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HUMAN INTERVENTION, NEUTRAL THEORY, AND THE ASSEMBLY OF AMAZONIAN SECONDARY FOREST COMMUNITIES IN NAPO, ECUADOR

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ABSTRACT
Amazonian forests host a very high biodiversity, but suffer deforestation for settling monocultures and livestock. Little is known about how different land-uses shape forest's biodiversity during further recovery. We investigated that by using the human-mediated community assembly-hypothesis, combined to the Unified Neutral Theory of Biodiversity and Biogeography (UNTB) as an Ockham's razor. We counted, marked, and identified all trees 10cm diameter at breast height on four 1-ha, secondary forest plots with already well-known land-use histories. We assessed the relative species abundances (RSA), richness, diversity, dominance, similarities, and species compositions of all plots. Plots A (12-15), B (22-25), and C (35-37y-old forests) were abandoned pastures and quasi-monocultures. Plot D (35-40y-old forest) was used for self-consumption agriculture (in Kichwa indigenous language *chakra*-and *ushun* periods) per six years (>50 planted species), then used for extracting resources –including fruits, medicine, and logs during fallow (*purun* period). For all plots, RSAs were lognormal (x^2; p>0.24) suggesting that random-and-symmetric birth, death, and immigration from the surrounding metacommunity are enough for explaining RSAs. Species richness, Shannon-, and Fisher's- diversities changed as follows: plotA<plotB<plotC<plotD while dominance varied in the opposite way. There was virtually no evidence of coppicing. Many species were useful for food, wood, and medicine. Dominant species are mainly wind-, animal-, and human-dispersed. Plot D's species composition was less similar to all other plots. Our results suggest that seed dispersal assembled forest communities according to UNTB, while humans mediated the secondary succession process after clear-cutting for agriculture and livestock by means of: planting, nursing, caring, and tolerating species, and opening gaps (selective logging) during fallow. For Amazonians, letting, respecting and enhancing highly diverse forests generated by natural processes guarantees a safer stock of resources so Amazonians may have no reason to make forest assembly to depart from neutral-and-symmetric birth, death, and immigration during succession.

KEY WORDS: Biodiversity, Community Assembly, Land-Use History, Secondary Succession, Trees.

INTRODUCTION
Amazonian forests are well known for hosting a great part of global biodiversity (Jenkins *et al*., 2013), mitigating Climate Change by catching Carbon Dioxide (Brienen *et al*., 2015), and being clear-cut for settling monocultures and livestock (Fearnside, 2005, Morton *et al*.,2006), which puts some 15 thousand species at risk (ter Steege *et al*., 2015). Yet most of such threats have occurred on late 20th- and early 21st centuries. Prior to that, Amazonians invented, improved, and practiced still-in-use ways to manage species, forests, plantations, landscapes, and soils (Clement 2006, Glaser and Birk, 2012). Each indigenous farmer clear-cuts 1 hectare each time, then plant, care, and use tens-to-hundreds of species (Perrault-Archambault and Coomes, 2008; Runashitu, 2009) while keeping both mature and secondary forests around crops (Cerón, 1990). Moreover, neighboring families and clans build-up agreements in order to keep people's-owned forests connected to their farms (*e.g*. Runashitu, 2010). Such a land-use regime facilitates forests' comeback throughout secondary succession (Chazdon, 2014). If all these are true, then Amazonian tree-communities should have an imprint from human intervention (Garrido-Pérez & Glasnovi , 2014) as some new evidence starts to show (Levis *et al*., 2017). Yet little is known about the mechanistic role of humans on Amazonian forest structuring. We assess that by combining two approaches: human-mediated community assembly –based on works by Arturo Gómez-Pompa (1987), and the Unified Neutral Theory of Biodiversity and Biogeography by Stephen P. Hubbell (2001) (hereafter UNTB).

Human-mediated- vs Neutral community assembly
How land-use by humans structures Neotropical forest communities has been widely studied in Mexico (*e.g.* Gómez-Pompa, 1987, Barrera-Bassols & Toledo, 2005), the Caribbean (*e.g.* Pascarella *et al*., 2000, Rivera *et al*., 2000, Salmerón López *et al*., 2015), and Brazil (*e.g.* Sampaio *et al*., 1998). That enabled others to formulate

hypotheses on human-mediated community structuring (*e.g.* Garrido-Pérez & Glasnovic, 2014). Since trees have longer life-spans than humans, and since tree species are differentially adapted to disturbance, it has been hypothesized that characteristics like relative abundance, diversity, and species composition of tree communities are a result of human-made disturbance occurring throughout land-use history (Garrido-Pérez & Glasnovi , 2014). *Homo sapiens'* environmental impacts are to be addressed by multi-disciplinarily reconstructing the land-use history of a forest stand using Ethnography, History, Remote sensing, and other information and methods; then interpreting forest's history under the scope of basic Ecology (e.g. Martinez-Ramos, 1994). From the perspective of forest ecology, *H. sapiens* is to be considered as (a): a producer of large-scale disturbance by clear-cutting and burning terrains. (b) A small-scale disturbance-maker by means of gaps; also enhancing the mortality of target tree species by means of selective logging. (c) A species-selective predator and disperser of seeds. (d) An herbivore; e.g., by taking-off leaves of palms for making roofs (Garrido-Pérez & Glasnovi , 2014); all these should affect forest characteristics.

Alternatively, tree-community assembly can result from random, among-species symmetric birth, death, and immigration from surrounding metacommunity (UNTB) (Hubbell, 2001, Rosindell *et al.*, 2011). That can even result in log-normal distributions of relative abundance of species (*e.g.* McKane *et al.*, 2000, Volkov *et al.*, 2003), suggesting that the mentioned processes, rather than human intervention or niche partition, are enough for explaining community assembly unless other processes fit better to field data (Hubbell, 2008). On its side, human mediated assembly may result in departures from lognormal. Some possible causes can be: enhanced populations of some species by active planting, differential pre-adaptation to anthropogenic disturbance, and reduced populations of weeded-and-selectively logged species (see also Garrido-Pérez & Glasnovi , 2014). Truly, explanations other than UNTB can also fit with lognormal, yet UNTB has fewer free terms and is easier to test than competition and other potential drivers of forest communities (Rosindell *et al.*, 2012). Hence we use UNTB as part of an Ockham Razor (Hubbell, 2008). If random migration, mortality and birth are not structuring secondary forest communities in the Amazon, then it is easier to find past human-made actions structuring plant communities by interviewing humans, than testing the role played by processes like competition and density-dependence in the past (Garrido-Pérez & Glasnovi , 2014).

The general goal of this paper is to throw some light on the mechanisms by which humans are able to contribute to the assembly of Amazonian forest communities. Specifically, we aim:

(a) To deduce what occurred to four plots on Amazonian forests during secondary succession based on field surveys and land-use history.
(b) To draw a mechanistic explanation to community assembly during secondary succession, based on land-use history. Our research questions are:
1. Do the relative abundance distributions of canopy tree communities in secondary forests follow lognormal-

or-logseries distributions (supporting UNTB), or any other distribution like geometric or broken stick (potentially favoring human-mediated assembly hypothesis)?
2. What are the changes of species richness, diversity, and composition among secondary forest plots, how similar are the communities, and how can land-use history explain such changes?

MATERIALS & METHODS
Study site and plots' settlement
This research was run in Atacapi, Canton of Tena, Napo, Ecuador (~7km from Tena City); buffer zone of the Colonso-Chalupas Biological Reserve, near rivers Colonso, Pashimbi and Tena (fig.1).
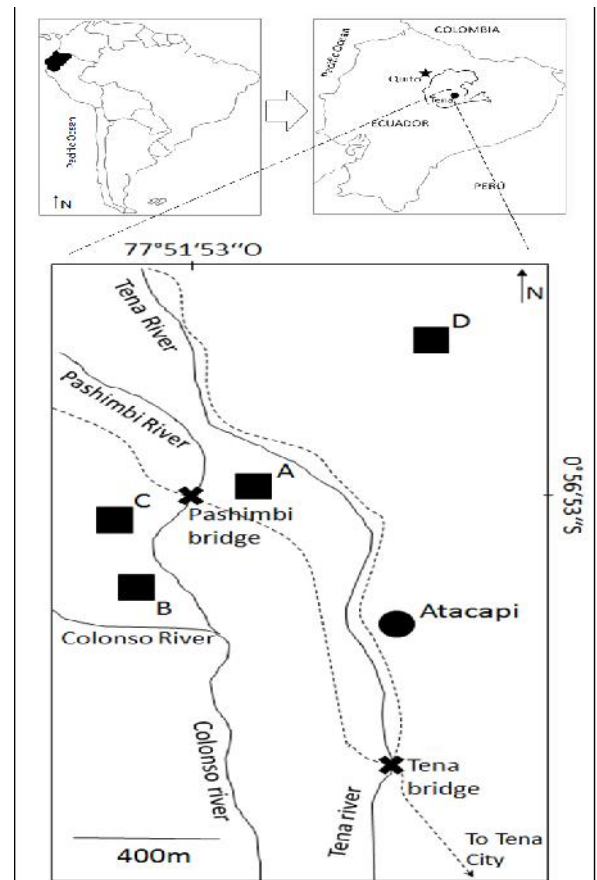

FIGURE 1: Study site and location of four 1-hectare plots on secondary, Terra Firme forests in Atacapi, province of Napo, Ecuadorian Amazon. Squares represent plots; dotted lines in the lower panel represent roads.

Life zone is Tropical Rainforest (*sensu* Holdridge *et al.*, 1971) located on Terra Firme; Evergreen High-canopy Jungle (*sensu* Miranda & Hernández, 1963). Altitude is ~650 m.a.s.l., annual rainfalls are ~4100 mm year^{-1} for nearby Jatun Sacha (Clinebell *et al.*, 1995); temperatures average 23°C (https://es.climate-data.org/location/2977/). Soils are well-drained inceptisols (MAGAP, 2011). Four 1ha-plots (50m x 100m) were randomly settled, and delimited following terrain's contour. Plot A was ~200m away of Tena River and other ~200m away of Pashimbi River. Plot B was ~100m away of Pashimbi- and ~200m

away of Colonso River. Plot C was ~200m of Pashimbi River, and Plot D was ~600m away of Tena River.

Surrounding vegetation and summarized land-use histories

Plot A occupied a 12-15y-old, smaller than two hectares stand surrounded by abandoned pastures, citric, two houses (one of them non-complete), and a two-way street paved on 2011. Plot B was surrounded by a secondary forests including: a 22-25y-old forest section where the plot was settled, and a 38-37y-old section where plot C was established. In the same forest area, but about 850m westwards from plot B the forest becomes even older. Plot C was located on a plateau some four meters above plot B; the plateau forms a ridge approximately 8m above Pashimbi River. Both plot B and plot C have smooth slopes leading to a crick inside. On another hand, plot D was settled at approximately 550m from Tena River (fig.1), upon a plateau approx. 10m above such a river. Although plot D has a crick inside, this appears at the bottom of a ridge 90° respect to the horizontal. Plot D is embedded inside a vegetation mosaic including: secondary forest of different successional ages, shifting-agriculture by Kichwa indigenous, small houses with gardens and backyards –instead of just secondary forests as occurred with plots A-C.

Land-use histories and occurring disturbances were not the same among plots (Table 1). Plot A was largely used for livestock and Agro-forestry oligocultures, plots B and C were devoted to two different intensities and duration of cattle and housing as well as oligoculture. Finally, plot D was used for shifting agriculture according to traditional, Kichwa-indigenous *chakra-ushun-purun* system (*e.g.* Vitery, 2015) which is similar to Maya land-use system (Gómez-Pompa, 1987).

Chakra is the Kichwa word for a period including: (a) clear-cutting by slash-mulch-and-burn, (b) collecting seeds of food- and wood species from the forest in order to nurse them, and (c) planting short-cycle species –mainly *Manihot esculenta* Crantz (Euphorbiaceae). In the mentioned language, *ushun* is the second period, starting at the end of the first *M. esculenta* harvest (nine months after planting). Then, short-cycle species are planted again, but being combined with other, longer-living species taken from the previously made nursery. Together, *chakra* and *ushun* periods comprehend >50 plant species in the crop, mainly perennials. Finally, *purun* is a period starting at approximately the sixth year from the beginning of the whole process. *Purun* is a fallowing period where growing forest is used for selectively extracting wood- and non-wood resources while training kids about the plants and processes of the forest and how to use them (Vitery, 2015). Thus, plot D was used by means of the *chakra-ushun-purun* shifting agriculture, while plots A, B, and C were preeminently used for commercial crops and livestock (Table 1) for the market (see Garrido-Pérez in review for full details of the land-use history and socio-economics of studied forests).

TABLE 1. Summarized land-use histories (1970-2015) of four 1ha plots (A, B, C & D) on secondary, Terra Firme forests in Atacapi, province of Napo, Ecuadorian Amazon (after Garrido-Pérez et al. in review). *Chakra*, *ushun*, and *purun* are Kichwa-indigenous words for three periods of planting, cultivating, and harvesting of more than 50 species during shifting agriculture and fallow management. Taxa mentioned by common names: citrus= *Citrus spp.*, Rutaceae; coffee= *Coffea canephora* Pierre ex A. Froehner, Rubiaceae; manihoc= *Manihot esculenta* Crantz, Euporbiaceae; plantain= *Musa* spp., Musaceae; guayusa= *Ilex guayusa* Loes., Aquifoliaceae.

Date (A.D)	Plot A	Plot B	Plot C	Plot D
1970-1980	Abundant cattle	Abundant cattle	Abundant cattle and horses. Big house with stable included. Abundant citrus, and fruit trees in oligo-culture; therefore: thinning.	Forest until 1971 –date of clear-cutting. Then *chakra* per nine months (until 1972). Then *ushun* per five years (1972-1976). About 50 planted species during *chakra* and *ushun* including edible, and wood-producing trees. Finally, *purun*- and managed fallow used for selective logging and extraction of non-wood resources (1976-2015).
1980-1992	Cattle on half of plot's area. On the second half: oligoculture with mainly coffee and citrus. Thinning was common; an unknown pesticide was used only once.	Oligoculture: mainly manihoc, plantain, citrus, and guayusa. Cattle. Small livestock (pigs). Small house for one person.	Fallow (1980-2015).	*Purun*-managed fallow, including selective logging and extraction.
1992-2001	Cattle on half of plot's area. On the second half: oligoculture –mainly coffee and citrus; thinning was common.	Fallow.	Fallow.	*Purun*-managed fallow, including selective logging and extraction.
2001-2015	Fallow with thinning and weeding.	Fallow	Fallow	*Purun* -managed fallow, including selective logging and extraction.

Floristic survey

All woody plants 10cm diameter at breast height (dbh =1.3m above ground level) were tagged, measured, and identified (method by the *Red Amazónica de Inventarios Forestales* –RAINFOR for putatively non-human-intervened forests; Phillips & Baker, 2003). Collecting vouchers was not allowed but in-situ research was. Fortunately, Morphological differences among most plants were clearly visible too, and other studies report consistent results when using morphospecies *vs* identified species (Duque *et al*., 2017). Plants were well recognized by our local co-authors (one 67y-old man, and one 35y-old man living all life-long in the area) using Kichwa-language names. Ambiguities were reduced to minimum by unifying nomenclature using Kichwa names according to names provided by our 67y-old co-author who was also the oldest member of our team, then using such a "para-taxonomy" for letting the survey to progress during the limited time of the project. Besides that, many families and genera were firstly identified in the field with the help of guides (*e.g.* Gentry, 1993). Cross-comparisons and other field-and-online sources were used to get the scientific names of species. Such resources included: The British Royal Botanical Garden's (Kew) *neotropikey* (http://www.kew.org/ science/ tropamerica/neotropikey.htm), the *Neotropical herbarium specimens of the Field Museum* (http://fm1.fieldmuseum org/vrrc/), the *Tropicos* guide of the Missouri Botanical Garden (MOBOT: http://www. tropicos.org/), the digital herbarium of the Smithsonian Tropical Research Institute (http://biogeodb. stri.si.edu/ herbarium/), as well as illustrated guides made for zones similar to our study site (*e.g.* Rojas & Martina, 1996, Dörfle, 2002, López & Montero, 2005, Flores Bendezú, 2013). Many of the found genera and species are economically useful so monographs on them were consulted too (e.g. Erkens *et al*., 2007, Mori & Cornejo 2013, Erazo *et al*., 2014). The same was made for highly specious families like the Melastomataceae (Mendoza & Ramírez, 2006).

Data analysis

(a) Relative abundances and species diversities

After determining species and numbers of individuals per species, we obtained best fits to relative abundance distributions for each plot testing for geometric, broken stick, log-series, and lognormal distributions. Because most of the very abundant species were useful for humans (see results), we re-ran best-fit tests for relative abundance distributions while progressively excluding such species in order to determine whether such species made results to depart from log-series distributions. By making that, we kept UNTB as an Ockham Razor, adding complexity to the simplest possible explanation to community assemblage (Hubbell 2008) by means of considering an additive role of species interesting for humans in the process of community assemblage.

We additionally ran best-fit abundance-distributions test for all plots together –assuming all plots as a sample of the meta-community. On another hand, used indexes of local species diversity (-diversities) (Krebs 1999) were: Fisher's- (extracted from the formula $S= /\ln(1+N/)$), Shannon-Wienner's H' ($H'= - \sum p_i \ln p_i$) where p_i= relative frequency of the ith species and ln= natural logarithm, and Simpson's dominance (D) index as well ($D= \sum p_i^2$).

(b) Similarities, and species compositions among plots

Among-plot differences of species and family composition were evaluated as follows: (a) rarefaction curves with 95% confidence interval –where overlapping confidence intervals of surveyed plots are considered more similar. It is worth to consider that species-cumulative curves are themselves indicators of diversity: communities with higher curves are more diverse compared to other communities. We also made paired comparisons of taxa (species and families separately) composition using: (b) Sørensen index (Sø): [Sø= (b+c)÷ (2a+b+c)], and (c) Jaccard index (J): [J= (b+c)÷ (a+b+c)]; where b=number of species or family occurring in one plot of the pair, c= number of species or family occurring only on the other plot of the pair, and a= number of species or family shared on both plots. Finally, (d) species lists were made, and compared among plots.

RESULTS

(a) Relative abundances and species diversities

All plots together had 1559 individuals belonging to 188 identified species, plus seven morpho-species identified by common names. Plot A had 323 individuals, plot B had 332 individuals, plot C had 489 individuals, and plot D had 415 individuals. For all plots, relative-abundance distributions of species were log-normal (Chi-square; p>0.24, Table 2, fig. 2) suggesting that random-and cross-species symmetric birth, death, and immigration are enough for explaining relative abundances according to UNTB. All other tested distributions did not fit with our data (p<<0.001).

TABLE 2. Significance (p-values after Chi-square) for best fit tests for the species relative abundances of trees 10cm diameter at breast height (dbh=1.30m above ground level) for four one-hectare plots on secondary, Terra Firme forests with different land-use histories in Atacapi, Ecuadorian Amazon, including and excluding hyper-abundant species.

Plot (forest age in years)	log-series		log-normal		Excluded species, their dispersal, and use.
	all species	after exclusion	all species	after exclusion	
A (12-15)	< 0.001	0.62	0.24	0.16	*Piptocoma discolor* (Kunth, Asteraceae) (n=129); anemocorous, wood for sale.
B (22-25)	< 0.001	0.87	0.64	0.74	*Matisia bracteolosa* Ducke (Malvaceae) (n=102); zoocorous, wood.
C (35-37)	< 0.001	0.88	0.49	0.22	*Vochysia bracelineae* Standl. (Vochysiaceae) (n=103), anemocorous, wood. *M. bracteolosa* (n=74); zoocorous, wood. *Pourouma cecropiifolia* Mart. (Cecropiaceae) (n=69); domestic, fruit for consuming and for sale.
D (35-40)	0.009	0.73	0.42	0.26	*Guadua angustifolia* (n=64); anemocorous, trunk for housing and fences. *P. discolor* (n=53); anemocorous, wood for sale. *Graffenrieda c.f. galeotti* (Melastomataceae) (n=50); zoocorous

Interestingly, relative abundance distributions reached log-series after excluding the most abundant species (Table 2), reinforcing the idea that neutral-symmetric processes drove the assembly of relative abundances during early succession even if the mentioned species are useful for humans. Best-fit analysis after pooling data for all plots showed that only log-normal (Chi-Square, p=0.38), instead of log-series (Chi-Square, p <0.001), or any other tested distribution (fig. 3) fitted better to the species relative abundance distributions, suggesting that the meta-community was not yet well represented by our four plots. On another hand, plot's species richness, Fisher's- , and Shannon's H' (Table 3), and the height of species rarefaction curves as well (fig.4a) changed as follows: A<B<C<D, pointing to a relevant role of *chakra-ushun-purun* as a way of enhancing tree-diversity compared to livestock and oligoculture –since plots C and D had similar successional ages. Consistent with all these, Simpson's dominance changed as follows: D<C<B<A (Table 3).
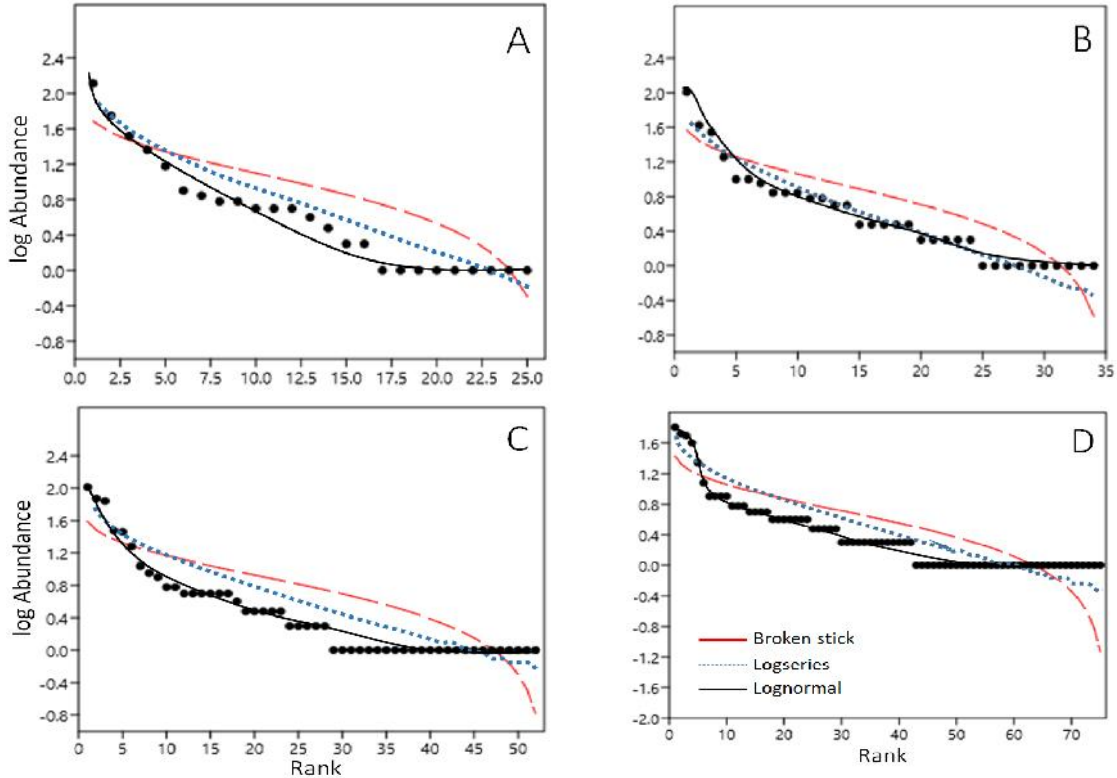

FIGURE 2. Species relative abundance distributions and fit curves for four 1-ha Amazonian secondary forest plots (A, B, C, and D) in Atacapi, Napo, Ecuador. Only lognormal fitted to data (p>0.24 for all plots). Black points represent species.

Table 3. Diversities of trees =10cm diameter at breast height (dbh=1.3m above ground level) for four one-hectare plots of secondary, Terra Firme Forests with different land-use histories in Atacapi, Ecuadorian Amazon. S= species richness, F= number of families (excluding morphospecies). Diversity indexes are: α= Fisher's α, H'= Shannon's H', and D=Simpson Dominance.

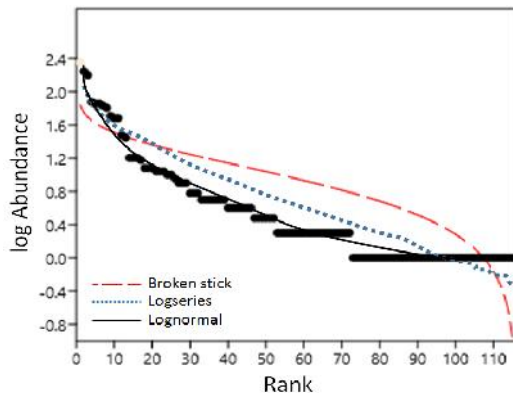| Plot (age in years)	S	F	α	H'	D
A (12-15)	29	15	6.36	2.09	0.22
B (22-25)	35	20	9.81	2.52	0.13
C (35-37)	52	26	15.24	2.73	0.10
D (35-40)	79	33	26.81	3.31	0.07

FIGURE 3. Species relative abundance distribution and it curves after joining data from four 1ha Amazonian secondary forest plots in Atacapi, Napo, Ecuador. Only lognormal fitted to data (Chi-Square, p=0.38). Black points represent species.

(a) Similarities, and species compositions among plots
Confidence intervals of rarefaction curves overlapped for plots A *vs* B, and mainly for plots B *vs* C (fig.4a) suggesting they had similar species compositions. Consistent with that, both Sørensen and Jaccard indexes were lower –showing higher floristic similarities for pairs of plots having more overlap after the mentioned rarefactions (Table 4). Moreover, overlapping enhanced after running rarefactions for families (fig.4b): there was a full overlap of confidence intervals for family-rarefaction

curves between plots B and C, an enhanced overlap between plots A and B, and even some overlap between plots C and D (fig. 4b) which did not appear after rarefaction for species (fig. 4a). Coherent with that, an oligarchy of species and families became very abundant in more than one plot during secondary succession (Tables 5 and 6), suggesting that dominant taxa strongly contributed to the overlap by colonizing several plots during succession.
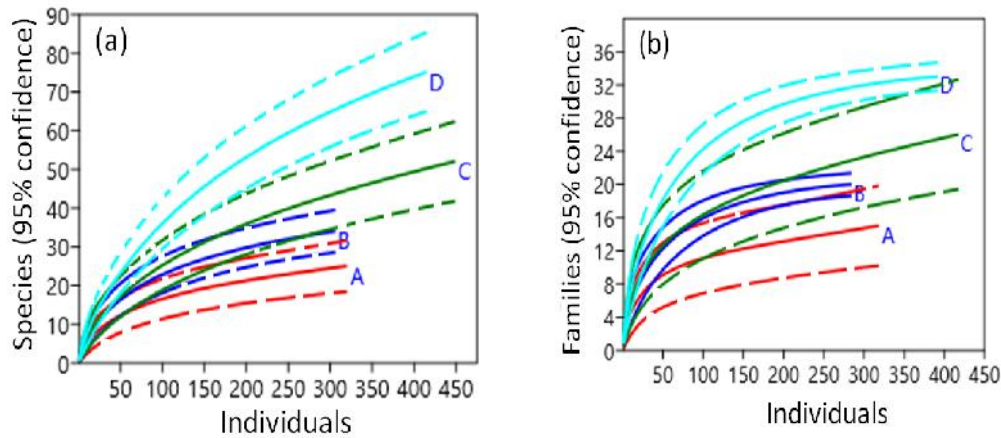

FIGURE 4. Rarefaction curves (95% confidence intervals) for communities of trees 10cm dbh for four one-hectare plots of secondary, Terra Firme forests with different land-use histories in Atacapi, Ecuadorian Amazon. (a) Curves for species. (b) Curves for families.

TABLE 5. Similarity Sørensen's (non-shadowed) and Jaccard's (shadowed) indexes for paired communities of trees 10cm diameter at breast height (dbh=1.3m above ground level) for four one hectare plots (A, B, C, and D) on secondary, Terra Firme forests with different land-use histories in Atacapi, Ecuadorian Amazon. (a) For species. (b) For families.

(a)	A	B	C	D
A	1	0.39	0.61	0.66
B	0.56	1	0.49	0.69
C	0.76	0.62	1	0.61
D	0.80	0.81	0.75	1

(b)	A	B	C	D
A	1	0.59	0.37	0.40
B	0.54	1	0.22	0.32
C	0.54	0.36	1	0.22
D	0.57	0.49	0.36	1

DISCUSSION
What occurred to forests during secondary succession
Our results confirm that clear-cut areas close to forests have a good potential for natural regeneration (Chazdon & Guariguata, 2016) and add information on how such a succession occurs. Thus, joining our results into a coherent history, secondary succession on our plots should have combined: (a) neutral processes assembling relative abundances for all plots (Rosindell *et al*., 2011). (b) Human intervention influencing richness, diversities, and species compositions on each plot, which is consistent with other studies (Sampaio *et al*., 1998, Pascarella *et al*. 2000, Rivera *et al*., 2000, Salmerón-López *et al*., 2015), yet without altering lognormalities of relative abundances.

TABLE 5. Most abundant species (n 7 individuals) of trees 10cm diameter at breast height (dbh=1.3cm above ground level) arranged from most abundant- to less abundant for four one-hectare plots of secondary, Terra Firme forests with different land-use histories in Atacapi, Napo, Ecuador. Numbers of individuals are in brackets.

Plot A (12-15 years)	Plot B (22-25years)	Plot C (35-37years)	Plot D (35-40years)
Piptocoma discolor (Kunth, Asteraceae) (129)	Matisia bracteolosa Ducke (Malvaceae) (102)	V. bracelinieae (Vochysiaceae) (103)	Guadua angustifolia Kunth (Poaceae) (64)
Cecropia longipes Pittier (Cecropiaceae) (56)	P. discolor (Asterceae) (42)	M. bracteolosa (Malvaceae) (74)	P. discolor (Asteraceae) (53)
Cecropia spp (Cecropiaceae) (33)	Miconia c.f. decurrens; Melastomataceae (35)	Pourouma cecropiifolia Mart. (Cecropiaceae) (69)	Graffenrieda c.f. galeotti (Melastomataceae) (50)
Dicksonia selloviana (Pr.) (Dicksoniaceae) (23)	V. bracelinieae (Vochysiaceae) (18)	Miconia c.f. decurrens (Melastomataceae) (30)	Dilodendron c.f. costaricense (Sapindaceae) (40)
Vochysia bracelinieae Standl. (Vochysiaceae) (15)	urku tamburu (10)	Pseudobombax sp1 (Bombacaceae) (29)	V. bracelinieae (Vochysiaceae) (22)
Bellucia pentamera Naudin (Melastomataceae) (8)	Pseudobombax sp1 (Bombacaceae) (10)	pikchiua (19)	Inga pavoniana Benth. & Hook. (Mimosoideae) (12)
Inga edulis Mart. (Mimosoideae) (7)	Graffenrieda c.f. galeotti (Melastomataceae) (9)	Iriartea deltoidea Ruiz & Pav. (Arecaceae) (11)	Hieronyma alchorneoides Allem. (Euphorbiaceae) (8)
	Macrolobium acaciifolium (Benth.) (Caesalpinioideae) (7)	Cedrela odorata L. (Meliaceae) (9)	Nectandra sp2 (Lauraceae) (8)
	Cecropia spp (Cecropiaceae) (7) pikchiua (7)	Wettinia maynensis Spruce. (Arecaceae) (8)	Guatteria sp2 (Annonnaceae) (8)
			Cecropia spp (Cecropiaceae) (8)

TABLE 6. Most abundant families (n 7 individuals) of trees 10cm diameter at breast height (dbh=1.3cm above ground level) arranged from most abundant- to less abundant for four one-hectare plots of secondary, Terra Firme forests with different land-use histories in Atacapi, Napo, Ecuador. Numbers of individuals are in brackets. Underlined families occupy a position in this ranking non-consistent to the rank of the most abundant species of the same family in Table 5, suggesting such a change was due to other members of the family.

Plot A (12-15 years)	Plot B (22-25 years)	Plot C (35-37 years)	Plot D (35-40)
Asteraceae (129)	Malvaceae (104)	Vochysiaceae (103)	Poaceae (64)
Cecropiaceae (90)	Melastomataceae (47)	Malvaceae (76)	Melastomataceae (54)
Dicksoniaceae (23)	Asteraceae (42)	Urticaceae (69)	Asteraceae (53)
Melastomataceae (18)	Vochysiaceae (18)	Melastomataceae (37)	Sapindaceae (40)
Vochysiaceae (17)	Cecropiaceae (12)	Bombacaceae (31)	Vochysiaceae (22)
Mimosoideae (11)	Bombacaceae (10)	Arecaceae (19)	Mimosoideae (16)
Clusiaceae (8)	Unknown 1 (7)	Unknown 1 (19)	Annonnaceae (14)
	Caesalpinioideae (7)	Annonnaceae (13)	Cecropiaceae (14)
		Mimosoideae (12)	Meliaceae (12)
		Meliaceae (10)	Lauraceae (11)
		Moraceae (9)	Clusiaceae (8)
		Cecropiaceae (8)	Euphorbiaceae (8)
			Urticaceae (7)

Above-mentioned synergy between neutral processes and human mediation may have assembled tree communities as follows.

1. Clear-cut areas should have been initially colonized by seeds and seed-bank representing the species pool of the surrounding, larger forest, according to symmetric-random sampling (Hubbell, 2001, Rosindell *et al*., 2011). Dispersal-based colonization is also supported by the virtual absence of large stumps on our plots and in the surrounding crops (Garrido-Pérez *et al*., in review): coppicing may have not played a significant role as it does in other Neotropical forests (e.g. Gómez-Pompa 1987, Sampaio *et al*. 1998).

2. Species coming first into clear-cut areas dominate during succession (Finegan, 1996) and that seems to have occurred in our plots. Most arriving seeds were wind dispersed (*e.g. Piptocoma discolor* (Kunth, Asteraceae) and *Vochysia bracelineae* Standl (Vochysiaceae)), whereas some were animal dispersed (*e.g. Matisia bracteolosa* Ducke (Malvaceae) and *Graffenrieda c.f. galeotti* (Melastomataceae)). Other species are domestic so they may have arrived by means of humans as dispersal agents before fallowing (e.g. *Pourouma cecropiifolia* Mart. (Cecropiaceae), *Inga edulis* Mart. (Mimosoideae), *Inga pavoniana* Benth. & Hook. (Mimosoideae)).

3. Colonization by dispersal "erased" the effects of previous land-use on further relative abundance distributions so the latter did not depart from lognormal. Lognormal is pervasive in old-grown Amazonian forests close to our study site at both 1- and 25ha scales (Duque *et al*., 2017). Therefore, we propose the "eraser effect" of seed dispersal plays a major role throughout succession.

4. UNTB is parsimonious enough for explaining species relative abundance distributions on all plots. Within the frame of the effects of dispersal, birth, and death, land-use by humans was associated to changed richness, diversity, and species composition among plots as has been reported somewhere else (Sampaio *et al*. 1998, Pascarella *et al*., 2000, Rivera *et al*., 2000, Salmerón-López *et al*., 2015). For plots A, B, and C, that occurred as a legacy of pre-abandonment livestock and quasi-monoculture, legating lower diversities and more similar species compositions compared to plot D. Since that occurred despite the different successional ages of the forests in plots A-C, they seemingly experienced a more similar successional path respect to plot D. Succession on plot D followed a different path due to manipulation during *chakra-ushun-purun* land-use.

5. For old forests around our study area, Duque *et al*. (2017) found ~210 species ha^{-1} in Yasuní (Ecuador), Amayacu (Colombia), and Manaus (Brazil). Also Pitman *et al*. (2001) found ~ 230 species ha^{-1} for Yasuni (Ecuador) and ~ 170 species ha^{-1} in Manu (Perú). These values are much higher than ours and suggest our studied stands need many years to recover tree-diversity.

However, our plot D had a clearly enhanced diversity compared A, B, and C suggesting that land-use by *chakra-ushun-purun* is better for further recovery of tree-diversity compared to livestock and quasi-monoculture. Yet, in another study (Garrido-Pérez *et al*. in review), we demonstrate *chakra-ushun-purun* delays the recovery of above-ground biomass –which mitigates Climate Change. That shows an aspect of the world-view of indigenous land-users: after thousands of years living in the area, plant diversity is desirable for indigenous land-users food security, medicine, and housing. In contrast, mitigating a climate change generated outside the Amazon has not yet become part of the interest of indigenous land-users in our study site.

Mechanisms of human-mediated Community assembly
Clear-cutting should have favored the arrival of anemochorous species producing thousands of seeds (Denslow, 1987, Martínez-Ramos, 1994). This should have applied for species like *Piptocoma discolor* (Kunth) (Asteraceae), *Vochysia bracelineae* Standl (Vochysiaceae), and *Cecropia spp*.

Planting (Gómez-Pompa 1987): *Chakra-ushun-purun* land-users directly plant edible species (*e.g. Inga spp*, *P. cecropiaefolia* and many Annonnaceae), and other useful species during *chakra* and *ushun*. By doing that, land users

act as seed dispersers themselves and facilitate succession by attracting animals bringing seeds of zoochorous wild species (Chazdon & Guariguata, 2016). That should have occurred to species like *Matisia bracteolosa* Ducke (Malvaceae) and *Graffenrieda c.f. galeotti* (Melastomataceae) which are dispersed by monkeys, birds, and bats (see also Renner 1989).

Nursing, caring, and tolerating species (Toledo *et al*., 2008): According to ours and other researches (Vitery 2015, Dörfle 2002) *chakra-ushun-purun* land users: (a) nurse seedlings of others species for planting them during *ushun* (e.g. wood-producer *Cedrela odorata* L. (Meliaceae)). (b) Take care of saplings and adults; for instance, by weeding around –which is much a sporadic activity in the *chakra-ushun-purun* compared to other land-uses. (c) Tolerate naturally-arriving species coming from surrounding forests based on the usefulness of such species (*e.g.* soft-wood-for-sale *P. discolor* (Erazo *et al*., 2014)), and housing-used *Guadua angustifolia* Kunth (Poaceae). Finally (d) tolerate rarely useful (*e.g.* sporadic sources of firewood) or virtually non-used species which are not weeds either (see Perrault-Archambault & Coomes, 2008, Runashitu, 2009 for lists of planted-and-tolerated species during land-use in Eastern Amazon).

Forming gaps: Land-use by *chakra-ushun-purun* recurrently enhanced gap-openning by means of selective logging. This is known to enhance plant diversity during *purun* (Brokaw 1987, Denslow 1987).

Humans *vs* other drivers of community assembly
Human-mediated community assembly does not dominate the mainstream, English-written ecological thought, probably because it looks into social science (*e.g.* Gómez-Pompa, 1987, Barrera-Bassols & Toledo, 2005, Bürgi *et al*., 2016). Also, UNTB is controversial (Rosindell *et al*., 2011, 2012) and has been questioned (*e.g.* McGill *et al*., 2006). Indeed, it is worth to discuss our results under the comparative scopes of human-mediated assembly and UNTB respect to other drivers of tree-communities widely accepted by ecologists.

As shown above, human-mediated assembly on our study area seemed compatible with gap dynamics and dispersal agents other than humans. Since pesticide was applied only once on Plot A, land-users had virtually no-interest in pathogens, herbivores, and pollinator insects. The role played by such agents during succession on our plots remains unknown. Still human-mediated assembly is compatible with currently recognized roles of vertebrates feeding from plants: pouching is a land-use enhancing plant fitness by reducing the herbivory and consumption of plants by vertebrates (Dirzo & Miranda, 1991, Wright *et al*., 2000). Pouching is strictly forbidden in our study site (Wildlife Ministry officers; personal communication), suggesting it may have been intense enough in the past for prohibiting it.

Human-mediated assembly does not reject competitive exclusion and facilitation. For instance, by means of planting, caring, and weeding, humans can alter competitive balances on tree communities (see also Oksanel *et al*., 2006). Yet such processes are difficult to be tested both in the present and in the past as well (Connell 1990, Garrido-Pérez *et al*. 2012). Although we ran no chemical analysis, we preliminarily measured soil salinities, bulk densities, pH, electric conductivity, and counted earth worms, and soil respiration for soil samples from some plots finding no significant difference among them. Water seems not to be a limiting resource either: the area has high precipitations, lacks any dry season, and all plots had fairly similar water bodies. Thus, we consider competitive exclusion as poorly plausible on our studied plots, and virtually impossible to test.

CONCLUSION
Our plant surveys and land-use histories suggest that random-and-symmetric birth, death, and seed dispersal from the surroundings played a major role on secondary forest assembly, while humans altered the successional paths within that "natural framework". For Amazonians, letting, respecting and enhancing highly diverse forests generated by natural processes guarantees a safer stock of resources. Therefore, Amazonians may have no reason to make forest assembly to depart from neutral-and-symmetric birth, death, and immigration during succession. All these are consistent with Amazonians' worldviews where even domestic trees are part of forest biodiversity and processes.

As well as UNTB, Human-mediated assembly does not deny other, widely recognized shapers of tree communities like gaps, herbivores, predators, and even competitors. However, none of the mentioned processes alone can explain secondary forests assembly better than human-mediation, which is able to unify all them.

While competition and other drivers of community assembly remain as "ghosts" in the past, human-mediated assembly is easier to test. Current humans are there for us to ask how they interacted with a land that today is a forest. The ancestors of the same humans inherited us the archaeological and floristic evidence of their actions too. Combined, Ecology and Social Science are able to unify a wide range of evidence related to deforestation and forest recovery. That is crucial for a better understanding, mitigation, and reversal of Global Change.

REFERENCES
Barrera-Bassols, N. & Toledo, V.M. (2005) Ethnoecology of the Yucatec Maya: symbolism, knowledge and management of natural resources. J Lat Am Geogr. 4(1), 9-41. DOI: http://www.jstor.org/stable/25765087.

Bendezú, Y.F. (2013) Manual para la identificación de las especies forestales en la región Ucayali. Ministerio de Agricultura del Perú, Pucallpa.

Brienen, R.J.W. and other 101 authors (2015) Long-term decline of the Amazon carbon sink. Nature 519, 344-348. DOI: 10.1038/nature14283.

Brokaw, N.V.L. (1987) Gap-phase regeneration of three pioneer tree species in a tropical forest. J Ecol 75, 9-19. DOI: 10.2307/2260533.

Bürgi, M., Östlund, L. and Mladenoff, D.J. (2016) Legacy effects of human land-use: ecosystems as time-lagged systems. Ecosystems 20(1), 94-103. DOI: 10.1007/ s10 021-016-0051-6.

Cerón, C.E. (1990) Manejo florístico Shuar-Achuar (Jíbaro) del ecosistema amazónico en el Ecuador. Ecuador: Ciencia y Tecnología número especial 68-76.

Chazdon, R.L. (2014) Second growth: the promise of tropical forest regeneration in an age of deforestation. The University of Chicago Press, Chicago.

Chazdon, R.L. and Guariguata, M.R. (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48(6), 716-730. DOI: 10.1111/btp.12381.

Clement, C.R. (2006) Domesticação de paisagens e plantas Amazônicas –a interação de etnobotânica, genética molecular e arqueología; in Pueblos y paisajes antiguos de la selva amazónica. Ríos, G.M., Camargo, S.M. and C.F. Calvo (eds.), pp. 97-112, Bogotá, Facultad de Ciencias – Universidad Nacional.

Clinebell, R.R., Phillips, O.L., Gentry, A.H, Stark, N. and Zuuring, H. (1995) Prediction of Neotropical tree and liana species richness from soil and climatic data. Biodivers Conserv 4, 56-90. DOI: 10.1007/BF00115314.

Connell, J.H. (1990) "Apparent" versus "real" competition in plants; in Perspectives in Plant Competition. Grace, J.O. and D. Tillman (eds.), pp. 9-26, San Diego, Academic Press. DOI: 10.1016/B978-0-12-294452-9.50006-0.

Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18, 431-451. DOI: 10.1146/annurev.es.18.110187.002243.

Dirzo, R. and Miranda, A. (1991) Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation; in Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. Price, P.W., Lewinsohn, T.M., Fernandes, G.W. and W. W. Benson (eds.), pp. 273-289, New York, John Wiley & Sons.

Dörfle, M. (2002) Árboles del bosque secundario en la comunidad de Challhua Yacu en la vía Hollín-Loreto. Proyecto Gran Sumaco, Challhua Yacu (Ecuador).

Duque, A., Muller-Landau, H., Valencia, R., Cárdenas, D., Davies, S., de Oliveira, A., Pérez, A.J., Romero-Saltos, H. and Vicentini, A. (2017) Insights into regional patterns of Amazonian forest structure, diversity, and dominance from tree large terra-firme forest dynamics plots. Biodivers

Conserv 26(3), 669-686. DOI: 10.1007/s10531-016-1265-9.

Erazo, G., Izurieta, J.C., Cronkleto, P., Larson, A. and Putzel, L. (2014) El uso de pigüe (*Piptocoma discolor*) por los pequeños productores de Napo, Ecuador. Manejo sostenible de una especie pionera de madera para los medios de vida locales. Brief CIFOR, Bogor.

Erkens, R.H.J., Chatrou, L.W., Maas, J.W., Niet, T. and Savolainen, V. (2007) A rapid diversification of rainforest trees (*Guatteria*; Annonaceae) following dispersal from Central into South America. Mol Phylogenet Evol 44(1), 399-411. DOI: 10.1016/j.ympev.2007.02.017.

Fearnside, P.M. (2005) Deforestation in Brazilian Amazonia: history, rates, and consequences. Conserv Biol 19(3), 680-688. DOI: 10.1111/j.1523-1739.2005.00697.x.

Finegan, B. (1996) Pattern and process in Neotropical secondary rainforest: the first 100 years of succession. Trends Ecol Evolution 11(3), 119-124. DOI: 10.1016/ 0169- 5347(96)81090-1.

Garrido-Pérez, E.I. and Glasnovi , P. (2014) The search of human-driven patterns of plant diversity: why and how? Brenesia 81-82, 96-107.

Garrido-Pérez, E.I., Durán, R. and Gerold, G. (2012) Las relaciones liana-árbol: repercusiones sobre las comunidades arbóreas y sobre la evolución de los árboles. Interciencia 37(3), 183-189.

Gentry, A.H. (1993) A field guide to the families and genera of woody plants of Northwest South America (Colombia, Ecuador, Peru) with supplementary notes on herbaceous taxa. The University of Chicago Press, Chicago.

Glaser, B., and Birk, J.J. (2012) State of the scientific knowledge on properties and genesis of anthropogenic dark earths in Central Amazonia (terra preta de Índio). Geochim Cosmochim Acta 82, 39-51. DOI: 10.1016/j. gca.2010.11.029.

Gómez-Pompa, A. (1987) On Maya sylviculture. Mex Stud 3(1), 1-17. DOI: 10.2307/4617029.

Holdridge, L.R., Grenke, W., Hatheway, W.H., Liang, T., and Tosi, J.A. (1971) Forest environments in tropical life zones: a pilot study. Pergamon, Oxford.

Hubbell, S.P. (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.

Hubbell, S.P. (2008) Approaching ecological complexity from the perspective of symmetric neutral theory; in Tropical Forest Community Ecology. Carson, W.P. and S.A. Schnitzer (eds.), pp. 43-159, Oxford, Wiley-Blackwell.

Jenkins, C.N., Pimm, S.L. and Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. Proc Natl Acad Sci USA 110(28), E2602-E2610. DOI: 10.1073/pnas.1302251110.

Krebs, C.J. (1993) Ecological Methodology. Benjamin/ Cummings, Menlo Park.

Levis, C. and other 152 authors (2017) Persistent effects of Pre-Columbian plant domestication on Amazonian forest composition. Science 355 (6328), 925-931. DOI: 10.1126/ science.aal0157.

López Camacho, I. and Montero González, M.I. (2005) Manual de identificación de especies forestales en bosques naturales con manejo certificable por comunidades. Instituto Amazónico de Investigaciones Científicas SINCHI, Bogotá.

MAGAP-Ministerio de Agricultura, Ganadería, Acuacultura y Pesca. (2011) Mapa de suelos del Ecuador continental (variable taxonomía) escala 1:250.000.

Martínez-Ramos, M. (1994) Regeneración natural y diversidad de especies arbóreas en selvas húmedas. Bol Soc Bot Mex 54, 179-224.

McGill, B.J., Maurer, B.A. and Weiser, M.D. (2006) Empirical evaluation of Neutral Theory. Ecology 87(6), 1411-1423. DOI: 10.1890/0012-9658(2006)87 [1411: EEONT] 2.0.CO;2.

McKane, A., Alonso, D. and Solé, R.V. (2000) Mean-field stochastic theory for species-rich assembled communities. Phys Rev E 62(6), 8466-8484. DOI: 10.1103/ Phys RevE. 62.8466.

Mendoza, H. and Ramírez, B. (2006) Guía ilustrada de géneros de Melastomataceae y Memecylaceae de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt –contribución #347, Bogotá.

Miranda, D. and Hernández Xolocotzi, E. (1963) Los tipos de vegetación de México y su clasificación. Bol SocBot Mex (Sobretiro), 29-176.

Mori, S. and Cornejo, X. (2013) Two new species (*Gustavia johnclarkii* and *G. hubbardiorum*) and other contributions to the systematics of *Gustavia* (Lecythidaceae). Brittonia 65(3), 330-341:(DOI. 10.1007/s 12228 -012-9282-9.

Morton, D.C., DeFries, R.S, Shimabukuro, Y.E, Anderson, L.O., Arai, E., Espirito-Santo, F.B., Freitas. R. and Morisette, J. (2006) Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon. Proc Natl Acad Sci USA 103(39), 14637-14641. DOI: 10.1073/pnas.0606377103.

Pascarella, J.B., Aide, T.M., Serrano, M.I. and Zimmerman, J.K. (2000) Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico.

Ecosystems 3(3), 217-228. DOI: 10.1007/s1 00210000 021.

Perrault-Archambault, M. & Coomes, O.T. (2008) Distribution of agrobiodiversity in home gardens along the Corrientes River, Peruvian Amazon. Econ Bot 62(2):109-126. DOI: 10.1007/s12231-008-9010-2.

Phillips, O.L. and Baker, T.R. (2003) Manual de campo para el establecimiento y remedición de parcelas permanentes. Cantua 12: 85-93.

Pitman, N.C.A., Terborg, J.W. Silman, M.R., Núñez, P., Neill, D.A., Cerón, C., Palacios, W., and Ulestia, M. (2001) Dominance and distribution of tree species in upper Amazonian Terra Firme forests. Ecology 82(8), 2101-2117. DOI: 10.1890/0012-9658(2001)082 [2101: DA DOTS]2.0.CO;2.

Renner, S.S. (1989) A survey of reproductive biology in Neotropical Melastomataceae and Memecylaceae. Ann Mo Bot Gard 76, 496-518. DOI: 10.2307/2399497.

Rivera, L.W., Zimmerman, J.K. and Aide, T.M. (2000) Forest recovery in abandoned agricultural lands in a karst region of the Dominican Republic. Plant Ecol 148(2), 115-125. DOI: 10.1023/A:1009825211430.

Rojas, M.R. and Martina, A.M.S. (1996) Manual de identificación de especies forestales de la subregión andina. Instituto Nacional de Investigación Agraria, Lima.

Rosindell, J., Hubbell, S.P. and Etienne, R.S. (2011) The unified neutral theory of biodiversity and biogeography at age ten. Trends Ecol Evol 26(7), 340-348. DOI: 10.1016/j.tree.2011.03.024.

Rosindell, J., Hubbell, S.P., He, F., Harmon, L.J., and Etienne, R.S. (2012) The case of ecological neutral theory. Trends Ecol Evol 27(4), 203-208. DOI: 10.1016/j.tree. 2012.01.004.

Runashitu (2009) Aprendamos a alimentarnos con productos de la chacra Kichwa Amazónica. PNUD, Quito.

Runashitu (2010) Plan de manejo del bosque de reserva de la comunidad Kichwa Runashitu de Humuyaku, cantón Tena, parroquia Chontapunta, provincia del Napo. CEDIME, Quito.

Salmerón López, A., González Rodríguez, A. and Geada López, G. (2016) Tipos funcionales de plantas según su respuesta a las perturbaciones en un bosque semideciduo micrófilo costero de Cuba Oriental. Bosque 37(1), 135-145. DOI: 10.4067/S0717-92002016000100013.

Sampaio, E.V.S.B, Araújo, E.L, Salcedo, I.H., and Tiessen, H. (1998) Regeneração da vegetação da caatinga após corte e queima em Serra Talhada, PE. Pesqui Agropecu Bras 33(5), 621-632.

ter Steege and other 157 authors (2015) Estimating the global conservation status of more than 15,000 Amazonian

tree species. Sci Adv 1(10), e1500936. DOI: 10.1126/ sciadv.1500936.

Toledo, V.M., Barrera-Bassols, N., García-Frapolli, E. and Alarcón-Chaires, E. (2008) Uso múltiple y biodiversidad entre los Mayas yucatecos (México). Interciencia 33(5), 345-352.

Vitery, P.V. (2015) Women as creators of biodiverse forests: Ecuadorian Amazon –ancestral system chakra ushun purun. United Nations Framework Convention on Climate Change.

<https://unfccc6.meta-fusion.com/sb42/events/2015-06-08-10-00/ms-pas-vitery-ecuador> (Accessed April 11, 2017).

Volkov, I., Banavar, J.R., Hubbell, S.P. and Maritan, A. (2003) Neutral theory and relative species abundace in ecology. Nature 424, 1035-037. DOI: 10.1038/ nature0 1883.

Wright, J.S., Zeballos, H., Domínguez, I., Gallardo, M.M., Moreno, M.C. and Ibáñez, R. (2000) Pouchers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. Conserv Biol 14(1), 227-239. DOI: 10.1046/j.1523-1739.2000.98333.x.