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Biodiversity function and resilience in tropical agroforestry systems including shifting cultivation

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Abstract

Agroforestry systems potentially deliver win-win solutions to production and biodiversity conservation in the tropics but they need to be adapted to farmers' needs. We reviewed the literature on functional roles of biodiversity and resilience in tropical agroforestry systems, and we evaluated the evidence base for the beneficial role of biodiversity on yield, and effects of farmer management practices. Most studies investigated the biodiversity of taxa assumed to have positive functions for farmers. Shaded commodities and shifting cultivation were the systems most frequently assessed. Half of studies investigated plants, while Hymenoptera and birds were other major groups. Many agroforests had lower diversity than forest, while less than half had higher diversity than agriculture. The effects of management within systems were rarely addressed, with shade level the most frequent factor. Papers on resilience, mainly from shifting cultivation systems, showed the positive influence of adjacent old-growth forest to biodiversity, and the negative effects of tillage. Better reporting of results for meta-analyses, and long-term experiments on key questions are needed to evaluate the potential of agroforestry more thoroughly.

Keywords: Agroforestry systems; biodiversity function; farmer management practices; agriculture; landscape management

1 Introduction

Tropical landscape management has two pressing needs – the production of food and goods to sustain rural livelihoods on the one hand, and the conservation of biodiversity on the other hand. Agroforestry is a land-use system that has raised huge interest in this respect, by agronomists and conservationists alike, as it may hold potential to reconcile these two seemingly opposing demands. Agroforestry preserves, most probably, much more of the (usually forest-bound) biodiversity than would the conversion of forests to non-forest agricultural systems. At the same time, there may be an economic benefit in maintaining high biodiversity, hence many beneficial ecological functions, in an agricultural system. This hope is sustained by experimental evidence from temperate-region grassland systems that showed a beneficial effect of biodiversity on biomass production [1]. Data from tropical biomes, particularly the humid forest zone, are scarce [2]. Agroforestry systems have been intensely studied in recent times, but due to the interdisciplinary, in parts policy-oriented nature of the topic it is not clear what claims are backed up by solid empirical knowledge.

1.1 What is agroforestry?

A simple definition of agroforestry is the use of trees in agricultural systems. More precisely, agroforestry has been defined as an intimate association of a minimum of two plant species of which at least one is a woody perennial, in a spatial mix with interactions through environmental processes or management [3]. More recent definitions have become less exclusive (**Table 1**). Many traditional farming systems fall into these categories, as tropical smallholder farmers have traditionally husbanded trees among their crops [9].

1.2 Defining the scope of tropical agroforestry systems with major groupings

Tropical agroforestry systems can be categorized along a gradient determined by whether they include planted timber trees, non-planted timber trees or other trees and shrubs and consequently whether the economic focus is more on forestry or on agriculture. They can also be classified by the length of the tree-crop interface. However, systems are extremely variable and can be included in multiple categories (**Fig. 1**). Some important types of agroforestry systems are described below (see also **Table 2**).

Shifting cultivation (or “slash-and-burn”, swidden) systems are characterized by alternated phases of cropping and fallowing, with the length of the fallow period exceeding greatly the length of the cropping period. During the fallow phase, soil nutrients are restored to allow low-input farming during cropping phases. Typically, an area of forest or fallow is partially cleared during the dry season and the cut vegetation is left to dry [10]. Remnant forest trees are often retained in the field [11-13], a practice that is often enshrined in traditional laws (e.g., for Central Africa [14,15]. Farmers then burn the debris and, after the first rains, cultivate the field. After a short cropping phase, the land is abandoned to a long fallow phase. Shifting cultivation has been in existence for millennia [16]. It is common across the humid tropics [17], particularly in areas with low human population density. Recent population growth has led to shorter fallowing phases in some parts of the world ([17]), and is assumed, unless management practices are adjusted, to result in a loss of sustainability and consequently create increases in demand for land to maintain production.

Homegardens comprise multipurpose trees or shrubs (used e.g. for fruits, firewood) grown with a large range of annual crops and vegetables. They have high levels of organic inputs, such as small livestock manure and kitchen waste [18]. Homegardens are distinguished from other agroforestry systems by being permanent, clearly delineated and located near homesteads.

In ***improved fallows***, trees or shrubs are tended or planted with the aim of either economically enriching the fallow so that more products (e.g., firewood, medicinal plants) are produced (in addition to crops), or biologically enriching the fallow by, for example, adding trees that improve soils (e.g., nitrogen fixing). Systems using herbaceous legumes, such as *Mucuna* spp. or *Pueraria phaseloides*, for this and other purposes, are functionally similar although they are not regarded as agroforestry.

In ***alley cropping***, food crops (e.g. maize) are grown between hedges of trees or shrubs, usually legumes (in Africa, e.g. *Leucaena leucocephala, Calliandra calothyrsus, Gliricidia sepium, Flemingia macrophylla*) that are pruned during the cropping phase. Alley cropping is often attributed to B. T. Kang [19], who developed this system in SW Nigeria in the 1970s. However, there are examples of similar smallholder systems that preceded it, such as the use of *Dactyladenia barteri* in fields in SE Nigeria [20] and *Leucaena leucocephala* in Timor, Indonesia [21]. In the Northwest Region of Cameroon, farmers plant lines of *Tephrosia vogelii* into their maize fields, stating that it suppresses the weed *Imperata cylindrica* (L. Norgrove, unpublished data).

Agrisilviculture (or agrosilviculture) distinguishes agroforestry systems that include planted timber trees as well as other perennial or annual crops. Two main types are common: (1) temporary intercropping systems (or *taungya*), in which food crops are grown between timber tree saplings before canopy closure; or (2) longer-term associations between timber trees and, usually, perennial crops, particularly *Musa* spp.

(1) ***Taungya*** was used in the 17th century by the Yao and Miao peoples in southern China to cultivate the conifer *Cunninghamia lanceolata* [22]. In 19th century Burma, the taungya system was used to produce teak (*Tectona grandis*) by the British Colonial Service while local farmers planted sweet potatoes, cotton and chillies between the tree seedlings [23]. The taungya system has spread worldwide and is usually institutionalised and instigated by forestry departments which permit smallholder farmers to crop between trees, saving on the labour cost of weeding the plantation. While the system has persisted, it has been severely criticised by some as being exploitational [24]. Indigenous taungya systems, designed and controlled by smallholders, are rare but do exist. For example, teak is grown with upland rice in Lao PDR [25] or with other food crops in Indonesia [26,27].

(2) There are only few references on traditional long-term associations between planted timber trees and crops. In the 'damar' (resin) system of Indonesia, *Shorea javanica* is planted by smallholder farmers for timber and resin production, combined with food crops and fruit trees [28-30].

Shade commodities: traditionally, smallholders have grown rubber and stimulants such as cacao, coffee and tea, under shade trees, whether planted or retained after partial forest clearance. Today, these crops are major agricultural commodities with globally combined production area amounting to ca. 36 x 10^6 ha (data from [31]). Although often managed in industrialized plantations, they are partly still grown under shade from timber trees.

1.3 Evaluating benefits and costs of agroforestry

Agroforestry systems can vary in scale (e.g., smallholder farming vs. industrialized plantation) and socio-economic characteristics vary accordingly. However, regardless of scale, agroforestry systems will generally have higher product diversity and a wider range of planting, weeding and harvesting times than an equivalent monocrop system. This leads to potential advantages for smallholder farmers in particular, such as (1) reduced risk of total crop failure (as the risk is spread between many species, akin to the "*spatial insurance hypothesis*" [63]); (2) increased diversity of products, hence improved nutrition for subsistence farmers; (3) less vulnerability to market price changes (for cash crops); (4) better distributed labour demands over the year; and (5) reduced seasonality of income (for cash crops). Apart from these, there are potentially positive effects on yields due to ecological effects such as complementarity and facilitation.

1.3.1 Complementarity

A central hypothesis in agroforestry is that 'the benefits of growing trees with crops will only occur when the trees are able to acquire resources of water, light and nutrients that the crops would not otherwise acquire' [64]. Trees and crops are complementary if they exploit more of the factors limiting growth, when grown together [65]. Where the different components have different root and stem architectures, or when their growth demands peaks are at different times, they are more likely to show complementarity [65-67]. For example, many food crop annuals are shallow rooting. In combination with a deep-rooting tree, more of the available soil volume is explored, and a greater amount of available water and nutrients accessed [68]. The most common mechanism for higher productivity in mixtures is the temporal sharing of resources. For example, mango trees (*Mangifera indica*) assimilate and produce leaves during the dry season when associated crops have been harvested or have reduced demands.

1.3.2. Facilitation

Different species may not only be unaffected in their growth by each other's presence, they may even benefit. A modification of the environment by one partner with benefits for the other describes the *'facilitative production principle*' [69]. For example, a reduction in light intensity may, under tropical, high-radiation conditions, have positive growth effects by, for example, avoiding stomatal closure at midday [70]. In some crops such as plantain (*Musa* spp.), light saturation density of leaves can be low and full light can lead to photorespiration rather than growth [71]. Shade can also alter pest and disease dynamics. Black sigatoka (*Mycosphaerella fijiensis*), the most important *Musa* disease globally, can be reduced under shade [72].

An agroforestry tenet is that trees perform a facilitative function by improving or maintaining soil fertility, in addition to the improved water and nutrient capture mechanisms mentioned above. Leaf-litter cover, tree root decomposition and the more stable soil microclimate created may maintain soil organic matter and also improve soil biological activity [73]. However, many of these assumptions have not been empirically proven, or only under specific circumstances [6]. Many data demonstrating positive effects of trees on soil qualities have been collected from natural [74], rather than planted tree systems. Therefore, it is not possible to clearly assess causalities, i.e. whether the trees improved the soil or whether good soils allowed the germination and growth of the trees.

1.3.3 Costs

There are also potential disadvantages of agroforestry, particularly for large-scale plantations. Among them are (1) difficult application of machinery for harvesting and planting; (2) greater requirement for technical knowledge; and (3) less benefits from 'economy of scale' effects [75,76], e.g. in processing, transporting and harvesting harvests. Furthermore, whether yields actually do increase, or possibly even decrease, is far from certain and requires quantitative study.

1.3.4 Cost:benefit analysis

The evaluation of yield benefits and, ultimately, economic advantages of agroforestry over other forms of productions is notoriously difficult. The criterion most frequently used to judge these quantitatively is the land equivalent ratio (LER) (see text box) [77]. It quantifies whether mixed cultivation yields more, or less, than what could be harvested in a monoculture. However, the performance of an agroforestry system varies locally due to the selected species' combination, absolute and relative densities and the limiting factors of the selected environment. The non-linearities inherent to economic as well as ecological processes (such as complementarity and facilitation) mean that outcomes could be very different depending on the exact mix and it is difficult to separate the effects of diversity, composition and management. It is therefore challenging to evaluate systems empirically in any general, transferable way, particularly systems with many components, and such attempts would require large experimental designs. For example, Leakey (2014) [78] discusses the uses of Nelder fan [79] and complex replacement series designs for determining optimum shade tree and shrub mixes in a cacao agroforestry trial. The timeframe of evaluations may also matter – for example, in grassland experiments ([1,80] particular monocultures in particular years performed better than more diverse systems, although longer-term average production of diverse communities always exceeded monocultures. When such ideas are applied to tree systems with longer growth cycles, even longer-term experiments are required and these should be a priority in the upcoming decades.

Furthermore, metrics such as the LER do not take account of the economic values of the different components and the outcome with the highest LER may not be the same as the one with the highest value [81]. Indeed, where the role of trees is not to produce a marketable product, but simply to provide benefits such as, e.g., maintain soil fertility or conservation of biodiversity (e.g., alley cropping), the adoptability of the system is greatly constrained. The "yield" of the hedgerow (e.g., its pruning) is not intrinsically of interest to farmers (although it can be used as mulch for the crop). For an alley cropping system to be successful economically, either the yield of the food crop would need to exceed that of a monoculture in the long term (despite reduced production area), or there needs to be an indirect economic benefit (e.g., conservation subsidies, offsets, etc.). In contrast, where the tree component produces edible or marketable products, farmers can be expected to be more tolerant of lower yields of their food crops, as they may gain economically, overall. Such calculations also need to take into account that smallholder farmers typically have short-time horizons and thus apply high discount rates [82], partly due to commonly high levels of tenure insecurity (for example, [83]), a disincentive to planting trees [84]. Thus farmers may favour short-term crops over trees and fast-yielding perennials, such as early fruiting trees, over timber trees with longer production cycles. Yet other authors have shown that incorporating trees into systems can reduce production risks and increase profitability compared to crop monocultures even under high discount rates [85].

Text box: The land equivalent ratio (LER)

LER allows the quantification of relative yield losses or benefits due to multi-cropping (e.g. a food crop and a tree) compared to monocrop systems [77]. It is calculated as

$$\mathrm{LER} = \frac{\mathrm{I_t}}{\mathrm{M_t}} + \frac{\mathrm{I_f}}{\mathrm{M_f}}$$

where
I_f = yield (per ha and unit time) of food crop, in mixed cultivation
I_t = yield (per ha and unit time) of tree, in mixed cultivation
M_f = yield (per ha and unit time) of food crop in monoculture at optimum density
M_t= yield (per ha and unit time) of tree in monoculture at optimum density
LER can take values between 0 (no yield at all) and >2 (if, due to facilitation, both crops yield more than in monoculture despite sharing the available area). If LER <1, the system is not economically beneficial (as judged on yield alone), as monoculture of one crop could produce more. LER = 1 indicates yield equivalence of the two crops, i.e. losses in one crop are perfectly balanced by gains in the other crop. If LER >1the multi-crop system is more productive than monoculture.

1.4 Biodiversity function in agroforestry systems and relevance for smallholder farmers

Apart from research assessing crop yield benefits of agroforestry systems, recent work has included potential biodiversity conservation benefits in agroforestry systems. For example, Leakey (2014) [78] collated data on biodiversity in tropical agroforestry systems as part of a more general review. Bhagwat et al. (2008) [86] focused on the potential for tropical agroforestry to maintain species diversity. Scales and Marsden (2008) [87] reviewed 52 studies that compared diversity indices between tropical agroforests and primary forest, and 27 studies that compared different types of agroforest. However, neither Bhagwat et al. (2008) [86] nor Scales and Marsden (2008) [87] distinguished between different types of biodiversity from the farmers' utilitarian perspectives, or assessed productivity data to test for a relationship between biodiversity and yield. They also did not consider the experimental designs to assess whether any confounding factors were present. For example, studies comparing the different stages of a land use sequence can either sample the same site repeatedly through the various phases (Type-I "chronosequence" data); or, different sites in different stages of the succession can be compared at the same time (Type-II "space-for-time" or "false chronosequence" data) [88]. Type-I chronosequence data collection requires large plots and is expensive, yet it is accurate and unequivocal. Drawbacks of type-II studies include spatial variation [89] and, often, unwarranted assumptions about site history [90]. Furthermore, type-II space-for-time studies comparing farmers' fields and fallows with remaining forest remnants rely on the farmer having randomly selected his plots, an unlikely condition as farmers have developed appropriate criteria to select the most productive fallows [91].

1.5. Resilience of biodiversity in tropical agroforestry system

Resilience is the capacity of an ecosystem to return to the pre-condition state following a disturbance, including maintaining its essential characteristics such as taxonomic composition, structures, ecosystem functions, and process rates [92,93]. Applying this concept to agroforestry systems can imply (1) that these systems have features that allow a recovery of biodiversity back to levels found in the previous land use system, prior to the disturbance of land conversion, and (2) that management features of the agroforestry system are sufficiently benign to avoid irreversible changes during its lifespan. Tittonell (2014) [94] has recently applied the resilience concept to tropical agroecosystems in Africa. Trenbath (1985) [95] developed a simulation model detailing how changes in management practice in shifting cultivation systems might alter succession of the future fallow. His model detailed how tree biomass and grass biomass may change under intensification comprising two stability domains with a separatrix. He postulated that with repeated cropping cycles and shortening fallow phases, a point will be reached at which tree regeneration fails completely and the system will move to the grassland domain. This would have severe implications for shifting cultivators as the utilitarian functions of a forest fallow, such as accumulating biomass and shading out agricultural weeds [96], would be lost, as well as their role as a biodiversity repository for forest species. More recently, a similar model to the Trenbath tree-grass model has been developed [97]. However, none of these models have been tested empirically, and the tipping point at which intensification creates a regime shift, as well as the dominant factors determining such a shift, have not been identified. Thus, as there is only limited empirical understanding of resilience in agroforestry systems, it is difficult to test and it may be premature to apply this concept based on assumptions alone.

1.6 Aims

In the next section, we assess and collate the results of peer-reviewed scientific studies on biodiversity of different taxa in agroforestry systems, to assess the relevance and utility from the viewpoint of the smallholder farmer, to assess how useful they are in deciding how effective the agroforestry system is in conserving biodiversity compared with a forestry agricultural landscape mosaic, and what is known about the relationship with productivity. We put particular emphasis on evaluating the evidence base for the beneficial role of biodiversity on yield and farm-level economy, which is the crucial argument for the high regard that agroforestry has. To assess the resilience of biodiversity in agroforestry systems, we used papers that examined changes over time within a particular system and those from shifting cultivation studies that assessed the residual management effects of the previous cropping phase.

2. A quantitative review of peer-reviewed studies on biodiversity function in tropical agroforestry systems

2.1 Methods: Literature search and processing

We conducted a literature search in SCOPUS on 1 June 2015 by searching for the following combinations of words in the title, abstract or keywords: (agroforestry OR swidden OR "hedgerow intercropping" OR "alley cropping" OR agrosilviculture OR home garden OR "shifting cultivation" OR "planted fallows" OR "improved fallows" OR taungya OR agrisilviculture OR "slash and burn") AND (biodiversity OR "ecosystem function" OR diversity OR "species richness" OR "Shannon-Wiener index" OR "Simpson index") AND (tropic*).We limited our search to journal articles within environmental and agricultural sciences. There was no time limitation.

The initial search resulted in 277 articles. We then manually excluded articles, such as review articles, those from outside the geographical tropics, those that did not contain biodiversity data, and two articles that we were unable to access. To limit the enormous potential scope, we also excluded articles where animals were a major component of the system, such as sylvopastoralism, leaving 146 articles. We extracted data on the following topics from these studies:

(1) To categorise different types of biodiversity functions in agroforestry systems, we used a system developed by Biala et al. (2005) [98] that can be adjusted to adequately describe the biodiversity of agroforestry systems:

i) ***Planned cultivated biodiversity***, consisting of the crop mix planted by the farmer;

ii) ***Spontaneous volunteer biodiversity***, i.e. marketable or useful species that were not planted, but are tended by the farmer;

iii) ***Within-system functional biodiversity***, e.g. regulators of soil fertility, natural enemies of crop pests, decomposer microbes, nitrogen fixers, pollinators of food crops and trees present within the agroforestry system;

iv) ***Out-of-system functional biodiversity***, which has a landscape-wide benefit in adjacent cropping systems, such as pollinators of crops or predators of crop pests not in the agroforestry system but in other production systems in the landscape;

v) ***Heritage biodiversity***, i.e. biodiversity not known to be directly linked to the functioning of the agroforestry system or production systems in the landscape, but of conservation value.

Some studies evaluated data for several of these categories. In such cases, we assigned the most valuable function, from a utilitarian farmer's perspective, to that study (i.e., highest: planned cultivated biodiversity, lowest: heritage biodiversity).

Other variables of interest were (2) country (for insular Southeast-Asia: island); (3) taxon studied; (4) type of agroforestry systems tested; (5) whether forest and agricultural controls were included; (6) the factors or covariables assessed, if any, and whether they related to smallholder management (if any); (7) whether the study was experimental (planted assemblages after randomly assigning plots, compared with agricultural and forestry controls), semi-experimental (some treatment imposed within the agroforest to elucidate functions) or descriptive (e.g., an existing type II "false chronosequence"); (8) whether productivity data (crop yields, economic value, carbon stocks) were presented; (9) what the relationship of biodiversity and productivity was (if investigated).

We identified a subset of papers that, in addition to comparing different land use systems, assessed the effects of farmer-relevant management practices within a system or looked at various landscape variables and categorized them by the type of agroforestry system investigated. We also identified those papers comparing similar systems in different stages of succession to estimate biodiversity resilience through time or those that looked at residual effects of management practices in the crop phase on the recovery of the following fallow. Of these, we only included studies that contained at least 3 age classes. Where secondary forests were mentioned without specifying age, we coded the age as 35 y. Similarly, primary forest and old growth forest were specified as 100 y old. We selected fallow succession studies that had a primary forest control. Of those, we calculated the proportion of recovery of species richness or species number, by comparing with the primary forest control. This is a simplistic measurement, yet it was chosen as many papers did not assess more complex indicators such as changes in functional composition. We then tested the significance of linear regressions of species against age and separated those that were significant. The age at which 80% of species recovery would be obtained was estimated from the linear regressions obtained.

2.2 Results

2.2.1 Categorizing studies by location, system, taxon, and other features

Studies found were from across the Americas, Africa and Asia with Mexico, Costa Rica, Brazil, Cameroon, and Sulawesi (Indonesia) having eight or more studies (**Fig. 2A**). One hundred and twenty studies (82%) were from humid forest ecoregions, 11 from sub-humid forest, 6 from montane forest, 1 from seasonally dry forest, 3 from the forest-savannah transition zone, and 5 from dry forest. The majority of studies assessed the biodiversity of taxa assumed to be of positive functional use to the farmer ("within-system"; **Fig. 2B**). Almost half of studies investigated the diversity of plants, while Hymenoptera (mainly ants) and birds were other major groups (**Fig. 2B**). Over a quarter of studies described biodiversity in shifting cultivation systems, and ca. half of studies described shaded commodity crops, predominantly cacao and coffee. Other shaded commodity systems were dominated by rubber [99,100], tea [53], coconut [101] and cardamom [102,103]. Other systems, such as homegardens, agrisilviculture and improved fallow were rarely studied. We did not find any study on biodiversity in *taungya* systems. Studies were predominantly of descriptive research design (**Fig. 2B**).

2.2.2 Biodiversity in relation to control habitats and yield

More studies contained forest controls (63%) than agricultural controls (20%), and only 19% contained both types of controls (**Table 3**). However, controls were not usually composed of the individual components of the agroforestry systems, thus it was not possible to conduct an LER-type analysis (see text box) to consider whether more biodiversity would be retained by the agroforestry system in contrast to its monocropped constituent parts.

Nevertheless, many agroforests (ca. 2/3) had significantly lower tested diversity than forest. For the remaining studies, there was no significant difference between agroforests and forests, however, this might be because of high variability and insufficient sampling and cannot be interpreted as meaning that there is no biodiversity loss. Less than half (41%) had significantly higher diversity than the agricultural control (**Table 3**).

Seventeen papers contained productivity data. Of these, only one study demonstrated a positive relationship between the number of cultivated species and total system (trees + crops) biomass production [124]. This study compared three tree species each planted in either a tree monoculture or intercropped in a polyculture with crops. Three years after planting, total system biomass production was increased in the polyculture versus the monoculture for the tree species *Cedrela odorata* and *Cordia alliodora*, but was not significantly difference for *Hyeronima alchorneoides* [124] . One paper found a negative effect of diversity in which higher cacao yields were associated with low richness of forest tree species [121], however, these data were derived from farmers' shaded cacao farms where the diversity of shade trees was confounded with shade level and therefore results simply demonstrate that very high shade levels can limit cacao production and do not test diversity *per-se.* Four studies tested the relationship but found no significant effect (**Table 3**). The remaining 11 studies presented data but did not explicitly address the link between diversity and yield or carbon stocks.

2.2.3 Biodiversity in relation to management

Studies on the effects of management within systems were few, with most of them addressing shaded commodity crops and analysing species richness as a response. For cacao, the effect of shade level was the factor most intensively studied (13 studies) while the density of flowering plants, weeding frequency and the application of fungicide, insecticide or nitrogen fertilizer were addressed in single studies only (**Table 4**). Many of the results were from the same, large project in Sulawesi, others were from Ecuador, Cameroon and Brazil. No study found a negative correlation between shade level and biodiversity, there were eight occurrences of significantly positive effects, and 17 results were non-significant. Shade levels and tree diversity were, generally, positively correlated. Shade effects were always positive on the diversity of birds, non-significant on amphibians, reptiles, and (mostly) invertebrates, and mixed on non-woody plants. However, these results are confounded by the higher probability of having more tree species when shade levels and therefore densities are higher, as data were mainly from descriptive studies of existing farmer managed systems rather than from planted experimental systems explicitly testing shade and diversity effects.

There was not sufficient information in the papers to assess which shade level was optimum. For coffee, some studies also investigated shade level as well as the distance from the agroforestry system to the nearest old growth forest (**Table 5**). Shade level generally had a non-significant effect, although it was only tested on ants and bats. Distance to the forest was negatively related to species richness of invertebrates.

2.3.4 Resilience

For assessments of biodiversity resilience (i.e., changes through time), we found one paper on homegardens in Indonesia, with ages ranging from 10 - 80 years old [141]. They found no relationship between tree species richness and age. Three studies from Ecuador [115,138,142] compared active coffee plantations with those abandoned 10-15 years ago, against a forest control. Whether or not pesticides were used was not reported. Total arthropod species richness was not significantly different between forest and abandoned coffee yet significantly lower in actively managed shaded coffee. There were no differences between actively managed and abandoned coffee in adult tree species richness, however, for both tree saplings and tree seedlings, abandoned coffee had higher species richness than active coffee and was not significantly different from the forest. These results suggest that this shaded coffee system was relatively benign from a viewpoint of biodiversity preservation and restoration can subsequently occur back to forest levels. We found no other studies in the shaded commodity, mixed multistrata, improved fallow or agrisilviculture categories.

All remaining papers on resilience dealt with temporal changes in biodiversity during the fallow period in shifting cultivation systems and most of these focused on the effect of the age of the current fallow (**Table 6**). Of papers including at least three age categories and a primary or old growth forest, 9 studies had significant positive linear regressions between species richness and age for any particular group, while the rest were non-significant (14). The greatest proportion of significant studies was for invertebrates (2/3), followed by "all plants" (4/7) (**Table 6**). With the exception of one study from the dry forest of Mexico (33 years) [90], it took at least 48 years for species richness to approach 80% of the value of the primary forest and this estimate did not vary consistently between taxa or ecoregion, however, the number of data points per time sequence was limited (**Fig 3**).

Eight papers looked at factors other than fallow age affecting biodiversity resilience in shifting cultivation (**Table 7**). Factors comprised a mix of residual management effects and landscape configuration. Three out of five studies assessing landscape configuration effects suggested effects of biodiversity reservoirs (e.g., nearby old-growth forests). Three studies from humid forest ecoregions assessed the effects of the number of previous crop-fallow cycles, with one reporting a negative effect on diversity (the two others were non-significant). Studies testing various effects of phase durations (e.g., cropping, previous fallow) did not find significant effects, while the effect of previous tillage was negative for plant and seedbank species richness.

3. Discussion

Increasing agricultural production in the tropics is jeopardizing conservation aims. There is currently much discussion on how to best compromise between these seemingly antagonistic needs: the land-sparing versus land-sharing debate [165,166]. Land-sparing is achieved by intensification of crop production to achieve higher yields. This saves other (e.g., forested) land for conservation purposes. Land-sharing is the application of farming practices that preserve or promote biodiversity within agricultural areas, often using low levels of inputs and minimal disturbance but at the cost of lower yields and therefore a greater area requirement for equivalent production. Traditional smallholder agroforestry systems are usually perceived as a land-sharing strategy [86]. While reviewing 146 original studies on biodiversity in tropical agroforestry systems, we focused on evaluating the evidence for three main conjectures in agroforestry research and policy: (1) it helps to preserve (forest-bound) biodiversity; (2) farming techniques are complementary to and not antagonistic with those promoting biodiversity conservation; and (3), there are economic advantages due to direct positive effects of biodiversity on productivity. If these conjectures are true, they provide strong arguments for environmental policies to maintain and promote agroforestry systems, in smallholder as well as plantation farming, across the tropics. A question of such global, applied relevance cannot be judged based on single studies, as they always refer to a particular system and region. As we have shown above, there is a wide variety of agricultural systems bunched together under the term agroforestry, which may react quite differently. Furthermore, single studies are prone to type-I statistical error [167], hence the requirement to assess results from multiple studies.

3.1 Methodological issues

Providing research results in a manner that facilitates review and meta-analysis is of high value. We noticed a relatively poor documentation of relevant factors in many studies, which may partly stem from the interdisciplinary nature of the research topic (i.e., ecology and agronomy; e.g., lacking information on age of system; planting densities; husbandry techniques such as weeding, pruning, etc.; variety of crops such as coffee and cacao used, which may have different shade responses [168]. Similarly, reporting on statistical test results was often not sufficient to carry out formal, quantitative meta-analyses [169], and the analysis of biodiversity in some papers was questionable (e.g., not considering effects of area size, under-sampling, and spatial non-independence).

It was challenging to address the three conjectures given above with the available studies. Many studies did not actually address them directly, even if some mentioned them to point out the relevance of agroforestry research. Furthermore, in the absence of a globally coordinated research program on data management, there is a huge variety of methods (including data analysis and its reporting), systems, spatial scales, and taxa studied. Different taxa can react very differently to the same environmental variation, jeopardizing overall conclusions [112, 170]. The majority of studies were not experimental, but compared already existing farmer-managed systems, which further weakened conclusions on causalities.

3.2 Testing the three conjectures

We found that many, but not a majority, of studies reported significantly higher biodiversity in agroforestry compared to agriculture, which moderately supports conjecture (1). Assumptions on the conservation benefits of agroforestry are also supported by conservation research from outside of agroforestry, which highlights the value of retaining forested secondary habitats in the tropics, in comparison to forest conversions to agricultural habitats (e.g., [171]). However, a majority of studies indicated significantly reduced diversity in agroforests compared to reference forests, so biodiversity preservation is far from complete and agroforestry cannot be viewed as a perfect substitute for forest protection. In line with this, a recent meta-analysis of biodiversity recovery after disturbance [172] indicated very long time-frames for reliably restoring reference-habitat levels (see also [173,174]).

As for conjecture (2), many studies addressed biodiversity types that were relevant to farmers and production (i.e., cultivated, volunteer and within-system biodiversity function), but surprisingly few studies looked at how agronomic practices used by farmers within their agroforestry systems affected biodiversity. Those that did overwhelmingly focused on shade level, with most of the studies on cacao, but not in a way that would allow quantification and facilitate practical advice to farmers. This finding supports the view of Franzen and

Borgerhoff Mulder (2007) [175], who, referring to shade cacao, stated that research often targets interventions that provide benefits either to farmers or biodiversity, but not both.

Shade had positive effects on ants in Cameroonian shaded cacao [134], which may help in controlling mirid (*Sahlbergella singularis*) populations, and on parasitoids in Brazilian shade cacao[128], although it was not clear what these were parasitizing and whether its host were cacao pests or not. Fungal diseases (witches' broom and blackpod), not insect pests, are generally considered the major yield constraints in South America. Other positive shade effects were on bird and plant biodiversity. Yet, the only study on cacao showing a significant biodiversity – productivity effect was from West Africa and a negative correlation was found [121]. Clearly, even so-called functional biodiversity will only show a positive impact on productivity if it is affecting a major yield constraint in the system.

Several studies suggested that landscape configuration was more important than management effects in determining biodiversity resilience, with biodiversity recovery in agroforestry systems depending on the existence of forest patches in the landscape. For example, Jakovac et al. (2015) [163], working in the Amazon, concluded that species diversity was more dependent on landscape configuration than on management intensity history of a fallow plot - although recovery of the structure of the forest was more dependent on the latter. However, the fallows in this study were rather young (5 y) so more and longer-term studies would be required to assess the importance of landscape configuration.

Conjecture (3), i.e. that high biodiversity in agroforest systems actually increases yields and therefore benefits farmers, was most poorly studied. This conjecture is backed by plausible ideas on ecological mechanisms, such as better nutrient cycling and lower potential for explosive population growth of pest organisms in diverse systems [176]. However, the few studies that addressed this in a tropical agroforestry context were quite equivocal (**Table 3**). Furthermore, results of descriptive studies on this topic are particularly susceptible to reversed causalities, as primary productivity (of which farmer's yield is a substantial part) is known to be a major determinant of biodiversity [177]. The correct assessment of the relationships between diversity and productivity or ecosystem functioning requires well-designed experimental approaches, analogous to those employed in some recent forest biodiversity experiments (for e.g.,[178,179].

Thus, in conclusion, the evidence base for the three conjectures is generally not strong. There is a lack of applied, practical advice resulting from studies on conjecture (2), and proof is particularly weak on conjecture (3). More studies, with improved designs, imposed treatments and from which the results are better documented are needed to test these conjectures with the required certainty. This is particularly relevant because they could, if proven, convince farmers and plantation owners to adopt more biodiversity-friendly management for their own, utilitarian advantage (which is a stronger incentive for action than any conservation policy).

Drawing more reliable conclusions from the available literature was hampered by the multitude of approaches, combined with weak-inference study designs (i.e., mostly descriptive studies) and often unclear reporting of statistical test results. Default publishing of raw data in electronic format, as it is becoming standard in many basic science ecological journals, would facilitate future meta-analyses. There is also still a gap between the approach used in the more ecologically focused, short-term studies initiated by universities, predominantly relying on comparing existing systems, and the longer-term, more agronomic studies that are less publishable but yield more practically relevant information for farmers. Additionally, systems are undergoing rapid changes. For example, Kusters et al. (2008) [30] predicted that farmers would cut down *damar* agroforests in Sumatra in the near future due to external economic factors; Ekadinata and Vincent (2011) [52] have confirmed this through remote sensing data. Cacao farmers in Ghana consider traditional cacao agroforests as an archaic system, preferring lightly shaded, commercially orientated systems with newer hybrid varieties [168]. Optimizing these systems before they disappear might be achieved by a series of collaborative, multi-locational long-term trials set up in farmers' agroforestry systems. Randomly allocated types of management, as planned by the farmers, could be compared with status-quo controls. Long-term data collection on yield, labour, inputs and biodiversity would allow the relevant open questions to be addressed (e.g., link of management actions, economic benefits, and biodiversity) simultaneously.

4 Conclusions

Agroforestry covers a wide range of different land management systems. It was studied in different regions, with reference to different taxa, using different methods, and analyzing different responses of biodiversity. Generalized statements on research findings may therefore not be warranted. Comparisons of biodiversity to those of control habitats suggest that agroforestry has more conservation potential than agriculture, but that it cannot substitute old-growth forests. Management practices (mostly shading regime in commodity crops) were studied either in relation to farmer's benefits or to biodiversity, but rarely both. While shade was often associated with higher biodiversity, most studies fell short of fully evaluating economic effects for farmers. Resilience, in the sense of biodiversity recovery to old-growth levels, was studied mostly in shifting cultivation systems (i.e., using fallow age as predictor). An initial review suggested recovery times of half a century, but better data are needed for reliable estimates. The distribution of old-growth habitat in the landscape (i.e., proximity of biodiversity reservoirs) emerged as an important predictor of resilience in many studies.

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Compliance with Ethics Guidelines

Conflict of Interest

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This article does not contain any studies with human or animal subjects performed by the author.

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- •• Of major importance

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CAPTION:

Figure 1 Depiction of selected tropical agroforestry systems along a forestry to agriculture gradient and according to the type and length of the tree-crop interface.

Figure 2 Properties of 146 reviewed studies on tropical agroforestry and biodiversity function. (A) Location of studies by country (in insular Southeast-Asia by island). (B) Frequencies of studies by Biodiversity function (CULT = planned, cultivated biodiversity; VOL = Spontaneous, volunteer biodiversity of use for the farmer; IN = biodiversity of positive, functional use for the farmer within the system (e.g. soil fertility, pest control, pollination); EX = biodiversity of positive, functional use outside the study system; HER = heritage biodiversity (without direct, studied link to study system), Taxon, Agroforestry system (ASC = Agrisilviculture; oSC = other shade commodity), and study design.

Figure 3 Estimate of species richness recovery (in percent of old-growth control levels) as a function of fallow age. Linear regressions (OLS) were fitted to published data as a crude, preliminary representation of recovery trajectories. Arrows indicate the age at which 80% of reference biodiversity would be restored according to these functions. Numbers give taxon, locality, ecoregion and r^2's of linear regressions (all were significant at $P < 0.05$): (1) Trees, Hainan (China), humid forest, $r^2 = 0.99$, n = 4 [147]; (2) Trees, NE India, humid forest, $r^2 = 0.94$, n = 5 [146]; (3) All plants, Mexico, dry forest, $r^2 = 0.47$, n = 15 [90]; (4) All plants, Madagascar, humid forest, $r^2 = 0.81$, n = 6 [156]; (5) All plants, Madagascar, semi-humid forest, $r^2 = 0.99$, n = 5 [158]; (6) All plants, Côte-d'Ivoire, semi-humid forest, $r^2 = 0.59$, n = 8 [159]; (7) Birds, NE India, humid forest, $r^2 = 0.81$, n = 5 [146]; (8) Beetles, Borneo, humid forest, $r^2 = 0.99$, n = 4 [100]; (9) Butterflies, Borneo, humid forest, $r^2 = 0.97$, n = 4 [148].

Table 1 Definitions of agroforestry by the minimum number and type of components, the requirement for spatial or only temporal mixing and the degree of interaction between components (updated after [8]). Key: ns – not stated

Table 2 Agroforestry systems with classes or individual components either named, or classified as present (X) or absent (). S = smallholder farmers, L = large-scale or institutionalised. *L. Norgrove unpublished data

Table 3 Number of studies with controls (agr. = agriculture), biodiversity differences of agroforestry compared to controls, and diversity-productivity effects, classified by type of agroforestry system. Note that the total surpasses the number of reviewed studies (146) as some papers presented data from several systems. The significance of effects was based on error probabilities given in papers ($p \leq 0.05$) or estimated from graphic data representation (e.g., non-overlap of 2*SE). Papers used for biodiversity comparison: [53, 104-118]. Papers used for biodiversity – productivity relationship: [119-124].

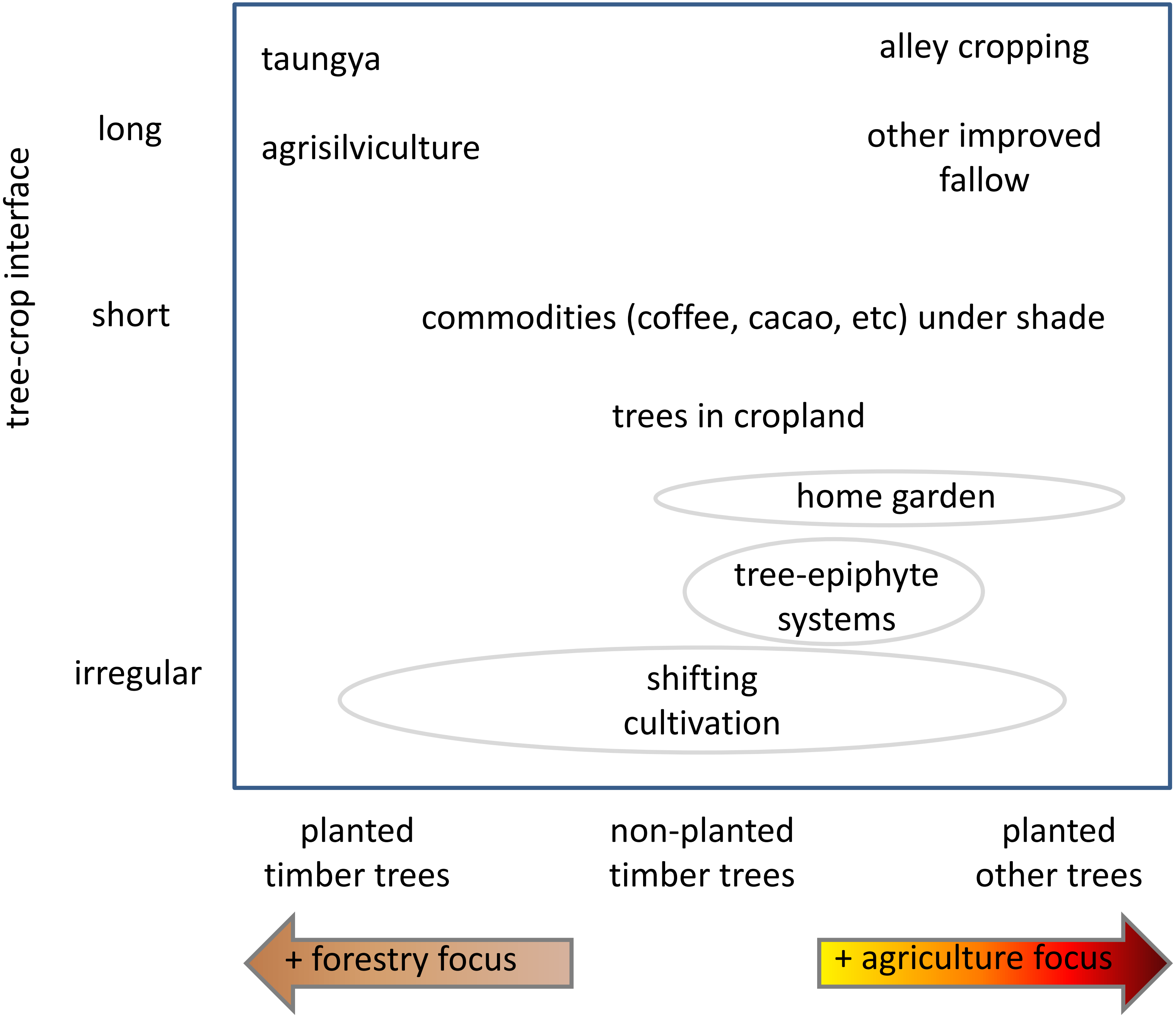
Two “other”s were both semi-experimental studies on Quesungual slash-and-mulch agroforestry [111] and fruit trees under shade [107].

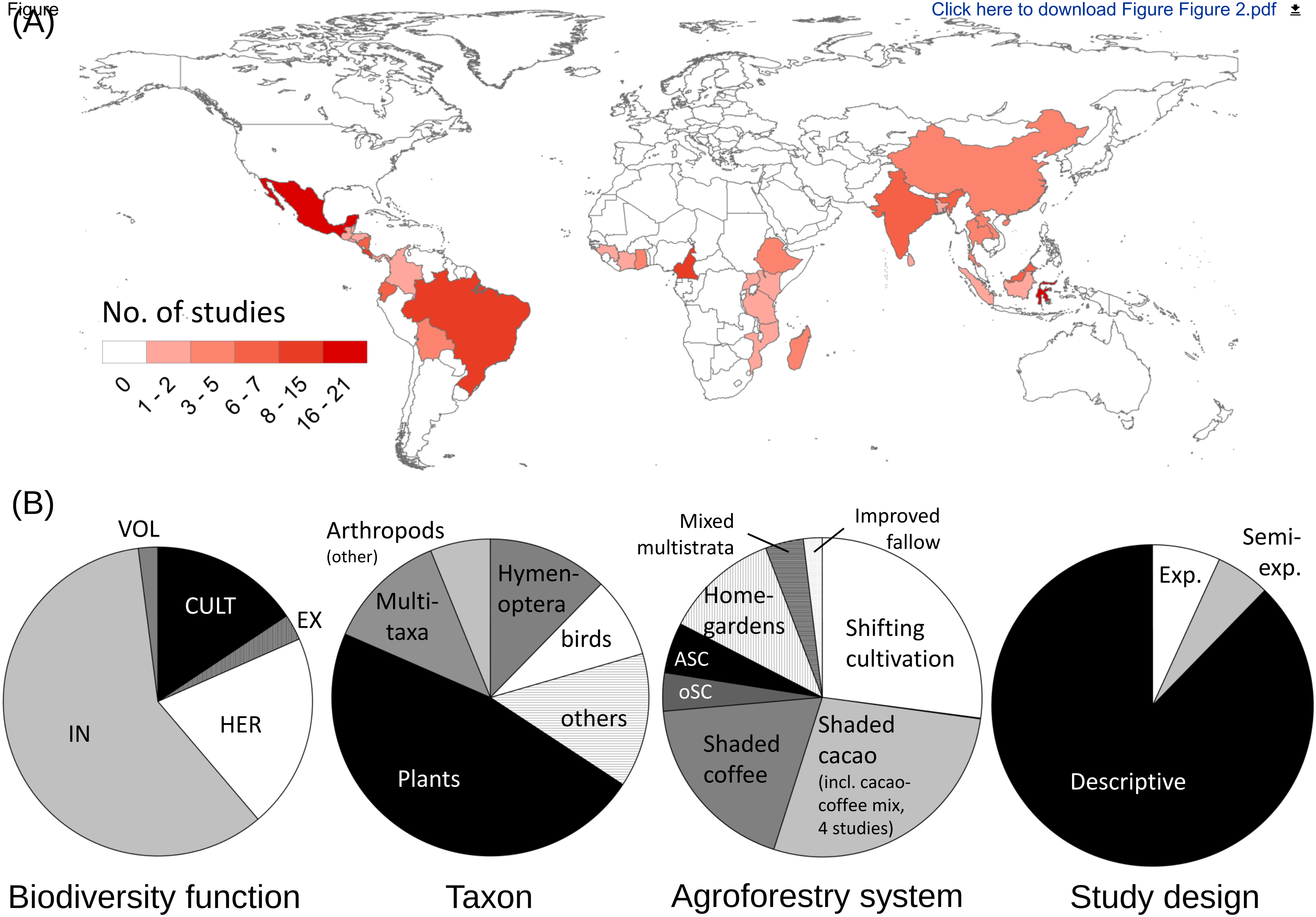
Table 4 Management influences tested on biodiversity in shaded cacao systems. All studies from the humid forest ecoregion.

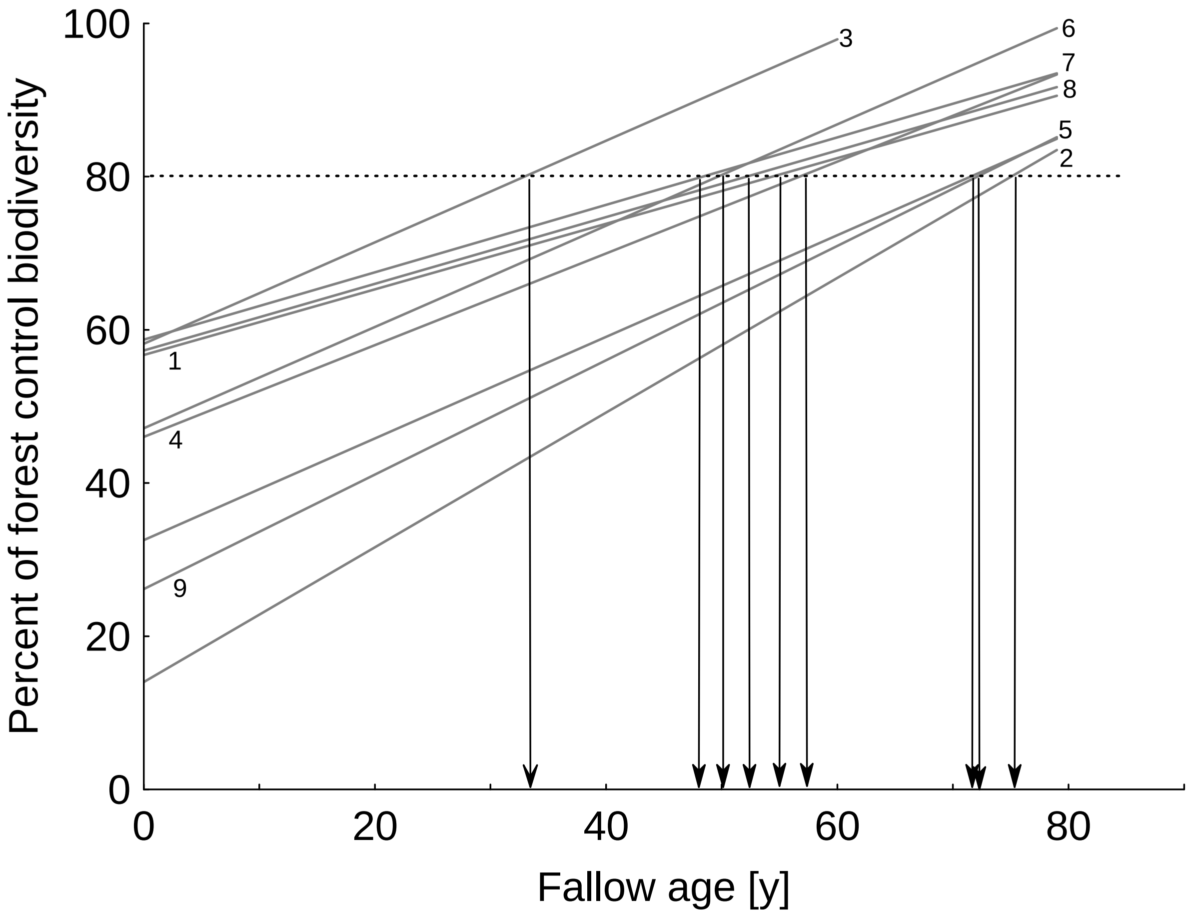
Table 5 Management influences tested on species richness in shaded coffee systems, all from humid forest ecoregions.

Table 6 Number of studies assessing effects of fallow age on biodiversity in shifting cultivation systems. NB Studies had at least 3 ages classes with a primary or old growth forest control; assessment of significance (sig., $p < 0.05$) is based on linear regression (ordinary least squares).

Table 7 Management and landscape configuration factors affecting biodiversity resilience in fallows of shifting cultivation systems.


tree-crop interface
long
short
irregular
taungya
agrisilviculture
alley cropping
other improved fallow
commodities (coffee, cacao, etc) under shade
trees in cropland
home garden
tree-epiphyte systems
shifting cultivation
planted timber trees
non-planted timber trees
planted other trees
+ forestry focus
+ agriculture focus


(A)
No. of studies
0
1 - 2
3 - 5
6 - 7
8 - 15
16 - 21
(B)
VOL
CULT
EX
HER
IN
Biodiversity function
Arthropods
(other)
Multi-
taxa
Hymen-
optera
birds
others
Plants
Taxon
Mixed
multistrata
Improved
fallow
Home-
gardens
Shifting
cultivation
ASC
oSC
Shaded
coffee
Shaded
cacao
(incl. cacao-
coffee mix,
4 studies)
Agroforestry system
Semi-
exp.
Exp.
Descriptive
Study design


Percent of forest control biodiversity
100
80
60
40
20
0
0
20
40
60
80
Fallow age [y]
1
2
3
4
5
6
7
8
9

	Huxley, (1983) [3]	**Young (1989)[4]**	**Nair (1991)[5]**	**Sanchez (1995)[6]**	**Zomer et al. (2009)[7]**
minimum components	minimum of two plant species of which at least one is woody. animals optional.	woody perennial & crop and / or animal	trees (shrubs?) crop and /or animal	tree and crop and / or animal	woody perennials included within farming system
spatial mix required or only time sequence?	spatial mix required (not time sequence)	spatial mix or time sequence possible	ns	ns	ns
types of interactions required	interactions through environmental processes or management	both ecological & economic interactions	not specified	interactions (competition)	ns

	Study region, References	Planted timber trees	Non-planted timber trees	Fruit or bean trees	Commodity tree crops	Other trees (e.g. N-fixing, shade)	Starchy food crops	Vegetables	Others
Homegardens									
S	Java, Indonesia[28,32-35]		sometimes	guava	sometimes		cassava	X	X
S	N Brazil [36-38]		X	X	X		X	X	X
S	Mexico[39]			orange, avocado			X	epazote *(Dysphania ambrosioides)*	coconut, *Aloe vera*
Improved fallow (alley cropping)									
S	SE Nigeria[20]					*Dactyladenia barteri*	maize, yam		
S	NW Cameroon*					*Tephrosia vogelii*	maize		
Agrisilvicultural systems: taungya									
S	Lao PDR[25]	Teak (*Tectona grandis)*					upland rice (*Oryza sativa*)		
L	Nigeria[40]	Teak, sapele (*Entandro-phragma cylindricum*), African mahogany (*Khaya ivorensis*), bibolo (*Lovoa trichilioides)*					X		

S / L	Ghana[41-43]	Teak, Cedrela (*Cedrela odorata*), Eucalypts, Cassia (*Cassia siamea*), Wawa (*Triplochiton scleroxylon*), Ofram / fraké (*Terminalia superba*), Emira / framiré (*Terminalia ivorensis*), Mansonia (*Mansonia altissima),* African mahogany, mahogany (*Khaya anthotheca*), and Edinam (*Entandrophragma angolense*)					cassava, plantain (*Musa* AAB), maize	pepper, okra, tomatoes, cabbage	
L	Thailand[44]	teak, *Eucalyptus camaldulensis*, chinaberry (*Melia azedarach*)					upland rice, maize, sorghum		
S /L	Indonesia[26,27]	teak					X		
L	India[45,46]	sal (*Shorea robusta*)							cotton, jute
L	Shamba, Kenya[47-49]	cypress (*Cupressus lusitanica*), pines (*Pinus patula, P. radiata),* *Eucalyptus*, *Araucaria*, *Acacia*			robusta coffee, cashew		maize, potatoes, peas		
Agrisilvicultural systems: long-term									

S	Indonesia[28-30]	damar (*Shorea javanica*)		durian (*Durio zibethinus*), rambutan (*Nephelium lappaceum*)	coffee			black pepper, *Piper nigrum*
Shade Commodities								
S	Indonesia[50-52]		X	rambutan, stink beans (*Parkia speciosa*), kerdas beans (*Archidendron bubalinum)*	rubber (*Hevea brasiliensis*),			palms
S	N Thailand[53]		remnant forest trees		tea, (*Camellia*)			
S	Ghana, S Cameroon[54-57]	X	X		cacao, safou (*Dacryodes edulis)*	X		
S	Brazil, particularly Bahia1[58,59]	*Caesalpinia echinata*	X	*Spondias mombin*	cabruca systems: cacao, rubber	*Erythrina sp.*, *Inga sp.*		
S	Venezuela [60,61]				cacao, arabica coffee	X	X	
S	Costa Rica[62]		X	X	arabica coffee			palms

	Control habitat present				**Biodiversity difference**			**Relationship biodiversity and productivity**		
System type	**N**	**Only forest**	**Only agr.**	**Both**	**N***	**Lower than forest**	**Higher than agr.**	**N**	**Positive**	**Negative**
Shifting cultivation	42	23	3	8	-	-	-	0	0	0
Homegarden	18	3	0	2	0	0	0	1	0	0
Agrisilviculture	8	2	0	1	0	0	0	1	1	0
Shade commodities	78	36	3	6	14	8	6	4	0	1
Other	9	3	0	0	2	2	0	0	0	0
Total	**155**	**74**	**8**	**24**	**16**	**10**	**6**	**6**	**1**	**1**

N = number of tests with relevant data; *) studies on fallows in shifting cultivation systems were excluded from this comparison.

Taxon, reference	**Localitry**	**shade level**	**density of flowering plants**	**fungicide application**	**insecticide application**	**weeding frequency**	**fertilizer app N**
V							
B	E	+ve	-	-	-	-	-
B	SI	+ve	-	-	-	-	-
A	SI	ns	-	-	-	-	-
R	SI	ns	-	-	-	-	-
I							
P	AB	+ve	-	-	-	-	-
B	SI	ns	+ve	-	-	-	-
S	SI	ns	-	-	-	-	-
B	SI	ns	-	-	-	-	-
C	SI	ns	-	-	-	-	-
B	SI	ns	-	-	-	-	-
W	SI	ns	-	-	-	-	-
P	SI	ns	-	-	-	-	-
A	SI	ns	-	-	-	-ve*	ns
A	SI	ns	-	-	ns	-	-
L	SI	ns	-	-	-	-	-
L	SI	ns	-	-	-	-	-
E	CC	-	-	ns	-	-	-
T	CC	-	-	ns	-	-	-
A	CC	+ve	-	-	-	-	-
P							
T	AB	+ve	-	-	-	-	-
T	SI	ns	-	-	-	-	-
T	CC	+ve	-	-	-	-	-
E	SI	ns	-	-	-	-	-
H	SI	ns	-	-	-	-	-
H	CC	+ve	-	-	-	-	-
L	SI	+ve	-	-	-	-	-
L	SI	ns	-	-	-	-	-

T	**+ve**	**8**	**1**	**0**	**0**	**0**	**0**
	-ve	**0**	**0**	**0**	**0**	**1**	**0**
	ns	**17**	**0**	**1**	**1**	**0**	**1**

Key: ns = not significant, **+ve** = significantly positive at P <0.05; **-ve** significantly negative at P<0.05; E = Ecuador, CC = central Cameroon, SI = Sulawesi, Indonesia, AB = Atlantic Brazil. *high (6 y^{-1}) or low (2 y^{-1}) frequency.

Reference	Region	Taxa	Shade level	Distance to forest
[137]	Sulawesi, Indonesia	Bees	-	-ve
[137]	Sulawesi, Indonesia	Wasps	-	-ve
[137]	Sulawesi, Indonesia	Parasitoids of bees & wasps	-	-ve
[138]	Ecuador	Ants	ns	-
[139]	Chiapas, Mexico	Bats	ns	-
[140]	El Salvador	Trees >2 m height	+ve	ns

Key: ns = not significant, **+ve** significantly positive at P <0.05; **-ve** significantly negative at P <0.05.

Taxon	**Sig.**	**Not sig.**	**Refs**
Vertebrates	1*	4[§]	[143-145, 146[y]]
Trees	2	6	[146-153]
Invertebrates	2**	1[§§]	[100,148,154]
All plants	4	3	[90,151,155-159]
Totals	**9**	**14**	

*) Birds; [§]) Bats, frogs & lizards, small mammals, forest birds; [y]compares all birds with forest birds**)Beetles, butterflies, [§§]) Ants.

refs		agroecoregion	taxa	fallow ages (y)	current fallow age	**# crop-fallow cycles**	previous cropping duration	previous fallow age	**previous tillage regime**	average fallow duration	**distance to forest edge**	**area of surrounding forest**
[160]	Lao PDR	HF	juvenile trees	7-10	-	ns	-	-	-	-	-	-
[161]	Belize	sDF	all plants	1 - 10	ns	-	-	-	-	-	ns	-
[156]	Madagascar	HF	tree seedlings	1-35	ns	**-ve**	-	-	-	ns	ns	-
			saplings	1-35	ns	**-ve**	-	-	-	ns	ns	-
			shrubs	1-35	ns	ns	-	-	-	ns	**-ve**	-
			herbs	1-35	**+ve**	ns	-	-	-	ns	ns	-
			adult trees	1-35	ns	ns	-	-	-	ns	ns	-
[162]	Madagascar	HF	all plants	1-5		-	ns	-	ns	-	-	-
			all plants	6 -10	**+ve***	-	ns	-	**-ve**	-	-	-
			all plants	11-29		-	ns	-	**-ve**	-	-	-

[163]	Amazonia, Brazil	HF	trees, shrubs, palms, lianas	5	-	ns	-	ns	-	-	-	**+ve**
[164]	Madagascar	HF	topsoil seedbank	1- 26	**+ve**	-	ns	-	**-ve**	-	-	-
[143]	S E Mexico	HF	bats	3,8	ns	-	-	-	-	-	ns	-
[148]	Sarawak, Malaysia	HF	butterflies	1, 5-13, 20-60	**+ve**	-	-	-	-	-	**-ve**	-
			Sums, by factors tested	+ve	**4**	**0**	0	0	**0**	0	**0**	**1**
				-ve	**0**	**2**	0	0	**3**	0	**2**	**0**
				ns	**6**	**5**	4	1	**1**	5	**6**	**0**

Key: *Significant between 1-5 and 6-10y fallows but not significant between 6-10 and 11-29 y fallows; ns not significant, **+ve** significant at P<0.05 and positively associated; **-ve** significant at P<0.05 and negatively associated; HF humid forest; sDF seasonally dry forest, - not tested. ^{x}refers to a no-tillage versus “heavy” tillage comparison.