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Individual-based analysis of interactions between plants: A statistical modelling approach applied to banana and cacao in heterogeneous multistrata agroecosystems in Talamanca, Costa Rica

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ABSTRACT

Understanding how the spatial organization of diversified plant communities alters their performance is an important step in designing and managing diversified agroecosystems. The high level of spatial heterogeneity in tropical agroforests makes this task challenging. In 19 agroforestry plots in Talamanca (Costa Rica), we analyzed the effect of the structure of the plant community in the neighborhood of each individual cacao tree and banana plant on their growth and yield parameters. We developed an individual-based analysis in two steps. First, we selected without *a priori* the distance at which the number of neighboring plants of a given functional group (banana plants, cacao trees, fruit trees, or wood trees) best explained the proportion of attainable yield (PAY) of cacao and banana plants. In a second step, we tested the significance of the abundances of the four groups of plants in a complete model that predicted the PAY of banana and cacao plants. The abundance of neighboring plants did not increase banana PAY except in the case of other banana plants, suggesting that banana plants yield better when aggregated. All other groups of plants tended to reduce both banana and cacao PAY. In the case of wood trees, these trends were not significant. Interestingly, our results suggests that it is possible to associate banana plants and cocoa trees to moderate densities of other plants without reducing their yield. The two complete linear models predicted about 60 % of the variance of the average response of the PAY to the neighboring plant assemblage. We suggest that in the future, it would be important to differentiate processes (resources partitioning, pest and diseases) inside our statistical approach. While requiring much more data, it could be useful to address the effect of cultural practices.

1. Introduction

Researchers have studied tropical agroforests, especially smallholder diversified production, as models for sustainable agricultural intensification (Sperber et al., 2004; Leakey et al., 2005; Tscharntke et al., 2011). Tropical agroforests are characterized by associations of multi-strata, multi-functional, and uneven-aged trees and crops, resulting in high species richness and high structural complexity of the vegetation (Sanchez, 1995; Ngo Bieng et al., 2013). Few authors have tried to link the structural complexity of different land uses to productivity (Steffan-Dewenter et al., 2007). Understanding how the local plant arrangement affects productivity is important for improving the design and management of complex systems (Monzeglio and Stoll, 2005). However, the substantial spatial heterogeneity of highly diversified systems makes this task challenging. In such complex systems, each plant has a unique "neighborhood" in terms of i) light availability, ii) competition for nutrients, and iii) pest and disease populations, making the establishment of generic rules at the field scale extremely difficult.

In the Talamanca region of Costa Rica, researchers have described how agroforests provide ecosystem services (such as carbon sequestration and biodiversity conservation) but have paid far less attention to how the overall productivity of such forests is related to their structure (Somarriba and Harvey, 2003; Suatunce et al., 2003). These descriptive studies led the authors to suggest that improvements in crop management, including improvements in spatial organization, are needed to increase overall productivity versus productivity of individual crops.

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The evaluation of productivity in the agroforestry systems in the Talamanca is challenging because of the diversity of the plants that are grown. These systems can include from one to more than 30 associated tree species (Guiracocha et al., 2001; Salazar-Díaz and Tixier, 2019). Two important cash crops in this region are cacao (*Theobroma cacao* L.) and organic banana (*Musa* spp.), which are perennial and semi-perennial, respectively. In addition to often being grown together, cacao and banana are usually grown with other fruit trees such as citrus (*Citrus* spp.), avocado (*Persea americana* Mill.), and peach palm (*Bactris gasipaes* Kunth), and also with shade trees from natural regeneration, 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.

Even when a field is composed of plants of the same species, the processes that determine how individual plants compete for resources are complex, because plants are forced to share limited resources (Sinoquet and Cruz, 1995). The spatial organization of individuals in a community may be one of the most important structural characteristics that influence complementarity between species, biodiversity, and ecosystem functioning (Mokany et al., 2008; Perfecto and Vandermeer, 2008; Pringle et al., 2010). Few studies of vegetation structure in agroforests, however, have dealt with spatial organization, i.e., the horizontal organization of individuals in space and the relationships between individuals in a "neighborhood" (Illian et al., 2008; Ngo Bieng et al., 2011). Although spatial heterogeneity of plants is recognized as a powerful promoter of coexistence between plants (Monzeglio and Stoll, 2005), explaining species performances remains challenging in fields where plant spatial organization is heterogeneous (Ripoche et al., 2012). In such fields, an individual-based analysis (i.e., an analysis of individual plants, their properties, and their surroundings) may be useful (DeAngelis and Grimm, 2014). Primarily, each individual plant is assumed to interact with neighboring plants through the resources they are sharing including light, nutrients and water. Here we hypothesized that the competition or the facilitation processes depends on the structural functioning of each plant species (e.g. canopy structure, depth of the root systems, temporal dynamics of use resources) and on the distance between plants. The hypothesis of the dependency of plants interactions to their distance directly relies on the processes involved in i) resources' capture with the canopies and roots overlapping (Roupsard et al., 2020), ii) the indirect effect on resource availability in the system as the restitution of dead biomass to the ground thus altering the local soil fertility (Rao et al., 1997; Sauvadet et al., 2019), and iii) the effects on biotic constraints through multiple processes including: dilution effect following the resource concentration hypothesis (Root, 1973), barrier to pathogens (Ngo Bieng et al., 2017), and alteration of microclimate (Ratnadass et al., 2012). Our other hypothesis in this work was that the effects of one group of plants on another plant should be quantitative, i.e. more plants are expected to have a stronger effect than fewer plants.

Ideally, a spatially explicit process-based modeling of such complex agroforestry systems would be valuable to better understand their functioning (Dupraz et al., 2019). However, such approaches are not easily applicable i) because of the extremely high number of data that would be needed for parameterization in highly diversified systems, and ii) because some basic knowledge on some species included in these systems still need to be acquired.

In this paper, we analyzed how the organization of the plant community in the neighborhood of individual cacao and banana trees affects their yield (assessed by the proportion of attainable yield, PAY). We used a data set of 19 plots of agroforestry systems in Talamanca, Costa Rica. In a first steps, we determined the area around each banana plant or cacao tree (as indicated by a radius) in which the number of trees of a given neighboring group (including banana plants, cacao trees, fruit trees, or wood trees) best explained the PAY of cacao and banana. In a second step, we tested the significance of the abundance of the four groups of plants in a complete model that predicted the PAY of banana and cacao plants. Based on the results, we finally discuss how the production of banana and cacao can be optimized in complex, multi-strata agroecosystems.

2. Methods

2.1. Field sites

This research was performed in the Bribri indigenous territory of Talamanca, Limón Province, south-eastern Costa Rica (9°00′–9°50′ N, 82°35′–83°05′ W). The average annual precipitation is 3570 mm, with short dry season in March-April and in September-October (Somarriba et al., 2014) and the average annual temperature is 25.9 °C. The climate is classified as tropical rain forest (bh-T) (Holdrige, 1978). The studied sites contain typical agroforestry systems in which the principal commercial crops, banana and cacao, are accompanied by a wide range of other tree species. We studied a set of 19 agroforestry fields; each field was 900 m^2 (30m × 30m). The selected cropping systems represent the smallholder farms (2 ha on average) in the Talamanca region, and most of times the species spatial design follows indigenous ancestral rules that are linked to the trees' functional roles in natural forests (Borge and Castillo, 1997). Nevertheless, there are some differences within plots, in the species spatial design, according to farmers' goals.

2.2. Local plant arrangement

From February to April 2015, we identified and determined the coordinates for all of the cultivated plants (with a commercial value, we did not accounted for weeds that are regularly control manually all over the fields) in each plot. Plants without commercial value were not included in this study. Plants with commercial value were identified to either the species or family level and were assigned to one of four categories: banana plants, cacao trees, wood trees, and fruit trees. Wood trees include timberwood trees and firewood trees, this group were the tallest, forming the top canopy layer (with a maximum height of 40 m). The intermediate vegetation layers were represented by fruit trees (with a maximum height of 26 m), and cacao and banana were located in the lower strata (with an average height of 6 m The locations of plants of each category in each plot are shown in Figure S1. Plants shorter than 1.5 m were not recorded. The data set included 2299 plants, and the plant taxa in the data set are listed in Table S1.

2.3. Determination of the PAY for banana plants and cacao trees

Our goal was to determine for each banana plant or cacao tree how much of their attainable growth or production was achieved. We assumed that the attainable growth (banana plants) and attainable production (cacao trees) was depending on the size of each plant at the first date of measurement. By plotting the growth or the production according to the initial biomass or circumference, we were able to define an envelope curve that we assumed to represent the attainable growth or production of a plant for a given initial size. This attainable growth or production represents the maximal values in the conditions of our set of plots. Similarly to classical yield gap analyses (Neumann et al., 2010), we selected the shape of the envelop curves according to biological hypotheses with the finalization of the growth after flowering for banana plants and a decrease of the production for older cacao trees. We had a sufficient banana plants and cocoa trees in contrasted growing conditions (from low densities in the full sun to higher densities under shade trees) to be sure that we reach their attainable growth.

In each mat from the three varieties of banana plants cultivated in this region (Cavendish, Gros Michel, and Lacatan), we measured the girth (1 m above ground level and then converted in girth at 0.3 m above the ground level using an allometric relationship) of the pseudostem of the mother plant from the three varieties cultivated in these plots. During the measuring period in which we followed the growth of banana plant (from April 2015 and during 17 weeks), we precisely measured the

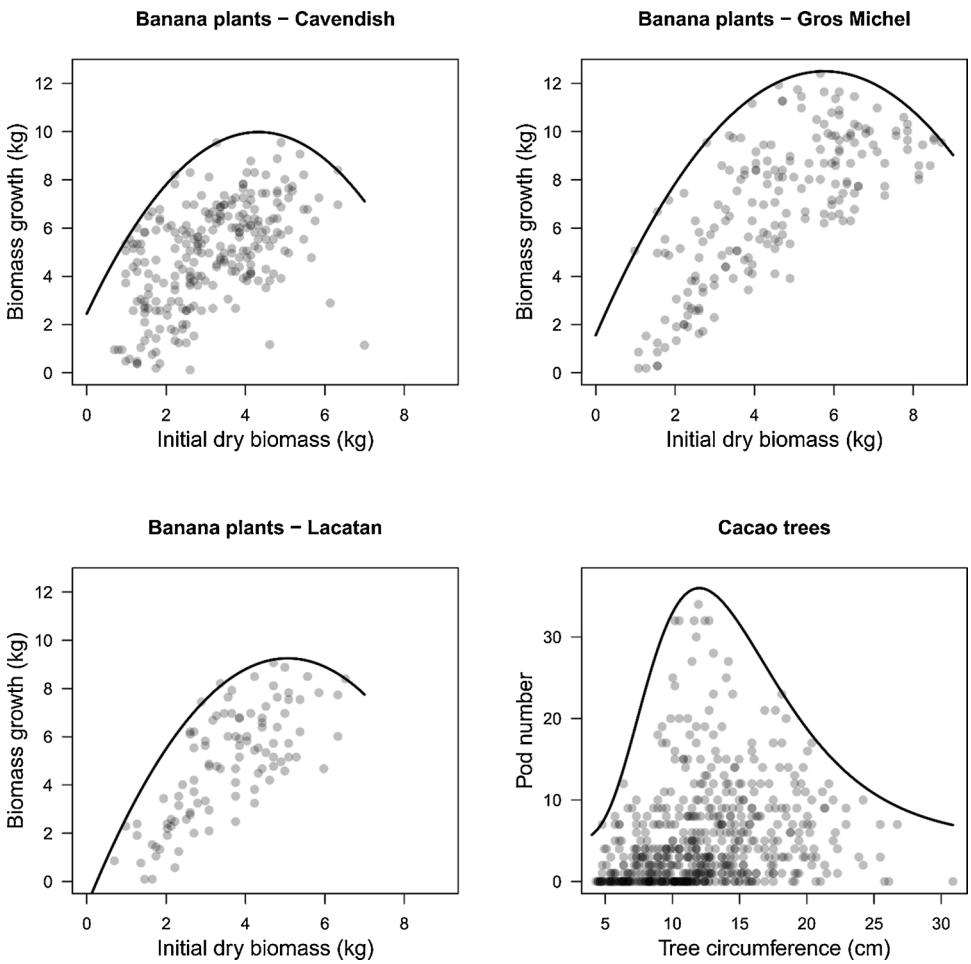

Fig. 1. Relationship between biomass increase and initial plant biomass for the three varieties of banana and between pod number and initial tree circumference (measured 1 m above soil) for the one variety of cacao. Each dot represents the data from a single banana plant or cacao tree. The increase in banana biomass was estimated over a 17-week period. Cacao pod numbers are the totals of two harvest periods. For the three banana varieties, the curves show that the vegetative growth rate increased up to the reproductive stage (partially linked to initial biomass) and then slightly declined. For cacao, the curve shows that the number of cacao pods increased as the initial tree circumference increased up to 13 cm and then greatly decreased.

mother plants that were harvested, and those lost by pruning or toppling-over.

We used allometric relationships to estimate banana vegetative dry biomass based on the circumference of the pseudostem of each mother plant (30 cm above ground level), following the equation (R. Achard, pers. com.):

$$\text{Dry Biomass} = 6.10^{-5}.\ \text{Girth}^{2.7116}$$

With the Dry Biomass in Kg and the Girth measured at 30 cm (in cm).

By measuring the circumferences again in July 2015, we were able to estimate the increase in vegetative biomass during the 17 weeks between measurements. The interval between measurements was identical for all plants. We assumed that the attainable growth of banana followed a parabolic curve. In this curve, the decrease in vegetative biomass growth for plants with bigger initial biomass corresponds to the progressive switch of banana from vegetative to reproductive growth (this later was not taken into account in our study). The proportion of attainable growth (PAY) for each banana plant was then calculated as the ratio of measured increase in biomass to attainable increase in biomass.

We estimated cacao yields by summing the healthy cacao pods counted on each tree during the two peaks of harvests in May and November 2015 (Deheuvels et al. (2012). We determined the attainable yield for each tree based on its circumference at 1 m above ground level in April 2015. Similarly to banana plants, we determined the gap between the observed and attainable yield for each cacao tree. We assumed that the attainable number of pods depended on the tree girth (measured in April 2015 and assumed not to dramatically change during the year of measures) following a log-normal curve. This type of curve allows taking into account the increase of the yield attainable for small to medium size trees and then its decrease for bigger (older) trees. The PAY of cacao tree was then calculated as the ratio between the measured number of pods and the attainable number of pods for the same girth.

2.4. Statistical analysis

Our aim was to determine the effect of neighboring plants on the PAY of banana and cacao plants. To this end, we used a linear mixed-effect model with the PAY as a response variable and the number of neighboring plants of each category as predictors. In all cases, the plot was included as a random factor on the intercept of the model, which enabled us to take account for the variability due to the conditions of each plot: pest and diseases, soil, landscape context, and crop management. We carried out the analysis in two steps. First, we determined the radius of the zone of influence of a given species that best explained the PAY. We used linear mixed models, with the number of plants of one category at a time (banana, cocoa, wood trees, fruit trees) as a predictor. The log-likelihood of the model was used as an estimator of the goodness of fit (McCullagh, 1984). For each category of plants, we selected the radius with the greatest log-likelihood. When more than one peak was observed, we selected the one with the smaller radius because a small radius has a minimal implication in terms of management for farmers (smaller area to consider). When two peaks had very close log-likelihood, we selected the one with the lowest p-value. In the second step, we tested the significance of the effect of the predictors (number of plants of each category of plants that were within the radius determined in the first step of the analysis) on the PAY in a complete model. We also determined whether the quadratic value of each

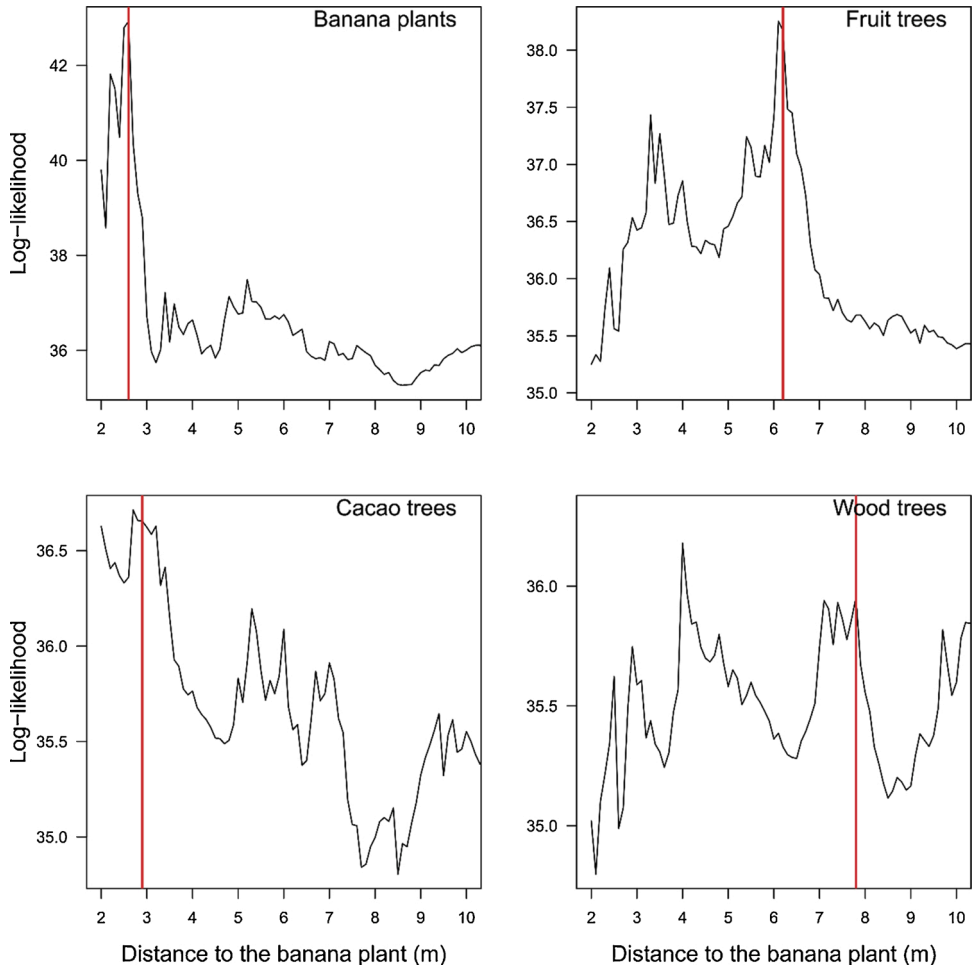

Fig. 2. Selection of the distances (radii) at which each category of neighboring plant had the most effect on the log-likelihoods of the predictions of the proportion of attainable yield (PAY) of banana. The distances correspond to the highest differences in AIC values from the null model (AIC). The red vertical lines show the radius that best predicted the PAY of banana plants that was 2.6 m for other banana plants, 2.9 m for cacao trees, 6.2 m for fruit trees, and 7.8 m for wood trees.

predictor was significant (significance would indicate a non-linear response to the predictor). All models were fitted with the 'lmer' function in the 'lme4' package (Bates et al., 2011). All statistical analyses were performed with R 3.3.0 (R Core Team, 2016) and with an alpha level of 0.05. We calculated the relative root mean square error (RRMSE) between measured and predicted values to quantify the precision of our models. To ensure that our approach is robust, we also carried out a bootstrap analysis with 100 iterations in which the dataset was randomly and equally divided in two; the first half was used for the calibration of the model and the other half was used for the validation. The distribution of the coefficient of determination and the RMSE were observed in the 100 iterations as predictors of the robustness of our analysis.

3. Results

The selected fields had diverse spatial arrangements with densities of banana ranging from 22 to 1778 plants per ha and those of cacao ranging from 0 to 900 plants per ha (see **Figure S1** for maps of plots). The patterns of biomass increase plotted on initial dry biomass were similar for the three varieties of banana (Fig. 1A, B, C). The vegetative growth of the banana plants increased as their initial biomass increased but then decreased slightly when reproductive growth began. The maximal increase and the variability in biomass accumulation differed among varieties; at 4 months, when the increase was greatest, the increase was 12, 10, and 9 kg for Gros Michel, Cavendish, and Lacatan varieties, respectively. For cacao most of the trees produced a small number of cacao pods, i.e., between 0–10 pods/tree (Fig. 1D). Only a few cacao trees produced more than 10 pods. The attainable number of pods produced increased as the stem circumference increased up to 13 cm and then decreased.

The radii that best predicted banana and cacao PAY based on the abundance of neighboring plants, i.e., banana plants (vb), cacao trees (vc), fruit trees (vf), and wood trees (vt), are presented in Figs. 2 and 3. The radius that best explained the variability in the PAY of banana plants was 2.6 m for other banana plants ($vb_{2.6}$), 2.9 m for cacao trees ($vc_{2.9}$), 6.2 m for fruit trees ($vf_{6.2}$), and 7.8 m for wood trees ($vt_{7.8}$). The radius that best explained the variability in the PAY of cacao trees has a radius of 3.9 m for banana plants ($vb_{3.9}$), 5.5 m for other cacao trees ($vc_{5.5}$), 3.9 m for fruit trees ($vf_{3.9}$), and 5.1 m for wood trees ($vt_{5.1}$). After backward selection, three predictors for banana PAY ($vb_{2.6}$, $vc_{2.9}$, and $vf_{6.2}$) and three for cacao PAY ($vb_{3.9}$, $vc_{5.5}$, and $vf_{3.9}$) were significant in a complete model; vt was not significant in either model (Table 1). For the banana PAY model, the quadratic terms of $vc_{2.9}$ and $vf_{6.2}$ were also significant or nearly significant. We graphically verified the normality of the residues of the two complete models (see **Figure S2**).

Interestingly, only $vb_{2.6}$ had a positive effect on banana PAY, and the relationship plateaued above 6 banana plants (Fig. 4). The other three predictors had a negative effect on banana PAY (Fig. 4). When the number of cacao trees exceeded 3 within a 2.9-m radius, the banana PAY clearly decreased. The three significant predictors had a negative effect on cacao PAY (Fig. 5). The negative slope was steepest for the effect of

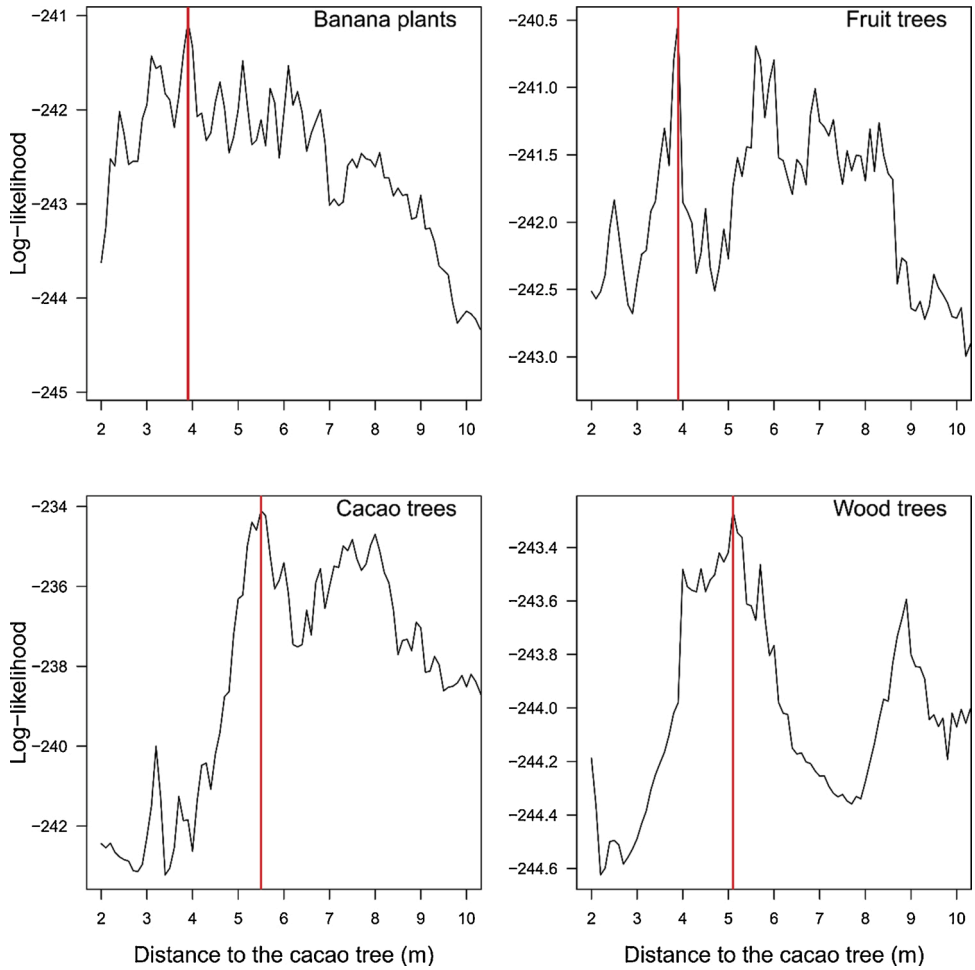

Fig. 3. Selection of the distances (radii) at which each category of neighboring plants had the most effect on the log-likelihoods of the predictions of the proportion of attainable yield (PAY) of cacao. The distances correspond to the highest differences in AIC values from the null model (AIC). The red vertical lines show the radius that best predicted the PAY of cacao trees that was 3.9 m for banana plants, 5.5 m for other cacao trees, 3.9 m for fruit trees, and 5.1 m for wood trees.

Table 1
Results of the analysis of deviance on the effect of neighboring plants on the proportion of attainable yield (PAY) of banana plants with a mixed-effect linear model (with the plot as a random factor on the intercept). The marginal and the conditional R^2 were equals to 0.05 and 0.19, respectively.

Predictors	Estimate (mean ± SE)	LRT	p
$vb_{2.6}$	0.017 ± 0.004	156.298	<0.001
$vc_{2.9}$	0.050 ± 0.033	21.704	0.141
$vc_{2.9}^2$	−0.021 ± 0.010	38.944	0.048
$vf_{6.2}^2$	−0.005 ± 0.003	35.886	0.058
$vt_{7.8}$	−0.006 ± 0.006	18.984	0.168

LRT: Likelihood-ratio test, p: p-value of the Chi-square test, vb: number of banana plants within a 2.6-m radius, vc: number of cacao trees within a 2.9-m radius, vf: number of fruit trees within a 6.2-m radius, vt: number of wood trees within a 7.8-m radius.

vc.

When the PAY values predicted by the complete model (a model that included all significant predictors; see Tables 1 and 2) for a given type of plant neighborhood were plotted on the observed PAY values for the same plant neighborhood, the R^2 value was 0.65 for banana and 0.59 for cacao (Fig. 6). In other words, the models that included the effects of all three categories of neighboring plants performed well, the RRMSE was equal 11.7 % and 21.0 %, for banana and cacao PAY respectively. The bootstrap analysis showed a relatively small variation or the R^2 and of RRMSE even when calibrated with half of the data (**Fig. S3**).

Our analysis (Fig. 4) suggests that 4 banana plants in a 2.6-m radius, 2 cacaos trees in 2.9-m radius, 2 fruit trees in 6.2-m radius, and 2 wood trees in 7.8-m radius should not reduce banana productivity compared to the productivity of a banana plant without neighbors as observed in our study. In the case of cacao (Fig. 5), 4 banana plants in a 3.9-m radius, 2 cacaos trees in 5.5-m radius, 2 fruit trees in 3.9-m radius, and 1 wood tree in 5.1-m radius should not reduce the cacao productivity.

4. Discussion

In the banana PAY model, the radius that had the largest effect on banana PAY was greater for the larger neighbors (fruit or wood trees) than for smaller neighbors (cacao trees or banana plants). This trend was not similar for cacao PAY. The radii that had the greatest effect on PAY were smaller in the cacao PAY model (Fig. 3) than in the banana PAY model (Fig. 2). We can hypothesize that this maximal effect of neighboring plant at smaller distances for cacao trees is due to the fact that their canopy has on average a larger horizontal extend; i.e. cacao trees are thus interacting with more far away plants than banana, especially in the exploitation of light and nutrients resources. The statistical individual based analysis presented in this work provide a quantitative approach to disentangle the huge variability observed in the PAY according to the initial biomass or circumference (Fig. 1). We found that the number of banana plants in a radius of 2.6 m had a significant positive influence on banana PAY, while cacao trees in a 2.9 m radius and fruit trees in a 6.2 m radius had significant negative influence. We

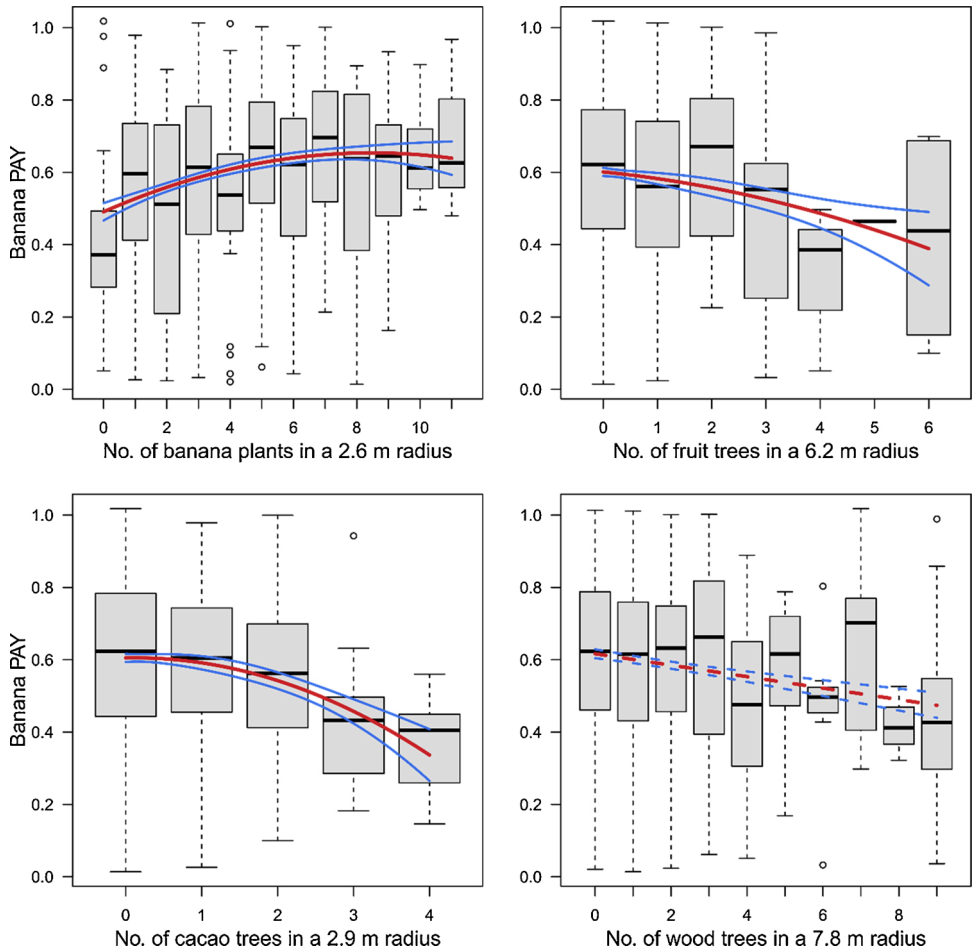

Fig. 4. Model fit of the predictions of the proportion of attainable yield (PAY) of banana according to the number of banana plants in a 2.6 m radius, fruit trees in a 6.2 m radius, cacao trees in a 2.9 m radius, and wood trees in a 7.8 m radius. The red lines show the mean responses, and the blue lines show the standard errors predicted by the 'lmer' (dashed-lines show non-significant relations).

suggest that this surprising result may be attributed to crop management, which tends to be better when banana density is high rather than low. For instance, we observed on the field that grouped banana plants tends to have a better leaf pruning and a more effective selection of suckers, resulting in a better exploitation of resources among banana mats. The high nutrients demand of fruit trees, especially citrus fruits (Scholberg and Morgan, 2012) which were particularly abundant in our study, is probably another factor that explains the decrease of the PAY of bananas and cacao plants for medium to high densities of fruit trees. These mutual negative effects at medium and high densities are probably also explained by competitions for nutrients. At low densities, complementarity between banana and cacao plants is possible. Additionally to radiation partitioning, this complementarity may be explained by root systems that is more superficial for banana plant than for cacao trees (Isaac et al., 2014). As suggested by Poeydebat et al. (2016), the production of a given plant in a multi-strata agroforestry systems is tight balance between light and nutrients.

Although our analysis included the plot identity as a random factor on the effect of the abundance of each plant type on PAY, we wanted to be verify that there was no co-variation between cultural practices and soil fertility. The banana density was even slightly negatively correlated with the soil organic matter content ($r=-0.531$, $p = 0.019$, see **Fig. S2-A** for details), showing that there was no bias on the trend that grouped banana plants better performed than isolated ones. Interestingly, there was no correlation between the mean field PAY and the soil organic matter content of each field (**Fig. S5-C&D**). This reinforces the fact that local conditions of each plant, largely explained by neighboring plants, are the main drivers of its growth and production.

Wood trees in the neighborhood of banana plants and cacao trees tended to reduce the PAY but the effect was not statistically significant. Even though wood trees were more numerous than fruit trees in the neighborhood of banana plants and cacao trees, the effect of fruit trees was statistically significant but that of wood trees was not. This difference may be attributed to the position of the trees in the canopy and to the resulting effects on shade intensity (Gidoin et al., 2014), fruit trees also have denser canopies than wood trees (Somarriba et al., 2014). Because wood trees are high in the canopy (Ngo Bieng et al., 2013), they provide a low level of uniform shading to the shorter banana plants and cacao trees. This suggests that wood trees at an adequate density and spatial distribution should not affect banana and cacao productivity, which is important because wood trees help provide other ecosystem services in cropping systems (Tscharntke et al., 2011). Relative to wood trees, fruit trees provide more localized and more intensive shade (Gidoin et al., 2014). This more localized shade may reduce banana and cacao productivity. Our results agree with previous studies that described a positive correlation between yields and light availability when growth is not limited by nutrient availability (Vernon, 1967; Jucker et al., 2014). This suggests that when light becomes scarce, complementarity is reduced. The latter hypothesis is consistent with findings of Zuidema et al. (2005), who showed that heavy shading (>60 %) in agroforestry systems reduced cacao crop yields by more than one-third. Similar to (Steffan-Dewenter et al., 2007) that conclude that low-shade agroforestry (40 %) provides the best available compromise between cacao crop yield and ecological needs.

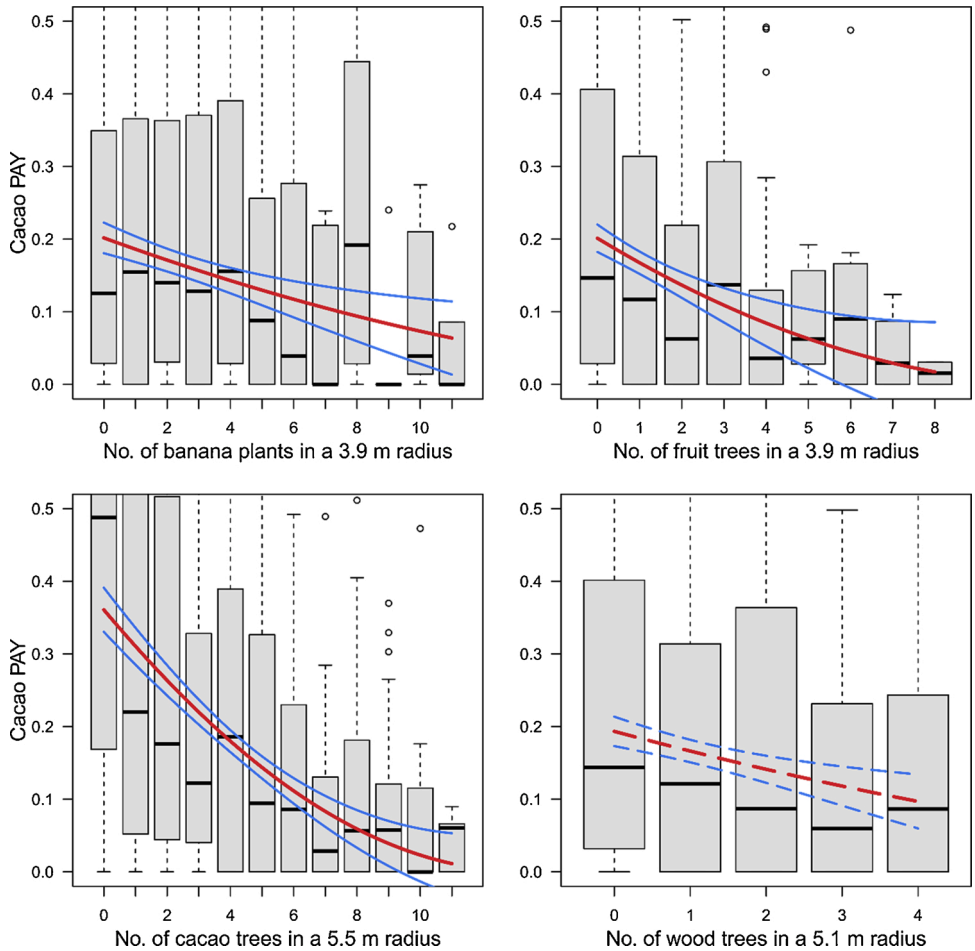

Fig. 5. Model fit of the predictions of the proportion of the cacao attainable yield (PAY) according to the number of banana plants in a 3.9 m radius, fruit trees in a 3.9 m radius, cacao trees in a 5.5 m radius, and wood trees in a 5.1 m radius. The red lines show the mean responses, and the blue lines show the standard errors predicted by the 'lmer' (dashed-lines show non-significant relations).

Table 2
Results of the analysis of deviance on the effect of neighboring plants on the proportion of attainable yield (PAY) of cacao trees with a mixed-effect linear model (with the plot as a random factor on the intercept). The marginal and the conditional R^2 were equals to 0.06 and 0.24, respectively.

Predictors	Estimate (mean ± SE)	δAIC	LRT	p
$vb_{3.9}$	−0.015 ± 0.006	4.551	5.960	0.015
$vc_{5.5}$	−0.031 ± 0.007	8.334	18.830	<0.001
$vf_{3.9}$	−0.044 ± 0.017	1.835	6.605	0.010
$vt_{5.1}$	−0.003 ± 0.011	9.209	0.063	0.802

LRT: Likelihood-ratio test, p: p-value of the Chi-square test, vb: number of banana plants within a 3.9-m radius, vc: number of cacao trees within a 5.5-m radius, vf: number of fruit trees within a 3.9-m radius, vt: number of wood trees within a 5.1-m radius.

Because our study was carried out on individual plants, it gains in statistical power compared to a whole field analysis. One output of this analysis is the definition without *a priori* of the radii until which it is needed to take into account neighboring plants to predict PAY. This assessment of distance also provides a first practical guidance for how neighboring plants may be organized to increase banana and cacao productivity in complex systems. For example, our analysis suggests that densities per ha correspond to 1884, 757, 166, and 105 for banana plants, cacao trees, fruit trees, and wood trees, respectively, should maximize the yield of banana. In the case of cacao, densities of 838, 210, 421, and 122 plants per ha of banana plants, cacao trees, fruit trees, and wood trees, respectively, should maximize the yield of cocoa. These recommendations probably hold only in systems with a similar level of complexity and with a similar level of management. Interestingly, the densities of banana plants and of cocoa trees that respectively optimize banana PAY and cocoa PAY are close to the recommended densities in monoculture 1600–1900 and 900–1100 (Robinson and Nel, 1985; Wood and Lass, 2008). In the case of recommended densities of fruits and wood trees that maximize banana and cocoa PAY are high close monocultures recommendations: 200–300, and 80–120 individuals ha^{-1}, respectively (Wheaton et al., 1986; Suatunce et al., 2009).

For cacao, the average production measured in this study (100 Kg ha^{-1}) was low compared to the attainable production (as high as 1800 Kg ha^{-1} in Malaysia, 800 Kg ha^{-1} in Ivory Coast, 350 Kg ha^{-1} in Ghana, and 250 Kg ha^{-1} in Central America) (Dormon et al., 2004). One possible reason for the low production of cacao trees in the current study was disease caused by the fungus *Moniliophthora roreri* and other pathogens (Leach et al., 2002).

In contrast to the production of cacao, the vegetative growth of bananas in the current study (which ranged from 9 and 11 Kg per banana plant in 17 weeks depending on the variety) is close to the potential of bananas as measured in intensively managed monoculture (Tixier et al., 2008; Ripoche et al., 2012). The high variability in PAY (up to nearly no growth with values with PAY close to zero) is clearly much greater to what could be observed in monocultures in which plants are relatively homogeneous. We can hypothesize that the negative effects of neighboring trees on banana plants in our study resulted from competition for light and mineral resources. On an applied perspective, it thus seems

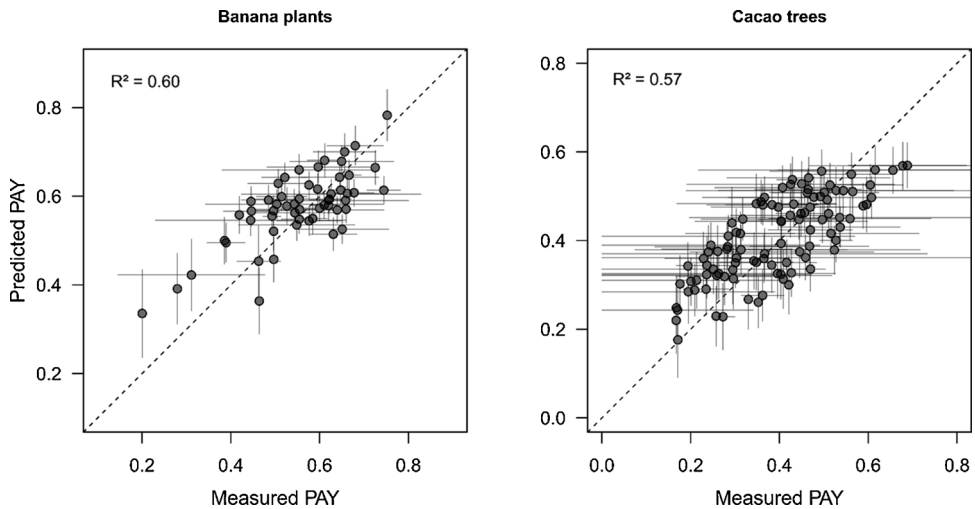

Fig. 6. Predicted vs. measured proportion of the attainable yield (PAY) for banana plants and cacao trees for each existing assemblage of neighboring plants (i.e., number of banana plants, cacao trees, and fruit trees within the radius considered in the PAY models). Horizontal bars indicate the standard error, and vertical bars indicate the prediction error. The two models used for banana and cacao PAY predictions are presented in Table 1.

possible to grow highly productive banana plants in association with trees, especially with cacao trees and with moderate densities of bigger trees.

Our statistical PAY models were relatively accurate in predicting the average effect of all plant assemblages (Fig. 6); both models explained about 60 % of the variance in PAY was explained, which could be considered as satisfying, especially when considering the low number of parameters used. This percentage of variance explained was relatively stable in the bootstrap analysis (**Fig. S3**), and the RRMSE was on average 12 % for banana PAY and 23 % for cacao PAY. The marginal R^2 (around 5% of variance explained) in the complete models (Tables 1 and 2) showed that the field random factor on the intercept moderately participated in the overall explanation of the variance.

The prediction of the attainable yield (PAY) for each existing assemblage of neighboring plants was more accurate for banana (RRMSE of 11 %) than for cacao (RRMSE of 21 %). We can suspect that the effect the fungal disease *Moniliophthora roreri* made this task more difficult, with probably more variability in the PAY itself and in its response to the local context compared to banana PAY. Indeed, the local plant context may not only play on nutrients and light resources partitioning, but also on the incidence of this disease (Ngo Bieng et al., 2017). Although our analysis integrates all the potential effects of these plants on the PAY (through the effect of neighboring plants), we can suspect that potential trade-offs between resources and disease effects are likely to make the prediction more uncertain. Although we used a wide diversity of situations for the calibration of our models, the extrapolation of our results to other situations should be done with care; future studies should attempt calibrating and validating this approach with contrasted regions. Future methodological improvements should challenge accounting for the effect of the size of the neighboring plants and not only their identity and distance to each crop (our attempts to do this were not successful, un-shown results).

It is not sure that process-based models can better explain the variance of plant productivity. However, it would certainly valuable to intend linking statistical models with more process-based models. The development of process-based models will certainly require a huge amount of measurements not only of plant growth (by organ) but also of environmental variables linked to the availability of resources (e.g., local soil nutrient content and radiation available for each plant). Such process-based model have only been obtained in relatively homogeneous systems as coffee agroforestry systems (Roupsard et al., 2011; Charbonnier et al., 2013). We suggest that models combining statistical approaches, to catch the effect of spatial and compositional effect on individual plant, with process-based equations to separate the effects on nutrients, light, and pest and diseases represents a great perspective to go further in the understanding and in the modelling of complex systems. However, it will requires more measurements for been parameterized (individual measurements of soil nutrients, lights, pest and diseases). We believe that integrating a bit of processes inside our spatial-individual-based statistical approach would be very helpful to account for potential cultural practices, especially thinning trees to manage light partitioning across strata.

In terms of recommendations to farmers, our results clearly suggests that it is possible to keep a significant density of associated trees with banana plants and cocoa trees while maintaining their yields. Nevertheless, over a given density (e.g. > 166 fruit trees associated to banana plants) competitions are likely to reduce yield.

CRediT authorship contribution statement

Ricardo Salazar-Díaz: Conceptualization of the experiment, Data acquisition, Data Analysis, Writing. **Philippe Tixier:** Conceptualization of the experiment, Supervision, Data Analysis, Writing.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.eja.2021.126295.

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