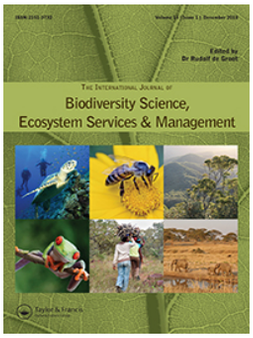


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REVIEW

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# Contribution of trees to the conservation of biodiversity and ecosystem services in agricultural landscapes

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**ABSTRACT**
The production of sufficient food for an increasing global population while conserving natural capital is a major challenge to humanity. Tree-mediated ecosystem services are recognized as key features of more sustainable agroecosystems but the strategic management of tree attributes for ecosystem service provision is poorly understood. Six agroforestry and tree cover transition studies, spanning tropical/subtropical forest zones in three continents, were synthesized to assess the contribution of tree cover to the conservation of biodiversity and ecosystem services. Loss of native earthworm populations resulted in 76% lower soil macroporosity when shade trees were absent in coffee agriculture. Increased tree cover contributed to 53% increase in tea crop yield, maintained 93% of crop pollinators found in the natural forest and, in combination with nearby forest fragments, contributed to as much as 86% lower incidence for coffee berry borer. In certain contexts, shade trees contributed to negative effects resulting from increases in abundance of white stem borer and lacebugs and resulted in 60% reduction of endangered tree species compared to forest. Managing trees for ecosystem services requires understanding which tree species to include and how to manage them for different socio-ecological contexts. This knowledge needs to be shared and translated into viable options with farming communities.

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## 1. Introduction

Agriculture is the most prevalent of the human–environment interaction and consumes more natural resources than any other human activity (FAO 2007). This has raised concerns about natural resource management trajectories as they relate to planetary boundaries and land degradation tipping points (Rockström et al. 2009). Conventional agriculture in the last century led to a dramatic increase in crop yields largely as a result of the introduction of new high-yielding crop varieties, the use of mineral fertilizers, chemical pesticides, mechanization and the expansion of irrigation infrastructure (Foley et al. 2005). While agriculture that overcomes production constraints through external inputs has been one way to increase yields per hectare, these agricultural systems have often resulted in negative economic and environmental side effects in part due to their low resource-use efficiency and negative impacts on biodiversity (Matson et al. 1997). Therefore, in recent years, increasing attention on productive agricultural systems that are resource-use efficient has placed biodiversity at the center-stage of discussions on agricultural intensification (Brussaard et al. 2010; Snapp et al. 2010; Barrios et al. 2015; Prabhu et al. 2015).

The valuable contribution of trees to more ecological forms of agricultural intensification has been increasingly highlighted in the literature (Schroth et al. 2004; Pretty et al. 2006; Tscharntke et al. 2012a). Ecological intensification can be defined as generating more output from the same area of land while reducing the negative environmental impacts by decreasing the reliance on anthropogenic inputs through the management of regulating and supporting ecosystem services in agricultural practices (Bommarco et al. 2013). Further, it also recognizes the valuable contribution of farmer's knowledge to the generation of technologies better adapted to context variation (Tittonell 2014). Agroforestry, broadly defined as the integration of trees and agriculture, has been increasingly recognized as a multifunctional land management option that can simultaneously contribute to income, food security and conservation of biodiversity and ecosystem services (Bhagwat et al. 2008; Tscharntke et al. 2011; Kuyah et al. 2016). Trade-offs among these potential benefits to rural

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communities, however, are common as it is well recognized that agroforestry trees can negatively influence crop production and income if not properly selected and managed due to competitive effects for light, water and nutrients (Beer et al. 1998; Ong et al. 2004; Steffan-Dewenter et al. 2007; Kuyah et al. 2016). Nonetheless, if we consider tree cover on agricultural land greater than 10% as agroforestry, this land use would represent over 1 billion ha of land inhabited by 900 million people (Zomer et al. 2016) and hence of significant importance to the agriculture sector. Recent concern, however, has been raised about the global decline in shade tree cover particularly in coffee agroecosystems and the potential implications for biodiversity, ecosystem services and livelihoods (Jha et al. 2014).

Biodiversity responsible for key ecological functions that provide benefits to society (i.e. ecosystem services) is a key component of agricultural sustainability strategies (Kremen 2005; Balvanera et al. 2006; Barrios 2007). Biodiversity in agricultural landscapes can be broadly separated into the better studied, visible aboveground biodiversity, which may be directly or indirectly managed by farmers like plants (e.g. shade trees) and insects with bio-control and pollination functions (e.g. parasitoid wasps, bees), and the less-studied, largely invisible and mostly unmanaged soil biodiversity contributing to soil health (Swift et al. 2004; Wall et al. 2010). Soil health is considered here as an integrative property that expresses the capacity of soil to respond to agricultural management where both agricultural production and the provision of other soil-mediated ecosystem services are maintained (Kibblewhite et al. 2008). The complexity of interactions between soil biodiversity and ecological functions underpinning soil health requires a focused approach on sets of soil organisms playing major roles (Beare et al. 1995; Barrios 2007). Efforts in this direction show that soil organisms can be grouped into four key functional assemblages: (1) decomposers, (2) nutrient transformers, (3) ecosystem engineers and (4) biocontrollers, each composed of several functional groups which contribute to four key aggregated ecosystem functions, namely carbon transformations, nutrient cycling, soil structure maintenance and population regulation, respectively, which, through a variety of soil-based delivery processes, generate and sustain soil health (Kibblewhite et al. 2008; Barrios et al. 2012). Trees in agricultural landscapes can provide more favorable habitats for soil biodiversity, through microclimate buffering and continuous supply of organic matter inputs, thus fostering 'hot spots' of biological activity responsible for many ecological functions underpinning soil health (Pauli et al. 2010; Ushio et al. 2010; Diedhiou-Sall et al. 2013; Kamau et al. 2017). Increased tree cover often, but not always, also reduces pest pressures and improves pollination services (Ricketts et al. 2004; Pumariño et al. 2015).

Agricultural landscapes, where agroforestry cover is significant, represent intermediate levels of complexity presumably most effective for the conservation of biodiversity and ecosystem services, yet also contributing to more resilient rural livelihoods (Schroth et al. 2004; Tscharntke et al. 2012b; Prabhu et al. 2015; Balvanera et al. 2016). In this paper, the contribution of trees to the conservation of biodiversity and ecological functions underpinning selected ecosystem services was evaluated across dominant land uses in agricultural landscapes representing different levels of tree cover (Figure 1).

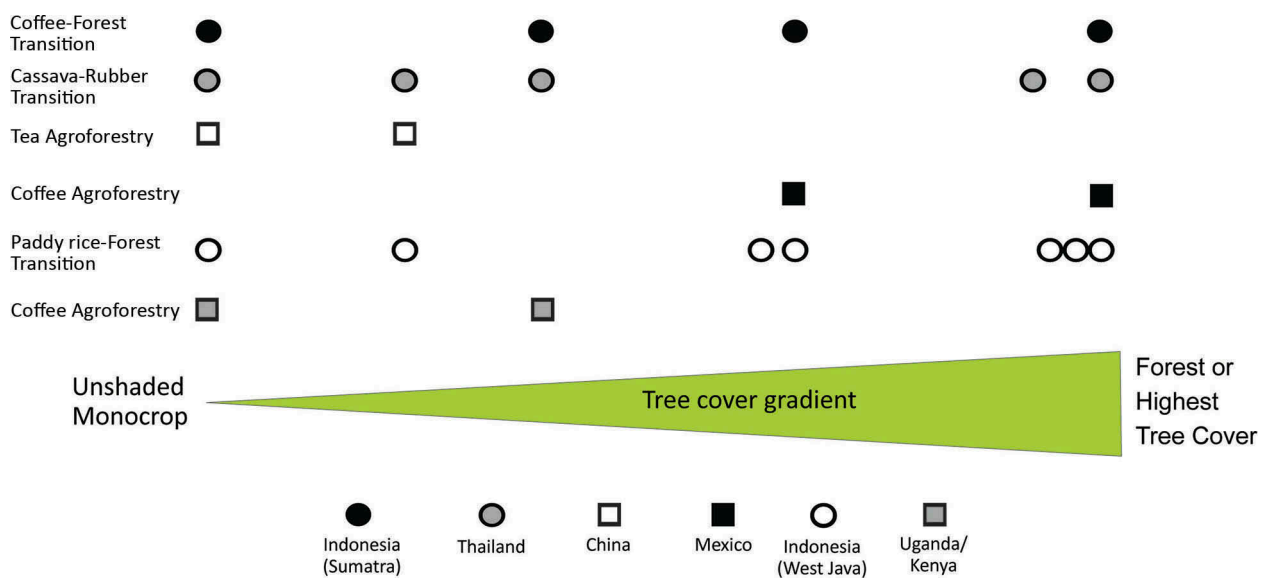


**Figure 1.** Approximate tree cover of dominant land uses in agricultural landscapes studied where each symbol represents a study site.

The objectives were to (1) assess the effects of changes in tree cover (e.g. presence/absence, density, diversity and functional traits) on belowground and aboveground biodiversity; (2) assess the effect of increasing tree cover on ecological functions of belowground organisms underpinning soil health and crop yield; (3) assess the effect of increasing tree cover on ecological functions of aboveground organisms underpinning habitat provision, pollination and biological control services and (4) examine the value of agroforestry as a biodiversity-based intervention contributing to more sustainable trajectories of agricultural intensification.

## 2. Approach and methods

We examined six study sites that investigated the impact of changing tree cover on biodiversity and ecosystem services in different agricultural landscapes (Table 1). We selected study sites occurring in areas described as biodiversity 'hotspots' (Myers et al. 2000) where agricultural expansion is threatening natural capital.

Agroecosystems studied included coffeeof differences in soil nutritional agroforestry, tea agroforestry and three agricultural landscapes in transition that resulted in tree presence/absence or tree cover gradients which presumably influence the belowground or aboveground biodiversity and associated ecosystem functions and services. Shade coffee agroforestry constitutes an intermediate intensification stage, and hence of tree cover, between the native forest and coffee monoculture that was a common feature in Mexico and Kenya–Uganda study sites (Figure 1). The tea agroforestry included the N-fixing tree, *Alnus nepalensis* D. Don, as companion tree to the otherwise monoculture tea plantations in southwestern China. The transitions from forest to unshaded coffee monocrop in Indonesia (Sumatra), from cassava monocrop to tree-based agroecosystems involving rubber in Thailand and from forest to paddy rice agriculture in Indonesia (West Java) generate decreasing and increasing tree cover gradients scenarios (Figure 1). All case studies provide different socio-ecological contexts in which to examine the effect of tree cover on biodiversity trends and selected ecosystem services aiming to contribute to generalizations on the role of agroforestry as a biodiversity-based intervention for ecological intensification of agriculture. Nevertheless, we do not address socio-economic dimensions in any detail. While farmers and the number of factors that influence their decisions are inherent to any agricultural intervention, we recognize that any principles proposed for agroecosystem management in addition to scientific validity must also be relevant and feasible. In order to compare different agroecosystems studied on a common basis, percent change in mean biodiversity measure or ecological process was calculated using the following formulae: [(monocrop − forest)/forest] × 100 and [(agroforestry − forest)/forest)] × 100. The forest was considered the baseline as it is the natural system and other agroecosystems were considered relative to it. In case forest was not part of land uses studied in a particular agricultural landscape, the land use of highest tree cover was used as a reference.

## 3. Results

### 3.1. Case studies

Land uses evaluated included dominant land-cover scenarios useful to comparatively assess the effects of trees on both belowground and aboveground biodiversity (Table 2). While unshaded monocrop/shaded agroforestry allowed the assessment of shade-tree absence/presence scenarios, respectively, the monocrop to forest/mature plantation transitions allowed examining a more gradual variation in tree cover. When considering natural forest as the baseline, and other systems relative to it, negative percent values are expected resulting from a loss in ecological function relative to forest when converted to agriculture (Table 2). Biodiversity-based interventions such as agroforestry would presumably cause less negative effects than monoculture because they can generate agricultural production while maintaining more biodiversity and ecological functions. Further, positive values would highlight additional virtues of agroforestry.

#### 3.1.1. Linking trees, belowground biodiversity and ecosystem services

The perennial nature of trees in agroforestry systems profoundly impacts microclimate and soil properties. By positively influencing the abundance, diversity and activity of soil biota, trees in agroforestry systems contribute to soil health and functional resilience (Barrios et al. 2012). In this section, we examine the impact of tree cover in coffee monocrop – forest transition on native earthworm populations influencing soil physical properties and water dynamics; the influence of canopy closure on the abundance and diversity of soil macrofauna in a cassava monocrop/agroforestry/rubber plantation transition; and the contribution of N-fixing trees to soil microbial biomass, diversity and crop yield in tea agroforestry.

*3.1.1.1. Coffee agroforestry transition in Indonesia (Sumatra).* Forest conversion to monoculture coffee systems in Sumatra (Indonesia) significantly affected the abundance and diversity of native earthworm populations and influenced soil physical properties (Hairiah et al. 2006). Four relatively large-bodied native earthworms were lost upon forest conversion to coffee agriculture (Figure S1, Table 2): (1) *Metaphire* sp. 1 (epigeic = feed on and live in the litter layer), (2) *Metaphire* sp. 2 (epigeic), (3) *Metaphire javanica* group

**Table 1.** General characteristics of study sites.

| Study site | Native vegetation types | Agroecosystem | Land uses | Altitude | Rainfall | Biodiversity emphasis | Ecosystem services |
|---|---|---|---|---|---|---|---|
| **Geographical location** | | | | (m a.s.l.) | (mm) | | |
| Lampung, Sumatra, Indonesia Lat. 5°01′–5°02′ S, Long. 104°26′–104°27′E | Tropical dipterocarp rainforest | Coffee agroforestry | Forest, coffee-based multistrata agroforestry, coffee agroforestry (*Gliricidia sepium* dominated), unshaded coffee monoculture | 600–1718 | 2614 | Soil macrofauna | Soil biodiversity conservation, soil water infiltration and storage |
| Chachoengsao – central Thailand Lat. 13°35′′N, Long. 101°28′E | Tropical dry dipterocarp forest | Cassava monocrop transition to rubber plantation | Unshaded cassava monocrop, intercropping + young rubber, mature rubber plantation | 70 | 1200 | Soil macrofauna | Soil biodiversity conservation |
| Changning county, Yunnan Province, China Lat. 24°47′ 34″–24°48′51″N, Long. 99° 35′35″–99°35′44″E | Subtropical evergreen broad-leaved forest | Tea agroforestry | Tea monocrop, tea agroforestry (*Alnus nepalensis* dominated) | 1728 | 1268 | Soil microoorganisms | Soil biodiversity conservation, soil nutrient availability, tea yield |
| La Sepultura Biosphere Reserve, Chiapas, Mexico Lat. 16°00′18″–16°29′01″N, Long. 93°24′34″–94°07′35″ W | Tropical deciduous forest | Coffee agroforestry | Coffee agroforestry (*Inga* spp. dominated), forest | 1100–1500 | 2000–2500 | Endangered tree species | Tree biodiversity conservation |
| West Java, Indonesia Lat. 06° 45′28″–06°47′53″S, Long. 107°04′18″–107°07′39″E | Tropical dipterocarp rainforest | Forest-agriculture transition | Forest, broad-leaved plantation, needle-leaved plantation, mixed-tree agroforestry, bamboo-dominated agroforestry, upland agriculture, unshaded paddy-rice monoculture | 600–1300 | 2000 | Insect pollinators | Pollination |
| East African Highlands, Uganda and Kenya Soono (Lat. 00°51′N, Long. 34° 25′E), Matokota (Lat. 00° 52′N, Long. 34°25′E) and Majanja (Lat. 00°52′N, Long. 34°26′E) in Bumbo subcounty in Manafwa District, Uganda Lat. 0° 57′–1°00′N, Long. 35°04′–35°09′E, Kitale District, Kenya | Tropical deciduous forest | Coffee agroforestry | Unshaded coffee monoculture, coffee agroforestry (diverse shade tree species) | Uganda: 1511–1840; Kenya: 1824–1992 | Uganda: 1500 Kenya: 1250 | Coffee pests | Biological population regulation |

**Table 2.** Effects of changes in tree cover on biodiversity and biological processes studied in dominant land uses across six agricultural landscapes (designs with sample sizes are summarized in Table 1S).

| Study site | Biodiversity or biological process measured (units) | Tree cover gradient: No tree cover | | | | Highest tree cover | Monocrop % change relative to highest tree cover | Agroforestry % change relative to highest tree cover |
|---|---|---|---|---|---|---|---|---|
| | | Coffee monocrop | Shaded coffee | | Mutistrata | Remnant forest | | |
| Coffee monocrop–forest transition Lampung, Sumatra, Indonesia | Native earthworm species (individuals $m^{-2}$) | 0 | nd | | 0 | 32 | −100% | −100% |
| | Exotic invasive species (individuals $m^{-2}$) | 463 | nd | | 351 | 0 | 100% | 100% |
| | Annual litterfall (Mg $ha^{-1}$ $year^{-1}$) | 4 | 6.6 | | 9.8 | 14 | −71% | −41% |
| | Standing litter (Mg $ha^{-1}$ $year^{-1}$) | 1.2 | 1.2 | | 1.8 | 2.1 | −43% | −29% |
| | Soil macroporosity (%) | 3 | 3.5 | | 3.6 | 12.3 | −76% | −71% |
| | | Cassava monocrop | Rubber agroforestry (1–3 years) | Rubber agroforestry (4–6 years) | Rubber (8–12 years) | Rubber (23-25 years) | | |
| Cassava monocrop transition to rubber plantation Chachoengsao, Central Thailand | Earthworm abundance (individuals $m^{-2}$) | 10.7 | 13.3 | 2.7 | 112 | 133.3 | −91% | −93% |
| | Termite abundance (individuals $m^{-2}$) | 10.7 | 2.7 | 0 | 80 | 32 | −81% | −98% |
| | Ant abundance (individuals $m^{-2}$) | 145.3 | 66.7 | 34.7 | 21.3 | 45.3 | 336% | 52% |
| | Total soil macrofauna biomass (g $m^{-2}$) | 2.2 | 1.3 | 0.8 | 7.5 | 10.4 | −75% | −89% |
| | | Tea monocrop | Tea agroforestry | | | | | |
| Tea agroforestry Changning county, Yunnan Province, China | Soil microbial biomass (Actinomycetes PLFAs) (nmol g $soil^{-1}$) | 5.1 | 7.4 | | | | −31% | |
| | Soil microbial biomass (Bacteria PLFAs) (nmol g $soil^{-1}$) | 51.3 | 67.0 | | | | −23% | |
| | Soil microbial biomass (fungi PLFAs) (nmol g $soil^{-1}$) | 6.3 | 8.0 | | | | −21% | |
| | Crop production (Mg $ha^{-1}$) | 249.2 | 466.7 | | | | −47% | |

(*Continued*)

**Table 2.** (Continued).

| Study site | Biodiversity or biological process measured (units) | Tree cover gradient: No tree cover | | | | | | Highest tree cover | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Shaded coffee | | | | Forest | | |
| Coffee agroforestry La Sepultura Biosphere Reserve, Chiapas, Mexico | Relative abundance of trees of conservation concern (% presence) | | | 10 | | | | 25 | | –60% |
| | Relative abundance of pioneer tree species (% presence) | | | 72 | | | | 29 | | 148% |
| | Relative abundance of *Inga* spp. (% presence) | | | 49 | | | | 10 | | 390% |
| | | Paddy (P) | Upland (U) | Bamboo-dominated agroforestry (BT) | Agroforestry (MT) | Needle-leaf plantation (NP) | Broadleaf plantation (BP) | Forest (F) | | |
| Paddy rice – forest transition West Java, Indonesia | Total insect pollinators – richness (number of species collected in 24 h) | 6 | 5 | 5 | 7 | 6 | 6 | 7 | –14% | 0% |
| | Efficient insect pollinators – richness | 4 | 3 | 4 | 5 | 4 | 4 | 6.5 | –38% | –23% |
| | Less efficient insect pollinators – richness | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 0% | 100% |
| | Total insect pollinators – abundance (individuals collected in 24 h) | 12 | 10 | 9 | 14 | 11 | 11 | 15 | –20% | –7% |
| | Efficient insect pollinators – abundance | 10 | 8 | 6 | 11 | 7 | 6 | 13 | –23% | –15% |
| | Less efficient insect pollinators – abundance | 2 | 2 | 2 | 4 | 4 | 3.5 | 1 | 100% | 300% |
| | | Unshaded coffee | | Shaded coffee | | | | | | |
| Coffeee agroforestry East African Highlands, Uganda | White stem borer (% coffee trunks infested) | 22 | | 72 | | | | | –69% | |
| | Coffee berry borer (% coffee berries infested) | 8 | | 5.5 | | | | | 45% | |
| Coffeee agroforestry East African Highlands, Kenya | Lacebugs (individuals per 240 leaves) | 2 | | 14 | | | | | –86% | |

(anecic = feed on litter layer and mix it with soil, and make vertical burrows) and (4) *Megascolex* sp. (endogeic = feed on and live in the soil) were completely replaced by six exotic and smaller bodied earthworms, dominated by the invasive exotic *Pontoscolex corethrurus* (endogeic) (Dewi et al. 2006; Dewi and Senge 2015).

The lower mean body size, and dominance of endogeic earthworms, in agroecosystems compared to natural forest resulted in 71–76% lower soil macroporosity (Table 2). The conversion of forest to agriculture also resulted in 71% and 43% reduction in annual litterfall and standing litter respectively in coffee monocrops which compared to lower reductions in coffee agroforestry (e.g. 41% and 29%) (Table 2). These observations suggest that encouraging land uses and management that maintain litter inputs and conserve native earthworm vertical burrowing activity could contribute to positive changes in soil macroporosity that can increase infiltration and reduce run-off and soil erosion (Hairiah et al. 2006). Nevertheless, there was some evidence that organic inputs from *Gliricidia sepium* shade trees may generate negative effects on some soil organisms and their contribution to soil function. Hence, further attention should be devoted to negative interactions resulting from agroforestry trees and future studies should explore how common *G. sepium* litter toxicity is to earthworms.

***3.1.1.2. Cassava monocrop transition to rubber plantation in Thailand.*** The shift from cassava to young rubber plantations in Thailand resulted in an initial sharp decrease in the density and biomass of the soil macrofauna. However, after canopy closure, when the habitat functions provided by trees become more prevalent, important changes were observed in the soil macrofauna community structure with an overall increase in biomass accompanied by a decrease in ant and increase in earthworms and termite populations (Figure S2, Table 2). The species richness of soil macrofauna was highest in the older rubber plantations. There was an important turnover of soil macrofauna functional groups along the rubber chronosequence caused by increased dominance of earthworms and presence of predators in the older plantations (8–12 → 23–25 years).

This study highlights that the conversion of annual monocrops to perennial monocrops generates system changes contributing to higher diversity and evenness (but lower abundance and higher biomass) in the soil macrofauna community, with a significantly greater earthworm population ($p < 0.05$) which is often associated with improved soil health (Pauli et al. 2011; Legname et al. 2012). Therefore, in this ecological context characterized by an adverse edaphic soil condition and a long dry season (Chambon et al. 2016), the shift from an annual cash crop such as cassava to rubber could bring positive impacts on soil biodiversity and associated ecological functions through continuity of organic inputs, reduced tillage, lower input of mineral fertilizers and maintenance of soil moisture.

***3.1.1.3. Tea agroforestry in China.*** Tea production in China increased by close to 50% when the tea was grown with *A. nepalensis* (Figure S3, Table 2). This finding is in line with past work relating to the positive effects of *A. nepalensis* on crop production (Vanlalhluna and Sahoo 2009; Das et al. 2010). These changes in crop production came about despite no significant changes in soil chemical characteristics (Mortimer et al.2015).

Although no significant change was detected in the overall soil microbial diversity between tea monoculture and agroforestry systems, significant increases of 21–23% were recorded in the microbial biomass of various functional groups in the soils associated with *A. nepalensis* (Table 2). The Actinomycetes biomass was significantly greater in the agroforestry soils, which concurs with the findings of Golinska and Dahm (2011) who reported an increase in the biomass of Actinomycetes in the soils associated with *Alnus glutinosa*. Furthermore, ectomycorrhizal biomass, as well as that of gram positive and negative bacteria, was found to be greater in the soils surrounding *A. nepalensis*. These findings are consistent with past studies showing the same trend of increased fungal and bacterial biomass in soils surrounding Alder trees of various species (Selmants et al. 2005; Prescott and Grayston 2013; Šnajdr et al. 2013).

This study clearly showed that the incorporation of *A. nepalensis* into monoculture tea plantations resulted in the improved productivity of the tea plantation (Mortimer et al. 2015). The lack of differences in soil nutritional status under both monoculture and agroforestry plots suggests that differences observed in tea production may be biologically driven by increased microbial biomass in the soils under agroforestry. A clear increase in the presence of certain functional groups known to aid plant growth, nutrient cycling and disease resistance provide evidence for this.

### *3.1.2. Linking trees, aboveground biodiversity and ecosystem services*

Agroforestry systems conserve plants, arthropods and vertebrates that have been linked to the delivery of habitat as well as important regulating services, such as pollination and pest control (Perfecto et al. 2004; Klein et al. 2008; Tscharntke et al. 2011). In this section, we examine the effect of shade-coffee agroforestry on tree species diversity and community composition; the effect of a tree cover gradient on insect pollinator species richness and abundance; and the effects of shade, landscape level tree cover and elevation on various pests in coffee agroforestry systems.

*3.1.2.1. Coffee agroforestry in Mexico.* While at the farm level (i.e. alpha diversity), coffee agroforests conserve lower tree diversity than forests, at the landscape level (i.e. gamma diversity) when the entire ensemble of coffee agroforestry farms is considered, forests and agroforests conserve comparable levels of tree richness (Valencia et al. 2014). However, stark differences were found between agroforests and surrounding forests when tree community composition considered trees of conservation concern status (i.e. listed as critically endangered, endangered or vulnerable in the IUCN Red List of Threatened Species in IUCN 2013; or The Red List of Mexican Cloud Forest Trees in Gonzalez-Espinosa et al. 2011) or succession traits (e.g. pioneer, intermediate and late stages of succession). The relative abundance of trees of conservation concern decreased by 60% in coffee agroforestry compared to the native forest (Figure S4, Table 2). Furthermore, agroforests showed close to 150% increase in relative abundance of pioneer trees, in particular native *Inga* spp. trees that increased by 390% (Table 2).

The uncovered differences in floristic patterns between agroforests and surrounding forests were explained primarily by farmers' tree preferences and selection criteria rather than as an unintended by-product of management (Valencia et al. 2015). Farmers believe that agroforests dominated by *Inga* spp. enhance ecosystem services such as soil fertility and production of higher yields; however, some studies have shown that this is not always the case (Romero-Alvarado et al. 2002; Peeters et al. 2003). Recent findings show that increasing the proportion of *Inga* spp. trees has a significant negative impact on the proportions of trees of late-successional stage and threatened species status that may be conserved in agroforestry systems (Valencia et al. 2016).

*3.1.2.2. Forest–agriculture transition in Indonesia (West Java).* The transition from forests to habitats with lower tree cover, as a result of increasing human modification, significantly affected the species richness, abundance and functionality of insect pollinators (Figure S5). A total of 453 insect pollinator individuals from 21 families were collected in pan traps that included eight species of bees, seven of wasps, seven of beetles, four of moths/butterflies and four of flies (Muhamad 2013). Of them, all eight bee species, three wasps, five beetles, one butterfly and all four flies are known as efficient insect crop pollinators. Species richness and abundance were significantly different among landscape element types, except those of less efficient insect crop pollinators.

Richness of total insect pollinators declined in monocrops (rice paddy fields) by 14% compared to natural forests, while it remained unchanged under mixed-tree (MT) agroforestry (Table 2). A decrease in richness of efficient insect pollinators close to 40% was observed under monocrops, but this decrease was only about 15% under MT agroforestry. Richness of less efficient pollinators, on the other hand, did not change under monocrops but slightly increased under MT agroforestry. Richness values for other land uses were intermediate between rice paddy fields and natural forests.

The abundance of total insect pollinators declined in monocrops by 20% compared to natural forests, and that of efficient pollinators by 23%, while increasing the abundance of less-efficient insect pollinators by 100% (Table 2). In contrast, MT agroforestry was colonized by 93% of crop pollinators found in the remnant forest and supported the highest richness of insect pollinators together with the natural forest. While MT agroforestry maintained 85% of the efficient insect pollinators found in the natural forest, an increase in abundance of less-efficient pollinators was also observed (Table 2). The abundance values for other land uses were intermediate between bamboo-dominated agroforestry and MT agroforestry. The lowest abundance values found in bamboo-dominated agroforestry could be related to bamboo species being largely wind pollinated and usually flowering at very long intervals of many years and decades (Janzen 1976).

Variations in pollinator richness and abundance observed across this forest–agriculture transition study are consistent with patterns reported by Ricketts et al. (2008) in their review of landscape effects on crop pollination services. Increased vegetation cover has been identified as an important factor fostering greater species diversity of insect pollinators in tropical landscapes with fragmented remnant forest (Donaldson et al. 2002; Potts et al. 2010). Furthermore, differences in vegetation structure could also affect the abundance and diversity of insect pollinators by influencing the abundance and distribution of flower resources, availability of nesting sites and light intensity levels (Klein et al. 2007, 2008). These findings emphasize the importance of human-modified landscapes, particularly MT agroforestry, in maintaining a high diversity and abundance of efficient insect crop pollinators. However, the protection of remnant forests as a source of crop pollinator diversity needs to be a conservation priority. The enhancement of agroforestry buffer zones around forest fragments stands out as a key feature of appropriate landscape design and habitat management. This is largely because this strategy would maintain a diversity of plant species of different life forms and phenology that can provide an abundant source of floral resources expected to maintain and attract more insect pollinators.

*3.1.2.3. Coffee agroforestry in east Africa (eastern Uganda and western Kenya).* The effect of shade differed between pest species (Figure S6). In Uganda, the coffee berry borer was more common in sun-exposed plantations, whereas the white stem borer was more common at shaded sites (Jonsson et al. 2015). The infestation of the coffee berry borer was on average about 45% higher in sun-exposed plantations compared to shaded ones (Table 2). The effect of shade on the white stem borer depended on altitude, with the differences between shade levels being most pronounced in plantations at lower altitudes. Stem borer infestations were on average 69% lower in plantations with full or moderate shade at low altitudes, compared to sun-exposed plantations (Table 2). The negative effect of agroforestry on coffee berry borer infestations may be due to both top-down and bottom-up factors. Natural enemies of coffee berry borers such as ants, parasitoids (Perfecto et al. 1996) and birds (Karp et al. 2013) are often more common in agroforestry systems and therefore biological control may be more effective there. The coffee berry borer populations could also have developed at a slower rate in shaded plantations due to lower temperatures (Jaramillo et al. 2009) and females may have had difficulties locating suitable berries due to altered biochemical composition (Jaramillo et al. 2013). Less is known about variables influencing white stem borers, but it appears likely that the positive effects of shade on this pest were due to improved microhabitat conditions rather than to predator attack rates as predators are usually more common under agroforestry practices.

In Kenya, results showed that the effect of shade on lacebugs depended on the amount of trees present in the surrounding landscape. More lacebugs were present in shaded plantations, but only in landscapes with a low tree-cover. The abundance of lacebugs was reduced by 86% in high shade sites compared to those with low shade and low tree cover (Table 2). This work shows that the impact of agroforestry on pest regulation in coffee is highly context dependent; it depends on the identity of the most important pests, altitude and landscape composition (Figure 2).

Coffee berry borers, white stem borers and lacebugs do co-occur in some areas of Africa, but often one of the species is the one causing most damage in a particular plantation. Coffee berry borers and white stem borers are currently primarily a concern below about 1700 m a.s.l. (Rutherford and Phiri 2006), whereas lacebugs thrive also at higher elevations. White stem borers are restricted to sub-Saharan Africa, whereas the coffee berry borer has spread through trade and is common in most coffee-growing regions of the world. White stem borers are especially serious in plantations established on poor soils (Rutherford and Phiri 2006). If coffee berry borers are the primary concern, then adding shade trees to a coffee plantation is likely to be an effective way of reducing pest problems. In contrast, if white stem borers are the key concern, then adding shade trees is likely to be detrimental, especially at lower altitudes. Finally, if lacebugs are the most destructive pests, then shade trees may also be detrimental, but only when coffee-growing areas are located in simplified agricultural landscapes with few trees.

## 4. Discussion

### 4.1. Agroforestry as a promising biodiversity-based agricultural intervention

Case studies highlighted in this paper provide examples of agricultural landscapes where tree-based land

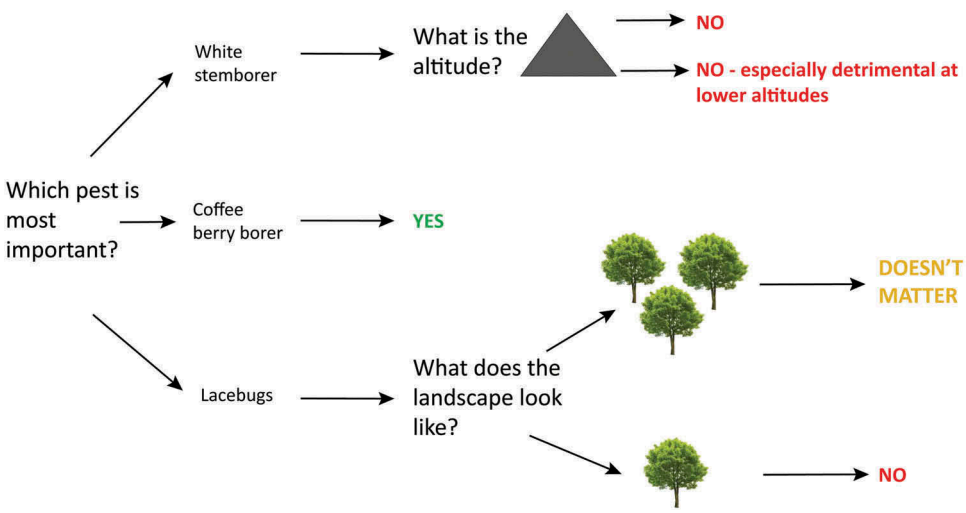


**Figure 2.** Diagram showing whether including shade trees into coffee plantations is likely to reduce pest problems (Yes), if it is likely to have no effect (Doesn't matter) or if it is likely to increase pest problems (No) depending on pest identity, altitude and tree cover in the surrounding landscape.

management practices contribute to the conservation of biodiversity and ecosystem services including agricultural production. Given the contrasting tree-based agricultural systems, organisms and ecosystem services considered, comparisons and general conclusions will be difficult to make and should be taken with caution. Coffee agroforestry landscapes were most common and the focus of three of the six study sites. The socio-ecological contexts in which they occurred, however, were contrasting and included an agricultural expansion frontier in Indonesia (Sumatra), smallholder agriculture inside a biosphere reserve in Mexico and smallholder farmer settlements in Kenya and Uganda. The cassava–agroforestry–rubber plantation transition in Thailand is an increasingly common agricultural practice where cassava, usually representing an attractive cash crop for bioethanol production, is replaced by rubber with higher market prices and hence greater profit. The introduction of N-fixing trees in tea agroforestry landscapes in China represents an increasingly common practice aiming at reducing fertilizer inputs and their contribution to high production costs and environmental pollution. The forest–agriculture transition in Indonesia (West Java) provides a good example of the impact of land-use intensification gradients on insect pollinators and the potential of agroforestry to conserve efficient insect crop pollinator species richness and abundance.

Protecting refuges and reproduction habitats for wild plants and animals in agroecosystems contributes to the *in situ* conservation of biological and genetic diversity that underpins regulation and production ecosystem functions (De Groot et al. 2002). Case studies, however, highlight the challenge of conserving native forest biodiversity in agroforestry systems (agroforestry-habitat hypothesis – Schroth et al. 2004). The Indonesia (Sumatra) study found the loss of native forest earthworms after conversion of natural forest to coffee monocrops or agroforestry practices which encouraged *G. sepium* as shade trees. Similarly, the Mexico case study found lower tree species diversity than the native forest when the agroforestry practice encouraged a single species of shade tree, *Inga* spp., in coffee agroforestry systems. These case studies highlight that changes in native biodiversity are a result of both the intended and unintended consequences of farmers' management. For example, in the Mexico study site, farmers' tree preferences and selection criteria intentionally modified tree species community composition in agroforests causing it to diverge from that found in natural forests. In Indonesia (Sumatra), the unintended results of removing tree cover (e.g. coffee monocrops) and of lower tree abundance and diversity in coffee agroforestry on the soil condition caused a reduction in the diversity and body size of earthworms. Significant replacement of native earthworm species by the invasive earthworm *P. corethrurus* has also been reported in the Colombian Andes in soils under *Indigofera constricta* L. tree fallows which, like *G. sepium*, produce fast-decomposing organic resources of high N content (Barrios et al. 2005). More recently, Marichal et al. (2010) showed that *P. corethrurus* density co-varied with soil N content in a study of agricultural landscapes in the Amazon. These results call attention to the need of identifying agroforestry systems which encourage tree cover diversity to reduce negative effects on biodiversity conservation and prevent creating environmental conditions that may favor invasion by exotic species.

Although the extent to which some agroforestry systems may conserve species richness and community composition similar to that in forests is debatable (Philpott and Dietsch 2003; Rappole et al. 2003; Valencia et al. 2016), an extensive body of literature has shown that increased tree cover improves the quality of the agricultural matrix, thus supporting metapopulations at the landscape level (Perfecto and Vandermeer 2002, 2008; Vandermeer and Perfecto 2007) and the ecosystem services that they provide. The Indonesia (West Java) case study is an example of the role that agroforestry systems play as buffer zones around forest fragments thus supporting the agroforestry-matrix hypothesis (Schroth et al. 2004). This case study highlights the importance of tree cover in agricultural plots, particularly MT agroforests, in supporting remnant forests in maintaining a high abundance and diversity of bees and other crop pollinators. Furthermore, a global study by Maestre et al. (2012) showed that preservation of plant biodiversity is crucial to maintaining multiple ecosystem functions and also to buffer negative effects of climate change. More recently, Jing et al. (2015) reported that the combined effects of above- and belowground biodiversity contributed to 45% of the variation in ecosystem multifunctionality.

Case studies also highlighted the ecologically restorative role of including trees in agricultural plots compared to tree-less monocultures. The Thailand case study shows that the transition from annual crop fields to tree plantations improves the capacity for restoring soil macrofauna diversity over time, and presumably their contribution to soil-mediated ecological functions. Similarly, rubber plantations in the Orinoco river basin also harbored more abundant and diverse soil macrofauna communities than those in annual crops (Lavelle et al. 2014). The China case study, on the other hand, showed that the inclusion of N-fixing trees in tea plantations, as compared to tea monocultures, was associated with increases in tea production, possibly related with increases in microbial biomass of various functional groups rather than increases in microbial diversity.

Nevertheless, it is important to note that the effects of agroforestry practices are not always positive and their effects on biodiversity and ecosystem services can be highly context dependent. While the Indonesia (Sumatra) case study showed that organic input from certain agroforestry tree species may have negative effects on soil animals and functions, agroforestry practices used in Thailand resulted in early reduction in soil macrofauna abundance and biomass, and the Uganda–Kenya case study showed that the effects of shade trees on pest problems can be negative depending on landscape context, altitude and the pest species that are of strongest concern in an area. All these issues need to be considered when designing agroforestry systems that minimize trade-offs and maximize synergies and complementarities that aim at biodiversity conservation and the delivery of multiple ecosystem services.

### 4.2. Challenges and opportunities to an ecological intensification of agriculture

The high levels of biodiversity and inherent ecological complexity of terrestrial ecosystems, particularly in the tropics, make the study of linkages between biodiversity and ecosystem functions/services supporting biodiversity-based agriculture difficult (Swift et al. 2004; Barrios 2007). Recent methodological reviews highlight the importance of using gradients of agricultural intensification as living laboratories at which biodiversity and ecosystem services are manifested at multiple scales (Balvanera et al. 2016). Furthermore, emphasis on agricultural landscapes where dominant practices maintain relatively high levels of aboveground and belowground biodiversity (e.g. agroforestry) has provided simpler but realistic scenarios to study linkages between biodiversity and the provision of ecosystem services (Perfecto et al. 1996; Steffan-Dewenter et al. 2007; Fonte et al. 2010; Tscharntke et al. 2011; Rousseau et al. 2013; Balvanera et al. 2016; Kamau et al. 2017).

The strong linkage between aboveground biodiversity (vegetation/crops) and belowground biodiversity (soil organisms) highlights the potential of tree cover management to influence the provision of soil-based ecosystem services in agricultural landscapes (Wardle et al. 2004; Diaz et al. 2007; De Deyn et al. 2008; De Bello et al. 2010). Research addressing key questions on the link between plant–soil feedbacks and the provision of ecosystem services (van der Putten et al. 2013; Bardgett and van der Putten 2014) should be conducted at scales relevant to management and this can be facilitated by integrating local and scientific spatial variability information on 'hot spots' of soil biological activity (Barrios 2007; Pauli et al. 2010, 2012; Barrios et al. 2012; Kamau et al. 2017). Furthermore, focusing on functions that are relatively specific, such as the roles of ecosystem engineers or specific nutrient transformations, would help with achieving more reliable assessments of the linkages between biodiversity and ecosystem services (Giller et al. 2005; Balvanera et al. 2016). Nevertheless, this focused approach should be integrated as part of an interdisciplinary framework where the continuous interaction between functional diversity components and priorities of social actors define land-use decisions and consequently the provision of ecosystem services (Díaz et al. 2011; Jackson et al. 2012).

After the conversion of natural ecosystems to agriculture and subsequent intensification, there is gradual replacement of ecological functions (e.g. nutrient mineralization, biological control of pests) by external inputs such as agrochemicals. This trend leads to a reduction in the capacity of agroecosystems for self-regulation, greater reliance on external inputs and thus greater vulnerability to environmental and market changes (Barrios et al. 2015). There is growing interest in agroecosystems characterized by greater internal resource-use efficiency, less reliance on external inputs, and that can sustain a suitable balance between productivity and the provisioning of other ecosystem services (Brussaard et al. 2010; Dore et al. 2011). The positive impact of agroforestry, compared to conventional agriculture, on biodiversity belowground and aboveground (e.g. N-fixing organisms, ecosystem engineers, pollinators, biological control agents) contributes to sustaining a greater diversity of ecological functions. Furthermore, agricultural practices that foster enhanced functional diversity increase the potential for multiple benefits but it is important to recognize the need to understand the interactions among multiple ecosystem services for greater resilience benefits and adaptation capacity to climate change.

The adaptation of ecological concepts and principles to the design and management of agroecosystems and food systems, defined as agroecology, is a key strategy that can contribute to addressing agricultural sustainability concerns (Altieri 1995; Gliessman 2007). Agroforestry is a good example of 'agroecology in practice' that has great potential to support a biodiversity-based and multifunctional agriculture that successfully addresses the challenge of optimizing crop productivity while conserving biodiversity and maintaining the provision of other ecosystem services (Prabhu et al. 2015). In order to realize this potential at scale, however, Coe et al. (2014) highlight that we need to better understand (1) how fine-scale variation in social, economic and ecological context creates a need for local adaptation of practices; (2) how to develop effective service delivery mechanisms, markets and institutional contexts in addition to technologies and (3) how to foster adaptive innovation processes that supports co-learning

amongst research, development and private sector actors. Moreover, Tomich et al. (2011) highlight the prospective role of agroecology in fostering the technological and institutional innovations, as well as the adaptive management and social learning, required to face global change challenges in the twenty-first century such as increasing global food production and resilience of agriculture and food systems in the context of increased environmental variability and socioeconomic vulnerability.

## 5. Conclusions

Increasing tree cover in agricultural landscapes can support plant and invertebrate biodiversity and significantly improve ecosystem functions that underpin ecosystem services based on the species/taxa studied here. While the results highlight a general pattern of trees promoting an increase in beneficial organisms, negative effects were also identified. This was particularly the case in agroforestry systems where single shade tree species were encouraged to replace a diverse tree cover or when different pests respond differently to tree shade level and altitude. The restricted number of studies examined which related increases in abundance and diversity with functional attributes, however, limited the wider attribution of functional benefits that trees may nurture. Agroforestry practices show great potential as biodiversity-based interventions contributing to an ecological intensification of agriculture. Nevertheless, the importance of matching tree-based management options to context for minimizing trade-offs, and maximizing synergies and complementarities, cannot be overstated. Developing understanding through knowledge sharing that encourages the blending of local and scientific knowledge could significantly facilitate this process by fostering the relevance, credibility and legitimacy required for the wide adoption of promising management options aiming at the sustainable management of lands for multiple ecosystem services and livelihood benefits.

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