); and coffee shade *income* (n=74;194). Before combining the results of Web of Science and SOLO databases, we removed 2271 and 3967 duplicates, respectively, and 817 duplicates after combining the two datasets, leaving a total of 1889 papers for screening.

2.2. *Literature screening*

We screened the literature in three stages: 1) assessed the relevance of titles; i.e., did the titles make reference to either conservation, species abundance/richness or biodiversity in addition to coffee/shade; 2) assessed the relevance of abstracts; i.e., does this paper provide a comparison between different shade management strategies; and 3) retrieved all remaining papers and removed all of those whose data did not align with the criteria listed in Figure 1. Consequently, out of 1889 papers screened, we retrieved 200 papers to check whether the data fit our criteria, and extracted data from 69 papers.

2.3. *Data retrieval*

In order to produce comparable results, papers had to conform to the following criteria: 1) compare species diversity or abundance between treatments (e.g., mean individual abundance, mean species richness, mean occupancy, Shannon Diversity Index, etc.); 2) define percentage canopy cover for each shade treatment; 3) canopy cover must be sufficiently different between studies (i.e., provide results for treatments with canopy cover relating to two or all of the following categories: 0-5%; 6-30%; and >30%); 4) the diversity metric must be provided with a corresponding measure of variance, or the means to calculate variance, and the number of samples taken; 5) the data must be a direct measure of species diversity or abundance (i.e., we could not extract data from studies that provided the outputs of statistical analyses alone); and 6) not relate to pest populations. We removed three papers as a result of not obtaining access.

In order to retrieve data, authors must have provided a measure of variance or have provided enough information for variance to be calculated manually. If they did not provide a measure of variance, but they provided the means and n for several sites within each treatment, we were able to calculate variance and include the data. Once we calculated the standard deviation for each data point, we calculated variance (v) by squaring the standard deviation. We were able to extract several data points from one paper in the following cases: the paper presented different measures of biodiversity (i.e., species diversity/richness, occupancy, abundance, etc.); or the paper presented results for different taxa. For papers that presented canopy cover as a continuous variable, or presented several treatments with varying shade cover, we calculated a mean value from all of the treatments that aligned with our canopy cover criteria.

We extracted relevant data from papers using tables, within-text references, and graphs, for which we used PlotDigitizer (PlotDigitizer, 2023) to accurately estimate the value. A map of the locations where studies took place can be seen in Figure 2. We categorised data into three shade management levels: sun (0-5% shade), low shade (6-30% shade) and high shade (>30%) (Philpott et al., 2008). Following this, we then separated data into two datasets: data points related to abundance (i.e., individual abundance, individual density, occupancy, visitation rate) and those related to species diversity (i.e., species richness, species diversity index, species density).

2.4. *Data analysis*

We analysed the data using R v 4.2.2 using the “metafor”, “DT”, “plyr” packages and visualised the data using “ggplot2” and “metafor” (R Core Team, 2022) and carried out an overall meta-analysis and further meta-regression analysis (Crystal-Ornelas, 2020; Harrer et al., 2021; Koricheva et al., 2013; Schwarzer et al., 2015). Firstly, we generated a response ratio (RR) between shade treatments (sun vs low shade; sun vs high shade; low shade vs high shade) for each line of data representing whether the mean value was higher in the higher shade treatment or the lower shade treatment. The RR was then transformed to the natural log of the RR, ln(RR). A negative ln(RR) indicates that the mean was higher in the higher shade treatment, e.g., ant abundance was higher in high shade farms than low shade farms, and a positive ln(RR) indicates that the mean was higher in the lower shade treatment, e.g., ant abundance was higher in sun farms than low shade farms. The ln(RR) for each paired species diversity/abundance measurements are the effect sizes we used for the meta-analyses. We calculated the effect sizes using the “escalc” function in the “metafor” package (R Core Team, 2022).

After we generated the ln(RR), we carried out random effects meta-analyses for each of the treatment comparisons. We used random effects analysis rather than fixed effects analysis as although all of the data were taken from coffee farms, these field sites were from all over the world and in highly variable environments, therefore the sampling process was not controlled enough to warrant fixed effects analysis. Random effects analysis takes into account both within and between study variance; therefore, this meta-analysis will not require a fixed effect model (Crystal-Ornelas, 2020; Harrer et al., 2021; Koricheva et al., 2013; Schwarzer et al., 2015). We ran six random effects meta-analyses comparing the species diversity/abundance values taken from each paper that we used for each shade treatment (n = number of papers; number of data points): 1) sun vs low shade (abundance: n=21;77; diversity: n=9;30); 2) sun vs high shade (abundance: n=13;36; diversity: n=12;44); and 3) low shade vs high shade (abundance: n=31;75; diversity: n=27;60). The random effects analysis was done using the "rma" function in the "metafor" package (R Core Team, 2022). Whilst running the analysis, we ensured that we accounted for non-independence, i.e., the model did not assume all data points to be independent, as some papers produced several data points. We did this by assigning the random effect to the last name of the author within the dataset.

In addition, we conducted meta-regression analyses to see whether trends existed within certain variables, such as between taxa, within insect taxa, and between regions (Crystal-Ornelas, 2020; Harrer et al., 2019; Koricheva et al., 2013; Schwarzer et al., 2015). The taxa and regions included in the meta-regression analyses for each treatment are summarised in Table S1 (abundance data) and Table S2 (species diversity data). For the meta-regressions, data points from studies that summarised taxa or region were removed; this meant removing one paper, Mokondoko et al. (2022), from each meta-regression for taxa and region. We were able to carry out an insect taxa meta-regression for each of the treatments due to insects making up the majority of papers used for the meta-analysis. The results of taxa making up fewer than two data points were not presented in the results. For abundance, these taxa included Fungi, Arthropods, and Nematodes; and for the insect taxa meta-regression, these included Blattodea, Coleoptera, Diptera, Hemiptera, Homoptera, Neuroptera, Orthoptera, Pscoptera, Scolopendridae. For species diversity data, these taxa comprised: Arthropods; and for insect taxa, comprised Coleoptera. A detailed summary of all taxa analysed in our meta-regressions is presented in Table S1 and S2. We used the "rma.mv" function in the "metafor" package to carry out the meta-regressions (R Core Team, 2022). We considered p=<0.05 to indicate significance, with p=<0.001 indicating high significance.

3. Results

3.1. *Overall random-effects meta-analyses*

We carried out six random effects meta-analyses, two for each treatment, to establish whether species diversity or individual abundance were significantly impacted by level of shade. The meta-analyses for species diversity revealed species diversity to be higher in higher shade systems, with a significant difference, or trending towards significance, found for each treatment (sun vs LS: estimate = -0.3006, p value = 0.051; sun vs HS: estimate = -0.3865, p value = 0.0182; LS vs HS: E=-0.1686, p=0.0141; fig. S1 and table 1). The meta-analyses for abundance were not significant for any of the treatments, showing that on average, the literature documented an increase in species diversity with increasing shade, with abundance seeming to be unaffected (see fig. S2 and table 2).

3.2. *Between taxa meta-regression*

We ran a meta-regression between taxa for each treatment to establish how different taxa varied in species diversity and abundance between shade treatments**.** We found significant results for abundance in the sun vs high shade treatment and species diversity in all treatments (fig. 3; fig. 4). For sun vs low shade, species diversity of birds was significantly higher in low shade farms (estimate = -0.5108, p value = <0.0001). For sun vs high shade, abundance and species diversity with relation to birds was found to be significantly higher in high shade farms (estimate = -0.3201, p value = 0.0160; estimate = -0.6573, p value = <0.0001). For low shade vs high shade, species diversity of birds (estimate = -0.2200, p value = 0.0234), mammals (estimate = -0.6242, p value = 0.0028) and epiphytes (estimate = -0.4801, p value = 0.0056) was higher in high shade farms. Regarding the significant results found for abundance, these are in contrast to the results presented in the previous paragraph as abundance is significant when looking at individual taxa, but not when examining all organisms combined. For non-significant between taxa meta-regressions, see Figure S3.

3.3. *Region meta-regression*

We ran a meta-regression using region as the categorical variable to establish whether biodiversity between management intensities were affected by region. We found significant results for almost all treatments for both abundance and species diversity (fig. 5; fig. 6). For the sun vs low shade treatment, abundance extracted from studies conducted in Africa was found to be significantly higher in sun farms (estimate = 0.5198, p value = 0.0355). Contrary to this, abundance extracted from Latin American studies was found to be significantly higher in low shade farms when compared to sun farms, and high shade farms when compared to low shade (estimate = -0.3823, p value = 0.003; estimate = -0.3756, p value = 0.0029). Latin American studies presenting species diversity showed the same trend in all treatments (sun vs LS: estimate = -0.3781, p value = <0.0001; sun vs HS: estimate = -0.3704, p value = 0.0014; LS vs HS: estimate = -0.1149, p = 0.0550).

3.4. *Insect taxa meta-regression*

We found significant results in all treatments (fig. 7; fig. 8). For the sun vs low shade treatment, insect abundance was not significantly affected by shade management, but Hymenoptera (ant) (estimate = -0.1485, p value = 0.0626, n = 4) and Lepidoptera species diversity was higher in low shade farms (estimate = -0.1219, p value = 0.0441, n = 6). For the sun vs high shade treatment, we found that Diptera abundance (estimate = -1.3421, p=0.0401, n = 3) and Lepidoptera species diversity were higher in high shade farms (estimate = -0.2591, p value = 0.0004, n = 4). Finally, in the low shade vs high shade treatment, ant species diversity was higher in the high shade system (estimate = -0.2690, p value = 0.0187, n = 11), whilst bee species diversity was lower in the high shade system (estimate = 0.4127, p=0.0023, n = 8). For non-significant between taxa meta-regressions, see Figure S4.

4. Discussion

Overall, we found species diversity to be higher in high shade systems when compared to sun farms and low shade farms. In contrast, there was no significant difference in abundance between shade treatments. This supports our hypothesis that increased shade cover promotes increased biodiversity, and whilst abundance may not be significantly lower in lower shade treatments, further meta-regressions have confirmed that high and low shade environments can be preferable for some taxa and in certain regions. Additionally, although ensuring viable species populations within an ecosystem is important, if preserving biodiversity is the primary goal, the literature shows that providing shade cover of >30% is required.

4.1. *Differences between taxa*

4.1.1. *Insects*

We found higher insect species diversity in high shade farms when compared to sun farms and low shade farms. Abundance did not significantly change between treatments, indicating that abundance is unaffected by shade management. Insects are by far the most studied taxa with regards to wildlife presence within coffee farms, which is likely due to their multi-functional ecosystem service provision.

We found significantly higher Lepidoptera species diversity in high shade farms when compared to sun farms and low shade farms. One potential explanation for this is that high shade coffee farms boast higher floristic diversity (Bandeira et al., 2004; Worku et al., 2015; Perfecto et al., 2004), which in turn encourages the presence of pollinators (Blaauw & Isaacs, 2014; Fisher et al., 2017; Ouvrard & Jacquemart, 2018). When studying butterfly abundance and movement in and between sun and shade farms, Muriel & Kattan (2009) found that butterfly species showed high behavioural plasticity, making them easily adaptable to heterogeneous landscapes. Movement changed significantly between the management intensities, with flight paths proving faster and more direct in sun farms

(Muriel & Kattan, 2009), which could mean that pollination efficiency is reduced if measuring efficiency through pollination time. Potential plasticity and adaptation to mosaic landscapes should be taken into account when designing conservation strategies, prioritising species that are not so quick to adapt.

We saw inconsistency within Hymenoptera between bees and ants. We will only discuss bees with regards to the low shade vs high shade insect taxa meta-regressions due to a lack of data when comparing sun and low and high shade systems. Whilst bee abundance in coffee farms was unaffected by either shade system, bee species diversity was significantly higher in low shade farms than in high shade farms. This trend is supported by other papers that we were unable to include in the meta-analysis due to them not providing specific definitions for shade cover, i.e., Berecha et al. (2015). The preference for sun farms could be due to a seasonal lack of floral resources in forested areas when coffee is blooming, meaning there is a seasonal attraction to sun coffee farms due to the higher density and concentration of floristic resources (Vogel et al., 2021). Additionally, bee visitation rate and time has been shown to increase with increasing temperature, showing a preference for sun farms (Manson et al., 2022a). This is further supported by Classen (2014), who found that honey bee (*Apis* spp.) visitation rate was higher in low shade farms and sun farms when compared to higher shade treatments, but found the opposite relationship for other pollinator species. This is in line with our findings that butterfly diversity increases with increased shade, showing a stark contrast between insect pollinator species. As discussed previously, we found that irrespective of bees, insects are generally sparser in sun farms both in abundance and diversity. This lack of diversity would risk leaving too heavy a reliance on bees for pollination, particularly as bees have been found to pollinate coffee less frequently than other taxa, such as butterflies (Berecha et al., 2015; Manson et al., 2022). Therefore, when discussing pollinators, conservation strategies (e.g., land-sparing or land-sharing) should prioritise bolstering pollinator diversity and, in turn, species complementarity, particularly with climate change threatening phenological synchrony (Bartomeus et al., 2013; Blüthgen & Klein, 2011).

Diptera abundance was found to be significantly higher in high shade farms when compared to sun farms. Although this result was taken from one paper, it comprises three separate measures of Diptera species abundance (all Diptera individuals, *Chrysopa* spp. adults and immature *Chrysopa* spp. individuals). Whilst Diptera are not considered to be an important pollinator of coffee, their presence has been recorded, and their presence could potentially contribute to species complimentarity in the face of phenological asynchronies. Researchers have generally not found Diptera abundance to be affected by agroforestry (Geeraert et al., 2019; Krishnan et al., 2012), with the exception of Hafsah et al. (2021) who found that Diptera individuals were more common in sun coffee farms. Dipterans have been documented as the most significant pollinator of cacao plants, a plant grown in similar conditions to coffee and often grown in a polyculture/rustic system alongside coffee (Vandromme et al., 2023). Therefore, although not directly important for the growth of coffee, our finding highlights the importance of high shade in promoting a diversity of pollinator species.

Ants make up one of the most studied taxa within this topic. Papers considering ant abundance within coffee farms were present in each of our treatments, leading to ants making up a relatively large proportion of data points within our meta-analysis (sun vs low shade=18; sun vs high shade=9; low shade vs high shade=20). This is further backed up by Philpott et al.'s (2008) major review of biodiversity in Latin American coffee farms. Interestingly, ant abundance was not found to be affected by shade management, and ant species diversity was only found to be significantly higher in the low shade vs high shade treatment, but trended towards significance in the sun vs low shade treatment. This is in line with the general trend of higher diversity in higher shade systems, but converse to the results found for bee populations in the low shade vs high shade treatment. Emphasis on ant population dynamics is understandably well-studied due to the important role of ants in the provision of ecosystem services, such as the biocontrol of pests. Moving forward, when discussing biodiversity provision within coffee farms of differing management intensities, more focus should be placed on more understudied ecosystem service providers, such as arthropods (Tatiana et al., 2022).

4.1.2. *Birds*

Bird species diversity was significantly higher in the higher shade system of all treatments. This is a well-documented finding within relevant literature with many reasons as to why this would be the case. Firstly, there are significantly more insects in high shade farms than in sun farms, providing increased food resources for birds in high shade farms. Related to this, Huang et al. (2015) found that areas with increased insect richness had a significant effect on the richness of breeding bird populations. However, habitat use by birds within shade coffee farms cannot be reduced to food resources alone; habitat use varies widely depending on season (breeding/non-breeding) and whether species are specialists or generalists (Huang et al., 2015; Valente et al., 2022). Forest specialists, species that are more at risk of extinction due to their narrow niches, tend to do better in land-sparing landscapes (Valente et al., 2022). In contrast, generalists do better in land-sharing landscapes. In this way, as long as shade is complex and cover is considerable enough, farmers still provide habitat for specialists whilst preserving functional and taxonomic diversity (Valente et al., 2022). Finally, not only is shade important for birds in terms of nesting sites and resources, but energetic load on birds reduces in shaded coffee farms due to microclimate regulation (Monge et al., 2022; Schooler et al., 2020). Bird abundance remained unaffected by shade management, but tended towards significantly higher in high shade farms over low shade farms. This is in line with Bohada-Murillo's (2019) review on bird populations in agroecosystems. They found that bird abundance declined with increased productivity, indicating that both abundance and species diversity is sacrificed with as canopy cover declines.

Shade coffee farms are important stop-over points for Nearctic-Neotropical migrants (Spidal & Johnson, 2016), such as black-throated blue warblers (*Setophaga caerulescens*), bird species that are highly sensitive to disturbance due to their reliance on habitat for nesting sites and wintering grounds (Mas & Dietsch, 2004; Price & Hayes, 2017; Sedinger et al., 2011). This is due to the seasonal resources shade farms provide for birds when over-wintering (Bakermans et al., 2012; Spidal & Johnson, 2016). Bakermans et al. (2012) found that migrant bird species density was significantly related to floristic and structural availability within coffee farms, with different species utilising different strata within shaded farms. Investing in the conservation of migratory birds is simultaneously contributing to the conservation strategies of multiple locations and benefiting the habitats where migratory birds provide key ecosystem services (Johnson et al., 2020; Wilson et al., 2021).

On the contrary, studies of birds in African coffee farms found the opposite trend. Smith et al. (2015) found higher richness and abundance of birds of all guilds in sun farms over low shade farms, but there was no community similarity between species present in each, suggesting that they produce and support entirely different species. Forest specialists made up the lowest proportion of the bird communities found in sun and low shade farms, which is in line with previous literature that states that forest undergrowth specialists are almost entirely absent in coffee plantations due to the near-complete transformation of undergrowth to coffee cultivation (Komar, 2006; Smith et al., 2015). As specialist species are of greater conservation concern, these results suggest that land-sparing strategies may be a better option in African coffee farms, as this will provide habitat for the two almost entirely distinct bird populations (Smith et al., 2015).

4.1.3. *Mammals*

We found significantly higher species diversity of mammals in high shade farms than in low shade farms, with Etana et al. (2021) documenting leopards (*Panthera pardus*) and blue monkeys in Ethiopia, both of which are classified as Vulnerable on the IUCN Red List (Stein et al., 2020; de Jong & Butynski, 2020). Much of the literature documents little difference in mammal biodiversity between shaded agriculture and nearby forest areas, which adds value to our results as not only is mammal presence significantly higher in largely shaded farms, but it is comparable to that of nondisturbed areas (Campera et al., 2021b; Caudill et al., 2014; Caudill et al., 2015; Caudill & Rice, 2016; Mertens et al., 2018). Coffee farms with increased shade may boast higher mammal presence due to increased connectivity within and between mammalian habitats, allowing for free movement for species that are highly sensitive to disturbance (Haggar et al., 2019). This is particularly true of coffee, above other agroforestry systems, which is considered to be an effective connector between forest habitats (Ocampo et al., 2019). Therefore, conservation strategies for mammals should prioritise connectivity and ensuring majority shade in agricultural landscapes. One example of this is implementing canopy bridges as part of land-sharing strategies to enable movement between habitats in mosaic, agroforest landscapes (Flatt et al., 2022; Nekaris et al., 2022). With increased connectivity come concerns regarding human-wildlife interactions, such as increased crop raiding, but there is evidence to suggest that shade-tree agriculture can mitigate human wildlife interactions by providing enough food resources to discourage crop raiding (Kerr, 2013). It is important to note that some studies document a decline in mammal species richness when comparing shade coffee and forested areas. Bedoya-Durán et al. (2023) documented lower mammal species richness and abundance in shade coffee farms in comparison to forest in Colombia, with distance from forest having the largest influence on mammal occupancy. This further bolsters the argument that land-sharing, promoting connectivity and providing habitat within and around farms, and land-sparing, ensuring that encroachment does not sacrifice untouched forest, must be used synergistically to achieve conservation success.

4.1.4. *Epiphytes*

Epiphytes were the only plants present within our meta-analysis, and we found that, similarly to mammals, there was significantly higher epiphyte species diversity in high shade farms than in low shade farms. Epiphytes are considered to be essential for biodiversity preservation due to their roles as ecosystem engineers, and they make up 10% of all vascular plants (Hietz, 2005; Zotz et al., 2021). Despite epiphytes' clear role in ecosystem service provision, qualitative research into farmers' perceptions of biodiversity within smallholder agriculture concluded that farmers were not aware of the important role of epiphytes and mostly associated epiphytes with aesthetics (Richards et al., 2021). Thus, the conservation of these plants is not only important for ecosystem functioning, but extinction would threaten a significant proportion of plants. Many studies document the importance of intact forest for epiphyte conservation, but it is not only the density of the forest that is pivotal; moreover, it is the diversity of the shade which regulates epiphyte presence (Hietz, 2005; Hundera et al., 2013; Koelemeijer et al., 2021; Zotz et al., 2023). Therefore, farmers must maintain not only high shade but diverse shade, i.e., higher number of different shade tree species providing different levels of strata; as Hietz (2005) reported, diverse shade maintains high epiphyte species richness. Diverse epiphytic vegetation is directly correlated to higher bird diversity and abundance due to the provision of nest sites (implying suitability for forest-undergrowth specialists) and the indirect increase in invertebrate abundance (Cruz-Angón et al., 2009; ; Hylander & Nemomissa, 2008). Globally, farmers are being encouraged to convert to intensive practices, meaning species kept for aesthetic purposes will fall by the wayside. High and diverse shade should be prioritised in relation to epiphyte conservation, and stakeholders should be made aware of the harmful impact of regular pollarding and over-pruning on epiphyte substrate attachment (Hietz, 2005).

4.2. *Differences between regions*

There were significantly higher levels of species diversity and abundance in Latin America in both high shade farms and low shade farms when compared to sun farms, and species diversity tended towards significantly higher in high shade farms over low shade farms. This is in line with previous reviews of the effect of management intensity on biodiversity in Latin America (Mendenhall et al., 2016; Philpott et al., 2008). Philpott et al. (2008) concluded that the loss of forest species increased with management intensity, and rustic coffee systems (coffee grown under complex, native shade) were the management strategy that protected the most species. Additionally, Mendenhall et al. (2016) documented that only 27% of species in their study region in Costa Rica were able to live in both “forest elements” and crop pastures, with 57% dependent on forest elements and 15% restricted to crop fields and pastures. These reviews, alongside our results, indicate that Latin American farms would be better investing in land-sharing strategies, with priority being given to rustic coffee systems and the restoration of sun farms (Philpott et al., 2008).

We found that African farms harboured higher abundance in sun farms over low shade farms. This may be due to species having adapted better to increased temperatures and prolonged sunlight, such as what are experienced in Uganda, Kenya and Tanzania where the studies took place. In the low shade vs high shade treatment, although it was only tending towards significant, species diversity was higher in the higher shade treatment. These results could further bolster the argument that low shade is not viable in maintaining biodiversity. In areas where diversity is high in sun, and dependent on existing geographic variables (i.e., existence of intact forest), land-sparing initiatives would both protect natural forest and provide viable habitat for wildlife.

4.3. *Benefits of agroforestry*

Agroforestry bolsters farmland against climate change due to the moderation of temperature extremes provided by shade trees (de Souza et al., 2012; Merle et al., 2022; Monge et al., 2022). This is particularly apt for arabica coffee due to its high sensitivity to increased temperature, but it will enable species, such as a diverse community of birds, to persist within an environment that would otherwise have not provided optimal climatic conditions. Additionally, other studies suggest that increased shade either has an insignificant effect on pest presence or pest presence is significantly reduced in higher shade (Borkhataria et al., 2012; Manson et al., 2022b; Piato et al., 2021; Soto-Pinto et al., 2002; Vogel et al., 2021). It is the very presence of species such as birds and bats that connect shade and pest presence in the literature. Ferreira et al. (2023a) found that in Cameroonian shaded cacao plantations, birds and bats provided a monetary benefit of \$478 ha−1y−1 in terms of pest removal, but were only able to do this in farms with high tree-level shade cover (>50%). In other words, the ecosystem services provided by birds and bats were not monetarily beneficial to farmers in low shade farms (Ferreira et al., 2023a). Whilst this study indicates the economic benefit of wildlife presence within farms, it highlights that in low shade environments, these benefits can be suppressed.

Additionally, agroforestry, and other organic farming practices, give farmers opportunities to join certification schemes. Certification schemes often require strict adherence to organic farming practices and act as an incentive to promote the use of them due to the price premium farmers receive. There are complicating factors that discourage farmers from joining certification schemes, such as high registration fees, products not being sold as "certified", increased labour and manpower, and rigorous and unrealistic assessments (Cabrera et al., 2020; Lyon, 2006). Whilst price premiums that come with entering certified and organic markets are a way of incentivising farmers to join certification schemes, Barham & Weber (2012) found that yield was still the driving force in improving net return for coffee farmers.

Although there is a lack of consensus within the literature, shaded agroforestry systems with an intermediate level of canopy cover can be monetarily beneficial in terms of yield (Clough et al., 2011; Piato et al., 2022). Whilst many studies have documented reduced yields in high shade, most studies see declines from shade levels of 30% and above, with some only seeing declines from 50% and above (Koutouleas et al., 2022; Soto-Pinto et al., 2000). Our results indicate that canopy cover of 30% and above is optimal in preserving species diversity, suggesting this level of canopy cover could be a potential "win-win" scenario for farmers and biodiversity alike.

In our meta-analysis, we examined the impact of increasing canopy cover on abundance and species diversity, showing that species diversity increases with increasing levels of shade. Whilst this is an important finding when establishing the effectiveness of agroforestry in providing viable habitat for species, the factors discussed above, outside of biodiversity preservation, benefit farmers through the creation of sustainable and resilient farmland. The results of this meta-analysis do not cover these factors, but we believe further research could be done to summarise the effect of increasing canopy cover on ecosystem functioning and biodiversity as a whole.

4.4. *Caveats in providing shade*

The primary limitation of this meta-analysis is that it does not take into account the type and diversity of shade occurring within coffee farms. Although one could assume that higher shade is equivalent to increased shade tree diversity, this is often not the case. As previously mentioned, when discussing Nesper et al. (2017) paper, growing coffee under the "correct" shade, and under the "wrong" shade, can affect not only the biodiversity present within coffee farms, but also coffee yield. For example, native bird species, species of regional conservation concern, are significantly more abundant and diverse when in habitats with higher numbers of native plant species (Burghardt et al., 2009). It is not just birds; in Cameroonian cocoa agroforests, with increasing native shade tree presence, researchers observed an increase in wasp and spider presence, both of which have been proven to be natural predators of insect pests (Bisseleua et al., 2013). Furthermore, a popular shade tree genus worldwide, *Inga* spp., have been found to be used more by species of conservation concern, such as in the case of cerulean warblers (*Dendroica cerulea*) (Bakermans et al., 2012). Conversely, Eucalyptus trees (*Eucalyptus* spp.) are often used as shade trees in South East Asia and Latin America as they are fast-growing and can generate income for smallholder farmers (Campera et al., 2021b; Manson et al., 2022c; Schaller et al., 2003). Eucalyptus trees reduce yield due to competition for root growth and release toxins causing soil acidification (Latini et al., 2020; del Moral et al., 1969). Finding fast-growing, income-generating, native alternatives to non-native species, such as eucalyptus trees, is vital if researchers, stakeholders and farmers are to address risk aversion in the adoption of shade. Finally, the provision of shade is not enough; shade trees should be diverse if they are to harbour diversity (Geeraert et al., 2019). As previously discussed, diversity breeds diversity, and through the provision of a diversity of floral resources, farms will attract a richer community of species (Blaauw & Isaacs, 2014; Fisher et al., 2017; Ricketts, 2004).

In complex agricultural systems, the likelihood of enhancing the provision of ecosystem services and, in turn, increasing the functionality of the system is increased due to optimising niche complementarity (Flombaum et al., 2014; Wood et al., 2015). The contribution of species and individuals to ecosystem functioning vary depending on their characteristics (i.e., traits); higher species diversity would increase the likelihood of species with traits valuable to ecosystem functioning being present within a system (Wood et al., 2015). Niche complementarity is higher in complex systems with high trait diversity as this allows for increased resource partitioning between species and increased ecosystem functioning through the mediation of biotic and abiotic factors by these species (Wood et al., 2015). Whilst shade tree diversity is a major factor in providing a habitable landscape for biodiversity, strata levels present within the provided shade dictates the ability of certain species to live in these agroecosystems. For example, farms with tall, large shade trees were found to harbour richer bat communities (Ferreira et al., 2023b), and farms with taller shade trees are better able to regulate maximum daily temperature, leading to richer communities of birds (Merle et al., 2022; Monge et al., 2022). Therefore, niche complementarity, and the presence of a wide variety of species able to contribute complimentarily to ecosystem functioning, must be prioritised in the provision of shade.

5. Conclusion

With demand for coffee growing exponentially over the past century, there has been ever increasing pressures on farmers, 70% of which are smallholders, to increase yield. The majority of major coffee producing countries are biodiversity hotspots, the 14 countries involved in this meta-analysis are all examples of this, putting a large responsibility on coffee farmers to maintain biodiversity whilst optimising yield. The two main strategies posed to preserve biodiversity within highly disturbed agricultural landscapes are land-sparing, leaving areas of forest undisturbed whilst intensifying areas of agricultural land, and land-sharing, providing habitat for species within agricultural land. Land-sharing is often achieved through shade grown coffee farming, a traditional practice that promotes optimal climatic conditions for coffee growth whilst also providing habitat for species and connectivity within fragmented landscapes. Within relevant literature, the benefit of shade for biodiversity has been mixed, thus provoking the discussion of whether farmers and conservationists should employ land-sparing or land-sharing conservation strategies. In this meta-analysis, we examined existing literature relating to full sun (0-5% shade), low shade (6-30% shade), and high shade (>30%) coffee farms and the species that exist within each management intensity. Using data that described individual abundance, species richness, species density, pollinator visitation rate and species diversity, we found that these values were significantly higher in high shade farms than in sun farms, with no significant differences found in the sun vs low shade treatment or the low shade vs high shade treatment. This indicates that if biodiversity is to be effectively preserved, shade must be considerable (>30%). In general, this was reflected in our between- and within-taxa and between region meta-regressions, but there were exceptions where some taxa and regions showed higher values in sun farms. This highlights the necessity for considering existing land-use, region and species of conservation value when discussing the applicability of sparing or sharing initiatives. Where species or regions tend to show higher biodiversity values in sun farms, as well as in regions of intensive, monoculture agriculture, sparing initiatives could be more successful. Whereas in areas where smallholder agriculture exists within an existing mosaic, agroforest landscape, land-sharing initiatives would be better suited. Moving forward, less emphasis should be placed on sharing vs sparing discussions, as in reality, these initiatives can be applied in parallel. Concerted efforts must be made to end further encroachment, maintain connectivity, and optimise yield through prioritising faunal and floral diversity.

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Tables and Figures

Table 1. A summary of the results of each random effect meta-analysis and meta-regression conducted within the three treatments for species diversity data: 1) sun vs low shade farms; 2) sun vs high shade farms; and 3) low shade vs high shade farms. Numbers in parentheses describe the number of papers used for each variable and the number of data points each variable produced. Papers were removed from meta-regressions if the biodiversity values they presented summarised taxa/global data. Results for taxa with fewer than two data points in taxa meta-regressions were not presented in this table. Data was analysed using R v 4.2.2 using the "metafor", "DT" and "ggplot2" packages (R Core Team, 2022).

Treatment (number of papers)	Model (number of data points)		Estimate	S.E.	Z value	P value
Sun vs Low Shade (9)	*Overall meta-analysis (30)*		-0.3006	0.1587	-1.8943	0.0582*
	Between taxa meta-regression (27)	Bird (2;5)	-0.5108	0.0932	-5.4809	<0.0001***
		Insect (5;18)	-0.0860	0.0677	-1.2705	0.2039
		Mammal (1;3)	-0.1937	0.2923	-0.6629	0.5074
	Region meta-regression (27)	Latin America (5;13)	-0.3781	0.0740	-5.1068	<0.0001***
		South East Asia (2;13)	-0.0346	0.0899	-0.3842	0.7008
	Insect taxa meta-regression (8)	Ant (1;3)	-0.1485	0.0797	-1.8622	0.0626*
		Butterfly (3;5)	-0.1219	0.0605	-2.0133	0.0441**
Sun vs High Shade (12)	*Overall meta-analysis (44)*		-0.3865	0.1637	-2.3613	0.0182**
	Between taxa meta-regression (41)	Bird (2;22)	-0.6573	0.1346	-4.8822	<0.0001***
		Fungi (1;4)	0.1617	0.2094	0.7720	0.4401
		Insect (8;12)	-0.2130	0.1317	-1.6176	0.1057
		Mammal (1;3)	-0.5942	0.3565	-1.6666	0.0956
	Region meta-regression (41)	Latin America (10;39)	-0.3704	0.1161	-3.1916	0.0014**
		South East Asia (1;2)	-0.2128	0.4104	-0.5184	0.6042

	Insect taxa meta-regression (10)	Ant (2;5)	0.0124	0.1140	0.1088	0.9134
		Butterfly (2;4)	-0.2591	0.0730	-3.5507	0.0004***
Low Shade vs High Shade (27)	*Overall meta-analysis (60)*		-0.1686	0.0687	-2.4543	0.0141*
	Between taxa meta-regression (57)	Arthropod (3;4)	0.0210	0.1816	0.1157	0.9079
		Bird (6;14)	-0.2200	0.0970	-2.2673	0.0234*
		Fungi (1;2)	0.4197	0.2480	1.6924	0.0906
		Insect (14;27)	-0.0192	0.0745	-0.2573	0.7969
		Mammal (2;4)	-0.6242	0.2087	-2.9915	0.0028**
		Epiphyte (3;6)	-0.4801	0.1734	-2.7687	0.0056**
	Region meta-regression (57)	Africa (1;2)	-0.6335	0.3252	-1.9483	0.0514*
		Latin America (23;52)	-0.1149	0.0599	-1.9187	0.0550*
		South East Asia (2;3)	-0.0328	0.2324	-0.1411	0.8878
	Insect taxa meta-regression (25)	Ant (7;11)	-0.2690	0.1144	-2.3514	0.0187**
		Bee (2;8)	0.4127	0.1351	3.0550	0.0023**
		Butterfly (3;6)	-0.1118	0.1628	-0.6868	0.4922

*: trending towards significance; **: significant; ***: highly significant

Table 2. A summary of the results of each random effect meta-analysis and meta-regression conducted within the three treatments for individual abundance data: 1) sun vs low shade farms; 2) sun vs high shade farms; and 3) low shade vs high shade farms. Numbers in parentheses describe the number of papers used for each variable and the number of data points each variable produced. Papers were removed from meta-regressions if the biodiversity values they presented summarised taxa/global data. Results for taxa with fewer than two data points in taxa meta-regressions were not presented in this table. Data was analysed using R v 4.2.2 using the “metafor”, “DT” and “ggplot2” packages (R Core Team, 2022).

Treatment (number of papers)	Model (number of data points)		Estimate	S.E.	Z value	P value
Sun vs Low Shade (21)	*Overall meta-analysis (77)*		-0.0148	0.2041	-0.0725	0.9422
	Between taxa meta-regression (76)	Amphibian (1;2)	-0.0057	0.8267	-0.0069	0.9945
		Arthropod (2;2)	0.7006	0.5544	1.2637	0.2063
		Bird (3;31)	-0.1937	0.2044	-0.9478	0.3432
		Insect (9;33)	-0.0936	0.1582	-0.5918	0.5540
		Mammal (2;2)	-0.7099	0.6658	-1.0662	0.2863
		Nematode (3;5)	0.2308	0.3486	0.6621	0.5079
	Region meta-regression (76)	Africa (5;9)	0.5198	0.2444	2.1265	0.0335**
		China (1;2)	0.0159	0.4673	0.0340	0.9728
		Latin America (12;53)	-0.3823	0.1399	-2.7318	0.0063**
		South East Asia (2;12)	0.1443	0.2019	0.7146	0.4748
	Insect taxa meta-regression (31)	Ant (4;19)	-0.3551	0.2129	-1.6679	0.0953
		Butterfly (4;4)	-0.1071	0.3379	-0.3171	0.7512
Sun vs High Shade (13)	*Overall meta-analysis (36)*		-0.2613	0.1810	-1.4432	0.1490
	Between taxa meta-regression	Fungi (2;2)	0.0233	0.5396	0.0431	0.9656
		Insect (7;29)	-0.3201	0.1329	-2.4081	0.0160**

	(35)	Mammal (2;2)	-0.2968	0.7053	-0.4208	0.6739
	Region meta-regression (35)	Africa (3;4)	0.2081	0.3126	0.6655	0.5057
		Latin America (7;29)	-0.3756	0.1263	-2.9748	0.0029**
		South East Asia (2;2)	-0.4167	0.5692	-0.7321	0.4641
	Insect taxa meta-regression (20)	Ant (4;5)	0.2319	0.4394	0.5277	0.5977
		Butterfly (3;3)	-0.5567	0.5741	-0.9697	0.3322
		Fly (1;3)	-1.3421	0.6539	-2.0522	0.0401**
Low Shade vs High Shade (45)	*Overall meta-analysis (75)*		-0.0983	0.0972	-1.011	0.3120
	Between taxa meta-regression (73)	Arthropod (1;2)	0.3396	0.4116	0.8251	0.4093
		Bird (4;16)	-0.2757	0.1499	-1.8390	0.0659*
		Insect (20;47)	-0.0794	0.1008	-0.7881	0.4306
		Mammal (3;6)	-0.4523	0.3129	-1.4457	0.1483
	Region meta-regression (73)	Africa (4;3)	-0.0877	0.3537	-0.2479	0.8042
		Latin America (25;67)	-0.1440	0.0828	-1.7385	0.0821
		South East Asia (2;2)	-0.1633	0.4303	-0.3864	0.6992
	Insect taxa meta-regression (39)	Ant (7;12)	0.0051	0.2613	0.0195	0.9845
		Bee (6;21)	-0.0999	0.1900	-0.5257	0.5991
		Butterfly (2;2)	-0.1438	0.5457	-0.2635	0.7922
		Wasp (3;2)	-0.0390	0.4647	-0.0840	0.9331

*: trending towards significance; **: significant; ***: highly significant

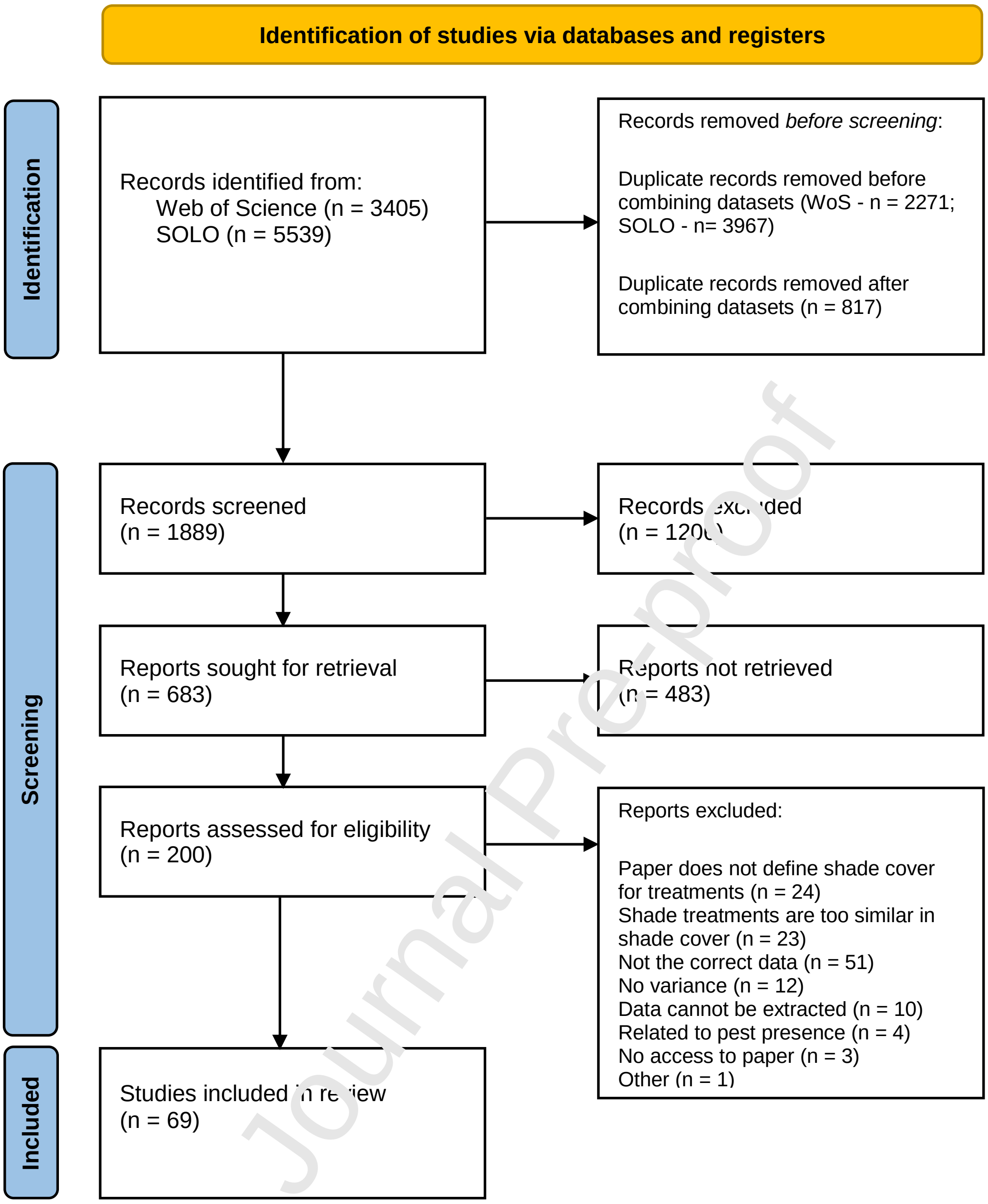


Figure 1. Systematic screening process, as outlined by the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) flow-chart. The database used was Web of Science; keyword searches produced 983 studies (deduplicated), of which 133 were retrieved and 51 were used for the overall meta-analysis.

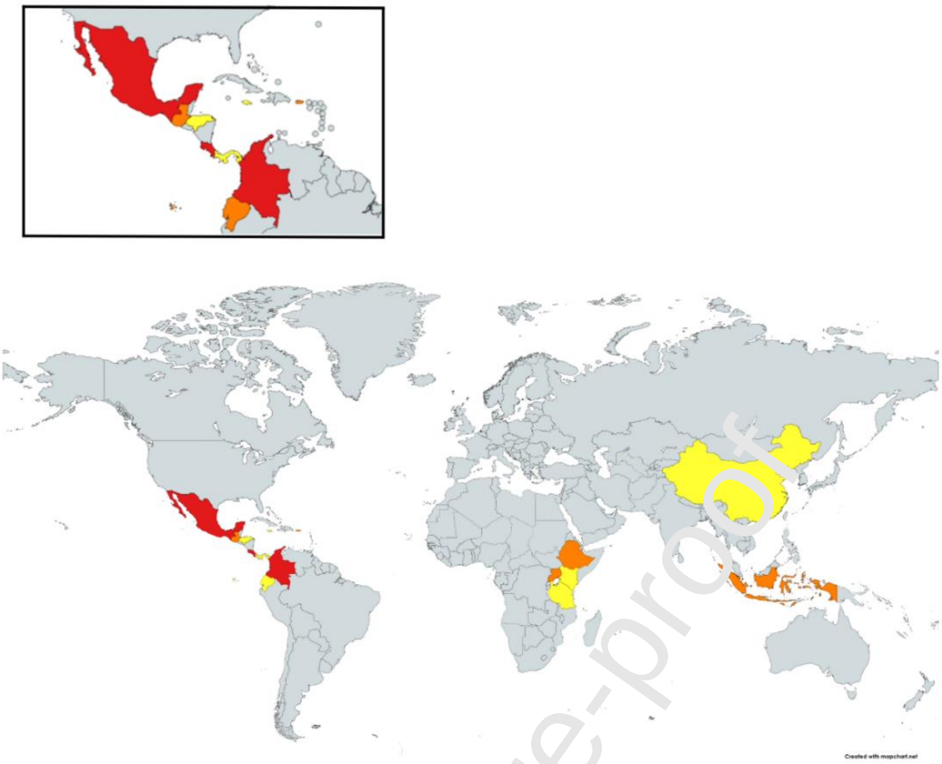


Figure 2. Map of the locations where studies included in the meta-analysis were carried out. Red: over five studies conducted; orange: two to five studies conducted; yellow: one study conducted. Map produced using MapChart.

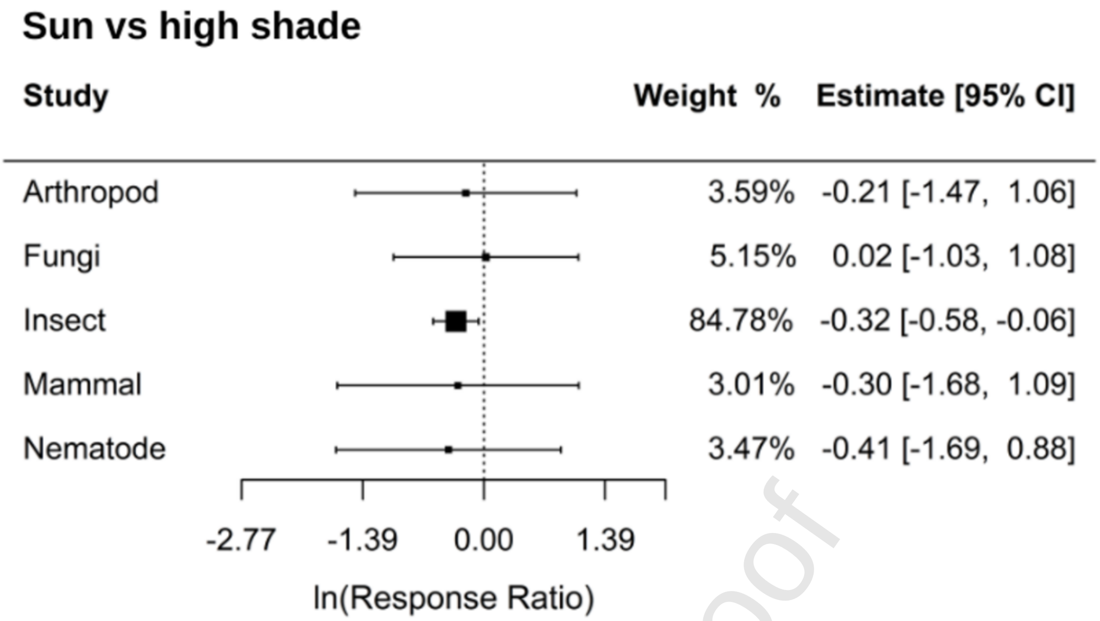


Figure 3. Forest plot presenting a meta-regression of the logged response ratios for taxa within the papers comparing individual abundance in sun farms (0-5% shade) and high shade farms (>30% shade). Sample sizes for taxa are as follows (number of papers; number of data points): Arthropod: 1,1; Fungi: 2,2; Insect: 7,29; Mammal: 2,2; Nematode: 1,1. This graph was produced using R v 4.2.2 using the “metafor”, “DT” and “ggplot2” (R Core Team, 2022).

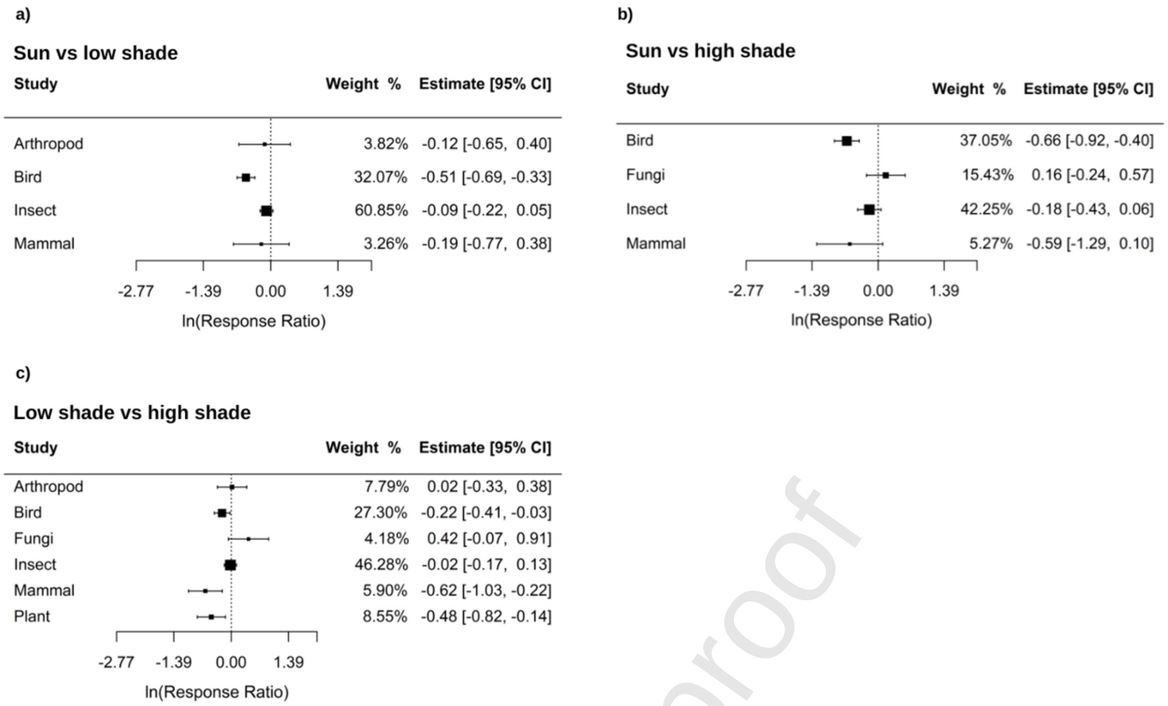


Figure 4. Forest plots presenting meta-regressions of the logged response ratios for taxa within the papers comparing species diversity in: a) sun farms (0-5% shade) vs low shade farms (6-30% shade); b) sun farms vs high shade farms (>30% shade), and c) low shade farms vs high shade farms. Sample sizes for taxa are as follows (number of papers; number of data points): a) Arthropod: 1,1; Bird: 2,5; Insect: 5,18; Mammal: 1,3; b) Bird: 2,22; Fungi: 1,4; Insect: 8,12; Mammal: 1,3; c) Arthropod: 3,4; Bird: 6,14; Fungi: 1,2; Insect: 14,27; Mammal; 2,4; Plant (epiphyte): 3,6. These graphs were produced using R v 4.2.2 using the “metafor”, “DT” and “ggplot2” (R Core Team, 2022).

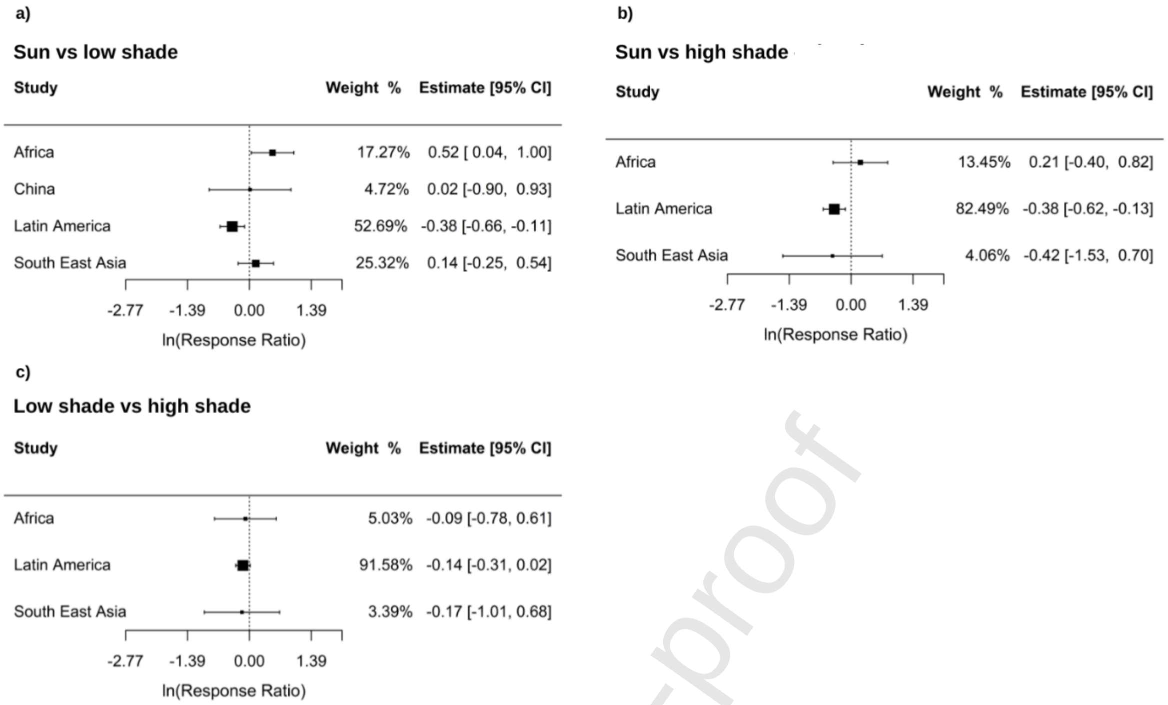


Figure 5. Forest plots presenting meta-regressions of the logged response ratios for each region within the papers comparing abundance in: a) sun farms (0-5% shade) and low shade farms (6-30% shade); b) sun farms and high shade farms (>30%); and c) low shade farms and high shade farms. Sample sizes for regions are as follows (number of papers; number of data points): a) Africa: 5,9; China: 1,2; Latin America: 12,53; South East Asia: 2,12; b) Africa: 3,4; Latin America: 7,29; South East Asia: 2,2; c) Africa: 4,3; Latin America: 25;67; South East Asia: 2,2. This graph was produced using R v 4.2.2 using the “metafor”, “DT” and “ggplot2” (R Core Team, 2022).

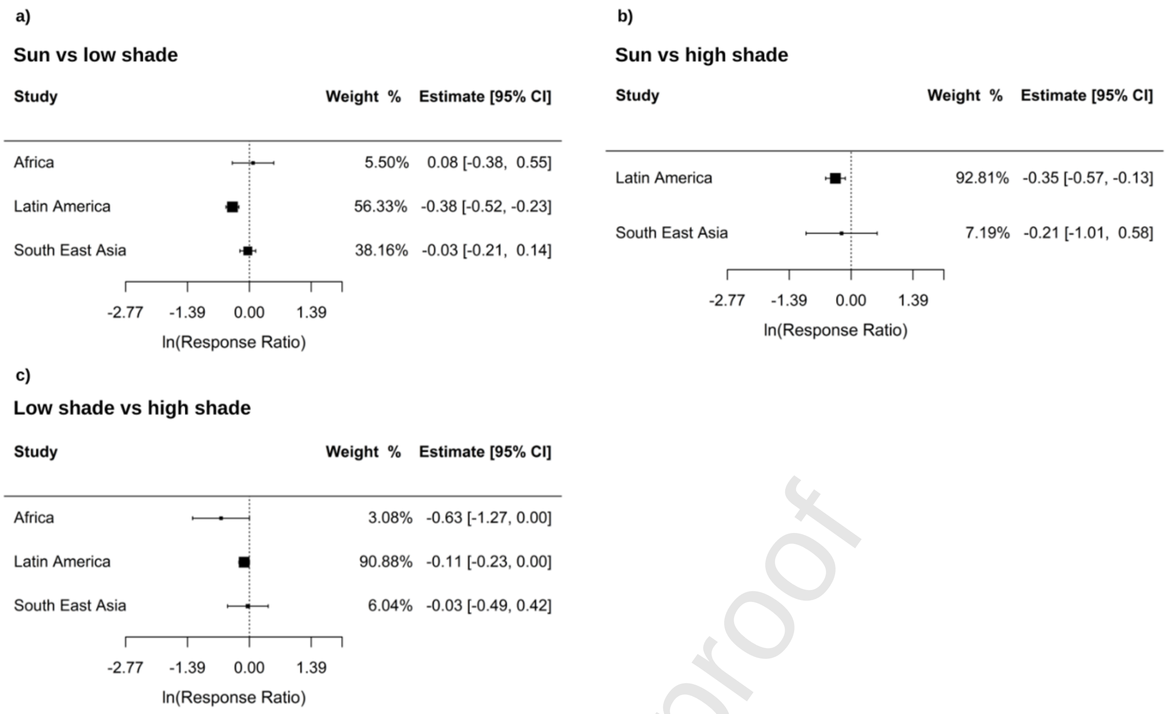


Figure 6. Forest plots presenting meta-regressions of the logged response ratios for each region within the papers comparing species diversity in: a) sun (0-5% shade) and low shade farms (6-30% shade); b) sun farms and high shade farms (>30% shade); and c) low shade farms and high shade farms. Sample sizes for regions are as follows (number of papers; number of data points): a) Africa: 1,1; Latin America: 5,13; South East Asia: 2,13; b) Latin America: 10,39; South East Asia: 1,2; c) Africa: 1,2; Latin America: 23,52; South East Asia: 2,3. This graph was produced using R v 4.2.2 using the "metafor", "DT" and "ggplot2" (R Core Team, 2022).

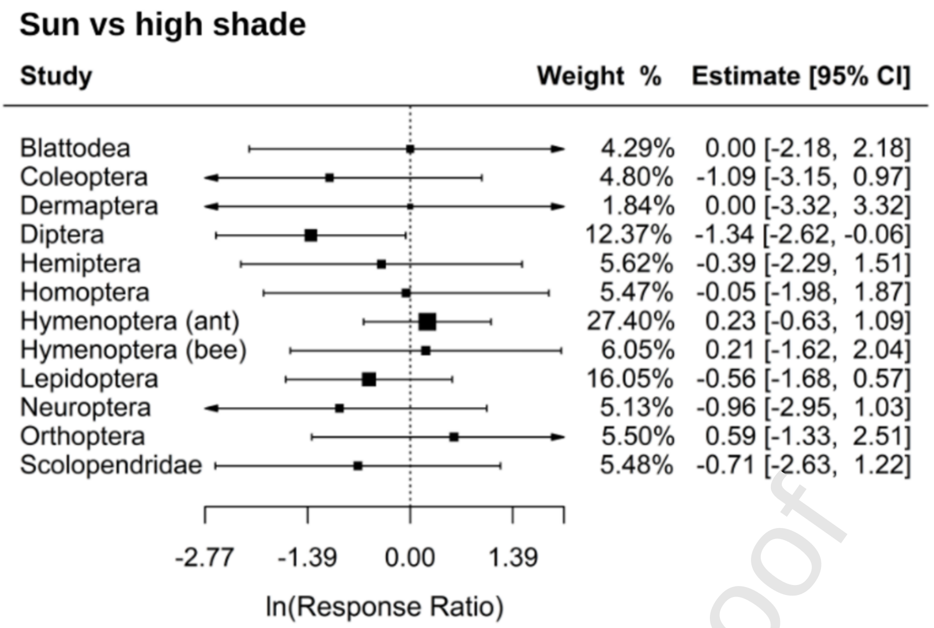


Figure 7. Forest plot presenting a meta-regression of the logged response ratios for insect taxa within the papers comparing abundance in sun farms (0-5% shade) and high shade farms (>30% shade). Sample sizes for taxa are as follows (number of papers; number of data points): Hymenoptera (ant): 4,5; Lepidoptera: 3,3; Diptera: 1,3; Blattodea: 1,1; Coleoptera: 1,1; Dermaptera: 1,1; Hemiptera: 1,1; Homoptera: 1,1; Hymenoptera (bee): 1,1; Neuroptera: 1,1; Scolopendridae: 1,1. (This graph was produced using R v 4.2.2 using the "metafor", "DT" and "ggplot2" (R Core Team, 2022).

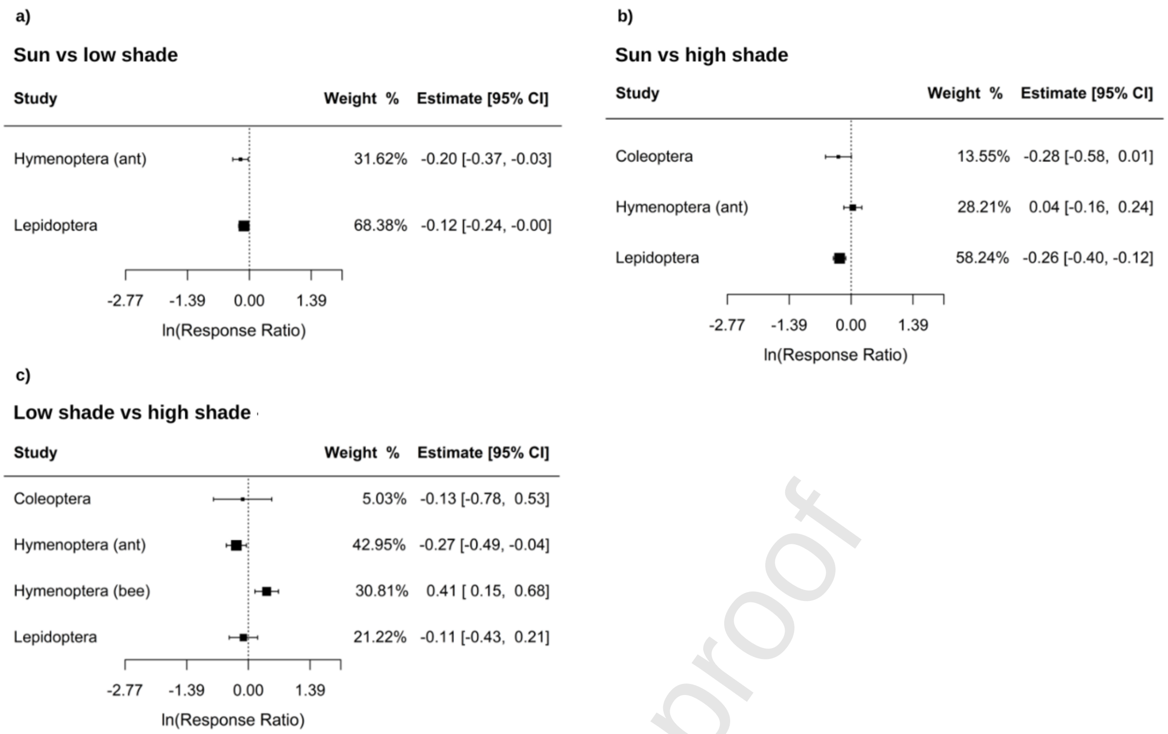


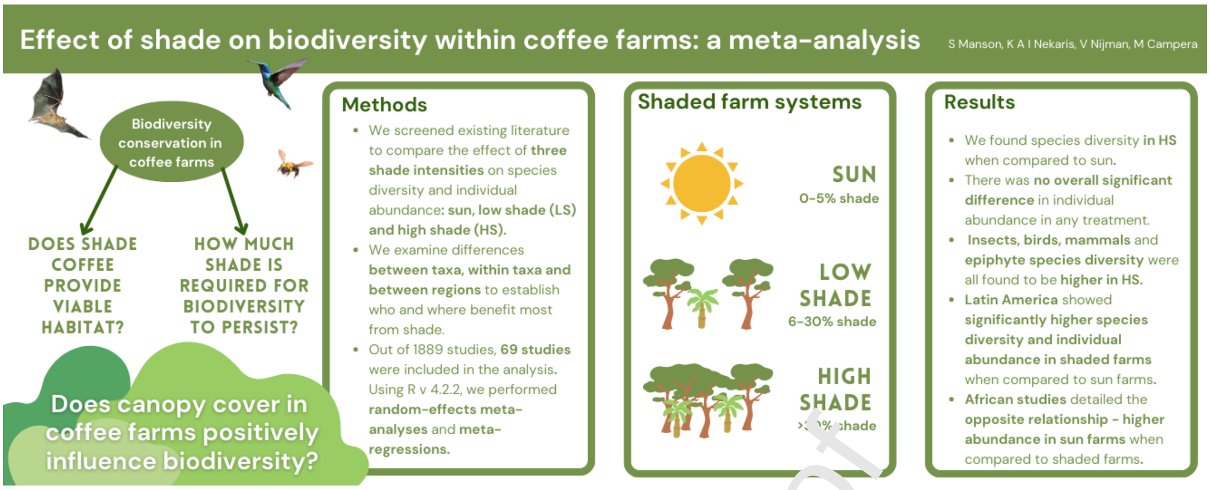
Figure 8. Forest plots presenting meta-regressions of the logged response ratios for insect taxa within the papers comparing species diversity in a) sun farms (0-5% shade) and low shade farms (6-30% shade); b) sun farms and high shade farms (>30% shade); and c) low shade farms and high shade farms. Sample sizes for taxa are as follows (number of papers; number of data points): a) Hymenoptera (ant): 1,3; Lepidoptera: 3,5; b) Hymenoptera (ant): 2,5; Lepidoptera: 2,4; Coleoptera: 1,1; c) Hymenoptera (ant): 7,11; Hymenoptera (bee): 2,8; Lepidoptera: 3,5; Coleoptera: 1,1. This graph was produced using R v 4.2.2 using the “metafor”, “DT” and “ggplot2” (R Core Team, 2022).

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Graphical abstract



Effect of shade on biodiversity within coffee farms: a meta-analysis

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Biodiversity conservation in coffee farms

DOES SHADE COFFEE PROVIDE VIABLE HABITAT?

HOW MUCH SHADE IS REQUIRED FOR BIODIVERSITY TO PERSIST?

Does canopy cover in coffee farms positively influence biodiversity?

Methods

- We screened existing literature to compare the effect of **three shade intensities** on species diversity and individual abundance: **sun, low shade (LS) and high shade (HS).**
- We examine differences **between taxa, within taxa and between regions** to establish who and where benefit most from shade.
- Out of 1889 studies, **69 studies** were included in the analysis. Using R v 4.2.2, we performed **random-effects meta-analyses** and **meta-regressions.**

Shaded farm systems

SUN
0-5% shade

LOW SHADE
6-30% shade

HIGH SHADE
>30% shade

Results

- We found species diversity **in HS** when compared to sun.
- There was **no overall significant difference** in individual abundance in any treatment.
- **Insects, birds, mammals** and **epiphyte species diversity** were all found to be **higher in HS.**
- **Latin America** showed **significantly higher species diversity and individual abundance in shaded farms** when compared to sun farms.
- **African studies** detailed the **opposite relationship - higher abundance in sun farms** when compared to shaded farms.

Highlights

Coffee farms with high shade (>30%) harbour higher species diversity than sun farms (0-5%).

Insects, birds, mammals and epiphytes benefit most from high shade.

The value of shade-grown coffee for wildlife varies between regions.

Conservation plans must be region-specific, maintain connectivity and optimise yield.