Plant biodiversity declines with increasing coffee yield in Ethiopia's coffee agroforests

Beyene Zewdie1 | Ayco J. M. Tack1 | Biruk Ayalew1 | Melaku Wondafrash2 | Sileshi Nemomissa2 | Kristoffer Hylander1

Abstract

1. Tropical agroforestry systems provide farmers with resources for their livelihoods, but are also well-recognized as refuges for biodiversity. However, the relationship between yield and biodiversity might be negative in these systems, reflecting a potential trade-off between managing for increased yield or biodiversity. The potential for synergies will depend partly on the shape of the biodiversity–yield relationship, where a concave relationship suggests a faster decline in biodiversity with increasing yields than a linear or convex shape.

2. We studied the relationship between biodiversity (plant species richness and composition) and coffee yield along a gradient of management in south-western Ethiopia, coffee’s native range. We inventoried species richness and community composition of woody plants, herbaceous plants and bryophytes at 60 sites. We also measured coffee management-related variables and assessed coffee yield for 3 consecutive years at each site.

3. Species richness of woody plants had a concave relationship with coffee yield, that is, tree richness declined fast initially before levelling out at higher yields, whereas there was no relationship between coffee yield and species richness of herbaceous plants or bryophytes. Species composition of woody plants, herbaceous plants and bryophytes all had a concave relationship with coffee yield.

4. From a methodological perspective, we found that multi-year data on yield were necessary to reliably assess the relationship between biodiversity and yield, and that the number of coffee shrubs or coffee dominance were poor proxies for yield when trying to capture the biodiversity–yield relationship.

5. Synthesis and applications. The concave relationship between biodiversity components (species richness and composition) and yield suggests that there is a strong conflict between the goals of increasing production and conserving biodiversity. However, it is important to recognize that this pattern is largely driven by the very low-yielding sites in natural forests. Here, even minor intensification of coffee management seems to rapidly erode biodiversity. Along the rest of...
INTRODUCTION

Sustainable resource use demand management of inevitable trade-offs that occur when one ecosystem service is enhanced at the expense of another, for example between provisioning and regulating ecosystem services (Deng et al., 2016; Inostroza et al., 2017). Dividing areas between conservation and production is one common strategy (see the land-sparing/land-sharing debate; Fischer et al., 2014). However, in most real-world situations, there is a need of simultaneously managing for both goals at the same place—protecting biodiversity, while still extracting provisioning services (MEA, 2005). A pattern of a negative relationship between regulating ecosystem services (e.g. biodiversity) and provisioning ecosystem services (e.g. yield) among a group of sites could be an indication that management for one property will trade off against the other property (Elmqvist et al., 2010). However, Elmqvist et al. (2010) proposed that this negative relationship could take different shapes: a concave, linear or convex relationship (Figure 1). If the relationship is convex, it suggests that it could be possible to somewhat increase the yield without losing substantial biodiversity, while if the relationship is concave, biodiversity values quickly erode with increasing yield (Elmqvist et al., 2010). Hence, a convex relationship offers more opportunities for conserving biodiversity, whereas a concave relationship indicates a strong conflict between the two goals already with little intensification. Thus, exploring the shape of such relationships is an important step in developing strategies and policies for sustainable future land use (Jiren et al., 2018; Steffan-Dewenter et al., 2007).

Tropical agroforestry systems, where crops are grown under a cover of shade trees (Schroth et al., 2004), are suggested as one promising approach for biodiversity conservation complementing strict forest protection, while simultaneously enhancing livelihoods of poor farmers (Bhagwat et al., 2008; Castle et al., 2021). For example, shade-grown coffee and cocoa can be associated with high levels of biodiversity (Perfecto et al., 2005; Tscharntke et al., 2011). However, trade-offs between biodiversity and productivity also exist in agroforestry systems (Bhagwat et al., 2008; Philpott & Dietsch, 2003, but see Clough et al., 2011 for several examples of less strong negative relationships between different biodiversity components and productivity in cocoa systems). For example, the total species richness of nine plant and animal taxa had a concave, nonlinear relationship with canopy cover in a cocoa agroforestry system in Indonesia (Steffan-Dewenter et al., 2007). It is likely that the relationship between regulating and provisioning ecosystem services will vary in different systems and for different biodiversity components investigated. As one example, Perfecto et al. (2003) found a concave relationship for the species richness of butterflies and a convex relationship for ants, whereas the species richness of birds did not change along a shade gradient in a Latin American coffee system. However, one should be careful when comparing studies since the management or yield gradient can be very different between studies, and that will affect the pattern of the relationships.

From a methodological perspective, most studies on the relationships between provisioning services and biodiversity components in agroforestry systems use indirect measures of provisioning ecosystem services (e.g. De Beenhouwer et al., 2013), and studies using actual yields are less common. Moreover, yield data from 1 year might not be informative, since the productivity of shade-grown crops such as coffee often shows a biennial pattern with alternating high and low yields (Bote & Jan, 2016), and there is also substantial inter-annual variation due to other environmental factors (DaMatta et al., 2008). Because of such fluctuations, it would be valuable to find good proxies for yield that could be used in analyses of the shape of biodiversity–productivity relationships when good yield data are missing.

**FIGURE 1** Hypothesized biodiversity–yield relationships, which all display a monotonic decline, but with different form of the curve. A concave curve (a) depicts a situation where low-yield sites have considerably lower biodiversity values with only slightly higher coffee yields, while a convex curve (c) suggests that intensification of coffee production from low to intermediate yields might have a small impact on biodiversity values (modified from Elmqvist et al., 2010)
In Ethiopia, the birth place of arabica coffee *Coffea arabica* (Tesfaye et al., 2014), coffee grows wild as an understorey shrub in the native forests while it is also cultivated across a broad management gradient, but exclusively under shade (Labouisse et al., 2008; Zewdie et al., 2020). This shade-based coffee production plays a positive role for biodiversity conservation by providing habitat complexity for many organisms (e.g. Buechley et al., 2015). Coffee management also has another positive role by reducing the rate of conversion of tree-covered habitats to open agricultural landscapes (Hylander et al., 2013). However, yields of the wild and semi-wild coffee in the forest habitats are extremely low due to low light levels, resulting in a growth form with few bearing shoots (Aerts et al., 2011; Schmitt et al., 2010). This leads the smallholder farmers to improve light conditions by thinning lower canopy shade trees and removing small shrubs and lianas, an activity that aims for coffee stems with larger crowns and a higher number of productive shoots (Aerts et al., 2011; Senbeta & Denich, 2006). With increasing management intensity, complex shade coffee systems become more simplified and dominated by a few preferred tree species (Geeraert et al., 2019). The negative relationship between biodiversity components and provisioning ecosystem services such as yield is likely to be true also in Ethiopia.

The general objective of this study was to describe the relationship between biodiversity components and coffee yield in a landscape where coffee management is economically very important, but yield still varies much along the broad management gradient from coffee grown with little or no management in the natural forest to more intensively managed plantations. More specifically, we tested the following two hypotheses:

1. Species richness of woody plants, herbaceous plants and bryophytes display a monotonic negative relationship with coffee yield.

2. Species composition of woody plants, herbaceous plants and bryophytes change monotonically with coffee yield.

For both of the hypotheses we explored if the relationships are concave (Figure 1a), linear (Figure 1b) or convex (Figure 1c). Moreover, we explored methodological challenges in establishing the relationships and discuss how to apply the results in practical conservation policy. To test these hypotheses, we inventoried woody plants (trees, shrubs and lianas), herbaceous plants (on the ground and epiphytic) and bryophytes (mosses and liverworts) at 60 coffee sites selected along a broad gradient of coffee management in south-western Ethiopia. We quantified coffee yield for 3 successive years in the same plots and measured a number of coffee management-related variables that could be used as a proxy for yield.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

We conducted this study in Gomma and Gera districts of Jimma zone, south-western Ethiopia (7°37′–7°56′N and 36°13′–36°39′E, Figure 2a,b). The area is characterized by a unimodal rainfall pattern with the main rainy season between May and September and the main dry season between December and March. The altitude of the area ranges between 1,506 and 2,159 m a.s.l. The mosaic landscape has a few large areas of weakly protected moist Afromontane forests (Friis et al., 2010), many small forest patches and open areas for annual crop agriculture. There are more areas with natural forests in the western than in the eastern part of the focal landscape (Koelemeijer et al., 2021). Coffee has a high social and cultural value for smallholder farmers and is the major cash crop in the area (Labouisse et al., 2008). In the larger intact forest areas, coffee management is minimal and farmers only pick ripe coffee berries and spices. In more managed sites, thinning of the upper canopy layer and regular removal of herbaceous vegetation is common (Aerts et al., 2011) and sometimes the famers also remove epiphytic vegetation from coffee shrubs (Hundera, Aerts, De Beenhouwer, et al., 2013). In the most intensively managed plantations, which are run by companies, regular management activities include pruning, weeding (or herbicide use) and fertilization. In the plantations, only a few shade tree species with desirable attributes such as *Albizia spp.*, *Acacia abyssinica* and *Milletia ferruginea* are used for coffee shade.

### 2.2 | Site selection and data collection

We made a preliminary site selection based on Google Earth images of the landscape and previous knowledge of the area. Then we visited numerous sites where we visually assessed the management intensity. We finally selected 60 coffee production sites representing a wide gradient of management ranging from little managed forest to the most intensively managed plantations while ensuring variation of management intensity across the whole study area. The sites are >1 km apart (with few exceptions) to avoid spatial autocorrelation and are likely forest-derived agroforestry (sensu Martin et al., 2020). At each site, we established a 50 × 50 m plot and further divided the plot into 10 × 10 m grid cells. We marked 16 coffee shrubs located closest to the intersections of the central 30 × 30 m grid cells (see Figure 2c). We quantified plant biodiversity during the rainy season, July–August 2018. We identified and counted all individuals of woody species (trees, shrubs and lianas) with DBH >20 cm in the 50 × 50 m plot; woody species with DBH <20 cm and height

**Figure 2** Study area and plot design. (a) Map of Ethiopia, with the study area in the south-western part marked with a rectangle. (b) An aerial view of the landscape with the 60 sites colour marked based on their management intensity (i.e. coffee structure index). The full circles represent sites with less to medium level of management and the triangles represent intensively managed plantations. (c) The layout of the individual plots, showing the 50 × 50 m plot and the 16 focal coffee shrubs. (d) Canopy cover and (e) site photographs taken along the gradient of management from left (less intensively managed forest coffee) to right (intensively managed plantations).
>1.5 m were identified and recorded as present/absent within the nine central 10 × 10 m quadrats; herbaceous plants, including both those on the ground and epiphytic species, were identified and assessed as dominant, frequent or rare in the central 30 × 30 m plot; and bryophytes (mosses and liverworts) were identified and ranked along a categorical scale reflecting abundance (see below) in the central 10 × 10 m quadrat. Species of vascular plants that could not be identified in the field were collected and identified using the Flora of Ethiopia and Eritrea at the National Herbarium of Ethiopia, Addis Ababa University (by MW). Bryophytes were collected from all major substrates and later identified at Stockholm University (by KH). See Appendix S1 in supporting information for more details on how the different species groups were assessed.

At each of the 60 sites, we recorded (a) coffee density as a count of coffee shrubs >1.5 m in the central 30 × 30 m plot that could be hypothesized to reflect a gradient from low intensity with few shrubs to highly managed sites with many shrubs; (b) coffee dominance as the proportion of coffee shrubs to all woody shrubs in the 30 × 30 m plot, that might reflect a management intensity gradient where farmers remove competing wild shrubs in more managed sites (see also Shumi et al., 2019); and (c) coffee structure index. The coffee structure index was created based on five attributes measured on each of the 16 coffee shrubs per site (see Appendix S2 and Figure S4). This index reflects the variation in coffee shrub architecture that results from variation in management and ranges from 1 (coffee with little or no management) to 3 (intensively managed coffee; see also Zewdie et al., 2020 for the details of how this index was created).

2.3 Coffee yield assessment

We assessed coffee yield on the 16 coffee shrubs in each of the 60 sites during the wet season from July to August, when the coffee berries were at the expansion stage towards maturity, for 3 consecutive years (2017–2019). On each shrub, we first visually assessed the berry-bearing status of each branch and selected three representative plagiotropic shoots (horizontal, fruit-bearing branches) and counted the number of healthy berries (i.e. excluding berries with signs of coffee berry disease or coffee berry moth attacks). Next, we counted the total number of plagiotropic shoots with berries on the shrub and multiplied the mean of the three branches with this value to get an estimate of the total number of berries per shrub. To avoid the risk of overestimation of total yield (since the multiplication at the shrub level sometimes yielded unrealistically high values), we used the median of the estimated berry yield of the 16 coffee shrubs (instead of the average). We then multiplied that with the average coffee yield as explanatory variable. As biodiversity–yield relationships might be nonlinear (Figure 1), we used GAMs with a smoothing parameter. In these models, we used a Gaussian distribution with identity link, and estimated the smoothing parameter with restricted maximum likelihood (REML) using the gam function in the r package mgcv (Wood, 2018).

To explore if the species composition of the different plant groups was related to coffee yield, we performed canonical redundancy analyses (RDAs) for each of the four species-by-site matrices as response variables and average coffee yield (averaged for the 3 years) as the explanatory variable. As biodiversity–yield relationships might be nonlinear, we fitted a GAM with the site scores extracted from the RDA models (first RDA axis of each species group) as response variable and average coffee yield as explanatory variable.

To determine if the frequency of occurrence of the three plant species groups (woody species, herbaceous plants and bryophytes) differed between the two yield categories, that is, low- (<1,000 kg/ha) or high-yielding (>1,000 kg/ha) sites, we performed a Chi-square goodness-of-fit test on the frequency distribution of the species groups belonging to the two yield categories.

To test whether sites with high yield in one year also had a high yield in other years, we performed Spearman’s rank correlation test between the site level coffee yield data for the 3 consecutive years. To assess if the biodiversity–yield relationships were consistent...
between the 3 years, we ran separate models for each year for both richness and composition following the same protocol as explained above for average coffee yield.

Furthermore, we explored the possibility of capturing the yield variation among sites with management-related proxies (coffee density, coffee dominance and coffee structure index). We performed Pearson's product-moment correlation tests between these proxies and average coffee yield. For the best proxy, we then ran the same analyses for richness and composition as for the average yield, as explained above. We implemented all statistical analyses in the R software v3.6.1 (R Core Team, 2019).

3 | RESULTS

3.1 | The relationship between plant species richness and coffee yield

We found a total of 407 plant species, including 71 woody plant species, 243 herbaceous plant species and 93 bryophytes in the 60 coffee sites (Table S1). As expected, the relationship between species richness of woody plants and coffee yield was negative. The shape of this negative relationship was concave, with a steep initial decline in species richness with increasing yields up to a. 750 kg/ha after which it levelled off ($R^2 = 0.30, p < 0.001$; Figure 3a; Table S2). There were no significant relationships between species richness of herbaceous plants or bryophytes and average coffee yield ($p = 0.12$ and $p = 0.75$ respectively; Figure 3b,c; Table S2). The relationship between all species richness and coffee yield mirrored the relationship between woody species and coffee yield, but was only marginally significant ($R^2 = 0.08, p = 0.06$; Figure 3d; Table S2).

In the two low-yield years (2017 and 2019; see Appendix S3: Table S5; Figure S1a), there were significant negative relationships between woody species richness and coffee yield ($R^2 \geq 0.05, p \leq 0.045$; Figure S1b,d; Table S2), but no relationship was detected in the year with high yield (2018; $p = 0.13$; Figure S1c; Table S2).

3.2 | The relationship between species composition and coffee yield

The species composition for all species groups changed significantly along the yield gradient ($R^2 \geq 0.16, p = 0.013$; Figure 4; Tables S3 and S4). The pattern was similar to species richness of woody plants with a fast turnover when yields increased from low to medium levels, but with a similar composition in sites with medium and high yield levels (Figure 4).

Species composition of all species groups changed significantly along the yield gradient in all 3 years, when analysed separately ($R^2 \geq 0.18, p \leq 0.005$; Tables S7 and S8).

Of the total number of woody species, 69% had their optimum in the low-yielding sites (≤1000 kg/ha), while among the herbaceous species 59% had their optimum in the low-yielding sites (Figure S2). The different bryophyte species on the other hand had their optimum nearly equally distributed, with 47% in the low-yielding and 53% in the high-yielding sites (Figure S2). The frequency distribution of the occurrences of the three species groups differed between the two yield categories ($\chi^2 = 7.89, df = 2, p = 0.019$; Figure S2).

3.3 | Using proxies for yield when analysing biodiversity–yield relationships

When we ran all models of species richness and species composition with the coffee structure index as the explanatory variable, we obtained the same general results as to when we used average yield (cf. Figure 3a vs Figure S3b; Figure 4c–d vs Figure S3c–d; Tables S9–S11), except that the relationship was linear and not concave for herbaceous species.

4 | DISCUSSION

We took advantage of a unique landscape with a broad coffee management gradient to explore the shape of the biodiversity–yield relationship for a number of plant groups. We found that tree species richness declined with increasing coffee yield, confirming our first hypothesis of a negative relationship, while richness of herbaceous plants and bryophytes did not decline with increasing yields. Yet, the species composition, not only of woody plants but all groups, changed along the yield gradient. All significant relationships showed a concave pattern with a sharp initial decline as yield increased and then a levelling off with even higher yields. From a methodological perspective, we found that yields were not consistent between years but that coffee structure index could well represent yield in models of biodiversity–yield trade-offs. The finding of an initial fast decline in biodiversity values with increasing coffee yield indicates that the very low-yielding forest sites are driving much of these patterns. This fact needs to be acknowledged both in terms of management implications in the Ethiopian context and when comparing these results with studies along management gradients in other parts of the world.

4.1 | Relationships between plant biodiversity components and coffee yield

Our observations show that there is a strong negative relationship between biodiversity and yield with a clear concave shape of the curve. Similar patterns have also been documented for coffee in other coffee-growing regions (Jha et al., 2014; Perfecto et al., 2005) and from cocoa agroforestry systems (Somarriba et al., 2013; Steffan-Dewenter et al., 2007), even if the gradients in these studies might have been less broad. The main reason seems to be that both coffee and cocoa, although being shade-tolerant plants, have a higher production under a thinned canopy (Beer et al., 1998; Somarriba et al., 2013). However, there are some studies showing
that it is possible to maximize biodiversity values without much effect on yield (Clough et al., 2011; Jezeer et al., 2019). It is important to point out that our study encompasses a very broad management gradient, and perhaps the relationship would have been less pronounced if the extreme end of the gradient (coffee growing with little or no management in the forests) would not have been included.

Our findings revealed that for species richness the negative relationship between biodiversity and coffee yield was much stronger for woody species than for herbaceous plants and bryophytes. The low-yield end of the gradient is characterized by little management where the rich diversity of woody species is maintained despite a high density of coffee in the understorey, similar to other landscapes in SW Ethiopia (Schmitt et al., 2010). This contrasts with the more intensively managed sites, which are characterized by a lower tree density and diversity. The low yield of coffee under dense canopies of shade trees is the reason that smallholder farmers gradually reduce the canopy of shade trees, and not least the mid-canopy trees and shrubs that directly compete with coffee for space (Aerts et al., 2011; Hundera, Aerts, Fontaine, et al., 2013). From a landscape perspective, the high diversity of woody species in the low-yield end of the gradient might be maintained also by landscape processes such as dispersal of seeds from the surrounding larger forest areas (Koelemeijer et al., 2021), suggesting that extinction debts are likely in places where the connectivity to continuous forest is broken (Hylander & Nemomissa, 2017).

While the composition of herbs and bryophytes changed—just like woody species richness—in a concave fashion along the yield gradient, the species richness of herbs and bryophytes did not decline along the yield gradient. Apparently, there were also many herbaceous and bryophyte species that were favoured by a more open canopy, counterbalancing the decline in the species adapted to denser shade in the low-yield end of the gradient. Thus, coffee sites with high yield still are rather species rich for these groups and contribute to biodiversity values in the landscape (Hylander & Nemomissa, 2008, 2009). That different groups can have different sensitivity to intensification has also been shown in some other studies. Steffan-Dewenter et al. (2007) demonstrated that plants were more affected than mobile species such as insects in a study of conversion from forest to cocoa agroforest in Indonesia and a study in Mexico showed that ants were less affected by intensification than butterflies (Perfecto et al., 2003). A subset of our biodiversity values is directly affected by management (e.g. slashing, removal of bryophytes from stems, thinning of canopy and removal of lianas), in contrast to other biodiversity components, such as butterflies and birds, which are always only indirectly affected by management.

![Figure 3](image-url)
4.2 | The relationship between biodiversity and yield for individual years and the search for a proxy for yield

While many studies on biodiversity–yield relationships use yield from a single year, our findings illustrate that single-year data did not consistently reveal the concave relationship between biodiversity and yield. Apparently, some sites have consistently low or high yields, while others display a strong tendency for a biennial pattern, but not necessarily with the same good and bad years. Such variability can be caused by many factors such as stress from heavy bearing during the previous year (DaMatta et al., 2008) and pest and disease damage (Cerda et al., 2017), which is outside the scope of this paper to examine. Irrespective of the cause, together these patterns lead to a changed rank order of productivity between sites in different years. It is thus not so easy to establish the gradient in yield to be used alongside the biodiversity data since it is necessary to have several years of yield data. Among the management variables that we suggested as possible proxies for yield, the coffee structure index did well represent the different biodiversity–yield relationships, even if coffee structure index only explained 30% of the variation in average yield (see Appendix S3). The reason why this index seemed to capture relevant aspects of the yield variation might be that the architecture of the coffee shrub is closely related to the number of fruit-bearing branches. One could argue that the value of the coffee structure index as a proxy for yield is questionable given the large amount of labour needed to establish it, but as a major advantage, it can be recorded within a single survey, and there is no need for multi-year yield data. However, the easy-to-assess proxies such as coffee dominance and coffee density can unfortunately not be used to predict plant biodiversity components in our study system.

4.3 | Implications for management

The concave nonlinear relationships between biodiversity values and yield in our data suggest that there is a strong conflict between the goals of improved production and biodiversity conservation. However, this pattern is due to the very rich biodiversity in sites with little or no management. If both the goals of conservation of biodiversity and improving yields are targeted, the most logical solution is to plan for different goals at different localities in the landscape,

FIGURE 4 The relationship between species composition and coffee yield for (a) woody species, (b) herbaceous species, (c) bryophytes and (d) all species. Ordination scores form an RDA of the respective species group shown as a function of average coffee yield. The scores should only be compared relative to each other in each graph, illustrating the similarity. Each dot represents an average of 3 years of coffee yield (kg/ha) for each of the 60 sites. Regression slopes with 95% confidence interval from a GAM are shown with solid trend lines for the significant relationships (see Table S4)
that is, a classical land-sparing approach (Phalan et al., 2011). This can be achieved by strict protection of the forest sites with little or no management, while the management is intensified in the other sites to close the yield gap. Besides biodiversity values such as the diversity of animals (Berecha et al., 2014; Samnegård et al., 2014), plants (Schmitt et al., 2010) and beneficial micro-organisms (Zewdie et al., 2021), these forests also harbour highly valued wild coffee genetic resources (Aerts et al., 2013). Also, from this perspective, the land-sparing approach should be advocated, whereby the intact forest areas would need a more strict protection for in situ conservation of coffee genetic resources (Aerts et al., 2015), while the other parts of the landscape perhaps can be more intensively managed to improve livelihoods.

In this paper we have examined biodiversity–yield relationships. However, what matters for a smallholder farmer might not be the yield alone, but the revenue (Mitiku et al., 2021). In our landscape, farmers often get a profit from the little managed sites through periodic harvesting of other resources such as spices, honey or firewood (Ango et al., 2014), which causes little or no damage to the system, while using their labour for other tasks than management to improve coffee yields. From such a perspective, the optimum strategy for a farmer might not be to have the highest possible yield. That might create an opportunity for having dual goals also for the forest sites (i.e. land-sharing) instead of the classical land sparing, that at a first glance would seem the most logical (see above). In the light of this, coffee certification with a payment of premium prices might further improve the revenue of farmers and thus be used to promote biodiversity-friendly coffee production (Mitiku et al., 2018; Perfecto et al., 2005). Yet, paradoxically, there is a concern that certification of the little managed forest areas could incentivize farmers to slowly intensify and simplify the remaining forests for coffee production (Geeraert et al., 2019; Gove et al., 2008; Tadesse et al., 2014). While much of the current conservation effort focuses on sites that are still natural, we suggest it may be worthwhile to design conservation strategies to maintain or enhance biodiversity values also in the more intensively managed sites. In agreement with this, we also found that many herbaceous and bryophyte species occurred in the more productive sites. Increasing biodiversity in more intensively managed sites could be possible through, for example, diversifying the shade tree species without much change in the amount of shade they provide.

While most studies compared either sites with low to medium management or medium to intensive management, our study is quite unique in that we focused on a broad management gradient ranging from more or less wild forest coffee with little or no management to intensively managed plantations. Despite the seemingly strong biodiversity–yield trade-offs when comparing sites with low and medium management, it also highlights that management intensification might have no negative consequences for biodiversity for sites with intermediate yields. Finally, we emphasize that it is important to take a landscape perspective when developing policy for biodiversity conservation. In such approaches it is important to acknowledge that sites with shade coffee are generally considered to provide a refuge for biodiversity, especially when compared with the alternative of deforestation for annual crop production (Buechley et al., 2015; Hylander et al., 2013). Moreover, the presence of coffee in the edges of the larger forest areas seems to protect the interior from deforestation, since the additional economic value from coffee outweighs problems from, for example, raiding animals that is a major obstacle associated with farming close to forests. In fact, at altitudes above where coffee can grow, large areas have been converted to annual crops, illustrating the positive role that coffee production can have at the landscape scale (Ango et al., 2020; Hylander et al., 2013). Thus, certification programs at the landscape scale that target both low and highly productive sites could have a potential to enhance the overall biodiversity of the area (Tscharntke et al., 2011, 2015). Although there is an inherent conflict between biodiversity conservation and increasing productivity at the low-yielding end of this unique gradient, there are still important arguments that coffee production has a positive implication for biodiversity at a landscape scale. The results from this and other similar studies are important to take into account when simultaneously targeting biodiversity conservation and smallholder farmers’ aspirations to improve their livelihoods.

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CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

AUTHORS’ CONTRIBUTIONS
B.Z., A.J.M.T., S.N. and K.H. conceived and designed the experiment; B.Z., B.A. and M.W. conducted the fieldwork; B.Z. analysed the data and wrote the first draft, and all authors contributed to the final manuscript.

DATA AVAILABILITY STATEMENT
Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.w0vt4b8t8 (Zewdie et al., 2022).

ORCID
Beyene Zewdie https://orcid.org/0000-0002-6020-916X
Ayco J. M. Tack https://orcid.org/0000-0002-3550-1070
Kristoffer Hylander https://orcid.org/0000-0002-1215-2648

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