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Effect of plant diversity on income generated by agroforestry systems in Talamanca, Costa Rica

Ricardo Salazar-Díaz · Philippe Tixier

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Abstract Optimal use of resources in agroforestry requires the evaluation of multi-species and multi-strata cropping systems. The current study evaluated the effect of plant diversity on the performance of agroforestry systems in Talamanca, Costa Rica. Plants in nine 100-m^2 plots in each of 20 fields were classified into five groups (banana, cacao, other fruits, timber, and firewood), and diversity was assessed by the Shannon–Wiener index. The production of each individual plant was estimated and converted into income according to local market prices. Our results indicated that as plant diversity increased, the income derived per plant increased for other fruits, firewood, and timber and also when all cultivated plants were considered as one group. In contrast, the income derived per plant decreased for banana and cacao as diversity increased. This suggests that complementarity between plants was stronger than competition for those plants occupying the higher strata of the canopy (i.e., other fruits, firewood, and timber) but that competition was stronger than complementarity for plants occupying the lower strata of the canopy (i.e., banana and cacao). These results increase our understanding of how the composition and the organisation of these agroforestry systems may be optimized.

Keywords Multi-strata agroforestry systems · Productivity · Musa · Cacao · Global evaluation · Economic value

R. Salazar-Díaz
ITCR, Escuela de Agronegocios, 7050, Cartago 30101, Costa Rica

R. Salazar-Díaz · P. Tixier (✉)
CIRAD, UPR GECO, 34398 Montpellier, France
e-mail: tixier@cirad.fr

R. Salazar-Díaz · P. Tixier
GECO, Univ Montpellier, CIRAD, Montpellier, France

P. Tixier
CATIE, Departamento de Agricultura y Agroforestería, 7170, Cartago, Turrialba 30501, Costa Rica

Introduction

Tropical agroforestry systems are often complex associations of multi-functional and uneven-aged trees and crops (Sanchez 1995). Such systems also have a complex spatial and temporal structure (Bhagwat et al. 2008) and are frequently presented as a sustainable alternative to modern intensive agricultural systems (Leakey et al. 2005; Ngo Bieng et al. 2013; Tscharntke et al. 2010). Many people in developing tropical countries depend on agroforestry systems for subsistence, economic income, and other services (Cerda et al. 2014; Malezieux et al. 2009; Paul et al. 2015). In addition to generating timber and firewood, agroforestry can also provide supplementary income from associated tree crops (Nair 2007). In many systems, however, the economic productivity, efficiency, and profitability of agroforestry farms have not been determined, i.e., there is need to quantify the costs and benefits of agroforestry farms in order to justify their propagation and adoption (Molua 2003). From both private and social perspectives, the economic potential of agroforestry farms has not been well studied (Franzel and Scherr 2002; Molua 2003; Rasul and Thapa 2006). The combined productivity and profitability of all cultivated plants in the system, i.e., have scarcely been addressed in complex agroforestry systems. This led us to determine whether farmers derive more income from complex than from simple agroforestry systems. The evaluation of multi-species and multiple-strata cropping systems remains a major challenge (Lamanda et al. 2012).

The practice of agroforestry, i.e., of growing trees and crops together, is frequently promoted based on the idea that trees benefit crops; otherwise, farmers would probably not include the trees (Vandermeer et al. 2002). Species richness and vegetation structure are key components of structural complexity and form the basis of biodiversity (Hooper et al. 2005b). Biodiversity increases the efficient use of resources and promotes positive interaction between species and other ecosystem processes (Cardinale et al. 2012; Hooper et al. 2005a; Nakamura 2008; Smith et al. 2008; Tilman and Pacala 1993). According to Lehman and Tilman (2000) and de Aguiar et al. (2013), diversity increases community productivity but may reduce the productivity of individual species. The negative effects of competition, which can lead to lower productivity in some species, are offset by complementarity and facilitation between other species, enabling greater productivity at the community level, i.e., greater global productivity.

The Talamanca region in Costa Rica is characterized by highly diversified cropping systems. The natural environment of the Talamanca region has been an inherent part of the life of the indigenous Bribris and Cabecares (Boza 2014). In this region, agroforestry systems tend to mimic the forest both in structure and in species. The association of species follows ancestral rules linked to their functional role (Borge and Castillo 1997). The variability in the composition and structure of the agroforestry systems, however, have been poorly described, and their relevance to ecosystem performance has been little investigated (Deheuvels et al. 2012). The evaluation of the global productivity in these systems is challenging because of the diversity of the plants that are grown.

The agroforestry systems in the Talamanca region include cacao (*Theobroma cacao* L.) and organic banana (*Musa* spp. AAA). Cacao is usually grown with other fruit trees and with shade trees, such as laurel (*Cordia alliodora* Ruiz and Pav.) or cedar (*Cedrela odorata* L.). These shade trees represent species from the natural forest and are either planted or are naturally growing remnants. Banana is an important crop for farmers and is grown with citrus (*Citrus* spp.), avocado (*Persea americana* Mill.), peach palm (*Bactris gasipaes* Kunth), and other fruit trees. Farmers claim that these other fruit trees grow well with cacao and banana (personal communication). Other species, such as jicaro (*Crescentia cujete* L.) and senko (*Carludovica palmata* Ruiz and Pav.), are used for crafts, while guava (*Inga* sp.) and turkey tail (*Cupania cinerea* Poepp.) are used for firewood.

In this study, we estimated the productivity and associated income of all plants cultivated in nine 100-m^2 plots in each of 20 agroforestry fields in the Talamanca region. We provide the first assessment of the global income generated by these systems. We also investigated how the cultivated plant diversity affects the global income and per type of plant.

Methods

Experimental site

This research was performed within the Bribri indigenous territory of Talamanca in Limón Province, south-eastern Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). In this region, most people obtain their livelihood from agriculture. The average annual precipitation is 3570 mm, and the average annual temperature is 25.9 °C. The climate is classified as tropical rain forest (bh-T) (Holdrige 1978).

Data collection

We studied a network of 20 agroforestry fields that included a wide range of diversity and spatial organization. Each field was 900 m^2 (30 m × 30 m). The fields were in four villages (Amubri, Dururpe, Katsi, and Watsi) and were located 200–400 m a.s.l. The farms were selected according to the following criteria: (1) the farmer was available and willing to participate in the research, (2) the farm area was relatively flat, and (3) the farm had the potential to produce at least one commercial crop. Each field was divided into nine plots (10 m $\times$ 10 m), and plot was the statistical unit used in the rest of the study.

We identified and determined the coordinates for all of the cultivated plants (with a commercial value) in all plots. Each plant was tagged, allowing multiple measures over time. Overall, our dataset included 2299 plants. Herbaceous plants were not recorded.

Global productivity

To estimate banana yield, we measured the circumference of the pseudostem of the mother plant (1 m above ground level) and the heights of the sucker plants. Using allometric relationships, we estimated the potential production of banana and vegetative tissue for each banana plant (Fernándes and García 1972). In addition, we measured the weight of available bunches and counted the fruits. Every banana stem was followed during 1 year to precisely measure those that were harvested or lost when plants were pruned or toppled-over.

To estimate cacao yield, we counted healthy cacao pods during the peak harvests in May and November. According to Braudeau (cited by Deheuvels et al. 2012), each pod produces an average of 185 g of fresh cacao beans. We multiplied this estimate of bean fresh weight by 0.56 to estimate the dry cacao commercial yield.

For every timber tree, total height, commercial height, and DBH (diameter at breast height) were measured with a hypsometer and a diametric tape. Cubic meters of wood were calculated based on empirical relationships reported by Almendarez et al. (2013) and with a form factor of 0.7 for timber species. With firewood species, we applied the same method using a form factor of 0.5.

Production of fruits other than banana and cacao was estimated for each tree using theoretical values reported by another study in the same region (Burgos et al. 2008).

We estimated the incomes generated by each category of plant according to local market surveys of product prices provided by an association of smallholder farmers from Talamanca (APPTA); the estimates were converted into US dollars. Costs of labour, crop management, and land use were not included in our analysis. The market price of the products considered in our study were: banana \$0.14/kg, cacao \$2.25/between species kg, timber \$5/m^3/yr (corresponding to \$75/m3 divided by the 15 years of the average age of commercial trees, regardless of species), firewood \$0.03/m^3, and other fruits between \$0.18 and \$1.80/kg depending on the species.

Plant diversity

Cultivated plant diversity in each plot was calculated using the Shannon–Wiener index, (Shannon 1948), which was calculated with the ‘diversity’ function of the ‘vegan’ package, version 2.2-1 (Oksanen et al. 2015).

We also assigned each plant to one of five categories: (1) banana, (2) cacao, (3) other fruit trees, (4) timber, and (5) firewood. Cacao and banana are mainly sold for the international market, while other fruit, timber, and firewood are sold locally or used for self-consumption.

Statistical analyses

Generalized linear mixed-effects models (Bolker et al. 2009) were used to examine the relationship between the income generated by each group cultivated plants and plant diversity in each of the 180 plots. We considered the field as a random effect. To analyse the effect of plant diversity on each group, income was expressed per plant to remove the effect of density. Income was considered globally when considered at plot scale. The GLMMs were fitted by the Laplace approximation using the ‘lmer’ function in the ‘lme4′ package (Bates et al. 2011). All statistical analyses were performed with R 3.3.1 (R Core Team 2016) and with an alpha level of 0.05.

Results

Cultivated plant diversity

Based on plant composition and spatial structure, the fields ranged from the relatively specialized (e.g., field 6 and 14) to the very complex (e.g., field 16 and 17) (Fig. 1). We identified 56 taxa (species and varieties) of cultivated plants in the 20 fields (Table 1). The timber category included 11 species; *Cordia alliodora*

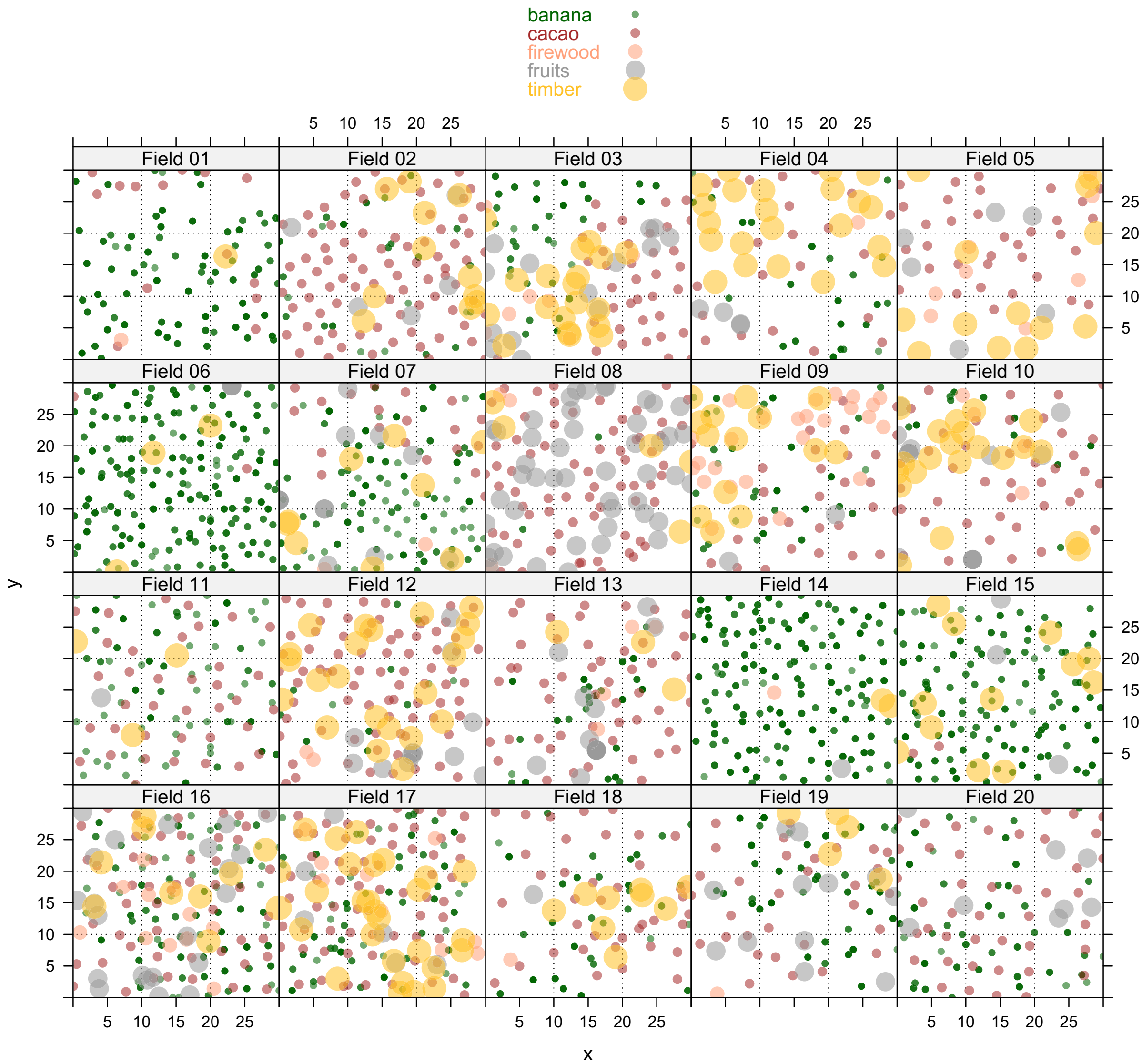

Fig. 1 The diversity and spatial distribution of individual cultivated plants in 20 agroforestry fields in Talamanca, Costa Rica. Each plant was assigned to one of the five categories indicated at the top. The *X* and *Y* coordinates are in meters. Plots within fields are delineated by dotted lines

Ruiz and Pav was the most abundant, representing 84% of the individuals. *Cedrela odorata* L., *Dipteryx panamensis*, and *Chloroleucon eurycyclum* were much less abundant species in the timber category. *Cupania cinerea* Poepp. and *Inga edulis* represented 56% of the 18 firewood species. Fruits other than banana or cacao was the most diverse group with 22 taxa; *Citrus* × *sinensis*, *Bactris gasipaes* Kunth, and *Persea americana* Mill represented 26, 21, and 13%, respectively, of the trees in this category. *Annona muricata*, *Morinda citrifolia*, and *Carica papaya* were also in the other fruits category but were represented by only one individual on specific farms. Cacao (*Theobroma cacao* L.) trees were all hybrids belonging to the Trinitarian variety. We identified eight varieties of banana *Musa* spp., and these were from the AA, AAA, AAB, and ABB groups.

Income

Income generated per plant was highest for the other fruits group, followed by the banana, cacao, and

Table 1 Names and abundances of the plants in the 20 agroforestry fields studied in Talamanca Costa Rica. The plants were assigned to five categories or groups. Abundance refers to the number of plants in all 20 fields

Group/taxa	Abundance	Group/taxa	Abundance
Cacao group		Timber group	
Hybrid	750	*Cordia alliodora*	178
		Cedrela odorata	15
Banana group		*Dipteryx panamensis*	3
Cavendish AAA	340	*Hyeronima alchorneoides*	1
Grosmichel AAA	277	*Chloroleucon eurycyclum*	3
Lacatan AA	158	*Gliricidia sepium*	2
Musa spp. AAA	248	*Brosimum alicastrum*	1
Musa spp. AAB	92	*Diphysa americana*	1
		Enterolobium cyclocarpum	1
Fruits group		*Brosimum lactensis*	2
Citrus × sinensis	38		
Citrus × paradisi	1		
Citrus × tangerina	5		
Citrus × aurantifolia	3	Firewood group	
Citrus × limonia	2	*Cupania cinerea*	24
Bactris gasipaes	32	*Inga edulis*	19
Persea americana	19	*Cecropia obtusifolia*	2
Crescentia cujete	10	*Erythrina costaricensis*	1
Nephelium mutabile	8	*Cordia panamensis*	8
Artocarpus communis	7	*Palicourea tetragona*	2
Averrhoa carambola	5	*Croton billbergianus*	3
Licania platypus	5	*Neea psychotrioides*	3
Eugenia malaccensis	3	*Naucleopsis naga*	1
Eugenia stipitata	3	*Trichospermum grewiifolium*	1
Cocos nucifera	2	*Cordia lucidula*	3
Annona purpurea	1	*Bursera simaruba*	2
Annona muricata	1	*Miconia trinerve*	1
Mangifera indica	1	*Spondias mombin*	2
Carica papaya	1	*Cestrum schlechtendalii*	1
Morinda citrifolia	1	*Alchornea costaricensis*	1
Bixa orellana	1	Ocotea mollifolia	1

timber groups, which had similar incomes (Fig. 2). Income generated was much lower for the firewood group than for the other four groups. Annually, the average production was 7351 kg ha^{-1} for banana, 191 kg ha^{-1} for cacao, 26 m^3 ha^{-1} for timber, and 5.25 m^3 ha^{-1} for firewood.

Cultivated plant diversity had a significant effect on the income generated per plant in each category. As diversity increased, income per plant decreased for banana and cacao but increased for other fruits, timber, and firewood, and also increased when all cultivated plants were considered as one group, i.e., global income increased with diversity (Table 2, Fig. 3).

Discussion

Cultivated plant diversity

The 180 agroforestry plots in Talamanca, Costa Rica, exhibited a large range of plant diversity (the Shannon–Wiener index ranged from 0 to > 2), and the high diversity in some of these fields confirmed previous

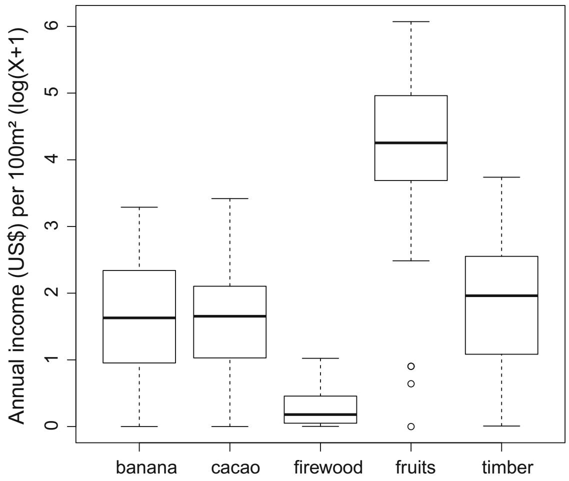

Fig. 2 Estimated mean incomes (log transformed) for each plant group summed in each of the 180 plots in 20 agroforestry fields in Talamanca, Costa Rica

reports (Borge and Castillo 1997; Deheuvels et al. 2012; Guiracocha 2000; Kapp 1989). Plant density and spatial organization (Fig. 1) suggested that farmers consider banana and cacao as the primary crops and timber and other fruits as secondary or complementary crops.

As pointed out by the farmers interviewed, these complex cultivated plant communities reflect two main management strategies: (1) to establish cacao and banana in remnant forests, and (2) to establish other fruits during the natural regeneration of timber and firewood trees. Trees from natural regeneration are usually preferred because they do not have to be purchased. In addition, regenerated trees are generally thought to be better adapted than planted trees to site conditions (de Sousa et al. 2016). The range in species diversity observed in this study was similar to that observed in previous studies (Anglaaere et al. 2011; Deheuvels et al. 2012; Ngo Bieng et al. 2013).

Global productivity

Banana was the most abundant group with an average population density of 1100 plants ha^{-1}, which is not very different from the population density in intensively managed commercial plantations (1600–1900 plants ha^{-1}). This highlights the importance of banana to the agroforestry farmers in Talamanca, Costa Rica.

The average productivity of cacao was 191 kg ha^{-1} year^{-1}, which was somewhat higher than the 136 kg ha^{-1} year^{-1} reported by Deheuvels et al. (2012) for similar agroforestry systems in Talamanca. Such yields are substantially lower than those of cacao agroforestry systems in Ghana and Ivory Coast, which average 456 and 214 kg ha^{-1} year^{-1}, respectively (Gockowski and Sonwa 2011). As noted by Deheuvels et al. (2012), the low cacao yields in Talamanca result from the absence of chemical input and from losses caused by the fungus *Moniliophtora roreri*, the agent of cacao frosty pod rot disease.

The average *C. alliadora* timber production in the current study (26 m^3 ha^{-1}) was substantially lower than the 48 m^3 ha^{-1} recently reported for Central America (Somarriba et al. 2014). This may result from differences in sites and planting densities. Although

Table 2 Relationship between income generated per plant (in each of five categories plus all categories of plants) and plant diversity in 180 plots in 20 agroforestry fields in Talamanca Costa Rica. A generalized linear model including field as a random effect was used for the analysis. The significance of plant diversity was tested against the null model. Note that increases in diversity decreased income per plant for banana and cacao but increased income per plant for the other categories

Response variable	Df	Estimate	AIC	ΔAIC	log-Likelihood	Chi-sq	*p*
All plants	3	66.61	2059.35	20.48	− 1026.67	22.48	< 0.0001
Banana	3	− 0.12	10.01	5.25	− 2.01	7.25	0.0071
Cacao	3	− 0.23	240.90	5.03	− 117.45	7.03	0.0080
Fruits	3	3.70	1197.72	7.15	− 595.86	9.15	0.0025
Firewood	3	0.01	− 753.33	2.50	379.67	4.50	0.0340
Timber	3	0.26	288.56	5.30	− 141.28	7.30	0.0069

Df degrees of freedom, *AIC* akaike information criterion, *ΔAIC* difference of AIC with the null model, *Chi-sq* value of the Chi square test, *p* p value of the Chi square test

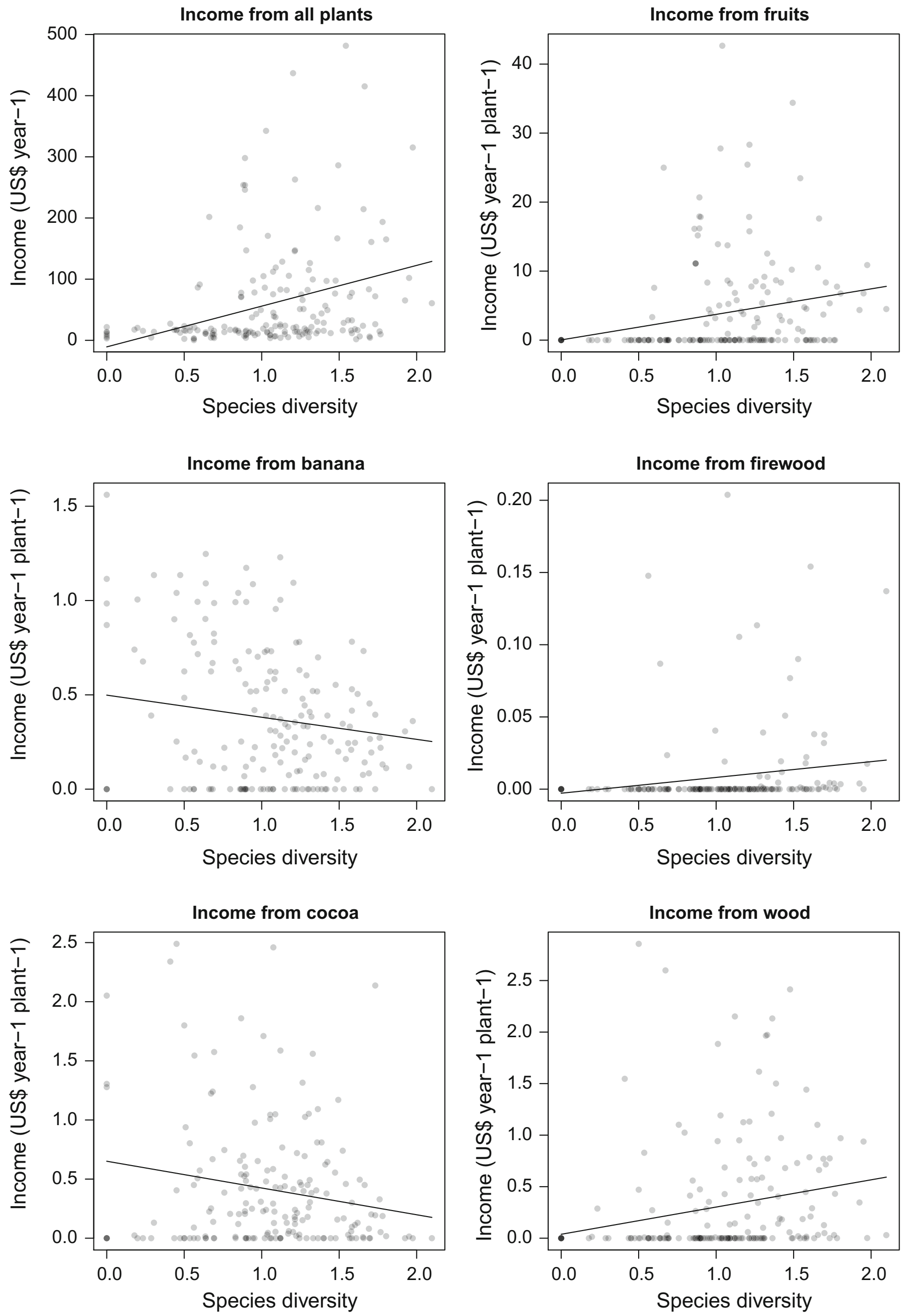

Fig. 3 Total mean income for all plants (global income) and in each group in response to plant species diversity in 20 agroforestry fields in Talamanca, Costa Rica. Diversity was assessed using the Shannon–Wiener index. Each circle indicates the mean value from one of the 180 plots. The lines show the prediction of the generalized linear model that included field as a random effect

the yields in the current study are low, they clearly represent a key economical input for smallholders, especially when cacao prices are low (Ramírez et al. 2001). Relative to timber, firewood is not a key economic input and averaged 43 trees ha^{-1}, which corresponds to 5.25 m^{3} ha^{-1}. According to the farmers interviewed, these species are not sold but are used by the farmers themselves.

The evaluation of the productivity of other fruits trees was difficult because of their seasonal variation. Our estimation of income from these fruits tree is clearly higher than other cultivated plants (Fig. 2). Although farmers don't have production records, this result is consistent with farmer's perception since they claim good yielding for fruit trees.

Relationships between income and plant diversity

Our results indicate that the effect of plant diversity on income depended on the plant group producing the income (Fig. 3). Income generated by higher strata plant groups (other fruit trees, timber, and firewood) were positively correlated with plant diversity, while income generated by lower strata plant groups (banana and cacao) were negatively correlated with plant diversity. These results suggest that complementarity rather than competition dominated for the higher strata plants. Similar results have been reported in tropical and temperate forests (Hooper et al. 2005b; Jucker et al. 2014; Zhang et al. 2012). In contrast, competition rather than complementarity apparently dominated for the lower strata cultivated plants. We suspect that the negative relationship between income generated by banana and cacao and plant diversity mainly resulted from competition for light.

For the higher strata, our results are in-line with other studies that showed that functional complementary or facilitation may occur in complex plant communities (de Aguiar et al. 2013; Franco et al. 2015; Hooper and Vitousek 1997; Smith et al. 2008). As noted, however, the effect of diversity became negative at a lower canopy level in the current study. This suggests that when light becomes scarce, complementarity is reduced. This hypothesis is consistent with previous studies that found that overyielding is reduced when the availability of an essential resource (mineral nitrogen in soil) decreases (Dybzinski et al. 2008; Jarchow and Liebman 2012; Lebauer and Treseder 2008; Reich et al. 2003). Our result is inconsistent with the gradient stress hypothesis, which predicts that interactions among plants shift from facilitation to competition as environmental stress decreases (Maestre et al. 2009). When all cultivated plants were treated as one group in the current study, the income per plant was positively related to plant diversity. This positive relationship was largely explained by the other fruits group, whose positive relationship with diversity more than countered the negative relationships for banana and cacao. Although we tried our best to assess the real value of other fruits, we may have slightly overestimated the value because some fruits are consumed by the grower and are not sold. This study suggests that an increase in the density of other fruit trees and therefore in fruit production could increase farmer income, but this possibility is limited by the poor access to markets in the region. Extension services and government incentives should probably focus on organizing distribution channels to facilitate the sale of fruit produced from these systems.

Our results show that the effect of diversification on farmer income reflects a close balance between complementarity and competition. The results also suggest that complementarity might be increased by increasing plant diversity within the same stratum of the canopy. This could lead to some specialisation within fields such that banana are grown in one part of the field and other trees are grown in other parts.

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