

Biodiversity, dynamics, and impact of chakras on the Ecuadorian Amazon

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Abstract

Aims

Deforestation and biodiversity loss are two alarming, closely related problems, and the main factors triggering changes in land use. Indigenous agricultural practices in the western Amazon Basin are known as chakras, and their structure and dynamics are seemingly optimal for forest management. However, the variability in tree species and the degree of forest recovery after abandonment is poorly documented in this agroforestry system (AFS). The goals of this study were: (i) to investigate whether the different AFSs (chakras) preserve similar levels of forest diversity, (ii) to determine the effect of transformation of mature forests (MF) to chakras, in particular, forest alpha and beta diversity levels, and (iii) to investigate whether native tree species recovery leads to the original forest structure following chakra abandonment.

Methods

We assessed the floristic composition in three AFSs (cassava, corn, and cocoa), the secondary forest (SF), and the forest remnants in the buffer zone of the Northern Ecuadorian Amazon (NEA). All tree species with a diameter at breast height (dbh) ≥ 10 cm were inventoried in 61 plots (0.28 ha average) representing 17.44 ha. Alpha diversity was calculated in all systems to determine the levels of variability using species richness and the Shannon diversity index. Also, beta diversity was examined to evaluate the degree of dissimilarity among all AFSs with the MF in order to analyze changes in floristic composition. The divergence between the SF and the MF was analyzed to ascertain forest recovery after chakra abandonment.

Important Findings

A total of 4,060 trees (dbh ≥ 10 cm) representing 109 species, 96 genera, and 43 plant families were inventoried in 17.44 ha sampled in five systems in the buffer zone of the NEA. The most dominant plant families were Arecaceae, Myristicaceae, Fabaceae, Meliaceae, and Malvaceae, and the most representative genera included *Iriartea*, *Virola*, *Guarea*, *Ocotea*, *Cordia*, *Chrysophyllum*, and *Inga*. The MF in this zone is composed of 81 tree species circumscribed in 74 genera and 30 plant families. Transforming this MF to different chakras leads to a decrease of alpha diversity between 52% and 75%, particularly in AFS practiced for local food security (corn and cassava). However, all the AFSs preserve ca. 56% of the native flora existing in the MF, in which at least 8% of the species are threatened; however, the status of the remaining 92% of species is still unknown, indicating that the assessment of the rarity of the native trees is virtually unexplored. Additionally, all sites investigated consistently formed three clusters that corresponded to AFS, MF, and SF. Thus, the trend of forests to recover the original structure is facilitated by native trees left intact in the chakras. These results strongly support the potential to execute sustainable forest management and preservation of endangered tree species practicing this AFS.

Keywords: agroforestry, biodiversity, chakra, climate change, tropical forest

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INTRODUCTION

The dynamic patterns, structural composition, and functional integrity of natural ecosystems are continuously threatened by deforestation. A growing body of evidence shows that changes in biodiversity are primarily attributed to a vast number of anthropogenic activities that have negatively impacted tropical and subtropical areas (Tapia-Armijos et al. 2015; Young and Clarke 2000). Although deforestation rates have decreased substantially from 8.5 million ha year⁻¹ in the 1990s to 6.6 million ha year⁻¹ in the last 5 years (FAO 2015), the main human activities linked to species extinction, habitat loss, and climate change still persist, especially in the tropics (Homeier et al. 2013; Porro et al. 2012; Tapia-Armijos et al. 2015).

Tropical forests (TF) still host the largest reserves of biodiversity in the world. These diversity-rich areas have important ecological roles, such as supporting a high number of endemic species of plants and animals (Duijvenvoorden et al. 2002), maintaining >50% of life forms on Earth (Gatti et al. 2015; Givnish 1999; Mishra et al. 2013), contributing to decreasing carbon dioxide (CO₂) from the atmosphere (DeFries et al. 2002; Houghton et al. 2000), storing 59% of the world's carbon (Malhi and Grace 2000), and protecting soils from wind and water erosion (FAO 2015), among others. These functions are essential for a healthy and integral ecosystem; however, human activities have altered the existing balance by converting the forest to other types of landscapes with lower structural complexity and biomass (Cochrane and Barber 2009; Malhi et al. 2009; Nobre and Borma 2009).

Transforming forest ecosystems to agricultural land and grasslands has been identified as the leading force causing forest loss with a concomitant contribution to shifting global climate and escalation in greenhouse gas emissions (Bhagwat et al. 2008; Gatti et al. 2015; Pan and Bilsborrow 2005). In fact, structural changes in TFs could be the main contributors to these deviations because these natural areas maintain ~120 t ha⁻¹ of carbon, which is 45 t ha⁻¹ more than the world average (FAO 2015). The Amazon Basin (AB), with an extension of >6.5 million km² (Mittmeier et al. 2003), undoubtedly stores large quantities of carbon that are eventually released into the atmosphere as a result of clearing of forests for agricultural use.

Within the AB, the Ecuadorian Amazon forest (EAF) is considered a salient biodiversity hotspot on Earth (Bass et al. 2010; Myers et al. 2000; Pérez et al. 2015), but in the last decades it has also been seriously affected by rapid changes in land use, an activity that has caused the highest deforestation rates in South America (Mena 2008; Tapia-Armijos et al. 2015). These human-mediated disturbances alter the structural composition and integrity of climax forest communities, as well as the capacity to provide ecosystem services. Because in the long run conversion of forest land may equate to desertification, recently, researchers have endeavored to document the effects of these rather fast-occurring and

alarming changes of natural landscapes to propose creative solutions to preserve protected areas (Bass et al. 2010; Becker and Ghimire 2003; Valencia et al. 2004). Unfortunately, the efforts to slow biodiversity loss are still unsatisfactory, especially with the pressure exerted by population growth and the increasing exploitation of natural resources.

While the protection of wild areas is a priority in conservation endeavors, the deliberate management in using native trees together with diverse agricultural crops is emerging as a potential alternative to safeguard biodiversity. This practice is known as agroforestry systems (AFSs) (Ashley et al. 2006), and its benefits to human society and environment have been widely discussed, e.g., Bhadwat et al. (2008) and DeClerck et al. (2010). The AFS provides several advantages, such as preserving biodiversity, reducing anthropological pressure on primary forest communities, and enhancing ecosystem services and connectivity with conservation or protected areas (Ashley et al. 2006; Schroth et al. 2004). Hence, the amalgamation of native trees and crops in indigenous farms might promote diversification and benefits to land users while preserving some components of the original ecosystem.

In the EAF, the AFSs are traditionally called chakras, a common and environmentally friendly farming tradition practiced by autochthonous groups. This AFS does not involve fertilizers, pesticides, and heavy machinery, and the advantage of this practice lies on the preservation of mature native trees for several purposes. Typically, this method encompasses a shifting agriculture in small land plots developed in forest gaps to satisfy food necessities, which after a few years are purposely abandoned to allow forest recovery (Arévalo 2009). The existence of different native tree species in various strata, which can have social and cultural significance for the Aboriginal groups, reveals a multifunctional system with the capacity of conserving high levels of floristic diversity (Perrault 2005; Porro et al. 2012); however, the extent of this tree diversity has not been evaluated nor quantified. Although the assessment of anthropological activities in natural areas is challenging, the analysis of this arboreal structure is significant to determine the disturbance threshold in highly diverse tropical areas to ensure sustainable forest management. Filling knowledge gaps about forest tolerance levels is particularly important in the Northern Ecuadorian Amazon (NEA) to improve the quality of zones surrounding biological reserves, e.g., the Sumaco Biosphere Reserve (Torres et al. 2014). In this reserve, new human settlements situated in the transitional and buffer areas have put extra pressure on natural resources, resulting in the threat to numerous native species and ecosystem functions due to the practice of more intensive and often more aggressive and inefficient production systems (Arévalo 2009).

The buffer zone in the NEA, an area in which agroforestry is quite active, represents ca. 12 500 ha (Torres et al. 2014). The diverse ecological characteristics along with the shared areas of mature forests (MF) communities and different AFSs make this zone an excellent example of the AB and a worthy

choice for investigation. To date, information regarding the characterization of chakras in the New World tropics is scanty. This study represents the first approach to characterize the AFS at the structural and biodiversity levels, in particular, the investigation of the forest alpha and beta diversity and organization levels in relation to different farming levels of management. The outcomes of this study will serve as a foundation to develop new approaches for sustainable agriculture practices in the tropical Amazon and other tropical and subtropical regions. We were particularly interested in (i) investigating whether traditional chakras preserve similar levels of forest diversity among the different types of AFS, (ii) determining the consequences of converting MFs to chakras on forest biodiversity levels, and (iii) evaluating whether native

tree species recovery leads to the original forest structure following chakra abandonment.

MATERIAL AND METHODS

Study area

This study was carried out in the buffer zone located in the northern Amazon Region in Ecuador (Fig. 1). The buffer zone lies in two provinces, namely Orellana and Napo, and covers ~10 606 km² of Ecuador's territory (INEC 2010). Within these two jurisdictions, a total of 18 areas, mostly located in the Napo province, have been declared as natural patrimony by the Minister of the Environment. This area covers the sub-basins of Jatun Yacu-Pano-Tena, Napo-Wambuno, and

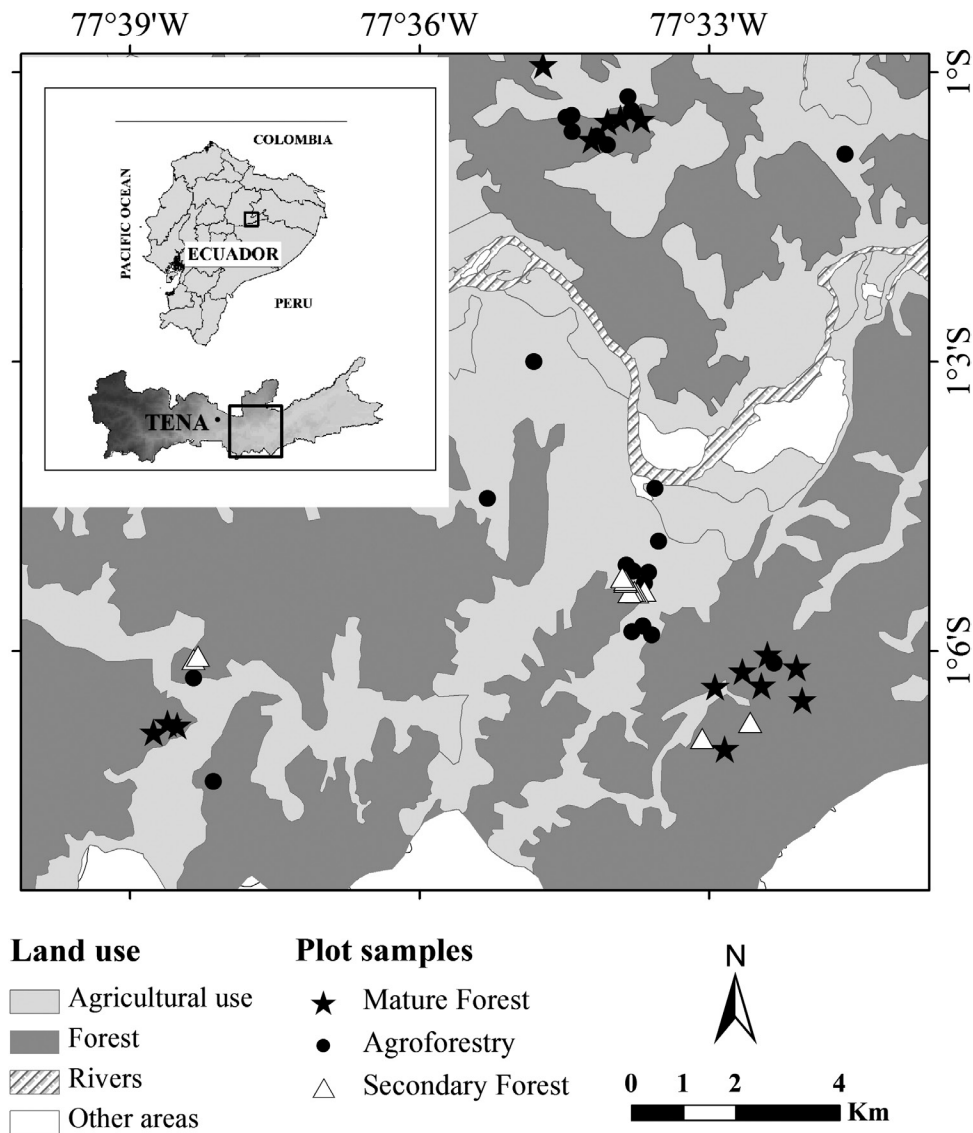


Figure 1: map showing the study area in the buffer zone of the Northern Ecuadorian Amazon. Top left shows Ecuador and Tena canton maps. Squares show the exact location of the region of study. The symbols on the map indicate the geographic location of the experimental plots. Forest plots are represented by black stars, secondary forest by white triangles, and black circles represent agroforestry plots. Different areas of land use are indicated in two different colors: light gray for agricultural land use and dark gray for forest cover.

Puni-Arajuno and is part of an extensive mixed evergreen tropical forest characterized by humid climate with mean annual rainfall of 3500 mm, monthly average temperature of 24°C, and altitudinal range from 300 to 600 m above sea level (m a.s.l.) (Arévalo 2009).

Field data

Sixty-one plots, each an average of 0.28 ha, representing a total of 17.44 ha were established in different fieldwork seasons from 2008 to 2016 as follows. Foremost, forest and agricultural areas for study were identified and selected from maps obtained from online databases available from the Ecuadorian Ministry of Agriculture (www.geoportal.agricultura.gob.ec). Then, four local indigenous communities were selected based on two main requirements. The first condition was that these communities should have areas under agricultural use (AFSs), post-disturbance or abandoned areas (secondary forest, SF), and undisturbed forest (MF). The second prerequisite was their relative accessibility to evaluate all the areas previously mentioned. Lastly, each plot was established following a disturbance gradient using stratified samples to capture the spatial variability of the MF, SF, and the AFS in the buffer zone.

The research plots included three of the most important AFSs (cocoa, corn, and cassava) in the NEA because the cultivated area dedicated to these three crops is substantially larger than the other crops grown in this zone. These crops are also relevant for their agricultural economy and cultural significance. Twenty-three plots were based on cocoa (*Theobroma cacao* L.), six dedicated to corn (*Zea mays* L.), and five with cassava (*Manihot esculenta* Crantz). In addition, 12 research plots of SF with ca. 15 to 20 years of abandonment and 15 of the MF were chosen (Table 1). The location and approximate ages of the SF were obtained through interviews with local landowners. The age of the climax forest was unknown and designated here as MF due to its relative inaccessibility and more diverse floristic composition. All AFS research plots varied in size because each lot represented the total land used by the landowner. The research plots belonging to the SF and MF were obtained by the aggregation of multiple plots. In the SF, 35 plots of 500 m² each near to each other were

grouped. That is, those plots that were always <100 m apart were aggregated. Thus, the cluster of adjacent plots prevents possible spatial pseudo replications. In the MF, six plots were obtained using combining six to seven plots of 500 m² each and two more from five plots of 1000 m² each. Overall, a total 61 plots (Table 1) were used in this study. The group of aggregated plots can be seen in online supplementary Table S4.

Species inventory

All tree species with a diameter at breast height (dbh) ≥10 cm were inventoried in each system being investigated (see Table 1) following Alder and Synnott (1992), a protocol with strategies to establish and measure permanent plots in mature tropical forests. The taxonomic identification of plants was conducted in the field at the generic and specific levels with the support of a multidisciplinary team with different areas of expertise, such as botanists (including local expert ethno-botanists), biologists, agronomists, and anthropologists. In addition, relevant literature and online resources were used to verify the identity of plants, i.e., the catalogue of Vascular plants of Ecuador (www.tropicos.org), (Jørgensen et al. (1995), (Jørgensen and León-Yáñez (1999), (Patzelt and Echeverría (1996), (Ståhl et al. (2015) and the Flora of Ecuador (<http://bioenv.gu.se>). Tree species that were not fully identified in the field were collected and processed at the Herbario Nacional (QCNE) and duplicate voucher specimens were deposited at the National Institute of Farming Research (INIAP), both institutions in Quito, Ecuador. The floristic inventory was compiled in a data matrix constructed in MS-Excel software encompassing a list with families and scientific names. The taxonomic authorities for the taxonomic species are based on the Tropicos nomenclatural database (www.tropicos.org).

Data analysis

Two analytical approaches were employed with the data. First, the alpha diversity was investigated with the species richness and diversity as unique response variables in the AFS, SF, and MF. Second, the beta diversity was evaluated to determine the degree of dissimilarity among systems using a multidimensional approach involving the tree species matrix.

Table 1: five different systems in the Northern Ecuadorian Amazon including number of plant families, genera, and the observed species in the total sampled area

System	<i>n</i>	Area (ha)	# Plant families	# Genera	# Species	Species diversity
<i>Manihot esculenta</i> (cassava)	5	0.59	18	20	20 ± 1.54	18 ± 5.19 b
<i>Zea mays</i> (corn)	6	6.19	21	30	32 ± 2.12	13 ± 4.47 b
<i>Theobroma cacao</i> (cocoa)	23	4.67	33	57	62 ± 2.37	19 ± 2.18 b
Secondary forest	12	1.75	31	52	54 ± 1.79	15 ± 1.54 b
Mature forest	15	4.24	38	74	81 ± 1.48	25 ± 0.99 a
Total	61	17.44	43	96	109 ± 9.90	37 ± 1.20

For fair comparison among the five systems the species diversity is expressed as the exponential alpha of the Shannon index ± standard error at 90% of sampling coverage. *n* = total numbers of plots investigated; ha = total sampled area. Same lower case letters in table represent overlapping confidence intervals at 95%.

Alpha diversity

Alpha diversity, that is, the number of plant families and genera, were estimated in each AFS, SF, and MF included in this study. Also, species richness and the Shannon diversity index (1) were calculated as follows:

$$H' = -\sum_{i=1}^S p_i \log_2(p_i) \quad (1)$$

Where H' represents the Shannon index and p_i is the relative abundance of each species

The Shannon index was converted using an exponential alpha to determine the effective number of species as described by Jost (2006, 2007). This more intuitive methodological approach allows the comparison of diversity levels among plant communities. The evaluation of species diversity among the five systems was based on the principle of completeness (Chao and Jost 2012), in which the samples are standardized by coverage rather than size. These different sampling efforts produce different numbers of the individuals collected. Therefore, this technique allows fair comparisons of species diversity. The estimation of these diversity indices also involved building intervals of 95% using a bootstrap method in the package iNEXT (Hsieh *et al.* 2016) using *R* statistical software (R Core Team 2017).

Beta diversity

Beta diversity or the change in floristic composition from one system to another, was also analyzed among the five systems investigated using the Bray-Curtis distance (2), which is an equation suitable for datasets with asymmetric characteristics:

$$d_{BC} = \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})} \quad (2)$$

Where x_{ij} is the abundance of species i on site j , and x_{ik} is the abundance of species i on site k .

This estimation consisted of an analysis in a dissimilarity matrix to evaluate the change in species composition from MF to AFS as well as the degree of forest recovery through the dissimilarity between the MF and the SF at the landscape level. In addition, a hierarchical approach including all sampled sites was used to determine small discontinuities in patterns of species composition among all sites. This approach aimed to investigate whether species composition is alike in all AFS sites regardless of the chakra type and whether forest recovery exhibits a common trend. In order to minimize the variance within groups, we used the Ward method followed by the application of the Bray-Curtis distance to calculate the dissimilarity index. Finally, a contingency analysis (CA) followed by a multiple correspondence analysis (MCA) was conducted to determine the putative significant degree of association among tree species, AFS, and forest types according to the chi-square distribution. These inquiries were performed using *R* statistical software (R Core Team 2017) and Infostat (Di Rienzo *et al.* 2015).

RESULTS

Among the three AFSs selected, corn and cassava represented the temporal crops, while cocoa had permanent production cycles. The largest cultivated areas of these AFSs corresponded to corn with an area of 1.03 ha on average, whereas the smallest farming spaces were those of cassava with 0.12 ha on average (see online supplementary Table S1). As expected, the three AFSs contained fewer trees (>10cm dbh) per hectare than the SF and MF (see online supplementary Table S1). Corn exhibited the lowest value of tree density (24 ± 7) followed by cassava (104 ± 30) and cocoa (200 ± 36). The highest tree concentration was found in the SF (469 ± 44) and MF (741 ± 68) (see online supplementary Table S1).

The floristic inventory of the 17.44 ha comprising the five different systems investigated included a total of 4060 individuals, representing, 109 tree species in 96 genera and 43 plant families (Table 1). The most dominant plant families were Arecaceae, Myristicaceae, Fabaceae, Meliaceae, and Malvaceae, and the most representative genera included *Iriarteia*, *Virola*, *Guarea*, *Ocotea*, *Cordia*, *Chrysophyllum*, and *Inga* (see online supplementary Table S2). This inventory varied in sampling coverage (SC) obtained per system. That is, $81.3 \pm 9.5\%$ of SC in cassava, $83.9 \pm 6.7\%$ in corn, $97.3 \pm 1\%$ in cocoa, $98.7 \pm 0.7\%$ in the SF, and $99.8 \pm 0.1\%$ in the MF (see online supplementary Table S1). Accordingly, the samples were standardized at 90% for fair comparison of species diversity without doubling any reference sample size in any community to avoid biases in the calculation (see Table 1).

Alpha diversity

The effect of transforming the MF into different AFSs is reflected in the alpha diversity among all systems. The MF in the buffer zone of the study area is composed of 81 ± 1.48 tree species, 74 genera, and 38 plant families (Table 1). The most common plant families were Arecaceae, Myristicaceae, Fabaceae, Moraceae, and Lauraceae, whereas the most frequent genera were *Iriarteia*, *Virola*, *Ocotea*, *Guarea*, *Chrysophyllum*, *Protium*, and *Inga* (see online supplementary Table S2). The use of forest remnants in the conversion to cocoa, corn, and cassava systems represents a significant decrease in tree species, particularly, in corn and cassava, with 32 ± 2.12 and 20 ± 1.54 species, respectively (Table 1), relative to the 81 ± 1.48 species in the MF. In terms of species diversity calculated as the number of effective species in each system, the samples standardized at 90% of SC had the highest diversity value in the MF (25 ± 0.99), whereas the cocoa, corn, and cassava showed values between 13 and 19 in species diversity (Table 1). This indicates that the anthropogenic influence alters the structural diversity in the MF and AFSs from 52% to 75%, respectively.

All the systems under investigation showed a significant degree of association with tree species (chi-square < 0.0001). Axes 1 and 2 separated chakras from forests and showed a group of tree species, such as *Cordia alliodora*, *Inga edulis*,

Cedrela odorata, and others, associated mainly with corn and cocoa, and a few species (*Aphandra natalia*, *Vernonia baccharoides*, and *Ceiba pentandra*) linked to cassava (Fig. 2). Another cohort of tree species, e.g., *Iriartea deltoidea*, *Vismia macrophylla*, *Pouteria lucuma*, typically associated with SF and MF, was also evident. Also, a number of trees, e.g., *Chimarrhis glabriflora*, *Terminalia oblonga*, *Cedrelinga cateniformis*, and several others, seemed not to exhibit habitat or system preference and occurred infrequently in all systems (Fig. 2).

Beta diversity

The impact of anthropogenic activities was also evident in the magnitude of dissimilarity (beta diversity) among systems. Changing MF to corn and cassava farming systems represented a modification of 56% of the floristic structure but slightly decreased to 51% when it was converted to cocoa AFS (Table 2). Additionally, all sites investigated consistently formed three clusters that corresponded to AFS, MF communities, and SF (Fig. 3). A divergence of 0.43 in tree species composition between the mature and SF represented ca. 60% of forest recovery following chakra abandonment (Fig. 4).

Discrepancies in the levels of dissimilarity are also apparent in terms of dominant tree species. In the cassava AFS, *C. pentandra*, *Iriartea deltoidea*, *A. natalia*, *Apeiba membranacea*, and *Cordia alliodora* represented 51% of the species. In the corn AFS, *C. alliodora*, *Cedrela odorata*, and *I. deltoidea* were the most dominant (56% abundance) trees (see online

supplementary Table S2). In contrast, in the cocoa AFS, *C. alliodora*, *Pseudolmedia rigida*, *I. edulis*, and *Vochysia leguiana* were the most frequent trees (52%). In the SF and MF, the dominant species were similar. For instance, in the SF *I. deltoidea*, *Virola flexuosa*, and *Guarea kunthiana* revealed 53% of the tree diversity, and in the MF *I. deltoidea*, *V. flexuosa*, *G. kunthiana*, *Ocotea bofo*, *Chrysophyllum amazonicum*, and *Protium amazonicum* were the most common (52% frequency) trees (see online supplementary Table S2).

Threatened, vulnerable, and endemic plant species

Our study revealed that the buffer zone of the NEA has nine species in the sensitive categories, particularly threatened, vulnerable, and endemic taxa, as proposed by Neill and Pitman (2004) and IUCN (2016). For instance, *Alseis lugonis* and *Minquartia guianensis* are among the threatened taxa, *C. odorata* and *Swietenia macrophylla* are vulnerable, and *A. lugonis* and *Stryphnodendron porcatum* are listed in the endemic category. Lastly, *C. alliodora*, *I. deltoidea*, *S. porcatum*, *Astrocaryum murumuru*, and *Inga pavoniana* are included in the group of least concern (see online supplementary Table S3). All these taxa were found both in chakras and forests and represented only 8% of the tree species inventoried in this zone. However, data regarding the remaining 92% of species are still lacking (see online supplementary Table S3), indicating that the assessment of the rarity status of native trees

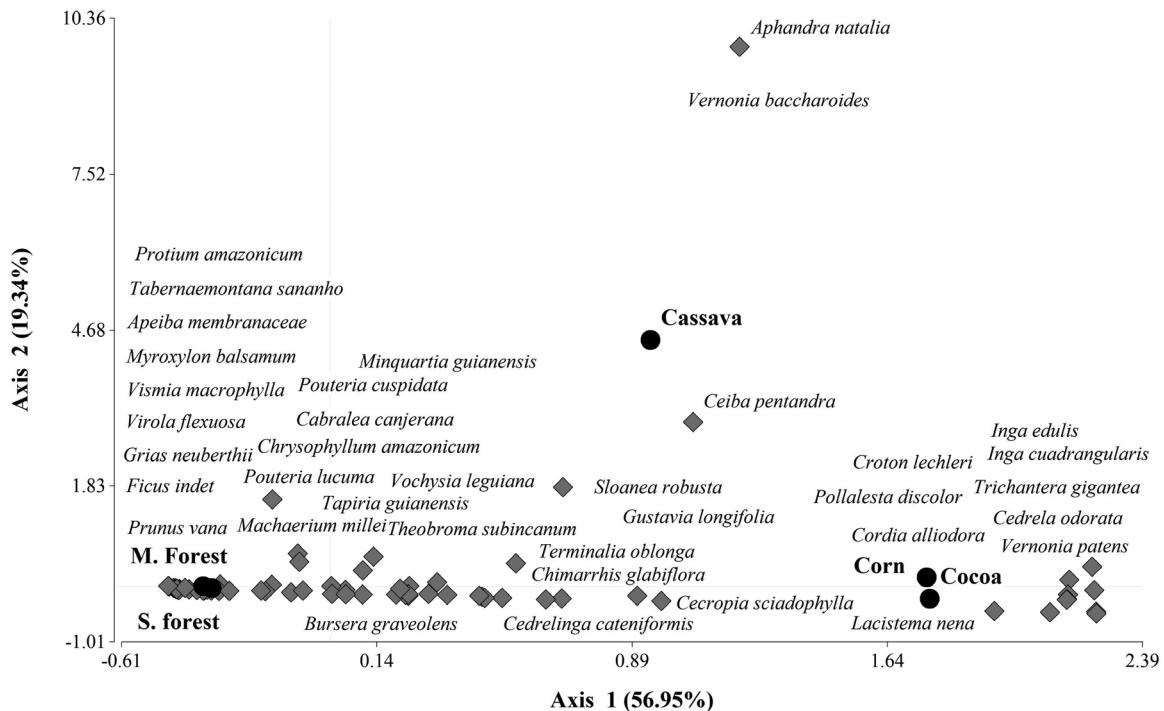


Figure 2: graph depicting the degree of association between species and systems, namely cassava (*Manihot esculenta*), corn (*Zea mays*), cocoa (*Theobroma cacao*), secondary forest, and mature forest in the buffer zone of the Northern Ecuadorian Amazon based on the correspondence multivariate analysis following a contingency analysis. Black circles show the position of the systems. Grey diamonds show the position of the tree species. For clarity of the graph, only a few species were included. Axes 1 and 2 together explain 76.29% of the total variance.

is virtually unexplored and needed to make more educated inferences about conservation practices of the NEA forests.

DISCUSSION

With the increase of agricultural land at the cost of removing natural vegetation to satisfy food and income needs in rural communities, the conservation of biodiversity hotspot areas is becoming a more complex challenge. Concrete actions to deal with this dichotomy in the tropics should be addressed to implement an efficient and sustainable integrated system involving protected and non-protected zones. For instance, the increasing use of the buffer zones with agroforestry practices (Bhagwat *et al.* 2008) should be considered as a multipurpose approach intended to reduce the vulnerability of forest reserves, but at the same time, adequate yield crop productivity, and the preservation of rare and/or endangered species is desired. Our study revealed that the chakra is a practical shifting agriculture system that maintains the natural components of surrounding areas because it is beneficial in the conservation of the forest structure and food production for local communities.

Table 2: dissimilarity matrix calculated with Bray–Curtis distance to analyze the change in tree species composition (≥ 10 cm dbh) among the five systems investigated in the buffer zone of the Northern Ecuadorian Amazon

	Cassava	Corn	Cocoa	SF	MF
<i>Manihot esculenta</i> (cassava)	0.00				
<i>Zea mays</i> (corn)	0.24	0.00			
<i>Theobroma cacao</i> (cocoa)	0.30	0.30	0.00		
Secondary forest	0.34	0.38	0.36	0.00	
Mature forest	0.56	0.56	0.51	0.43	0.00

Overall, the chakras involve an adaptive strategy directly associated with socio-economic conditions aimed at food security, land management, and balanced use of forest resources using environmentally friendly approaches. The first aspect of this approach is to guarantee adequate food supplies and income. For example, corn and cassava are two of the most important crop plants for global foodstuff in the tropics (Godfray *et al.* 2010), but cocoa beans are preferred for economic returns in this and other areas of South and Central America, Africa, and Asia (Cerda *et al.* 2014; Porro *et al.* 2012; Schroth and Harvey 2007). The second feature of this farming strategy is the cultivated area. The chakra plots in the NEA oscillated from 0.05 to ~ 3.0 ha (see online supplementary Table S1). Similar integrated crop systems in the East African highlands have comparable sizes from 0.4 to 3.0 ha (Abebe *et al.* 2005). These small areas theoretically represent a strategic organization to optimize a family's labor force capacity to secure adequate crop yields. A third characteristic of the chakras is the deliberate change of MF into AFS, which does not necessarily represent a random tree selection for logging but rather the result of a systematic process intended to provide suitable ecological and soil resources for crops to thrive. For example, cocoa farmers in Ghana prefer nutrients and incidence of light; thus, certain tree species are selected in order to harmonize the above-ground interaction with the shade trees to enhance root systems and maintain more consistent levels of soil moisture (Abebe 2005; Anglaere *et al.* 2011). Although a farmer's tree selection is intended exclusively to increase crop productivity, the presence of some native trees, such as *Ilex guayusa*, *Urtica urens*, and *Aphandra natalia* (see online supplementary Table S3) in AFS of study area, suggests preferences for arboreous species that are associated with the preservation of the indigenous identity and cultural beliefs, e.g., traditional beverages, rituals, and handcrafts

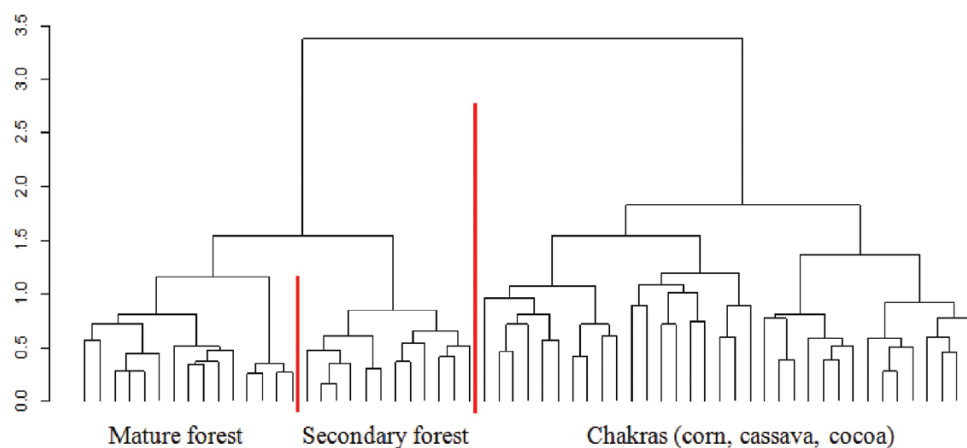


Figure 3: dendrogram showing the degree of qualitative dissimilarity among all sites investigated in the five systems: cassava (*Manihot esculenta*), corn (*Zea mays*), cocoa (*Theobroma cacao*), SF, and MF in the buffer zone of the Northern Ecuadorian Amazon. The Ward and the Bray–Curtis distance methods were used. The Y axis shows the height of the Bray–Curtis distance as it was calculated using the *vegan* package and the *hclust* function in the R statistical software. Note two different groups divided by a line: the secondary forest and mature forest group and the AFS. The scale line indicates the degree of dissimilarity. A pair of branches close to 0 means more similarity in sites.

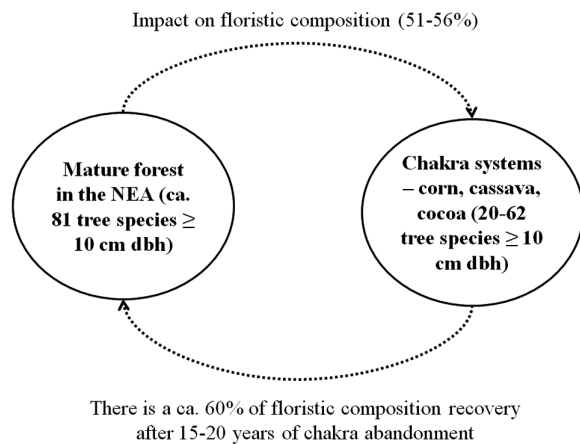


Figure 4: cyclic description of the chakra system in the buffer zone of the Northern Ecuadorian Amazon. The two circles represent the tree species richness in the MF and the chakras. The lines indicate the process of transforming MF to chakras, the forest recovery after chakra abandonment, and their effects in the floristic composition, respectively. This cycle starts when the MF is transformed into different chakra systems with their impacts in alpha and beta diversity. Then, the chakra is abandoned allowing forest recovery.

(Arévalo 2009; Perreault 2005). Thus, the Kichwas culture of the western Amazon is also represented in the chakras. In all, AFSs in the NEA are adaptations to more diversified, ecologically healthy, and sustainable agrosystems based on use of resources adjacent to forests.

Our inquiries also showed that the shifting agriculture in the buffer zone of the NEA denotes a permanent dynamic structure between MF and chakras that keep significant levels of alpha and beta diversity (see Fig. 4). The first feature regarding this interesting configuration is that the alpha diversity in the MF is limited by continuous modifications of the arboreal strata. Our results disclosed ca. 81 tree species (>10 cm dbh) in 4.04 ha (Table 1). It is noticeable that this value is lower compared to other similar inventories of tree species >10 cm dbh. For instance, 307 tree species ha⁻¹ inventoried in the *Reserva Faunística Cuyabeno* (Valencia et al. 1994), 251 tree species ha⁻¹ in the Yasuní National Park (Valencia et al. 2004), and 217 tree species ha⁻¹ in the Jatun Sacha forest (Palacio and Jaramillo 2001), all of these reserve forests in the NEA, a region with remarkably high biodiversity values. This information suggests that the degree of maximum post-disturbance recovery and biodiversity levels of the MF communities in the Ecuadorian Amazon buffer zone is significantly lower compared with protected forests as shown by the 81 species (Table 1), which is the result of the uninterrupted use of this forest for agriculture. In all, this structural richness may well represent the adequate threshold for recovery when Aboriginal people use forests plots for farming.

Following the conversion of the MF to chakra, the second dynamic characteristic is directly related to the impact of decreasing levels of alpha diversity from as low as 52% to up 75%. However, even after this transformation, the AFSs have

slightly higher effective number of species of trees ≥10 cm dbh, i.e., 13 in corn, 18 in cassava, and 19 in cocoa (Table 1), than other AFSs in the tropics, specifically compared with cocoa systems in Ghana (Asase and Tetteh 2010) and Mexico (Ramírez-Meneses et al. 2014), with 15 and 13 effective number of tree species ≥10 cm dbh, respectively. This means that there are higher biodiversity levels in the AFSs of Ecuador, as evidenced by >20% of tree species, compared to other tropical regions. Hence, the degree of intensification exercised in MF in the conversion to AFS in the western Amazon is likely lower than the integrated systems in other tropical areas of the world. The combination of MF and chakras increases ca. 25% the total diversity, which translates in a contribution of ca. 28 species to the total floristic richness (Table 1). Thus, both types of land use (109 ± 10 species richness) have a synergetic effect in the alpha diversity of the buffer zone of NEA. Although these species richness values are relatively low compared to protected forests in the same area (Valencia et al. 1994, 2004) and other preserved regions of the upper Amazon (Gentry 1988), the dominant plant families in the buffer zone are the same as those reported in the *Reserva Faunística Cuyabeno* located also in the same zone. That is, 7 of the 10 main plant families, i.e., Fabaceae, Lauraceae, Sapotaceae, Annonaceae, Moraceae, Burseraceae, and Myristicaceae, concur with the list presented in Valencia et al. (1994). This finding supports the idea that changes in alpha diversity in the buffer zone are mostly driven at the species level.

Specific structural dynamics were also observed between the MF and chakras in relation to changes in the floristic composition (Fig. 4). Our results showed that beta diversity varied between 51% and 56% in tree species ≥10 cm dbh (Table 2). These changes are significantly lower than the cocoa AFSs in Africa. For instance, the modification of natural forests to young replanted cocoa (3–5 years old) plots represented an estimated 88% change of the floristic structure in Ghana (Anglaaere et al. 2011) and ca. 82% in Cameroon (Zapfack et al. 2002), values substantially higher than those reported in this study, i.e., 51% and 56%. Thus, unlike Africa, the anthropogenic actions in the NEA appear to have fewer negative effects on forests communities, which is illustrated by higher levels of Shannon diversity found in this study, which fluctuated between 13 and 19 effective number of species. Evidently, the management of tree diversity by farmers is intended to preserve stratified floristic components associated with ecological functions more similar to the natural climax forest, which ultimately benefit crop establishment and development.

Another major argument for the preservation of levels of plant diversity is in connection with the active cycle of shifting agriculture, which concludes with the abandonment of the chakra. The spatial and temporal practice of the AFS facilitates rapid forest recovery as suggested by our dissimilarity values (0.43) between the SF (~15–20 years old) and the MF. These indices denote a significant floristic recovery of ca. 60% after chakra abandonment (Fig. 4), which is consistent

with a small-scale shifting agriculture in which pioneer species and surrounding vegetation in ecozone areas drive a new successional process (Chazdon 2003). Specifically, these characteristics could influence the AFSs in the buffer zone of the NEA allowing seeds from native species to germinate and re-emerge regardless of the chakra type, eventually leading to a singular floristic structure. Therefore, despite the existence of diverse AFSs with different floristic composition, upon abandonment, these tree assemblages are less differentiated during the recovery process until the characteristic structure of the MF is reached, suggesting a remarkable forest resilience (Fig. 2).

An additional central aspect underlying the significance of chakra farming is the opportunity for biodiversity conservation, particularly endemic, vulnerable, and threatened species as well as basic ecological and genetic fingerprints. Based on our findings, the existence of two endemic species, i.e., *A. lugonis* and *S. porcatum*, has probably been facilitated by indigenous farming practices and the resilience and stability of forests. The same can be said for endangered species because the buffer zone includes four taxa listed in this category, which along with other species form part of the dominant elements of this unique floristic assemblage. These plants are also useful resources for both local indigenous people and fauna. For example, *C. odorata*, *S. macrophylla*, and *Cedrelinga cateniformis* are valuable for timber (Porro *et al.* 2012); *Croton lecheri* is used for medical purposes (Jones 2003); and *P. rigida* is eaten by animals, especially spider monkeys (Suarez 2006). Nonetheless, according to the IUCN (2016), the rarity status of the vast majority (92%) of the species in this area remains to be evaluated, which is a serious knowledge gap posing constraints to propose proactive options for conservation of species. On the other hand, the intrinsic dynamics of the chakras may have repercussions on diverse ecological attributes associated with species turnover. It is known that AFSs and other wooded areas generate different ecosystem services, such as preventing erosion of soils from wind and water and retaining nutrients and water table levels (FAO 2015); nevertheless, the replacement of tree species from MF to AFS can influence the carbon balance. In this scenario, the new dominant and fast-growing species in chakras, such as *C. alliodora* and *Ochroma pyramidale*, can play a critical role as a carbon sink during the initial successional stages (Chazdon 2003). Although this activity may vary depending on resource availability and intensity and duration of the disturbance (Baker *et al.* 2003; Chazdon *et al.* 2007), the chakra system can be considered as a farming alternative to mitigate climate change. In all, the preservation of threatened and vulnerable taxa and the enhancement of natural corridors to connect wild fauna and flora make this system an efficient alternative for farming practices in vulnerable and fast-changing ecosystems.

In conclusion, the attributes of chakras in relation to AFSs intersect in the production of local foodstuffs, conservation of adequate levels of alpha and beta biodiversity, and culturally representative native species and ethnic traditions. These

are tangible characteristics allowing a more harmonious and less labor intensive farming system used by indigenous communities to obtain major supplies for their well-being while preserving forests, natural habitats, and plant diversity. Concisely, land use involving intercropping systems, i.e., chakras, in the Amazon Region and other tropical countries has a strong potential to mitigate food security and ameliorate climate change at the local and regional levels by preserving forest ecosystem structure, integrity, and functional dynamics of natural landscapes. Similar positive effects of this agrosystem in conjunction with fundamentals of forest resilience can benefit other tropical regions of the world.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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