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Journal of Applied Ecology



The impacts of tropical agriculture on biodiversity: a metaanalysis

Journal:	Journal of Applied Ecology
Manuscript ID	JAPPL-2022-00125.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	17-Aug-2022
Complete List of Authors:	Oakley, Joseph; University of Kent Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation Bicknell, Jake; University of Kent Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation
Key-words:	Agriculture, Biodiversity, Food systems, Tropical, Meta-Analysis, Crops, Ecosystem services, Intensification

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The impacts of tropical agriculture on biodiversity: a meta-

2	analysis
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Abstract

- 1. Biodiversity underpins all food production and strengthens agricultural resilience to crop
- failure. However, agricultural expansion is the primary driver of biodiversity loss,
- particularly in the tropics where crop production is increasing and intensifying rapidly to
- meet a growing global food demand. It is therefore crucial to ask, how do different crops
- and crop production systems impact biodiversity?
- 2. We first use the FAO database of harvested crop area to explore temporal changes in crop
- area and intensification across the entire tropical realm. We show that the harvested area of
- tropical crops has more than doubled since 1961, with ever-increasing intensification. The
- 21 harvested area in 2019 was 7.21 million km², equivalent to 5.5% of global ice-free land area,
- or 11.5% of land area in the tropics.
- 3. Second, we conducted a meta-analysis of 194 studies and 1,368 pairwise comparisons to
- assess the impact of tropical agriculture on biodiversity, comparing biodiversity values in
- 25 food crop sites versus natural reference habitats.
- 4. Our meta-analysis shows that crop type, rotation time and level of shading are important
- determinants of biodiversity assemblages. Perennial tropical crops that are grown in shaded
- plantations or agroforests (e.g., banana and coffee) support higher biodiversity, while crops
- cultivated in unshaded and often homogeneous croplands (e.g., maize, sugarcane, and oil
- palm), and particularly annual crops, have impoverished biodiversity communities.
- 31 5. Policy implications: These findings inform our understanding of how different crops and
- 32 crop production systems impact biodiversity, and may serve as a warning sign for
- agricultural systems that rely on the ecological functions provided by biodiversity.
- 34 **Keywords:** agriculture, biodiversity, crops, ecosystem services, food systems, intensification,
- 35 meta-analysis, tropical

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Introduction

Biodiversity underpins all food production and strengthens agricultural resilience to crop failure due to the ecological functions that animals provide (Bélanger & Pilling 2019). However, many of the species that perform these functions are disappearing, in part due to the intensification of agricultural systems (Bélanger & Pilling 2019; Foley et al. 2005; Figure S1). With the demand for food predicted to double by 2050 from 2010 levels (Springmann et al. 2018), food security is an increasingly important global issue (Rosegrant & Cline 2003). It is therefore important to consider how different crop production systems impact biodiversity communities. Agricultural expansion is a major driver of habitat loss (Curtis et al. 2018; Foley et al. 2005; Phalan et al. 2013) and one of the most detrimental disturbances to biodiversity assemblages (Gibson et al. 2011; Green, 2005; Newbold et al. 2014). Over the last sixty years, the production of different tropical crops has increased by varying degrees (Phalan et al. 2013). In the next three decades, to meet a growing demand for food, it is predicted that agricultural expansion will continue to increase. This is expected to occur mostly in poorer countries throughout the tropics, where land for crop production often comes at the expense of natural habitats (Tilman et al. 2011). The tropics are extremely biodiverse, with tropical forests alone containing more than twothirds of the world's terrestrial biodiversity (Giam 2017). The presence of wild animals in ecosystems is important due to the ecological functions and ecosystem services that they provide, such as pollination, seed dispersal, nutrient cycling, energy flow through trophic levels, and pest control (Bélanger & Pilling 2019; Mathieu et al. 2005; Valencia-Aguilar et al.

2013; Willig et al. 2007). Therefore, the promotion of biodiversity in agricultural systems,

alongside appropriate management, can provide these benefits in addition to high crop yields (Bélanger & Pilling 2019; Clough *et al.* 2011). In some taxa, particularly birds and bats, agricultural conversion affects the relative composition of functional groups. Insectivorous and carnivorous species that provide pest control services often decline, whilst the proportion of frugivores, nectarivores and granivores may increase, depending on food availability within the cropland (Mtsetfwa *et al.* 2018; Tscharntke *et al.* 2008; Willig *et al.* 2007). These changes affect the ability of biodiversity communities to perform functions important to food production, particularly pollination and pest control (Bélanger & Pilling 2019).

The magnitude to which agriculture affects biodiversity varies greatly between different crops and agricultural management practices. For example, rice fields are generally less biodiverse than the natural forests or wetlands that they replace (Mathieu *et al.* 2005; Tscharntke *et al.* 2008). However, well-managed rice fields can maintain biodiversity and provide important foraging and breeding grounds for some birds, including rare species (Elphick *et al.*, 2010). Forest conversion for oil palm is the one of the greatest threats to biodiversity in Southeast Asia, characterised by the loss of high conservation value species, and overall, harbouring fewer species than natural forests (Fitzherbert *et al.* 2008; Wilcove & Koh 2010). Crops such as coffee and cacao, when grown in shaded plantations, support a greater diversity than those grown in open monocultures, since they provide arboreal habitats and are more structurally similar to natural forests (Estrada, *et al.* 1997; Zermeño-Hernández *et al.* 2016). In addition to the ecological conditions of croplands, crop rotation times (e.g., perennial or annual), proximity to natural habitats, fragmentation, and connectivity are other major factors that influence the capacity for agricultural areas to support biodiversity (Haddad *et al.* 2015; Şekercioğlu *et al.* 2019).

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Despite numerous studies on the impacts of tropical food crops on biodiversity, most are limited to certain crops, taxa, and geographic regions. Therefore, a global analysis to identify and compare the impacts of individual tropical food crops on biodiversity assemblages is needed. Here we explore trends in crop production in the tropics between 1961 and 2019, identifying the crops which have expanded the most. We then present a meta-analysis to assess the impacts of tropical agriculture on animal diversity. We investigate whether biodiversity impacts vary between different crops, shading levels, crop rotation times, taxonomic groups, and geographic regions. We expected that agricultural systems that are structurally complex, or similar to natural counterparts (e.g. shaded crops), would maintain biodiversity closer to natural levels, whilst crop sites that are homogeneous and structurally simple (e.g. unshaded crops) would harbour impoverished biodiversity assemblages. Furthermore, we hypothesised that perennial crops such as coffee, cacao and banana would better support biodiversity than annual crops such as maize and sugarcane. We also expected to see differences in agricultural impacts between different geographic regions, due to the variation in crop species and agricultural practices in different parts of the world. Quantifying the impacts of different food crops and their cultivation approaches on biodiversity can inform our understanding of changes to the ecological contribution of biodiversity in tropical agricultural landscapes. In turn, this may inform potential improvements to agricultural practices, and the long-term sustainability of tropical food production.

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Materials and Methods

Quantifying tropical crop expansion

In order to quantify crop expansion in the tropics, following Phalan *et al.* (2013), we defined tropical countries as those with at least one-third of their land area situated within the tropics. We used this definition because data on crop harvesting were only available as totals per

country for each crop. We used data from FAOSTAT (fao.org/faostat/) on the production and area harvested for all food crops in 115 tropical countries for the years 1961-2019. The harvested area of each of the 137 crops was totalled in each year to compute pan-tropical estimates for each crop's total harvested area per year, and changes in harvested area.

While the FAO provides some of the best available data on crop harvesting, it must be acknowledged that it has some limitations, so caution must be taken when interpreting the data. Where annual crops are harvested in rotation on the same land multiple times a year, they are all counted towards crop harvesting data, so may lead to overestimations of the true harvested land area. Conversely, underestimations may also occur since crop harvesting data excludes areas where crops were planted but not harvested due to natural calamities or economic reasons. Additionally, there are discrepancies in the reporting of data between countries, with some reporting the entire cultivated area of perennial crops, while others report only the productive area (FAO 2011). Therefore, there may be some discrepancies between the reported and true harvested areas of crops, but the results are likely to be indicative of trends.

Literature search to quantify agricultural impacts on biodiversity

To quantify the relative impacts of different tropical crops on biodiversity, we first conducted a rapid evidence assessment (REA) to search for peer-reviewed studies measuring biodiversity in both food crops sites and natural reference sites, based on inclusion and exclusion criteria (described below). We used Web of Science to search for studies published prior to 9th June 2020.

After trialling various search strings, we finally conducted our search using the query: TS = (*tropic* AND (agricultur* OR farm* OR plantation* OR crop* OR agroforest*) AND

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(biodiversity OR wildlife OR *fauna* OR bird* OR mammal* OR bat* OR reptil* OR amphibia* OR insect* OR invertebrate*) AND (abundance* OR *diversit* OR richness* OR communit*)). We restricted search results to journals within the subject areas: ecology, environmental sciences, biodiversity conservation, entomology, forestry, multidisciplinary sciences, agriculture multidisciplinary, zoology, and ornithology. We limited our search to English language studies, with no restrictions on the date of publication. This search returned 3,900 results (Figure 1).

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The lead author (JLO) subsequently screened the retrieved studies for relevance based on the title, abstract, and full text of the articles. A conservative approach was taken in the inclusion of papers during the title and abstract screening to reduce errors of omission. Both authors screened a subset of studies independently and assessed the level of agreement using Cohen's kappa statistic (Cohen 1960), scoring 0.8, to ensure the inclusion criteria were applied consistently. Studies that met our inclusion criteria: (a) reported vertebrate or macroinvertebrate species richness, density, or abundance within both an area cultivated for food crops and a paired natural landscape of any size with little or no disturbance - yielding us a pairwise comparison for the calculation of effect sizes in the meta-analysis, (b) were located within the tropics, and (c) provided or allowed us to calculate the mean, standard deviation, and sample size, from which we could compute an effect size. We were unable to calculate effect sizes for pairwise comparisons where the standard deviation was zero or the sample size was one, therefore they were excluded. We also excluded pairwise comparisons where food crops were mixed with other anthropogenic land uses (e.g., pasture). Studies that measured biodiversity in aquatic ecosystems within agricultural and reference sites (e.g., streams, irrigated croplands or wetlands) were included.

Our screening process resulted in 194 studies (Figure 1; Table S1) which contributed to our final dataset, amounting to a total of 1,364 pairwise comparisons for 13 crop categories (Table S2), from 34 countries (Figure S2), spanning five geographic regions (Tables S1-S2): Africa (N_{studies}=38, N_{comparisons}=281), Asia (N_{studies}=55, N_{comparisons}=432), Central America (N_{studies}=48, N_{comparisons}=371), South America (N_{studies}=52, N_{comparisons}=278), and Oceania (N_{studies}=1, N_{comparisons}=2). Brazil, Malaysia, Mexico, and Indonesia were the most well-studied countries, comprising more than 50% of all studies (Figure S2). Macroinvertebrates were the most well-represented group (N_{comparisons}=613), followed by birds (N_{comparisons}=428), mammals (N_{comparisons}=248), herpetofauna (N_{comparisons}=65), and fish (N_{comparisons}=10).

Data extraction and meta-analysis

The data that met the inclusion criteria were extracted by JLO with a second opinion from JEB where necessary. For each pairwise comparison, we extracted the mean and standard deviation of the biodiversity data. Where studies reported median values, we used these directly (Higgins et al., 2019). We converted standard error, interquartile ranges and confidence intervals to standard deviation. Data were extracted from tables, figures or the text of each study. For those that presented data graphically, we used WebPlotDigitiser (https://apps.automeris.io/wpd/) to extract the data. Where studies provided multiple pairwise comparisons (e.g., different crops, taxonomic groups, or geographic locations) we recorded each separately. For those that provided separate pairwise comparisons for food crops and other agricultural or anthropogenic habitats with reference sites, we only extracted the food crop comparison. We considered sample sizes as the number of independent sites within a study. For each pairwise comparison, we also recorded the taxonomic group (birds, fish, herpetofauna, invertebrates, or mammals), geographic region (Africa, Asia, Central America, South America, or Oceania), crop rotation time, and level of shading. We divided shading into three categories: 'Shaded crops' were those

characterised by natural or planted shade trees above the crop in question. This was most common in cacao and coffee; 'Unshaded crops' contained crops grown in open land with sparse or no shade trees. In the case of large crops, e.g. oil palm, where the mature trees create shade we considered these unshaded crops because they were not being shaded by a second vegetation type; finally, 'Crops with some vegetation' included those which the authors stated had moderate levels of shade trees, understory vegetation, or something to a similar effect. These were classified to the best of our ability with the information available in the papers. We calculated an effect size for individual crops if there were at least four studies reporting data for that crop. For single crops represented by fewer than four studies, we grouped these and reported them as 'all other tropical crops' (e.g., 'brazil nut', or 'pineapple'). When biodiversity values were provided for sites that did not distinguish between multiple different crops, we reported them as 'mixed tropical crops' (e.g., 'annual crops', or 'sugarcane, pineapple, and banana'). We divided data into four categories for crop rotation time, classified as 'annual', 'perennial', 'mixed', or 'unknown' if the crops were not specified.

To assess the magnitude of the impact of tropical agriculture upon biodiversity, we calculated the Hedges' *g* effect size of the standardized mean difference between agricultural and natural reference sites. Some studies provided multiple pairwise comparisons with a common control (natural reference) site, so we accounted for the potential non-independence of these by nesting them within study, computing a mean for each study (Borenstein *et al.*, 2009). We used a random-effects model, which weighted each comparison by the inverse of within-study variance and between-study variance (Borenstein *et al.* 2009; Koricheva *et al.* 2013).

In cases where data were extracted from figures, and the variance was so small that it was indiscernible from the mean, we recorded the variance as 0.001 so that an effect size could be

computed. The effect direction was reported as positive for cases where the biodiversity value was more favourable in the reference site than the agricultural site, and negative for cases where the biodiversity value was less favourable in the reference site than agricultural site. In cases where there was a greater abundance and/or diversity of invasive species in the agricultural site, this was deemed negative. Therefore, a negative effect size indicates that the agricultural site had an impoverished biodiversity community, and a positive effect size indicates that the agricultural site supported higher levels of biodiversity than the reference site. We considered effect sizes to be significant if the confidence interval did not overlap zero (Koricheva *et al.* 2013).

We calculated the mean effect size for the overall dataset, and the mean effect size for each of the moderator variables (crop type, shading, crop rotation time, taxonomic group, geographic region, and biodiversity metric – richness or abundance). Where fewer than four studies were used for each category, they contributed to the calculation of the overall effect size, but were otherwise not displayed separately in Figure 3.

To test for publication bias, we followed Nakagawa *et al.* (2017). As such, we plotted funnel plots of standard error and precision for Hedges' *g* (Figure S3), and calculated the Classic Failsafe N. The Classic Fail-safe N was 5,151, which means that we would need to locate and include 5,151 null studies in order to overturn the significance of our results (Borenstein *et al.* 2009; Koricheva *et al.* 2013). The symmetry of the funnel plots and high Fail-safe N suggest that publication bias is minimal or non-existent in our dataset. We conducted all meta-analyses in the Comprehensive Meta-analysis v3.0 software (Borenstein *et al.* 2013).

Results

Crop expansion

According to the FAO data, the summed harvested area of crops in tropical countries in 2019 was 7.21 million km² (Figure 2), equivalent to 5.5% of global ice-free land area, or 11.5% of land area in the tropics (i.e., approximately equivalent to the size of the Australian continent). The top ten crops by harvested area in tropical countries in 2019 were rice, maize, soybeans, wheat, sorghum, beans, millet, oil palm, cassava, and groundnuts, which together accounted for two-thirds (67%) of total harvested area (Figure 2a). Across the tropics, the total area of harvested land has more than doubled between 1961 and 2019 (Figure 2b). The mean annual rate of expansion has accelerated in the past two decades, almost doubling in 2000-2019 compared to that of 1980-1999. Production has increased at a greater rate than harvested area (Figure S1), showing the overall increasing intensification of tropical food production.

Between 1961 and 2019, soybeans were the most rapidly expanding crop both in terms of absolute area, increasing by 0.54 million km² (Figure 2c), and percentage, increasing by 4,597% (Figure 2d). After soybeans, maize, rice, and oil palm expanded most in absolute area, while oil palm, cow peas, and sugarcane increased by the greatest percentage.

Biodiversity impacts

Our results suggest that, overall, food crop expansion has contributed towards biodiversity loss in tropical regions, although the direction and magnitude of the impact depends on the crop, level of shading, rotation time, taxonomic group, and geographic region. The overall effect of tropical agriculture upon biodiversity is negative and significantly different from zero (Figure 3; mean Hedges' g [\pm 95% CI] =-0.59 [-0.67 to -0.51], p<0.001; Table S3).

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Exploring the data by crops, we found that effect sizes were negative and significantly different from zero in maize, oil palm, sugarcane, 'all other tropical crops', tea, rice, cacao, and 'mixed tropical crop' sites, compared with natural habitats (Figure 3a; Table S3). Biodiversity responses were in general negative but not significant in citrus, allspice, and coffee plantations, while banana and mixed cacao and coffee plantations showed a positive effect size, though not significantly different from zero. Examining our results by level of shading, we found that for shaded and unshaded crops, biodiversity showed a negative and significant difference from zero, with unshaded crops having a considerably greater negative effect size than shaded crops (Figure 3b; Table S3). However, we do not find a significant affect for crops with some vegetation where the confidence intervals were particularly wide and overlapped zero. We find that crop rotation time is an important determinant of impacts, with annual crops showing a greater negative response than perennial crops that have longer rotation periods, though both categories had a significantly negative effect size (Figure 3c). Effect sizes were negative but not significantly different from zero for croplands with 'mixed' annual and perennial crops, and for 'unknown' where studies didn't specify whether crops were annual or perennial. Exploring the results by taxonomic group, we found that bird, herpetofauna, and invertebrate assemblages showed significantly negative effect sizes of similar magnitudes in response to agricultural treatments, while mammal responses were negative but not significant (Figure 3d; Table S3). Examining our results by geographic region, we found there was a significantly negative effect of agriculture on biodiversity in all tropical regions (Figure 3e; Table S3). Asia showed the greatest negative response, followed by South America, Africa, and lastly, Central America. Finally, comparing by biodiversity metric, effect sizes for both richness and abundance were negative and significantly different from zero, with richness showing the strongest response to agriculture (Figure S4). Breaking this down by crop, in all cases, the effect sizes for richness were consistently more negative than those for abundance, more likely to be significant, and in the case of coffee, there was evidence of a positive effect on abundance (Figure S4).

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Discussion

Our study supports the existing literature highlighting the adverse impacts of tropical agriculture upon animal assemblages (Chapman et al. 2019; Gibson et al., 2011; Ocampo-Ariza et al. 2019; Ramamonjisoa et al. 2020). Adding to this, our meta-analysis is the first to compare the magnitude and direction of the impacts of different food crops across the whole of the tropics, and demonstrates that agricultural conversion across a range of ecosystems has an effect on biodiversity, depending on the type of crop and intensity of land use. We also demonstrate the sheer scale of tropical crop expansion (Figure 2), with our findings of increased acceleration of crop expansion over the past two decades corroborating those of Potapov et al. (2022), which are based on remote sensing data. Potapov et al. (2022) further emphasises the magnitude of crop expansion in the tropics, showing that globally, conversion of natural vegetation to croplands was proportionately largest in Africa, Southeast Asia, and South America. Our results demonstrate that intensification is increasing year-on-year due to production increases out-accelerating area increases (Figure S1). Intensification is particularly concerning because there is increasing evidence that croplands with impoverished biodiversity communities can produce lower yields, and require higher levels of chemical inputs (Bélanger & Pilling 2019). This is therefore due in part to intensification undermining the pollination and other services provided by biodiversity, because of the impact intensification has on biodiversity assemblages as illustrated herein. Indeed, in general, it is known that crop systems support widespread, common, and generalist species, while more specialist, disturbancesensitive, endemic, and threatened species are likely to be absent (Gallmetzer & Schulze 2015; Şekercioğlu 2012), and along with them, their specific functions lost.

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A particularly important finding from our study is the relative impacts from different crop production systems. We show that unshaded crops result in the most impoverished biodiversity communities, however, the effects varied greatly depending on the crop species. Impoverished biodiversity in agricultural sites could be associated with reduced structural complexity, the removal of understory vegetation, destructive land management practices (Bohada-Murillo et al. 2020; Castaño-Villa et al. 2014; Zermeño-Hernández et al. 2016), use of agrochemicals (Smith et al., 2016; Zermeño-Hernández et al. 2016), reduced resource availability (Mang & Brodie, 2015), changes in soil quality and communities (Franco et al. 2019; Smith et al. 2016), and an increase in pest or invasive species (Paini et al. 2016; Suzán et al. 2008). Crops grown in systems that are structurally complex or similar to natural ecosystems, such as agroforests (e.g., some cacao, coffee, and banana plantations), harbour biodiversity closer to natural levels (Estrada et al. 1997; Zermeño-Hernández et al. 2016). The substantially smaller impact of shaded crops than unshaded crops highlights the potential for improving agricultural practices to reduce biodiversity loss, and this may explain why abundance in some coffee plantations can increase. The wide confidence intervals for crops with some vegetation could be due to fewer studies, or variation in the capacity for different types of vegetation to support biodiversity (e.g., croplands with scattered shade trees provide a different habitat from those with an intact understory). Better measures of agricultural intensity could include chemical inputs, monoculture vs polyculture, and weed richness and cover, however, these details were often not reported in studies. We also show that crops that are harvested on an annual basis, such as maize, sugarcane and rice, result in greater biodiversity impacts when compared with crops that have longer rotation periods, such as coffee, tea, citrus, allspice, cacao and banana. However, oil palm (a perennial with ~25-year rotation cycles) which has significant impacts on biodiversity, does not follow this trend. This may be due to oil palm often being planted within large-scale, high-yield monocultures, but also the fact that 80% of oil palm is produced in the highly biodiverse Southeast Asia biodiversity hotspot, much of this replacing tropical forests (Fitzherbert *et al.* 2008).

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While our findings provide insights into the impacts of different crops on biodiversity, there is a distinct lack of data for most crops. Of the top ten crops in terms of harvested area in the tropics, our REA only returned enough studies for rice, maize, and oil palm to be analysed individually. The large negative effect size of the 'all other tropical crops' category highlights the need for more research on understudied crops to identify their individual impacts. Despite soybeans being the most rapidly expanding crop in recent decades, we only found one study reporting biodiversity in soybean sites with data that met our criteria for the meta-analysis (Moura et al. 2013). Soybean expansion is well documented, particularly in Brazil. It has been responsible for large areas of deforestation of the Amazon and habitat loss in the globally important Cerrado biome (Kastens et al. 2017; Soterroni et al. 2019). Nonetheless, the biodiversity impacts of soybeans are understudied compared with other tropical crops such as cacao, coffee, and oil palm, which account for considerably less harvested land area (fao.org/faostat/). Many lesser-known crops are grown by small-scale subsistence farmers and are less likely to gain attention from conservationists than industrially produced crops that are traded internationally (Balmford et al. 2012). Our REA also showed some geographic bias in the papers we found. In the Neotropics, research is concentrated in Brazil, Mexico, Costa Rica, Colombia, and Peru, and in Asia the majority of studies come from Malaysia, Indonesia, and India (Figure S2). Most other countries provided few or no studies; research in tropical Oceania is particularly limited. Gaps in our dataset may be due in part to our restricting of the literature search to English language studies. It must therefore be acknowledged that language bias presents a limitation to our study. The inclusion of non-English languages could provide further data and consequently potentially alter effect sizes (Konno et al. 2020). However, as demonstrated by our assessments of publication bias (described in the Methods), any changes to effect sizes as a result of missing articles, are highly unlikely to overturn the conclusions of the study.

In our analysis, richness metrics declined more than abundance metrics. Both are concerning, because there is an abundant literature to show that, in general, the first species to be lost under habitat conversion (and therefore reduce richness), are the most sensitive species that are typically of conservation concern (e.g. Newbold *et al.* 2015 and studies therein). On the other hand, reductions in abundance metrics (and richness metrics) indicate potential declines in the provisioning of ecosystem functions performed by key groups. As such, birds which are important mobile seed dispersers and pest controllers, showed the greatest negative response to agricultural conversion while mammals displayed the most tolerance, reflecting the findings of Gibson *et al.* (2011). It has been suggested that large-bodied mammals are often extirpated due to habitat loss, whereas small nonflying mammal and bat populations can thrive in agricultural habitats (Daily *et al.* 2003; Gibson *et al.* 2011; Wearn *et al.* 2017).

In many studies used in our meta-analysis, reference sites were fragmented landscapes. Evidence suggests that due to fragmentation, 70% of global forest lies within 1 km of the forest edge (Haddad *et al.* 2015). Agricultural land can have adverse impacts upon biodiversity at considerable distances into natural habitats (Hurst *et al.* 2013; Scriven *et al.* 2018). Therefore, biodiversity levels in reference sites would be influenced by factors such as proximity to agricultural land, patch size, connectivity, edge effects, and the intensity of land use in the surrounding matrix (Prugh *et al.* 2008). Consequently, the true effects of agricultural conversion are likely to be greater than our estimates, when considering the additional impacts

of fragmentation (Haddad *et al.* 2015). Nonetheless, the relative differences between the impacts of different crops are likely to remain largely the same.

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Understanding the consequences of food cultivation on biodiversity can help to identify improvements to agricultural practices and influence consumer choice. Since much of the food produced in tropical regions is exported internationally, a large proportion of impacts on tropical biodiversity are remotely driven by industrialised countries (Green et al. 2019; Lenzen et al. 2012). This study therefore provides us with food for thought regarding the positive and negative environmental impacts caused by our food choices. It is particularly pertinent as we are trying to improve the transparency of food supply chains and connecting consumer markets and biodiversity loss through projects such as destruction (http://www.trase.earth). The knowledge gained from this study could also be incorporated into the modelling of future agricultural expansion scenarios (e.g., Chaplin-Kramer et al. 2015), helping to identify areas for crop expansion with minimal adverse impacts on biodiversity. Most of all though, our findings may serve as a warning sign for agricultural systems that rely on the ecological functions provided by biodiversity to maximise their yields. This is crucial, because with an ever-increasing global food demand, yield deficits could result in further expansion to the area footprint of tropical agriculture.

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405	Author contributions
406	JLO led the manuscript writing, conducted the REA and analysed the data. JEB conceived the
407	study, co-wrote the manuscript and assisted with data analysis.
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409	Acknowledgments
410	We would like to thank C. Gardner for initial discussions regarding the study concept.
411	
412	Conflicts of interests
413	The authors declare no conflicts of interests.
414	

Should the manuscript be accepted, the dataset will be archived in the repository Dryad, and

Data availability

the data DOI will be included at the end of the article.

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607 Figures

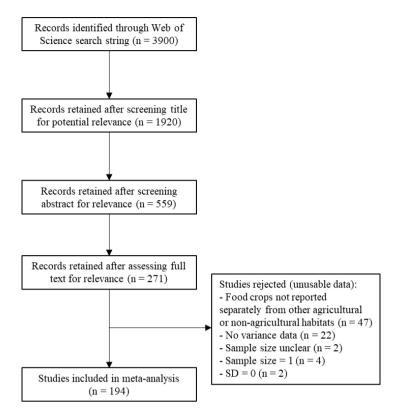


Figure 1. PRISMA diagram of the number of studies included during each filtering stage of

the rapid evidence assessment. See methods for inclusion criteria.

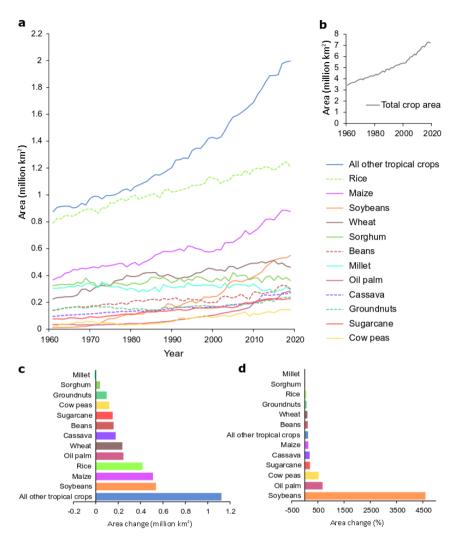


Figure 2. Changes in harvested area of tropical crops from 1961-2019. (a) Harvested area of individual food crops. (b) Total harvested area of food crops. (c) Increase in harvested area of food crops by absolute area and (d) by percentage, in tropical countries from 1961-2019. The top ten tropical crops by area in 2019 are shown. Additionally, sugarcane and cow peas, which were in the top ten by area increase, are also shown. The harvested areas of 'all other tropical crops' were combined. Data: FAOSTAT.

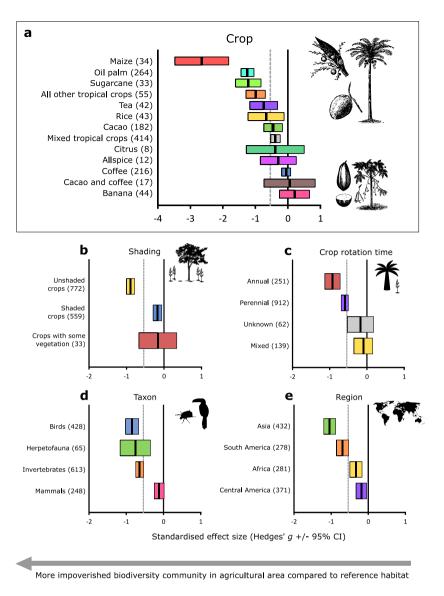


Figure 3. Effect sizes of agricultural impacts on biodiversity by (a) crop, (b) intensity, (c) crop rotation time, (d) taxonomic group (omitting fish N_{studies}=3), and (e) geographic region (omitting Oceania N_{studies}=1). The number of pairwise comparisons between agricultural and reference sites per category is reported in parentheses. The black vertical lines show the mean standardised effect size (Hedges' g), and 95% CI are indicated by the width of the boxes. Effect sizes are significant if the confidence intervals do not overlap zero. The tall vertical black lines and grey dashed lines represent an effect size of zero and mean overall effect size respectively. For single crops represented by fewer than four studies, we grouped these and reported them as 'all other tropical crops'. When biodiversity values were provided for sites that did not distinguish between multiple different crops, we reported them as 'mixed tropical crops'

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5	The impacts of tropical agriculture on biodiversity: a meta-
6	analysis
7	Joseph L. Oakley and Jake E. Bicknell
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10	Supporting Information

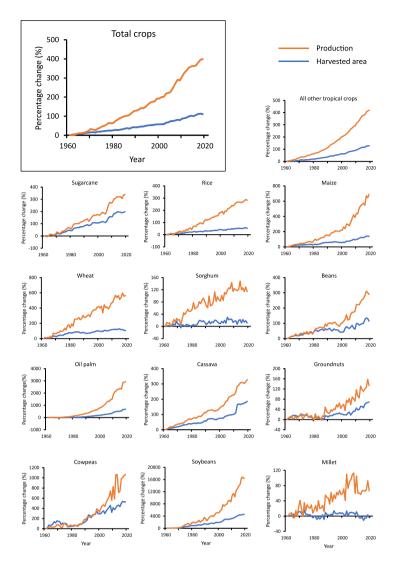


Figure S1. Changes in crop production by weight and harvested area from 1961 to 2019.

Changes are measured as the percentage changes for each year compared to 1961. The top ten crops by harvested area in 2019 are shown, as well as sugarcane, cowpeas, 'all other tropical crops' and the total. Data: FAOSTAT.

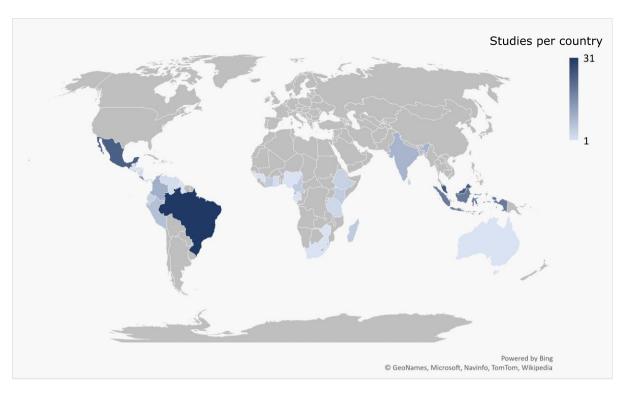
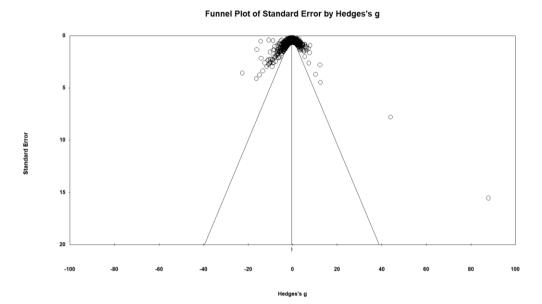


Figure S2 Map of study sites by country. Country colour illustrates the number of studies per country (N_{countries}=34, N_{studies}=194).

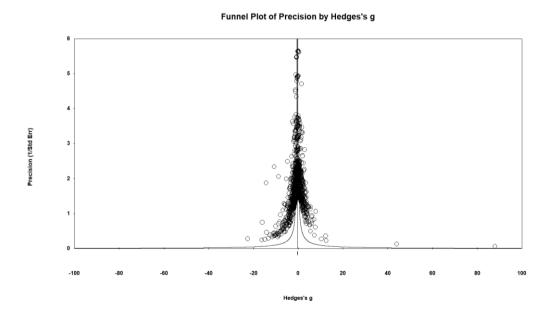
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Figure S3. Publication bias in the meta-analysis. (a) Funnel plot of the relationship between mean effect size and standard error for each study. (b) Funnel plot of the relationship between mean effect size and the precision of each study.

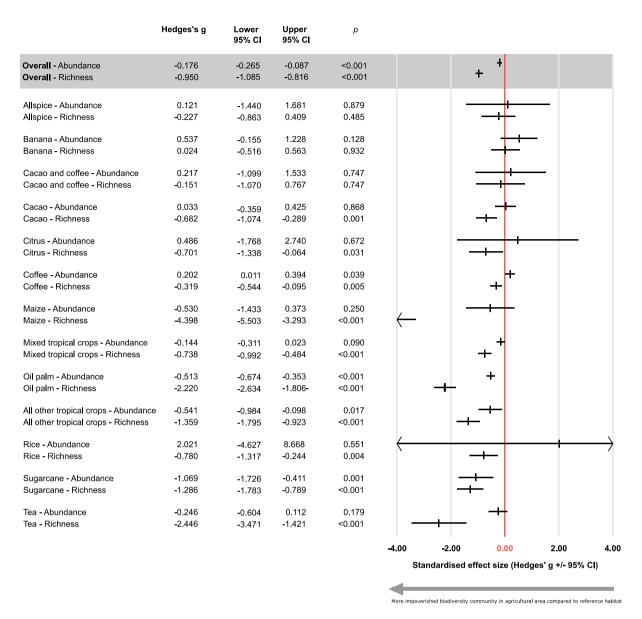


Figure S4. Effect sizes of agricultural impacts on biodiversity, broken down by crop type and by biodiversity metric (richness or abundance). The black vertical lines show the mean standardised effect size (Hedges' *g*), and 95% CI are indicated by the width of the lines. Where these go beyond the scale of -4 to +4, this is indicated by an arrow. Effect sizes are significant if the confidence intervals do not overlap zero. For single crops represented by fewer than four studies, we grouped these and reported them as 'all other tropical crops'. When biodiversity values were provided for sites that did not distinguish between multiple different crops, we reported them as 'mixed tropical crops'. Overall effect sizes for abundance and richness are found in Table S3.

Table S1. Details of the studies included in the meta-analysis

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Ackerman IL, Constantino R, Gauch, Jr HG, Lehmann J, Riha SJ, Fernandes ECM. 2009. Termite (Insecta: Isoptera) Species Composition in a Primary Rain Forest and Agroforests in Central Amazonia. Biotropica 41:226–233.	Shaded crops	Mixed tropical crops	Invertebrates	South America	Unknown
Adedoja O, Kehinde T. 2018. Changes in interaction network topology and species composition of flower-visiting insects across three land use types. African Journal of Ecology 56:964–971.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Annual
Allen L, Reeve R, Nousek-McGregor A, Villacampa J, MacLeod R. 2019. Are orchid bees useful indicators of the impacts of human disturbance? Ecological Indicators 103:745–755.	Unshaded crops	Banana	Invertebrates	South America	Perennial
	Shaded crops	Banana	Invertebrates	South America	Perennial
Almeida SM, Silva LC, Cardoso MR, Cerqueira PV, Juen L, Santos MPD. 2016. The effects of oil palm plantations on the functional diversity of Amazonian birds. Journal of Tropical Ecology 32:510–525.	Unshaded crops	Oil palm	Birds	South America	Perennial
Alonso-Rodríguez AM, Finegan B, Fiedler K. 2017. Neotropical moth assemblages degrade due to oil palm expansion. Biodiversity and Conservation 26:2295–2326.	Unshaded crops	Oil palm	Invertebrates	Central America	Perennial
Alvarez-Alvarez EA, Corcuera P, Almazán-Núñez RC. 2018. Spatiotemporal variation in the structure and diet types of bird assemblages in tropical dry forest in southwestern Mexico. The Wilson Journal of Ornithology 130:457.	Unshaded crops	Mixed tropical crops	Birds	Central America	Mixed
Arellano L, Favila ME, Huerta C. 2005. Diversity of dung and carrion beetles in a disturbed Mexican tropical montane cloud forest and on shade coffee plantations. Biodiversity and Conservation 14:601–615.	Shaded crops	Coffee	Invertebrates	Central America	Perennial
Arenas-Clavijo A, Armbrecht I. 2019. Soil ants (Hymenoptera: Formicidae) and ground beetles (Coleoptera: Carabidae) in a coffee agroforestry landscape during a severe-drought period. Agroforestry Systems 93:1781–1792.	Unshaded crops	Coffee	Invertebrates	South America	Perennial
	Shaded crops	Coffee	Invertebrates	South America	Perennial
Ashwini KM, Sridhar KR. 2006. Seasonal abundance and activity of pill millipedes (Arthrosphaera magna) in mixed plantation and semi-evergreen forest of southern India. Acta Oecologica 29:27–32.	Shaded crops	Mixed tropical crops	Invertebrates	Asia	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Azhar B, Lindenmayer DB, Wood J, Fischer J, Manning A, McElhinny C, Zakaria M. 2011. The conservation value of oil palm plantation estates, smallholdings and logged peat swamp forest for birds. Forest Ecology and Management 262:2306–2315.	Unshaded crops	Oil palm	Birds	Asia	Perennial
Bakermans MH, Vitz AC, Rodewald AD, Rengifo CG. 2009. Migratory songbird use of shade coffee in the Venezuelan Andes with implications for conservation of cerulean warbler. Biological Conservation 142:2476–2483.	Shaded crops	Coffee	Birds	South America	Perennial
Barnes AD et al. 2017. Direct and cascading impacts of tropical land-use change on multitrophic biodiversity. Nature Ecology & Evolution 1:1511–1519.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
	Unshaded crops	Oil palm	Birds	Asia	Perennial
	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Basset Y et al. 2008. Changes in Arthropod Assemblages along a Wide Gradient of Disturbance in Gabon. Conservation Biology 22:1552–1563.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed
Beck J, Schulze CH, Linsenmair KE, Fiedler K. 2002. From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. Journal of Tropical Ecology 18:33–51.	Unshaded crops	Mixed tropical crops	Invertebrates	Asia	Mixed
Belshaw R, Bolton B. 1993. The effect of forest disturbance on the leaf litter ant fauna in Ghana. Biodiversity and Conservation 2:656–666.	Unshaded crops	Cacao	Invertebrates	Africa	Perennial
Bennett RE, Leuenberger W, Bosarreyes Leja BB, Sagone Cáceres A, Johnson K, Larkin J. 2018. Conservation of Neotropical migratory birds in tropical hardwood and oil palm plantations. PLOS ONE 13:e0210293.	Unshaded crops	Oil palm	Birds	Central America	Perennial
Benstead JP, Douglas MM, Pringle CM. 2003. Relationships of stream invertebrate communities to deforestation in eastern Madagascar. Ecological Applications 13:1473–1490.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Annual
Bobo KS, Waltert M, Fermon H, Njokagbor J, Mühlenberg M. 2006. From Forest to Ffarmland: Butterfly Diversity and Habitat Associations Along a Gradient of Forest Conversion in Southwestern Cameroon. Journal of Insect Conservation 10:29–42.	Shaded crops	Cacao and coffee	Invertebrates	Africa	Perennial
	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Annual
Bos MM, Steffan-Dewenter I, Tscharntke T. 2007. The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. Biodiversity and Conservation 16:2429–2444.	Shaded crops	Cacao	Invertebrates	Asia	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Braga RF, Korasaki V, Audino LD, Louzada J. 2012. Are Dung Beetles Driving Dung-Fly Abundance in Traditional Agricultural Areas in the Amazon? Ecosystems 15:1173–1181.	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Unknown
	Shaded crops	Mixed tropical crops	Invertebrates	South America	Perennial
Buechley ER, Şekercioğlu ÇH, Atickem A, Gebremichael G, Ndungu JK, Mahamued BA, Beyene T, Mekonnen T, Lens L. 2015. Importance of Ethiopian shade coffee farms for forest bird conservation. Biological Conservation 188:50–60.	Shaded crops	Coffee	Birds	Africa	Perennial
Cabra-García J, Bermúdez-Rivas C, Osorio AM, Chacón P. 2012. Cross-taxon congruence of α and β diversity among five leaf litter arthropod groups in Colombia. Biodiversity and Conservation 21:1493–1508.	Unshaded crops	Sugarcane	Invertebrates	South America	Annual
Cajaiba RL, Périco E, Dalzochio MS, da Silva WB, Bastos R, Cabral JA, Santos M. 2017. Does the composition of Scarabaeidae (Coleoptera) communities reflect the extent of land use changes in the Brazilian Amazon? Ecological Indicators 74:285–294.	Unshaded crops	Cacao	Invertebrates	South America	Perennial
	Unshaded crops	Cacao	Invertebrates	South America	Perennial
	Unshaded crops	Cacao	Invertebrates	South America	Perennial
Carvalho RL, Andresen E, Barônio GJ, Oliveira VHF, Louzada J, Braga RF. 2020. Is dung removal a good proxy for other dung beetle functions when monitoring for conservation? A case study from the Brazilian Amazon. Ecological Indicators 109:105841.	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Mixed
Castillo LE, Martínez E, Ruepert C, Savage C, Gilek M, Pinnock M, Solis E. 2006. Water quality and macroinvertebrate community response following pesticide applications in a banana plantation, Limon, Costa Rica. Science of The Total Environment 367:418–432.	Unshaded crops	Banana	Invertebrates	Central America	Perennial
Céspedes LN, Bayly NJ. 2019. Over-winter ecology and relative density of Canada Warbler Cardellina canadensis in Colombia: the basis for defining conservation priorities for a sharply declining long-distance migrant. Bird Conservation International 29:232–248.	Shaded crops	Coffee	Birds	South America	Perennial
Chapman PM, Loveridge R, Rowcliffe JM, Carbone C, Bernard H, Davison CW, Ewers RM. 2019. Minimal Spillover of Native Small Mammals From Bornean Tropical Forests Into Adjacent Oil Palm Plantations. Frontiers in Forests and Global Change 2:2.	Unshaded crops	Oil palm	Mammals	Asia	Perennial
Chellaiah D, Yule CM. 2018. Riparian buffers mitigate impacts of oil palm plantations on aquatic macroinvertebrate community structure in tropical streams of Borneo. Ecological Indicators 95:53–62.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
	Shaded crops	Oil palm	Invertebrates	Asia	Perennial
	Crops with some vegetation	Oil palm	Invertebrates	Asia	Perennial
Chiawo DO, Kombe WN, Craig AJFK. 2018. Bird responses to land use change: guild diversity in a Kenyan coastal forest and adjoining habitats. Emu - Austral Ornithology 118:281–292.	Unshaded crops	Mixed tropical crops	Birds	Africa	Annual
Clough Y et al. 2016. Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. Nature Communications 7:13137.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
	Unshaded crops	Oil palm	Birds	Asia	Perennial
Costa C, Oliveira VHF, Maciel R, Beiroz W, Korasaki V, Louzada J. 2017. Variegated tropical landscapes conserve diverse dung beetle communities. PeerJ 5:e3125.	Shaded crops	Coffee	Invertebrates	South America	Perennial
Coulibaly T, Akpesse AAM, Boga J-P, Yapi A, Kouassi KP, Roisin Y. 2016. Change in termite communities along a chronosequence of mango tree orchards in the north of Côte d'Ivoire. Journal of Insect Conservation 20:1011–1019.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed
	Crops with some vegetation	All other tropical crops	Invertebrates	Africa	Perennial
	Shaded crops	All other tropical crops	Invertebrates	Africa	Perennial
da Cunha Bitar YO, Juen L, Pinheiro LC, Santos-Costa MC dos. 2015. Anuran Beta Diversity in a Mosaic Anthropogenic Landscape in Transitional Amazon. Journal of Herpetology 49:75–82.	Unshaded crops	Mixed tropical crops	Herpetofauna	South America	Annual
Daily GC, Ceballos G, Pacheco J, Suzán G, Sánchez-Azofeifa A. 2003. Countryside Biogeography of Neotropical Mammals: Conservation Opportunities in Agricultural Landscapes of Costa Rica. Conservation Biology 17:1814–1826.	Unshaded crops	Coffee	Mammals	Central America	Perennial
DaRocha WD, Neves FS, Dáttilo W, Delabie JHC. 2016. Epiphytic bromeliads as key components for maintenance of ant diversity and ant–bromeliad interactions in agroforestry system canopies. Forest Ecology and Management 372:128–136.	Shaded crops	Cacao	Invertebrates	South America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Davies TE, Clarke RH, Ewen JG, Fazey IRA, Pettorelli N, Cresswell W. 2015. The effects of land-use change on the endemic avifauna of Makira, Solomon Islands: endemics avoid monoculture. Emu - Austral Ornithology 115:199–213.	Unshaded crops	Cacao	Birds	Asia	Perennial
	Unshaded crops	Mixed tropical crops	Birds	Asia	Perennial
	Shaded crops	Mixed tropical crops	Birds	Asia	Mixed
De Beenhouwer M, Geeraert L, Mertens J, Van Geel M, Aerts R, Vanderhaegen K, Honnay O. 2016. Biodiversity and carbon storage co-benefits of coffee agroforestry across a gradient of increasing management intensity in the SW Ethiopian highlands. Agriculture, Ecosystems & Environment 222:193–199.	Shaded crops	Coffee	Invertebrates	Africa	Perennial
De la Mora A, Murnen CJ, Philpott SM. 2013. Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. Biodiversity and Conservation 22:871–888.	Unshaded crops	Coffee	Invertebrates	Central America	Perennial
	Shaded crops	Coffee	Invertebrates	Central America	Perennial
de Lima RF, Dallimer M, Atkinson PW, Barlow J. 2013. Biodiversity and land-use change: understanding the complex responses of an endemic-rich bird assemblage. Diversity and Distributions 19:411–422.	Shaded crops	Mixed tropical crops	Birds	Africa	Mixed
Delabie JHC, Jahyny B, do Nascimento IC, Mariano CSF, Lacau S, Campiolo S, Philpott SM, Leponce M. 2007. Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil. Biodiversity and Conservation 16:2359–2384.	Shaded crops	Cacao	Invertebrates	South America	Perennial
Dosso K, Roisin Y, Tiho S, Konaté S, Yéo K. 2017. Short-term changes in the structure of termite assemblages associated with slash-and-burn agriculture in Côte d'Ivoire. Biotropica 49:856–861.	Shaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed
Edwards DP et al. 2014a. Selective-logging and oil palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. Ecological Applications 24:2029–2049.	Unshaded crops	Oil palm	Birds	Asia	Perennial
	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
	Unshaded crops	Oil palm	Mammals	Asia	Perennial
Edwards DP, Hodgson JA, Hamer KC, Mitchell SL, Ahmad AH, Cornell SJ, Wilcove DS. 2010. Wildlife-friendly oil palm plantations fail to protect biodiversity effectively: Farming and the fate of tropical biodiversity. Conservation Letters 3:236–242.	Unshaded crops	Oil palm	Birds	Asia	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Edwards FA, Edwards DP, Hamer KC, Davies RG. 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. Ibis 155:313–326.	Unshaded crops	Oil palm	Birds	Asia	Perennial
Edwards FA, Edwards DP, Larsen TH, Hsu WW, Benedick S, Chung A, Vun Khen C, Wilcove DS, Hamer KC. 2014b. Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot?: Functional diversity and land-use change in Borneo. Animal Conservation 17:163–173.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Elisei T, Valadares E, Martins CF, Albuquerque FA. 2017. Diversity and Structure of Social Wasps Community (Hymenoptera: Vespidae, Polistinae) in Neotropical Dry Forest. Sociobiology 64:111.	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Unknown
Estrada A, Coates-Estrada R, Dadda AA, Cammarano P. 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. Journal of Tropical Ecology 14:577–593.	Unshaded crops	Citrus	Invertebrates	Central America	Perennial
	Shaded crops	Coffee	Invertebrates	Central America	Perennial
	Unshaded crops	Allspice	Invertebrates	Central America	Perennial
	Shaded crops	Cacao and coffee	Invertebrates	Central America	Perennial
	Shaded crops	Cacao	Invertebrates	Central America	Perennial
Estrada A, Coates-Estrada R, Meritt D. 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography 17:229–241.	Unshaded crops	Citrus	Mammals	Central America	Perennial
	Unshaded crops	Allspice	Mammals	Central America	Perennial
	Shaded crops	Coffee	Mammals	Central America	Perennial
	Shaded crops	Cacao	Mammals	Central America	Perennial
	Shaded crops	Cacao and coffee	Mammals	Central America	Perennial
Estrada A, Coates-Estrada R, Meritt Jr DA. 1997. Anthropogenic changes and avian diversity at Los Tuxtlas, Mexico. Biodiversity and Conservation 6:19–43.	Unshaded crops	Banana	Birds	Central America	Perennial
	Unshaded crops	All other tropical crops	Birds	Central America	Annual

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
	Unshaded crops	Maize	Birds	Central America	Annual
	Unshaded crops	Allspice	Birds	Central America	Perennial
	Shaded crops	Cacao and coffee	Birds	Central America	Perennial
	Unshaded crops	Citrus	Birds	Central America	Perennial
	Shaded crops	Coffee	Birds	Central America	Perennial
	Shaded crops	Cacao	Birds	Central America	Perennial
Estrada A, Coates-Estrada R. 2005. Diversity of Neotropical migratory landbird species assemblages in forest fragments and man-made vegetation in Los Tuxtlas, Mexico. Biodiversity and Conservation 14:1719–1734.	Unshaded crops	Mixed tropical crops	Birds	Central America	Annual
	Unshaded crops	Mixed tropical crops	Birds	Central America	Perennial
	Shaded crops	Mixed tropical crops	Birds	Central America	Perennial
Estrada A, D AA, Coates-Estrada R. 1999. Tropical rain forest fragmentation, howler monkeys (Alouatta palliata), and dung beetles at Los Tuxtlas, Mexico. American Journal of Primatology 48:253–262.	Unshaded crops	Citrus	Invertebrates	Central America	Perennial
	Unshaded crops	Allspice	Invertebrates	Central America	Perennial
	Shaded crops	Coffee	Invertebrates	Central America	Perennial
	Shaded crops	Cacao and coffee	Invertebrates	Central America	Perennial
	Shaded crops	Cacao	Invertebrates	Central America	Perennial
Faria D, Baumgarten J. 2007. Shade cacao plantations (Theobroma cacao) and bat conservation in southern Bahia, Brazil. Biodiversity and Conservation 16:291–312.	Shaded crops	Cacao	Mammals	South America	Perennial
Faria D, Laps RR, Baumgarten J, Cetra M. 2006. Bat and Bird Assemblages from Forests and Shade Cacao Plantations in Two Contrasting Landscapes in the Atlantic Forest of Southern Bahia, Brazil. Biodiversity and Conservation 15:587–612.	Shaded crops	Cacao	Birds	South America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
	Shaded crops	Cacao	Mammals	South America	Perennial
Faria D, Paciencia MLB, Dixo M, Laps RR, Baumgarten J. 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil. Biodiversity and Conservation 16:2335–2357.	Shaded crops	Cacao	Herpetofauna	South America	Perennial
Faria D. 2006. Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. Journal of Tropical Ecology 22:531–542.	Shaded crops	Cacao	Mammals	South America	Perennial
Faruk A, Belabut D, Ahmad N, Knell RJ, Garner TWJ. 2013. Effects of Oil-Palm Plantations on Diversity of Tropical Anurans: Effects of Oil-Palm Plantations on Anurans. Conservation Biology 27:615–624.	Unshaded crops	Oil palm	Herpetofauna	Asia	Perennial
Fayle TM, Turner EC, Snaddon JL, Chey VK, Chung AYC, Eggleton P, Foster WA. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. Basic and Applied Ecology 11:337–345.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Feijoo A, Carvajal AF, Zúñiga MC, Quintero H, Fragoso C. 2011. Diversity and abundance of earthworms in land use systems in central-western Colombia. Pedobiologia 54:S69–S75.	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Mixed
	Shaded crops	Mixed tropical crops	Invertebrates	South America	Perennial
Filgueiras BKC, Tabarelli M, Leal IR, Vaz-de-Mello FZ, Iannuzzi L. 2015. Dung beetle persistence in human-modified landscapes: Combining indicator species with anthropogenic land use and fragmentation-related effects. Ecological Indicators 55:65–73.	Unshaded crops	Sugarcane	Invertebrates	South America	Annual
	Unshaded crops	Sugarcane	Invertebrates	South America	Annual
Fotso AK, Hanna R, Tindo M, Doumtsop A, Nagel P. 2015. How plants and honeydew-producing hemipterans affect ant species richness and structure in a tropical forest zone. Insectes Sociaux 62:443–453.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Unknown
Franco ALC, Bartz MLC, Cherubin MR, Baretta D, Cerri CEP, Feigl BJ, Wall DH, Davies CA, Cerri CC. 2016. Loss of soil (macro)fauna due to the expansion of Brazilian sugarcane acreage. Science of The Total Environment 563–564:160–168.	Unshaded crops	Sugarcane	Invertebrates	South America	Annual
Freudmann A, Mollik P, Tschapka M, Schulze CH. 2015. Impacts of oil palm agriculture on phyllostomid bat assemblages. Biodiversity and Conservation 24:3583–3599.	Unshaded crops	Oil palm	Mammals	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Frishkoff LO, Karp DS, M'Gonigle LK, Mendenhall CD, Zook J, Kremen C, Hadly EA, Daily GC. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science 345:1343–1346.	Unshaded crops	Mixed tropical crops	Birds	Central America	Mixed
	Crops with some vegetation	Mixed tropical crops	Birds	Central America	Mixed
Furtado IS, Martins MB. 2018. The impacts of land use intensification on the assembly of drosophilidae (Diptera). Global Ecology and Conservation 16:e00432.	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Perennial
	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Annual
Gallmetzer N, Schulze CH. 2015. Impact of oil palm agriculture on understory amphibians and reptiles: A Mesoamerican perspective. Global Ecology and Conservation 4:95–109.	Unshaded crops	Oil palm	Herpetofauna	Central America	Perennial
Geissen V, Peña-Peña K, Huerta E. 2009. Effects of different land use on soil chemical properties, decomposition rate and earthworm communities in tropical Mexico. Pedobiologia 53:75–86.	Unshaded crops	Banana	Invertebrates	Central America	Perennial
	Shaded crops	Banana	Invertebrates	Central America	Perennial
Gillespie GR, Ahmad E, Elahan B, Evans A, Ancrenaz M, Goossens B, Scroggie MP. 2012. Conservation of amphibians in Borneo: Relative value of secondary tropical forest and nonforest habitats. Biological Conservation 152:136–144.	Unshaded crops	Oil palm	Herpetofauna	Asia	Perennial
Gilroy JJ, Prescott GW, Cardenas JS, Castañeda PG del P, Sánchez A, Rojas-Murcia LE, Medina Uribe CA, Haugaasen T, Edwards DP. 2015. Minimizing the biodiversity impact of Neotropical oil palm development. Global Change Biology 21:1531–1540.	Unshaded crops	Oil palm	Birds	South America	Perennial
	Unshaded crops	Oil palm	Invertebrates	South America	Perennial
	Unshaded crops	Oil palm	Herpetofauna	South America	Perennial
Glor RE, Flecker AS, Benard MF, Power AG. 2001. Lizard diversity and agricultural disturbance in a Caribbean forest landscape. Biodiversity and Conservation 10:711–723.	Unshaded crops	Oil palm	Herpetofauna	Central America	Perennial
	Shaded crops	Cacao	Herpetofauna	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Goodale E, Kotagama SW, Raman TRS, Sidhu S, Goodale U, Parker S, Chen J. 2014. The response of birds and mixed-species bird flocks to human-modified landscapes in Sri Lanka and southern India. Forest Ecology and Management 329:384–392.	Unshaded crops	Mixed tropical crops	Birds	Asia	Unknown
Gordon C, Manson R, Sundberg J, Cruz-Angón A. 2007. Biodiversity, profitability, and vegetation structure in a Mexican coffee agroecosystem. Agriculture, Ecosystems & Environment 118:256–266.	Shaded crops	Coffee	Mammals	Central America	Perennial
	Shaded crops	Coffee	Birds	Central America	Perennial
Gove AD, Hylander K, Nemomissa S, Shimelis A, Enkossa W. 2013. Structurally complex farms support high avian functional diversity in tropical montane Ethiopia. Journal of Tropical Ecology 29:87–97.	Unshaded crops	Mixed tropical crops	Birds	Africa	Unknown
Gray CL, Lewis OT, Chung AYC, Fayle TM. 2015. Riparian reserves within oil palm plantations conserve logged forest leaf litter ant communities and maintain associated scavenging rates. Journal of Applied Ecology 52:31–40.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Greenler SM, Ebersole JJ. 2015. Bird communities in tropical agroforestry ecosystems: an underappreciated conservation resource. Agroforestry Systems 89:691–704.	Shaded crops	Cacao	Birds	Central America	Perennial
Guéi AM, N'Dri JK, Zro FGB, Bakayoko S, Tondoh JE. 2019. Relationships between soil morpho-chemical parameters and earthworm community attributes in tropical agroecosystems in the Centre-West region of Côte d'Ivoire, Africa. Tropical Ecology 60:209–218.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Unknown
	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed
	Unshaded crops	Cacao	Invertebrates	Africa	Perennial
Halffter G, Pineda E, Arellano L, Escobar F. 2007. Instability of Copronecrophagous Beetle Assemblages (Coleoptera: Scarabaeinae) in a Mountainous Tropical Landscape of Mexico. Environmental Entomology 36:1397–1407.	Shaded crops	Coffee	Invertebrates	Central America	Perennial
Harada LM, Araújo IS, Overal WL, Silva FAB. 2020. Comparison of dung beetle communities (Coleoptera: Scarabaeidae: Scarabaeinae) in oil palm plantations and native forest in the eastern Amazon, Brazil. Revista Brasileira de Entomologia 64:e2019102.	Unshaded crops	Oil palm	Invertebrates	South America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Harterreiten-Souza ÉS, Pujol-Luz JR, Sujii ER. 2016. Influence of Various Farmland Habitats on Abundance of Taeniaptera (Diptera: Micropezidae). Florida Entomologist 99:740–743.	Unshaded crops	Mixed tropical crops	Invertebrates	South America	Annual
Harvey CA, Gonzalez J, Somarriba E. 2006. Dung Beetle and Terrestrial Mammal Diversity in Forests, Indigenous Agroforestry Systems and Plantain Monocultures in Talamanca, Costa Rica. Biodiversity and Conservation 15:555–585.	Unshaded crops	All other tropical crops	Invertebrates	Central America	Perennial
	Unshaded crops	All other tropical crops	Mammals	Central America	Perennial
	Shaded crops	Banana	Invertebrates	Central America	Perennial
	Shaded crops	Cacao	Invertebrates	Central America	Perennial
	Shaded crops	Cacao	Mammals	Central America	Perennial
	Shaded crops	Banana	Mammals	Central America	Perennial
Harvey CA, González Villalobos JA. 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodiversity and Conservation 16:2257–2292.	Unshaded crops	All other tropical crops	Birds	Central America	Perennial
	Shaded crops	Banana	Birds	Central America	Perennial
	Shaded crops	Cacao	Birds	Central America	Perennial
	Unshaded crops	All other tropical crops	Mammals	Central America	Perennial
	Shaded crops	Banana	Mammals	Central America	Perennial
	Shaded crops	Cacao	Mammals	Central America	Perennial
Helbig-Bonitz M, Ferger SW, Böhning-Gaese K, Tschapka M, Howell K, Kalko EKV. 2015. Bats are Not Birds - Different Responses to Human Land-use on a Tropical Mountain. Biotropica 47:497–508.	Shaded crops	Coffee	Birds	Africa	Perennial
	Shaded crops	Mixed tropical crops	Birds	Africa	Unknown

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
	Shaded crops	Mixed tropical crops	Mammals	Africa	Unknown
	Shaded crops	Coffee	Mammals	Africa	Perennial
	Shaded crops	Mixed tropical crops	Mammals	Africa	Mixed
Hoehn P, Steffan-Dewenter I, Tscharntke T. 2010. Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. Biodiversity and Conservation 19:2189–2200.	Unshaded crops	Mixed tropical crops	Invertebrates	Asia	Mixed
	Shaded crops	Mixed tropical crops	Invertebrates	Asia	Mixed
Horgan FG. 2009. Invasion and retreat: shifting assemblages of dung beetles amidst changing agricultural landscapes in central Peru. Biodiversity and Conservation 18:3519–3541.	Shaded crops	Coffee	Invertebrates	South America	Perennial
Horner-Devine MC, Daily GC, Ehrlich PR, Boggs CL. 2003. Countryside Biogeography of Tropical Butterflies. Conservation Biology 17:168–177.	Unshaded crops	Coffee	Invertebrates	Central America	Perennial
Huang JC, Rustiati EL, Nusalawo M, Kingston T. 2019. Echolocation and roosting ecology determine sensitivity of forest-dependent bats to coffee agriculture. Biotropica 51:757–768.	Shaded crops	Coffee	Mammals	Asia	Perennial
Huerta E, Kampichler C, Geissen V, Ochoa-Gaona S, Jong B de, Hernández-Daumás S. 2009. Towards an ecological index for tropical soil quality based on soil macrofauna. Pesquisa Agropecuária Brasileira 44:1056–1062.	Unshaded crops	Maize	Invertebrates	Central America	Annual
	Unshaded crops	Mixed tropical crops	Invertebrates	Central America	Mixed
	Unshaded crops	All other tropical crops	Invertebrates	Central America	Perennial
Kapoor V. 2008. Effects of rainforest fragmentation and shade-coffee plantations on spider communities in the Western Ghats, India. Journal of Insect Conservation 12:53–68.	Shaded crops	Coffee	Invertebrates	Asia	Perennial
Kessler M et al. 2009. Alpha and beta diversity of plants and animals along a tropical landuse gradient. Ecological Applications 19:2142–2156.	Shaded crops	Cacao	Birds	Asia	Perennial
	Shaded crops	Cacao	Invertebrates	Asia	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
King DI, Hernandez-Mayorga MD, Trubey R, Raudales R, Rappole JH. 2007. An Evaluation of the Contribution of Cultivated Allspice (Pimenta Dioca) to Vertebrate Biodiversity Conservation in Nicaragua. Biodiversity and Conservation 16:1299–1320.	Shaded crops	Allspice	Mammals	Central America	Perennial
	Shaded crops	Allspice	Herpetofauna	Central America	Perennial
	Shaded crops	Allspice	Birds	Central America	Perennial
Klarner B, Winkelmann H, Krashevska V, Maraun M, Widyastuti R, Scheu S. 2017. Trophic niches, diversity and community composition of invertebrate top predators (Chilopoda) as affected by conversion of tropical lowland rainforest in Sumatra (Indonesia). PLOS ONE 12:e0180915.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Knowlton JL, Mata Zayas EE, Ripley AJ, Valenzuela-Cordova B, Collado-Torres R. 2019. Mammal Diversity in Oil Palm Plantations and Forest Fragments in a Highly Modified Landscape in Southern Mexico. Frontiers in Forests and Global Change 2:67.	Unshaded crops	Oil palm	Mammals	Central America	Perennial
Kone M, Konate S, Yeo K, Kouassi PK, Linsenmair KE. 2012. Changes in ant communities along an age gradient of cocoa cultivation in the Oumé region, central Côte d'Ivoire: Ant communities in cocoa plantations. Entomological Science 15:324–339.	Unshaded crops	Cacao	Invertebrates	Africa	Perennial
	Shaded crops	Cacao	Invertebrates	Africa	Perennial
	Crops with some vegetation	Mixed tropical crops	Invertebrates	Africa	Mixed
	Unshaded crops	Cacao	Invertebrates	Africa	Perennial
	Crops with some vegetation	Mixed tropical crops	Invertebrates	Africa	Mixed
	Shaded crops	Cacao	Invertebrates	Africa	Perennial
Konopik O, Steffan-Dewenter I, Grafe TU. 2015. Effects of Logging and Oil Palm Expansion on Stream Frog Communities on Borneo, Southeast Asia. Biotropica 47:636–643.	Shaded crops	Oil palm	Herpetofauna	Asia	Perennial
Kudavidanage EP, Wanger TC, Alwis C, Sanjeewa S, Kotagama SW. 2012. Amphibian and butterfly diversity across a tropical land-use gradient in Sri Lanka; implications for conservation decision making: Land-use change affects amphibians and butterflies. Animal Conservation 15:253–265.	Crops with some vegetation	Mixed tropical crops	Herpetofauna	Asia	Unknown

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
	Crops with some vegetation	Mixed tropical crops	Invertebrates	Asia	Unknown
Kühnert K, Grass I, Waltert M. 2019. Sacred groves hold distinct bird assemblages within an Afrotropical savanna. Global Ecology and Conservation 18:e00656.	Unshaded crops	Mixed tropical crops	Birds	Africa	Annual
Kuppler J, Fricke J, Hemp C, Steffan-Dewenter I, Peters MK. 2015. Conversion of savannah habitats to small-scale agriculture affects grasshopper communities at Mt. Kilimanjaro, Tanzania. Journal of Insect Conservation 19:509–518.	Unshaded crops	Maize	Invertebrates	Africa	Annual
Lees AC, Moura NG, de Almeida AS, Vieira ICG. 2015. Poor Prospects for Avian Biodiversity in Amazonian Oil Palm. PLOS ONE 10:e0122432.	Unshaded crops	Oil palm	Birds	South America	Perennial
Livingston G, Jha S, Vega A, Gilbert L. 2013. Conservation Value and Permeability of Neotropical Oil Palm Landscapes for Orchid Bees. PLOS ONE 8:e78523.	Unshaded crops	Oil palm	Invertebrates	Central America	Perennial
López-Ricaurte L, Edwards DP, Romero-Rodríguez N, Gilroy JJ. 2017. Impacts of oil palm expansion on avian biodiversity in a Neotropical natural savanna. Biological Conservation 213:225–233.	Unshaded crops	Oil palm	Birds	South America	Perennial
Love K, Kurz DJ, Vaughan IP, Ke A, Evans LJ, Goossens B. 2017. Bearded pig (Sus barbatus) utilisation of a fragmented forest—oil palm landscape in Sabah, Malaysian Borneo. Wildlife Research 44:603.	Unshaded crops	Oil palm	Mammals	Asia	Perennial
Lucey JM, Tawatao N, Senior MJM, Chey VK, Benedick S, Hamer KC, Woodcock P, Newton RJ, Bottrell SH, Hill JK. 2014. Tropical forest fragments contribute to species richness in adjacent oil palm plantations. Biological Conservation 169:268–276.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Luke SH, Fayle TM, Eggleton P, Turner EC, Davies RG. 2014. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodiversity and Conservation 23:2817–2832.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
MacGregor-Fors I, Blanco-García A, Lindig-Cisneros R. 2010. Bird community shifts related to different forest restoration efforts: A case study from a managed habitat matrix in Mexico. Ecological Engineering 36:1492–1496.	Unshaded crops	Maize	Birds	Central America	Annual
MacGregor-Fors I, González-García F, Hernández-Lara C, Santiago-Alarcon D. 2018. Where are the birds in the matrix? Avian diversity in a Neotropical landscape mosaic. The Wilson Journal of Ornithology 130:81–93.	Shaded crops	Coffee	Birds	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
MacGregor-Fors I, Schondube JE. 2011. Use of Tropical Dry Forests and Agricultural Areas by Neotropical Bird Communities: Birds in Modified Landscapes. Biotropica 43:365–370.	Unshaded crops	Mixed tropical crops	Birds	Central America	Annual
	Unshaded crops	Mixed tropical crops	Birds	Central America	Perennial
Mandal J, Shankar Raman TR. 2016. Shifting agriculture supports more tropical forest birds than oil palm or teak plantations in Mizoram, northeast India. The Condor 118:345–359.	Unshaded crops	Oil palm	Birds	Asia	Perennial
Martin EA, Viano M, Ratsimisetra L, Laloë F, Carrière SM. 2012. Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. Agriculture, Ecosystems & Environment 149:1–9.	Unshaded crops	Rice	Birds	Africa	Annual
	Unshaded crops	Mixed tropical crops	Birds	Africa	Annual
Mas AH, Dietsch TV. 2004. Linking shade coffee certification to biodiversity conservation: butterflies and birds in Chiapas, Mexico. Ecological Applications 14:642–654.	Shaded crops	Coffee	Invertebrates	Central America	Perennial
Mathieu J, Rossi J-P, Mora P, Lavelle P, Martins PF da S, Rouland C, Grimaldi M. 2005. Recovery of Soil Macrofauna Communities after Forest Clearance in Eastern Amazonia, Brazil. Conservation Biology 19:1598–1605.	Unshaded crops	Rice	Invertebrates	South America	Annual
Mendenhall CD, Frishkoff LO, Santos-Barrera G, Pacheco J, Mesfun E, Quijano FM, Ehrlich PR, Ceballos G, Daily GC, Pringle RM. 2014. Countryside biogeography of Neotropical reptiles and amphibians. Ecology 95:856–870.	Unshaded crops	Coffee	Herpetofauna	Central America	Perennial
Mendes-Oliveira AC, Peres CA, Maués PCR de A, Oliveira GL, Mineiro IGB, de Maria SLS, Lima RCS. 2017. Oil palm monoculture induces drastic erosion of an Amazonian forest mammal fauna. PLOS ONE 12:e0187650.	Unshaded crops	Oil palm	Mammals	South America	Perennial
Méndez-Castro FE, Rao D. 2014. Spider diversity in epiphytes: Can shade coffee plantations promote the conservation of cloud forest assemblages? Biodiversity and Conservation 23:2561–2577.	Shaded crops	Coffee	Invertebrates	Central America	Perennial
Milder JC, DeCLERCK FAJ, Sanfiorenzo A, Sánchez DM, Tobar DE, Zuckerberg B. 2010. Effects of farm and landscape management on bird and butterfly conservation in western Honduras. Ecosphere 1:art2.	Shaded crops	Coffee	Birds	Central America	Perennial
Milheiras SG, Guedes M, Augusto Barbosa Silva F, Aparício P, Mace GM. 2020. Patterns of biodiversity response along a gradient of forest use in Eastern Amazonia, Brazil. PeerJ 8:e8486.	Shaded crops	All other tropical crops	Invertebrates	South America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Moura NG, Lees AC, Andretti CB, Davis BJW, Solar RRC, Aleixo A, Barlow J, Ferreira J, Gardner TA. 2013. Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. Biological Conservation 167:339–348.	Unshaded crops	Mixed tropical crops	Birds	South America	Annual
	Unshaded crops	Mixed tropical crops	Birds	South America	Mixed
Moya-Raygoza G, Cuevas-Guzmán R, Pinedo-Escatel JA, Morales-Arias JG. 2019. Comparison of Leafhopper (Hemiptera: Cicadellidae) Diversity in Maize and Its Wild Ancestor Teosinte, and Plant Diversity in the Teosinte Habitat. Annals of the Entomological Society of America 112:99–106.	Unshaded crops	Maize	Invertebrates	Central America	Annual
Muhamad D, Okubo S, Miyashita T, Takeuchi K. 2013. Effects of habitat type, vegetation structure, and proximity to forests on bird species richness in a forest–agricultural landscape of West Java, Indonesia. Agroforestry Systems 87:1247–1260.	Shaded crops	Mixed tropical crops	Birds	Asia	Perennial
Mulwa RK, Böhning-Gaese K, Schleuning M. 2012. High Bird Species Diversity in Structurally Heterogeneous Farmland in Western Kenya. Biotropica 44:801–809.	Unshaded crops	Sugarcane	Birds	Africa	Annual
	Crops with some vegetation	Mixed tropical crops	Birds	Africa	Unknown
Mulwa RK, Neuschulz EL, Böhning-Gaese K, Schleuning M. 2013. Seasonal fluctuations of resource abundance and avian feeding guilds across forest-farmland boundaries in tropical Africa. Oikos 122:524–532.	Unshaded crops	Mixed tropical crops	Birds	Africa	Annual
	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Annual
Mumme S, Jochum M, Brose U, Haneda NF, Barnes AD. 2015. Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia. Biological Conservation 191:750–758.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Murillo-Pacheco J, López-Iborra GM, Escobar F, Bonilla-Rojas WF, Verdú JR. 2018. The value of small, natural and man-made wetlands for bird diversity in the east Colombian Piedmont. Aquatic Conservation: Marine and Freshwater Ecosystems 28:87–97.	Unshaded crops	Rice	Birds	South America	Annual
Murrieta-Galindo R, González-Romero A, López-Barrera F, Parra-Olea G. 2013. Coffee agrosystems: an important refuge for amphibians in central Veracruz, Mexico. Agroforestry Systems 87:767–779.	Shaded crops	Coffee	Herpetofauna	Central America	Perennial

Page 50 of 62

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Muvengwi J, Mbiba M, Ndagurwa HGT, Nyamadzawo G, Nhokovedzo P. 2017. Termite diversity along a land use intensification gradient in a semi-arid savanna. Journal of Insect Conservation 21:801–812.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Annual
Naughton-Treves L, Mena JL, Treves A, Alvarez N, Radeloff VC. 2003. Wildlife Survival Beyond Park Boundaries: the Impact of Slash-and-Burn Agriculture and Hunting on Mammals in Tambopata, Peru. Conservation Biology 17:1106–1117.	Unshaded crops	Mixed tropical crops	Mammals	South America	Annual
Ndriantsoa SH, Riemann JC, Raminosoa N, Rödel M-O, Glos JS. 2017. Amphibian Diversity in the Matrix of a Fragmented Landscape Around Ranomafana in Madagascar Depends on Matrix Quality. Tropical Conservation Science 10:194008291668606.	Crops with some vegetation	Banana	Herpetofauna	Africa	Perennial
	Unshaded crops	Rice	Herpetofauna	Africa	Annual
Nicolas V, Barrière P, Tapiero A, Colyn M. 2009. Shrew species diversity and abundance in Ziama Biosphere Reserve, Guinea: comparison among primary forest, degraded forest and restoration plots. Biodiversity and Conservation 18:2043–2061.	Unshaded crops	Mixed tropical crops	Mammals	Africa	Mixed
Norfolk O, Asale A, Temesgen T, Denu D, Platts PJ, Marchant R, Yewhalaw D. 2017b. Diversity and composition of tropical butterflies along an Afromontane agricultural gradient in the Jimma Highlands, Ethiopia. Biotropica 49:346–354.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Annual
	Shaded crops	Coffee	Invertebrates	Africa	Perennial
Norfolk O, Jung M, Platts PJ, Malaki P, Odeny D, Marchant R. 2017a. Birds in the matrix: the role of agriculture in avian conservation in the Taita Hills, Kenya. African Journal of Ecology 55:530–540.	Shaded crops	Mixed tropical crops	Birds	Africa	Mixed
	Unshaded crops	Mixed tropical crops	Birds	Africa	Annual
Ocampo-Ariza C, Denis K, Njie Motombi F, Bobo KS, Kreft H, Waltert M. 2019. Extinction thresholds and negative responses of Afrotropical ant-following birds to forest cover loss in oil palm and agroforestry landscapes. Basic and Applied Ecology 39:26–37.	Unshaded crops	Oil palm	Birds	Africa	Perennial
	Shaded crops	Mixed tropical crops	Birds	Africa	Mixed
Paoletti A, Darras K, Jayanto H, Grass I, Kusrini M, Tscharntke T. 2018. Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest. Global Ecology and Conservation 16:e00492.	Unshaded crops	Oil palm	Herpetofauna	Asia	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Pardo LE, Campbell MJ, Edwards W, Clements GR, Laurance WF. 2018. Terrestrial mammal responses to oil palm dominated landscapes in Colombia. PLOS ONE 13:e0197539.	Unshaded crops	Oil palm	Mammals	South America	Perennial
Perfecto I, Mas A, Dietsch T, Vandermeer J. 2003. Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. Biodiversity and Conservation 12:1239–1252.	Shaded crops	Coffee	Invertebrates	Central America	Perennial
	Shaded crops	Coffee	Birds	Central America	Perennial
Perry J, Lojka B, Quinones Ruiz L, Van Damme P, Houška J, Fernandez Cusimamani E. 2016. How natural Forest Conversion Affects Insect Biodiversity in the Peruvian Amazon: Can Agroforestry Help? Forests 7:82.	Unshaded crops	All other tropical crops	Invertebrates	South America	Annual
	Shaded crops	Cacao	Invertebrates	South America	Perennial
	Shaded crops	All other tropical crops	Invertebrates	South America	Perennial
Peters MK, Fischer G, Schaab G, Kraemer M. 2009. Species compensation maintains abundance and raid rates of African swarm-raiding army ants in rainforest fragments. Biological Conservation 142:668–675.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed
Petit LJ, Petit DR, Christian DG, Powell HDW. 1999. Bird communities of natural and modified habitats in Panama. Ecography 22:292–304.	Shaded crops	Coffee	Birds	Central America	Perennial
Pineda E, Halffter G. 2004. Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. Biological Conservation 117:499–508.	Shaded crops	Coffee	Herpetofauna	Central America	Perennial
Potapov AM et al. 2020. Functional losses in ground spider communities due to habitat structure degradation under tropical land-use change. Ecology 101:e02957.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Prabowo WE, Darras K, Clough Y, Toledo-Hernandez M, Arlettaz R, Mulyani YA, Tscharntke T. 2016. Bird Responses to Lowland Rainforest Conversion in Sumatran Smallholder Landscapes, Indonesia. PLOS ONE 11:e0154876.	Unshaded crops	Oil palm	Birds	Asia	Perennial
Pringle CM, Ramírez A. 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. Freshwater Biology 39:359–373.	Unshaded crops	Banana	Invertebrates	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Ramamonjisoa N, Sakai M, Ndriantsoa SH, Kakehashi R, Kurabayashi A, Tomaru N, Natuhara Y. 2020. Hotspots of stream tadpole diversity in forest and agricultural landscapes in Ranomafana, Madagascar. Landscape and Ecological Engineering 16:207–221.	Unshaded crops	Mixed tropical crops	Herpetofauna	Africa	Mixed
Raman TRS. 2006. Effects of Habitat Structure and Adjacent Habitats on Birds in Tropical Rainforest Fragments and Shaded Plantations in the Western Ghats, India. Biodiversity and Conservation 15:1577–1607.	Shaded crops	Mixed tropical crops	Birds	Asia	Perennial
Ranganathan J, Chan KMA, Daily GC. 2007. Satellite detection of bird communities in tropical countryside. Ecological Applications 17:1499–1510.	Unshaded crops	Mixed tropical crops	Birds	Central America	Annual
	Shaded crops	Coffee	Birds	Central America	Perennial
Ranganathan J, Daniels RJR, Chandran MDS, Ehrlich PR, Daily GC. 2008. Sustaining biodiversity in ancient tropical countryside. Proceedings of the National Academy of Sciences 105:17852–17854.	Unshaded crops	All other tropical crops	Birds	Asia	Perennial
Ribeiro J, Colli GR, Caldwell JP, Ferreira E, Batista R, Soares A. 2017. Evidence of neotropical anuran community disruption on rice crops: a multidimensional evaluation. Biodiversity and Conservation 26:3363–3383.	Unshaded crops	Rice	Herpetofauna	South America	Annual
Ricketts TH, Daily GC, Ehrlich PR, Fay JP. 2001. Countryside Biogeography of Moths in a Fragmented Landscape: Biodiversity in Native and Agricultural Habitats. Conservation Biology 15:378–388.	Unshaded crops	Coffee	Invertebrates	Central America	Perennial
Roberts DL, Cooper RJ, Petit LJ. 2000. Use of Premontane Moist Forest and Shade Coffee Agroecosystems by Army Ants in Western Panama. Conservation Biology 14:192–199.	Shaded crops	Coffee	Invertebrates	Central America	Perennial
Rocha J, Laps RR, Machado CG, Campiolo S. 2019. The conservation value of cacao agroforestry for bird functional diversity in tropical agricultural landscapes. Ecology and Evolution 9:7903–7913.	Shaded crops	Cacao	Birds	South America	Perennial
Rocha R, Virtanen T, Cabeza M. 2015. Bird Assemblages in a Malagasy Forest-Agricultural Frontier: Effects of Habitat Structure and Forest Cover. Tropical Conservation Science 8:681–710.	Unshaded crops	Mixed tropical crops	Birds	Africa	Mixed
Roth DS, Perfecto I, Rathcke B. 1994. The Effects of Management Systems on Ground-Foraging Ant Diversity in Costa Rica. Ecological Applications 4:423–436.	Unshaded crops	Banana	Invertebrates	Central America	Perennial
	Shaded crops	Cacao	Invertebrates	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Rousseau L, Fonte SJ, Téllez O, van der Hoek R, Lavelle P. 2013. Soil macrofauna as indicators of soil quality and land use impacts in smallholder agroecosystems of western Nicaragua. Ecological Indicators 27:71–82.	Unshaded crops	Mixed tropical crops	Invertebrates	Central America	Annual
	Shaded crops	Mixed tropical crops	Invertebrates	Central America	Annual
Sambhu H, Nankishore A, Turton SM, Northfield TD. 2018. Trade-offs for butterfly alpha and beta diversity in human-modified landscapes and tropical rainforests. Ecology and Evolution 8:12918–12928.	Unshaded crops	Sugarcane	Invertebrates	Oceania	Annual
Sambhu H, Northfield T, Nankishore A, Ansari A, Turton S. 2017. Tropical Rainforest and Human-Modified Landscapes Support Unique Butterfly Communities That Differ in Abundance and Diversity. Environmental Entomology 46:1225–1234.	Unshaded crops	Sugarcane	Invertebrates	South America	Annual
Santos A de C, Sales PCL, Ribeiro DB, Silva PRR. 2020. Habitat conversion affects beta diversity in frugivorous butterfly assemblages. Studies on Neotropical Fauna and Environment: 1–13.	Unshaded crops	Sugarcane	Invertebrates	South America	Annual
Schulze CH, Waltert M, Kessler PJA, Pitopang R, Veddeler D, Mühlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I, Tscharntke T. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. Ecological Applications 14:1321–1333.	Shaded crops	Cacao	Birds	Asia	Perennial
	Unshaded crops	Maize	Birds	Asia	Annual
	Shaded crops	Cacao	Invertebrates	Asia	Perennial
	Unshaded crops	Maize	Invertebrates	Asia	Annual
Scriven SA, Gillespie GR, Laimun S, Goossens B. 2018. Edge effects of oil palm plantations on tropical anuran communities in Borneo. Biological Conservation 220:37–49.	Unshaded crops	Oil palm	Herpetofauna	Asia	Perennial
Seidu I, Danquah E, Ayine Nsor C, Amaning Kwarteng D, Lancaster LT. 2017. Odonata community structure and patterns of land use in the Atewa Range Forest Reserve, Eastern Region (Ghana). International Journal of Odonatology 20:173–189.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed
Sewlal J-AN, Hailey A. 2019. Diversity and species composition of Araneidae, Tetragnathidae and Nephilidae in different levels of disturbed habitats in Trinidad, West Indies. Journal of Natural History 53:1889–1903.	Unshaded crops	Mixed tropical crops	Invertebrates	Central America	Annual
	Shaded crops	Cacao	Invertebrates	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Shahabuddin S, Hidayat P, Manuwoto S, Noerdjito WA, Tscharntke T, Schulze CH. 2010. Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. Journal of Tropical Ecology 26:53–65.	Shaded crops	Cacao	Invertebrates	Asia	Perennial
Shahabuddin S, Schulze CH, Tscharntke T. 2005. Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). Biodiversity and Conservation 14:863–877.	Unshaded crops	Maize	Invertebrates	Asia	Annual
	Shaded crops	Cacao	Invertebrates	Asia	Perennial
Sidhu S, Raman TRS, Mudappa D. 2015. Prey abundance and leopard diet in a plantation and rainforest landscape, Anamalai Hills, Western Ghats. Current Science 109:323–330.	Unshaded crops	Tea	Mammals	Asia	Perennial
	Shaded crops	Coffee	Mammals	Asia	Perennial
Sodhi NS, Koh LP, Prawiradilaga DM, Tinulele I, Putra DD, Tong Tan TH. 2005. Land use and conservation value for forest birds in Central Sulawesi (Indonesia). Biological Conservation 122:547–558.	Unshaded crops	Mixed tropical crops	Birds	Asia	Mixed
Soh MCK, Sodhi NS, Lim SLH. 2006. High sensitivity of montane bird communities to habitat disturbance in Peninsular Malaysia. Biological Conservation 129:149–166.	Unshaded crops	Tea	Birds	Asia	Perennial
Sreekar R, Srinivasan U, Mammides C, Chen J, Manage Goodale U, Wimalabandara Kotagama S, Sidhu S, Goodale E. 2015. The effect of land-use on the diversity and massabundance relationships of understory avian insectivores in Sri Lanka and southern India. Scientific Reports 5:11569.	Crops with some vegetation	Mixed tropical crops	Birds	Asia	Unknown
Srinivas A, Koh LP. 2016. Oil palm expansion drives avifaunal decline in the Pucallpa region of Peruvian Amazonia. Global Ecology and Conservation 7:183–200.	Crops with some vegetation	Oil palm	Birds	South America	Perennial
Strauß L, Faustino de Lima R, Riesbeck F, Rödel M-O. 2018. São Tomé Island Endemic Treefrogs (Hyperolius spp.) and Land-Use Intensification: A Tale of Hope and Caution. Tropical Conservation Science 11:194008291877643.	Unshaded crops	Mixed tropical crops	Herpetofauna	Africa	Mixed
Trainor CR. 2007. Changes in bird species composition on a remote and well-forested Wallacean Island, South-East Asia. Biological Conservation 140:373–385.	Unshaded crops	Mixed tropical crops	Birds	Asia	Mixed
Trimble MJ, van Aarde RJ. 2014. Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemicity: Herpetofauna over a land-use gradient. Animal Conservation 17:441–453.	Unshaded crops	Sugarcane	Herpetofauna	Africa	Annual

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Turner EC, Foster WA. 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. Journal of Tropical Ecology 25:23–30.	Unshaded crops	Oil palm	Invertebrates	Asia	Perennial
Tylianakis JM, Klein A-M, Lozada T, Tscharntke T. 2006b. Spatial scale of observation affects alpha, beta and gamma diversity of cavity-nesting bees and wasps across a tropical land-use gradient. Journal of Biogeography 33:1295–1304.	Shaded crops	Coffee	Invertebrates	South America	Perennial
	Unshaded crops	Rice	Invertebrates	South America	Annual
Tylianakis JM, Klein A-M, Tscharntke T. 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86:3296–3302.	Unshaded crops	Rice	Invertebrates	South America	Annual
	Shaded crops	Coffee	Invertebrates	South America	Perennial
Tylianakis JM, Tscharntke T, Klein A-M. 2006a. Diversity, ecosystem function, and stability of parasitoid–host interactions across a tropical habitat gradient. Ecology 87:3047–3057.	Shaded crops	Coffee	Invertebrates	South America	Perennial
	Unshaded crops	Rice	Invertebrates	South America	Annual
Umetsu F, Pardini R. 2007. Small mammals in a mosaic of forest remnants and anthropogenic habitats—evaluating matrix quality in an Atlantic forest landscape. Landscape Ecology 22:517–530.	Unshaded crops	Mixed tropical crops	Mammals	South America	Annual
Urrutia-Escobar MX, Armbrecht I. 2013. Effect of Two Agroecological Management Strategies on Ant (Hymenoptera: Formicidae) Diversity on Coffee Plantations in Southwestern Colombia. Environmental Entomology 42:194–203.	Unshaded crops	Coffee	Invertebrates	South America	Perennial
	Shaded crops	Coffee	Invertebrates	South America	Perennial
van Biervliet O, Wiśniewski K, Daniels J, Vonesh JR. 2009. Effects of Tea Plantations on Stream Invertebrates in a Global Biodiversity Hotspot in Africa: Effect of Tea Plantations on Stream Biodiversity. Biotropica 41:469–475.	Unshaded crops	Tea	Invertebrates	Africa	Perennial
Vasconcelos S, Rodrigues P, Palma L, Mendes LF, Palminha A, Catarino L, Beja P. 2015. Through the eye of a butterfly: Assessing biodiversity impacts of cashew expansion in West Africa. Biological Conservation 191:779–786.	Unshaded crops	All other tropical crops	Invertebrates	Africa	Perennial
Waltert M, Bobo KS, Kaupa S, Montoya ML, Nsanyi MS, Fermon H. 2011. Assessing Conservation Values: Biodiversity and Endemicity in Tropical Land Use Systems. PLOS ONE 6:e16238.	Unshaded crops	Mixed tropical crops	Invertebrates	Africa	Mixed

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
	Shaded crops	Mixed tropical crops	Invertebrates	Africa	Perennial
	Unshaded crops	Mixed tropical crops	Birds	Africa	Mixed
	Shaded crops	Mixed tropical crops	Birds	Africa	Perennial
Waltert M, Bobo KS, Sainge NM, Fermon H, Mühlenberg M. 2005. From forest to farmland: habitat effects on Afrotropical forest bird diversity. Ecological Applications 15:1351–1366.	Unshaded crops	Mixed tropical crops	Birds	Africa	Annual
	Shaded crops	Mixed tropical crops	Birds	Africa	Perennial
Waltert M, Mardiastuti A, Mühlenberg M. 2004. Effects of Land Use on Bird Species Richness in Sulawesi, Indonesia. Conservation Biology 18:1339–1346.	Shaded crops	Cacao	Birds	Asia	Perennial
	Unshaded crops	Maize	Birds	Asia	Annual
Wearn OR, Carbone C, Rowcliffe JM, Bernard H, Ewers RM. 2016. Grain-dependent responses of mammalian diversity to land use and the implications for conservation set-aside. Ecological Applications 26:1409–1420.	Unshaded crops	Oil palm	Mammals	Asia	Perennial
Wearn OR, Rowcliffe JM, Carbone C, Pfeifer M, Bernard H, Ewers RM. 2017. Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multispecies modelling approach. Biological Conservation 212:162–171.	Unshaded crops	Oil palm	Mammals	Asia	Perennial
Wilkinson CL, Yeo DCJ, Tan HH, Fikri AH, Ewers RM. 2018b. Land-use change is associated with a significant loss of freshwater fish species and functional richness in Sabah, Malaysia. Biological Conservation 222:164–171.	Unshaded crops	Oil palm	Fish	Asia	Perennial
	Shaded crops	Oil palm	Fish	Asia	Perennial
	Unshaded crops	Oil palm	Fish	Asia	Perennial
	Unshaded crops	Oil palm	Fish	Asia	Perennial
Williams-Guillén K, Perfecto I. 2010. Effects of Agricultural Intensification on the Assemblage of Leaf-Nosed Bats (Phyllostomidae) in a Coffee Landscape in Chiapas, Mexico: Phyllostomid Diversity in Shade Coffee Plantations. Biotropica 42:605–613.	Shaded crops	Coffee	Mammals	Central America	Perennial

Study bibliographic details	Crop shading	Crop category	Taxa	Continent	Perennial or Annual
Williams-Guillén K, Perfecto I. 2011. Ensemble Composition and Activity Levels of Insectivorous Bats in Response to Management Intensification in Coffee Agroforestry Systems. PLOS ONE 6:e16502.	Shaded crops	Coffee	Mammals	Central America	Perennial
Willig MR, Presley SJ, Plante J-L, Bloch CP, Solari S, Pacheco V, Weaver SC. 2019. Guild-level responses of bats to habitat conversion in a lowland Amazonian rainforest: species composition and biodiversity. Journal of Mammalogy 100:223–238.	Unshaded crops	Mixed tropical crops	Mammals	South America	Mixed
Wordley CFR, Sankaran M, Mudappa D, Altringham JD. 2018. Heard but not seen: Comparing bat assemblages and study methods in a mosaic landscape in the Western Ghats of India. Ecology and Evolution 8:3883–3894.	Unshaded crops	Tea	Mammals	Asia	Perennial
	Shaded crops	Tea	Mammals	Asia	Perennial
	Shaded crops	Coffee	Mammals	Asia	Perennial
Zuluaga GJC, Rodewald AD. 2015. Response of mixed-species flocks to habitat alteration and deforestation in the Andes. Biological Conservation 188:72–81.	Shaded crops	Coffee	Birds	South America	Perennial

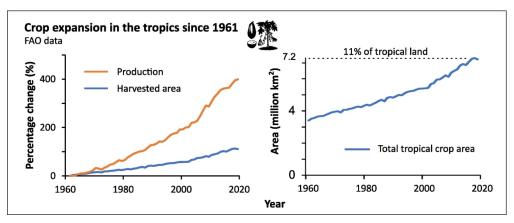
Table S2. Crops analysed in the meta-analysis per pairwise comparison by region

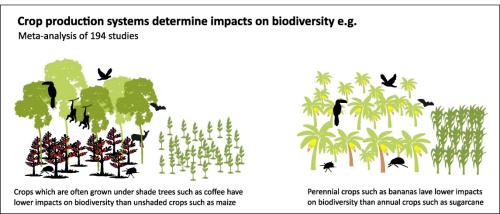
Crops	Central America	South America	Africa	Asia	Oceania	Total
Allenias	12	_	_	_	_	12
Allspice Banana	38	4	2	_	_	44
	50	45	11	- 76	-	182
Cacao	8		9	70		162
Cacao and coffee		-	-	-	-	
Citrus	8	-	-	=	-	8
Coffee	102	51	31	32	-	216
Maize	9	-	2	23	-	34
Mixed tropical crops	78	65	186	85	-	414
Oil palm	38	50	2	174	-	264
All other tropical crops	28	8	15	4	-	55
Rice	-	32	11	-	-	43
Sugarcane	_	23	8	_	2	33
Tea	-	-	4	38	-	42

Table S3. Effect sizes calculated in the study as displayed in Figure 3. For single crops with fewer than four studies, we grouped these and reported them as 'all other tropical crops'. When biodiversity values were provided for sites that did not distinguish between multiple different crops, we reported them as 'mixed tropical crops'

Analysis	Mean Hedges' g	Lower 95% CI	Upper 95% CI	p	
Overall	-0.588	-0.671	-0.505	<0.001	
Crop (Fig. 3a)					
Allspice	-0.29	-0.848	0.258	0.296	
Banana	0.20	-0.258	0.665	0.387	
Cacao	-0.43	-0.717	-0.152	0.003	
Cacao and coffee	0.05	-0.737	0.841	0.897	
Citrus	-0.39	-1.281	0.499	0.390	
Coffee	-0.05	-0.198	0.098	0.509	
Maize	-2.65	-3.479	-1.820	< 0.001	
Mixed tropical crops	-0.39	-0.539	-0.247	< 0.001	
Oil palm	-1.23	-1.429	-1.030	< 0.001	
All other tropical crops	-0.98	-1.290	-0.675	< 0.001	
Rice	-0.67	-1.224	-0.118	0.017	
Sugarcane	-1.22	-1.610	-0.828	< 0.001	
Tea	-0.73	-1.155	-0.295	0.001	
Shading (Fig. 3b)					
Crops with some vegetation	-0.160	-0.674	0.354	0.542	
Shaded crops	-0.168	-0.290	-0.046	0.007	
Unshaded crops	-0.876	-0.987	-0.766	< 0.001	
Crop rotation time (Fig. 3c)					
Annual	-0.927	-1.132	-0.721	< 0.001	
Mixed	-0.121	-0.378	0.135	0.354	
Perennial	-0.605	-0.707	-0.504	< 0.001	
Unknown	-0.173	-0.525	0.179	0.334	
Taxonomic group (Fig. 3d)					
Birds	-0.841	-1.025	-0.656	< 0.001	
Fish	0.324	-0.551	1.199	0.468	
Herpetofauna	-0.756	-1.151	-0.360	< 0.001	
Invertebrates	-0.626	-0.735	-0.518	< 0.001	
Mammals	-0.109	-0.252	0.033	0.132	

Analysis	Mean Hedges' g	Lower 95% CI	Upper 95% CI	p	
Geographic region (Fig. 3e)					
Africa	-0.339	-0.503	-0.174	< 0.001	
Asia	-1.043	-1.213	-0.873	< 0.001	
Central America	-0.196	-0.345	-0.046	0.010	
Oceania	1.064	-2.950	5.079	0.603	
South America	-0.698	-0.862	-0.534	< 0.001	





895x764mm (72 x 72 DPI)