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Tempo and Mode in Secondary Succession: Above-Ground Biomass, and Forest Structure on the Coiba Island, Panama (1919-2023)

Tiempos y modos de la sucesión secundaria: biomasa en pie y estructura forestal en la isla de Coiba, Panamá (1919-2023)

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Abstract

Ecology needs a unified view of the patterns and processes of secondary succession; we addressed that on the Coiba Island, Panama. We measured tree diameters and determined the land-use histories and structural properties for nine stands. We detected land-use history-legacy gradients ranging from no-use to still-in-use sites (Linear Regressions, $R^2 \geq 0.87$ for Above-Ground Biomass and Basal Area, n=7 stands). Three successional pathways derived from a meadow, another from shifting agriculture, another from a >400y-old forest, and four were related to a river and a camp. Our results clarify discussions like convergence-vs-divergence, organismic-vs-individualistic successions, chance-vs-determinism, and provide land-use history-based suggestions for conservation.

Keywords: Carbon Capture, Forest Plots, Land-use History, Penal Island, Tropical Rainforest.

Resumen

La Ecología necesita una visión unitaria de los patrones y procesos de sucesión secundaria. En la isla de Coiba, Panamá, determinamos los diámetros arbóreos, estructura forestal e historias de uso del suelo en nueve parcelas. Hallamos gradientes de legados de historia de uso que van desde «sin usar» hasta

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todavía en uso (Regresiones Lineales, $R^2 \geq 0.87$ para las biomasas aéreas y áreas basales, n=7 parcelas). Tres rutas de sucesión provinieron de un potrero, otra de agricultura itinerante, otra de una selva >400 años, y cuatro se asociaban a un río y un campamento. Nuestros resultados aclaran discusiones como las de convergencia-vs-divergencia, sucesión organísmica-vs-individualista y casualidad-vs-causalidad, y proporcionan recomendaciones para la conservación basadas en la cultura agropecuaria.

Palabras clave: Bosque Húmedo Tropical, Captura de carbono, Historia de uso del suelo, Isla penal, Parcelas forestales.

1. INTRODUCTION

The time for Ecology to appeal to History for understanding forests is already here. In a world losing nearly 18 million hectares of forests, and where more than 90% of forest coverage corresponds to secondary ones (FAO, 2020), detecting which land-use histories resulted in differentiated second-growth stands is fundamental for both Ecology and Conservation. Fully addressing the plurality of land-use histories of the world is needed to detect human behaviors to be incentivized for conserving forests (Garrido-Pérez *et al*., 2021). Human intervention is recognized as a key driver of secondary succession (Mesquita *et al*., 2015, Chazdon, 2008, Guariguata and Ostertag, 2002). However, Ecology barely addresses how the different behaviors displayed by *Homo sapiens* L. result in altered forest structure and captured Carbon Dioxide. Fortunately, Ecology is a science of synthesis; able to combine information from History, Ethnography, Geography, and other humanities into forest histories (Garrido-Pérez and Glasnović, 2014). According to such authors, these relations can be interpreted from a Plant Biology's viewpoint in order to detect how human intervention in the past generated current forest properties. No reason for Ecology to reject a historical approach for studying today's biota: a similarly holistic approach is being largely and successfully used by Evolution (Mayr, 1998; Dobzhansky, 1973).

Forest Ecology describes land-use histories by saying "agriculture", "pasture", "orchard", "field", and so on. These are just land-use names; histories are something else. Land-use histories should be chronologically ordered sequences of human-made manipulations occurring to a given place during a certain period. Like any other history, land-use histories should provide information for readers to deduce explanations to ongoing, apparently non-connected phenomena (see also Dobzhansky, 1973). That's possible because many of the complexities of the present are consequence of the facts of the past, doesn't matter whether such facts were stochastically, or deterministically generated (deduced from Mayr, 1998). Therefore, detailed land-use histories can clarify whether some abandoned "fields" now hold more vigorous forests than other stands due to previous addition of fertilizer. Land-use history can reveal whether emergent forest trees are there because farmers let them for shadowing, instead of being fast-growing competitors. Land-use history can unveil whether human-made fire limited further forest recovery, whether long-distance seed dispersal was relevant during succession, or to what extent the planting of fruit trees accelerated secondary growth (see also Mesquita *et al*., 2015; Chazdon, 2008).

Spatially changing land-use histories produce a plurality of neighboring forest patches. Forest surveys and tree-measurements simply portray snapshots of the ongoing process of secondary succession (see Chazdon, 2014). By laying in the same region, interacting with the same source of seeds, and exposed to the action of the same human groups, all secondary forests of a zone are "variations of the same theme" (Chazdon, 2008) for which the rates and ways of recovery comprehend the tempo and mode of secondary succession (concepts borrowed from Simpson, 1984 for evolution). Historical Ecology can discover such tempo and mode by exhaustively looking into the history of human-land interactions.

The goal of this paper is contributing to explain why some secondary forests have different structures respect to others. Such structural features include Aboveground Biomass (AGB). We measured the diameters and determined the AGB for nine contrasting stands on the Coiba Island, Panama. Complementarily, we thoroughly reconstructed each stand's land-use history. Two stands represented the extremes of a single land-use gradient. Thus, Control 1 was a >500 y-old, virtually never used forest (Ibáñez, 2011). Control 2 was a still-in-use stand keeping food trees from at least 1919-to date. From the remaining seven stands, five were 33 y-old secondary forests with different land-use histories. Indeed, the among-stands uneven time after abandonment is not a descriptor of their structural variation. One of the remaining two stands is a mixture of 73- with 33 y-old forest resulting from two fallowing periods in the past. Finally, the remaining stand is a 51 y-old novel ecosystem where no forest has grown yet. All stands were randomly chosen so there was no bias towards any successional age or land-use history type. We ordered all experimental plots from the highest to the lowest AGB values. Thanks to that, readers will see which land-use histories resulted in better- or worse mitigation of Climate Change by our studied forest patches. There are many, not fully precise ways to estimate AGB (e.g. Chave *et al*., 2015; Mascaro *et al*., 2014). Indeed, we determined other, more precisely measured structural aspects like stem density, tree-diameters, and total-and-averaged basal areas as well. This was made for both complementing results from AGB and providing more comprehensive interpretations of the effects of land-use. Moreover, Ecology recognizes that forest succession is related to seed-dispersal from older, nearby forests, and to the differential response of plant species to both natural, and human-made (micro)habitat modifications (Guariguata and Ostertag, 2002; Chazdon, 2014, 2008). Hence, we included the changes of the surrounding landscape as part of our land-use histories.

In this paper we answer the following questions:

1. Which land-uses of the past resulted in enhanced, or worsened Aboveground Biomass of current secondary forest patches?

2. To what extent each forest plot remained in contact- or near mature forest during the past?

3. Which land-uses took place on each stand, per how many years, which plant or animal species were produced, and which were the agricultural behaviors

inherent to such activities? Some instances of these activities include weeding, direct planting, tolerance to remnant trees, soil removal, addition of fertilizer or manure, among others.

4. Which major events occurring during the land-use of each stand were related to the history of the other stands and their surroundings?

Our working hypothesis was two-folded. Firstly, the world and its landscapes comprehend a vegetation mosaic resulting from divergent degrees and types of human-made impacts due to land-use (Garrido-Pérez and Glasnović, 2014; Chazdon, 2008). If this is true, then secondary forests can be arranged into a gradient of land-use history legacies as follows. Towards one extreme of the gradient there should be stands without any land-use (old-grown forests); conversely, towards the other extreme there should be stands still being used. Finally, in-between there should be an array of forests in a declining order of numerical values for each studied characteristic (e.g. AGB, basal area, and other forest properties).

Secondly, if all land-use histories of the world or a landscape are made by the same species namely *Homo sapiens*, and if the humans using the lands operate throughout time, then the secondary forests of any studied location should have different degrees of relationship with the other stands in the area. The later should result from both the commonalities and the divergence of human-made manipulations. Consequently, thorough relations of the particular land-use histories running along a single time scale should reveal the mechanisms leading to both divergence and similarity among human-affected forests.

2. MATERIALS AND METHODS

2.1. Study site, and field work

The Coiba island (7°30′50.3′′N, 81°41′44.1′′W; surface = 503 km^2, Fig. 1) is in the Gulf of Chiriquí, Western Pacific shore of the Republic of Panama, and is part of the Coiba National Park. According to our calculations based on FAO-AQUASTAT (2023) Coiba's mean annual temperature is 26.27 ºC, annual rainfall = 3275 mm, and has three months (January to March) of dry season (rainfall < evapotranspiration). The island was inhabited by a penal colony devoted to agriculture and livestock per 84 years (1919-2004). From 2005 onwards, Coiba and surrounding waters and islands are UNESCO's Natural Heritage of the Humankind (ANAM, 2009). Coiba's geology comprehends sedimentary and volcanic rocks distributed among shales and sandstones, basalts and pillow lavas, basalts and diabase, limestone and tuff as well as alluvium and other sedimentary forms (ANAM 2009). About 40% of Coiba existed ~70 million years ago (MYA) as part of the Galapagos Hot Spot; the rest was completed between 3-8 MYA (Ibáñez, 2011: 17-196). Coiba was joined to the Panama Isthmus during the Pleistocene (~10 000 years ago; last glaciation) so a great deal of current Coiba's biota arrived from the mainland (Ibáñez, 2011: 17-196). Coiba's mountains are not very high (highest peak is the *Cerro de la Torre* hill, 416 m.a.s.l.), but the topography is very broken on the northern, western, and southern sides of the island (Berbey de Quijano, 1972; Fig. 1). That results in a dense network of rivers and creeks (1.48 km km^{-2}, Duquette et al. 2020). Combined to the broken terrain, the soft soils – mainly frank, clayish inceptisols, alfisols and ultisols (Villarreal *et al*., 2013) generate landslides on ridges, even where the later are covered by mature forest (pers. obs.). Prisoners inhabiting Coiba were mainly devoted to agriculture, livestock, and poultry, with a quasi-total exclusion of other civilians particularly from 1941 onwards (Bastidas 2019). From 2004 to date Coiba is exclusively used for environmental conservation, non-intrusive ecotourism, ranging, and science (Bastidas, 2019).

We randomly chose four sites on Western Coiba for establishing large plots (> 0.5 ha) thereby settling our plots Coi 1, Coi 2, Coi 3, and Coi 7 (Fig. 1) while ignoring their land-use histories. While surveying (three visits from May 5th to November 15th, 2023) and reconstructing a general Land-use history for the whole Coiba Island (Garrido-Pérez and Bastidas, in prep.), we confirmed that the Central Camp concentrated the largest percentage of Coiba's population, infrastructures, and variety of land-uses besides the *Catival* Camp (Berbey de Quijano, 1972; Bastidas, 2019). Therefore, we complemented our sample by adding five, randomly chosen plots in the surroundings of the Central Camp (plots Coi 4, Coi 5, Coi 6, Coi 8). We left plot Coi 1 as Control I (no land-use) because it corresponds to a > 500 y-old forest for which we found no evidence of land-use. Berbey de Quijano (1972) reports selective logging on an old forest area outside Coi 1. We realized that the gardens of the Central Camp are still being used so we settled plot Coi 9 there (Control II = land still in use). Recall that all our secondary forest stands were randomly chosen, and their land-use histories are a result from our study and not part of our methodology. We measured each plot's terrain. For plots Coi 4, Coi 6, Coi 8, and Coi 9 the terrain of the whole stand was measured. Meanwhile, plot Coi 1 is 0.5 ha and belongs to the larger, old-grown forest covering ~80% of Coiba's surface (Berbey de Quijano, 1972; ANAM, 2009). Finally, Coi 2, Coi 3, Coi 5, and Coi 7 are 1 ha plots embedded in larger stands (see results). All plots were measured following the contour of the terrain as much as possible. Inside all plots we counted, measured, and identified all tree stems ≥ 10 cm diameter at breast height (DBH = 1.3 m above ground level). We warn that our species identification is still going on for plot Coi 1. Taxonomic identification follows the works by Pérez *et al*. (1996), Ibáñez (2011), ForestGeo (2023), and the Herbarium of the University of Panama (PMA, 2023).

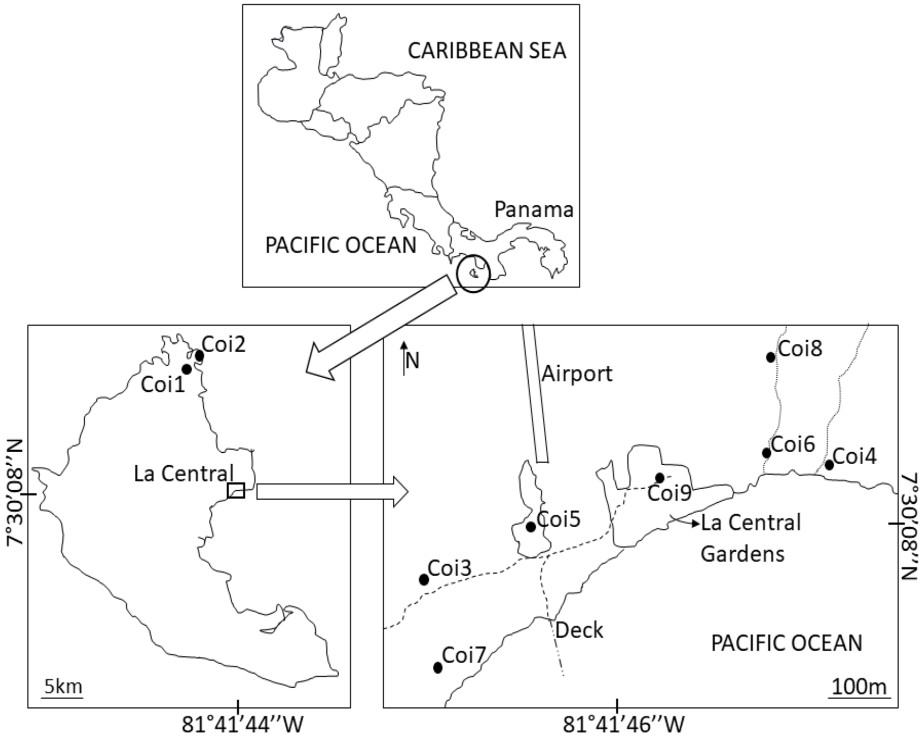

Figure 1. Location of the Coiba island, and position of nine forest plots there.
Source: this study.

2.1.1. Numerical analysis

After counting and measuring all stems in each plot, we calculated and extrapolated to hectares the stem density, average tree diameter, basal area, and average basal area (m^2 $stem^{-1}$). We also determined the diameter of the largest stem and estimated the Aboveground Biomass (AGB). For the later, we borrowed the wood density for each of our found species from the Global Wood Densities Database (Zanne *et al*., 2009), particularly for Central America. When more than one wood density was reported in such a database, we calculated and used the average. For species non present in the database we averaged values from reported species of the same genus. For alien species like the mango (*Mangifera indica* L., Anacardiaceae) we averaged wood densities reported for India, Tropical Asia, and Africa. We repeated this procedure for other exotics like teak (*Tectona grandis*), and tamarind (*Tamarindus indica* L.). In order to cope with the elusive taxonomy of trees on plot Coi 1 we profited from the following two facts. First: After ten years working on the Coiba flora, Alicia Ibáñez published an in-depth identification of the trees living in her seven 1 ha plots located in the same old-grown forest around Coi 1 (Ibáñez, 2011). Second: most of the tree species in Tropical Rainforest plots are represented by one single individual (Hubbell 2001). Indeed, we considered legitime to assume that our plot Coi 1 was a sample of the ~101 tree species enlisted by Ibáñez (2011) in a one-to-one species: individual ratio. Thus, we randomly assigned a putative species name from Ibáñez (2011) to every not-yet identified single individual of our plot Coi 1. After constructing such a species list, we obtained wood densities for each tree as we already explained. Then, with all wood densities enlisted, we estimated the (AGB) in kilograms per hectare for each tree using the following formula (Chave *et al*., 2005):

$$AGB = \varrho * \exp(-1.499 + 2.148 lnD + 0.207(lnD))^2 - 0.0281(ln\,(D))^3$$

Where ϱ = wood density in g cm^3, and D = stem diameter in cm. Finally, we summed AGB for all trees per plot and extrapolated the result into Mg ha^{-1}. After obtaining the average diameters, maximum tree-diameter, total-and average basal area, and AGB for each plot, we re-organized our experimental plots in descending order for each one of such characteristics. For that ordination, we kept Controls I and II in the extremes as references for detecting any gradient of land-use history legacies on current stand characteristics. Data analyses were made using non-parametric ANOVA (Kruskall-Wallis), Tukey, and Linear Regression tests for assessing patterns of forest properties related to land-use history gradients. For that, our a priori assumption was that high R^2 values for declining curves represent strong evidence favoring the existence of a land-use history-determined gradient.

2.2. Reconstructing land-use histories

One of us (currently 61 years-old, Chronist of the Coiba Island) lived and worked Coiba's lands as a *machetero* (cutting plants with a machete) for 10 years (1988-1998). After such a job, the same person worked other 20 years as a scientific assistant, and game-warden (2000-2018). Such two periods summed 30 years of participatory and direct observations (Bastidas, 2019). We consulted a prolific description of Coiba's physical, and human geography published > 50 years ago (Berbey de Quijano, 1972). We also checked a paper and photos taken 66 years ago by ornithologist Alexander Wetmore (1956, 1957). Besides these, we read theses and testimonies made by students of the Faculty of Law of the University of Panama who studied the situation of the prisoners (Moncada Luna Vargas, 1989, Blades, 1973, 2021) looking for casual descriptions or comments on the every-day life regarding human-nature relationships. Additionally, we semi-structurally interviewed six key informants whose timespans related to Coiba ranged from the years 1928 to the present (2023) (Table 1). For making easier the examination of all data, we arbitrarily segmented our study period into decades. Then, we organized our found information into such decades, determined the labors made for every decade, and assembled the facts into timelines for each one of our studied plots (1919-2023).

The history of every secondary forest plot belongs to the one of its surroundings. For instance, a current 1 ha plot may have been used as a meadow being part of a larger meadow. Moreover, the current position of the plot can be nearer, or farer-away of the edge of an old-grown forest and such a distance may have changed throughout time. The later may have altered the history of seed rainfall among plots (Guariguata and Ostertag, 2002, Martinez-Ramos and Garcia-Orth, 2007). Indeed, for the purposes of our research we consider both the within-plot manipulations made by humans and the history of the vegetation around it as part of the land-use history for each plot. Therefore, we took the coordinates of each plot, then looked into satellite images from 1984 to date (Google Timelapse © 2023) for checking how was each plot's surrounding vegetation throughout history. We combined that with the photos and relations of Wetmore (1956, 1957), Berbey de Quijano (1972), Blades (1973, 1974, 2021), Moncada Luna Vargas (1989). Additionally, both the personal- observations of one of us and the information provided by our informants of Table 1 were integrated to the whole data. Furthermore, on the most recent satellite images we visually estimated the percentage of each plot's perimeter in direct contact with forest. When such a contact did not exist, we measured the distance from the target plot to n = 5 points on the nearby old forest' edges. That was for assessing to what extent the history of seed dispersal from the old forest (as part of land-use history) explains current secondary forest properties. Finally, we articulated the data from all these sources into a thorough, coherent version of each plot's land-use history, considering such version as the most parsimonious.

After finishing the reconstruction of land-use histories we: (a) kept the timeline as a vertical axis with the present on top. (b) Took advantage of the fact that all studied plots are part of the same land namely the Coiba Island. (c) Assumed that all current stands originally belonged to one single "primary" forest from which humans unevenly started to clear-cut and use different areas. (d) Represented the further land-use divergence of each plot respect to the others as a cladogram. The extremes of such a cladogram are the current plots, while the clades are groups of plots sharing an original land-use in the past represented as a node in the cladogram. Thus, (e) each branch of the cladogram represents a period of continued land-use, while each node or "split" represents spatially located differentiation of land-uses occurring during history.

Table 1

Characteristics of six key informants interviewed for studying land-use history and human-nature relationships on the Coiba Island (Panamanian Pacific), penal colony from 1919 to 2004. All interviewed persons were men.

Informant	Age range (y)	Relationship with Coiba Island	Date of interview	Period covered during interview
1	> 80	guard per 32 years	years 2000	1928-1960
2	50-55	official visitor	June 2023	< 5 days in 2002
3	50-55	guard	July 2023	2011-present
4	< 35	Son-in-law of a > 90year-old fisherman born and inhabiting an island nearby	July 2023	c.a. 1940-2000
5	< 35	Guard since < 4 years ago	July 2023	2011-present
6	> 40	none. Countryman related to folklore	January 2024	1988-present

Source: this study

3. RESULTS

All nine plots totalized 1538 stems. However, one plot (Coi 5) was an unfinished airport now having virtually no stems and all such stems were < 10 cm DBH. Plots' surface ranged from 0.25 ha to 1 ha (Table 2). Except for Coi 5 and Coi 8 (see further), all plots rapidly acquired stem-diameters, basal areas, and AGB tending to, or even surpassing the ones of the old-grown forest (Figs. 2, and 3). That occurred in 33 years suggesting a rapid secondary succession taking place in Coiba respect to other tropical forests. Two potential explanations are the fertile, young soils of Coiba (STRI-DATA 2023), and an appropriate arrival of water and nutrients from Coiba's highlands (Garrido-Pérez *et al.*, in prep). Three plots held higher AGB compared to the old-grown forest of Control I (Coi 1, Table 2). Similar patterns occurred for average, and maximum tree diameters as well (Figs. 2, and 3a).

Regarding our question 1, after re-organizing the experimental plots in descending order of AGB, the slope of the resulting line was -17.95, and $R^2 = 0.48$ (n = 9 plots; $R^2 = 0.87$ when excluding controls I and II). This suggested that land-use histories explained a great deal of the among-plots variation of AGB, fitting very well into our proposed concept of land-use history gradient (Fig. 3b). Plot Coi 4 had the highest AGB, followed by plots Coi 2, 7, 6, 3, 8, and 5, respectively (Table 2, Fig. 3b).

3.1 Relations of the land-use histories

3.1.1. Control-I (Plot Coi 1), Coiba AIP Station, > 500 y-old forest, Appendix 1a, and 2a)

This stand was located inside Coiba's great, old-grown Tropical Rainforest. Berbey de Quijano (1972) reports selective logging for such a mature forest, but outside our plot Coi 1. Therefore, we found no evidence of land-use during our studied period (Appendix 1a).

Table 2

Woody-vegetation structural characteristics of nine stands with different land-use histories on the Coiba Island, Panama. All plots were randomly chosen so their characteristics including age were not a priori looked for. All percentages are respect to Coi 1 (old grown forest). n = number of stems, SD = Standard Deviation, DBH = Diameter at Breast Height namely at 1.3 m above ground level. Land-use keywords provide hints on what each plot was used for.

Plot (age, and land-use keywords)	**n**	**Surface (ha)**	**Density (stems ha^{-1})**	**DBH (cm, ±SD)**	**Largest tree DBH (cm)**	**Total Basal Area (m^2 ha^{-1})**	**Average Basal Area (m^2 stem^{-1})**	**Estimated Above Ground Biomass (Mg ha^{-1})**
Coi 1 (>500y; Control I, virtually no use)	137	0.5	274 (100%)	20.23 (14.50)	72.77	5.79 (100%)	419.49	116.41 (100%)
Coi 2 (73y, and 33y; small-scale agriculture)	373	1	370 (135%)	19.21 (10.68)	124.84	13.80 (238%)	338.00	130.51 (112%)
Coi 3 (33y, meadow, then festivals)	323	1	323 (118%)	17.98 (9.86)	90.25	9.75 (168%)	321.88	94.10 (80.8%)
Coi 4 (33y, sawmill)	92	0.25	368 (134%)	24.75 (16.15)	84.78	6.28 (108%)	690.61	259.62 (223%)
Coi 5 (51y, unfinished jets-airport)	0	1	0 (0%)	0	0	0 (0%)	0	~0 (~0%)
Coi 6 (33y, bakery, rooster-fighting, and open yard)	66	0.25	264 (96.3%)	23.61 (12.08)	53.60	22.30 (385%)	3379.49	110.25 (94.7%)
Coi 7 (33y, meadow, then abattoir)	308	1	308 (112.4%)	20.00 (11.28)	89.17	12.80 (221%)	412.94	126.23 (108.4%)
Coi 8 (33y, tannery)	15	0.30	50.50 (18.4%)	26.72 (18.74)	76.24	1.23 (21.2%)	817.82	45.62 (39.2%)

Coi 9 (in use since 1919, Control II, Central Camp Gardens)	22	2.58	86.82 (31.7%)	32.65 (21.01)	151.9	26.09 (50%)	1052.17	92.37 (79.3%)

Source: this study

3.1.2. Plot Coi 2: Gambute (Appendix 1b, 2b)

Rectangular, 200 m × 50 m plot. Nearly 100 m (22%) of the perimeter has been to date in contact with the old-grown forest. That implied high chances of a direct arrival of seeds from the old-grown forest. Survivorship and backyard, shifting agriculture, small livestock (poultry, pigs), and perennials occurred (1919-1941). After that, there was a first fallow period (Fallow I, 1941-1954), then small-scale agriculture (1954-December 1989), and then fallow again until today (Fallow II, Fig. 2b). Satellite pictures (e.g. 1984, Google Timelapse © 2023) show Fallow I was surrounding about 200 m (44%) of current plot's perimeter, and the fallow itself occupied ~50% of the plot. The remaining half was part of a wider area under shifting agricultural use (1954-December 1989). From January 1990 onward, such a section became Fallow II (Bastidas, in prep.; Google Timelapse © 2023). Thus, current plot Coi 2's surface combines Fallow I (73 y-old forest) and Fallow II (33 y-old forest). Moreover, the mentioned Fallow II surrounds nearly 150 m of current plot's perimeter (33.3%). Also, the terrain of Fallow I becomes steep (c.a. 20° respect to the horizon). The location of Coi 2 is a kind of isthmus on Northern Coiba (Fig. 1). The later, plus its steep terrain exposed the vegetation to strong winds contributing to a visibly dynamic gap formation (e.g. plot Coi 2 in Appendix 2). In summary, 22% of Coi 2 remained in contact with old-grown forest receiving seed rainfall from there. At the same time, there was an added complexity resulting from the two fallowing processes: the planting-and-keeping of some fruit tree species as part of survivorship agriculture, and the enhanced gap dynamics supplying sunlight (Guariguata and Ostertag, 2002; Chazdon, 2008). For Coi 2, all these is ought to have resulted in: a fast recovery of AGB respect to the old-grown forest, a large size of the biggest tree respect to all other stands (Fig. 3-a), and the highest stem density of our studied plots (135% respect to old-grown forest, Table 2).

3.1.3. Plot Coi 3: La Feria (The Festivals, Appendix 1c, 2c)

The terrain of Coi 3 was part of the same meadow to which Coi 7 belonged to. The average distance from Coi 3 to the nearest old-grown forest edges was 1.91

km so this plot was surrounded by the open areas of the old meadow (1941-1980). This plot, however, had the second largest remnant tree of all experimental plots (Fig. 3-b) namely a *Ficus popenoyi* Standl. (Moraceae). Yet such a tree as well as other two individuals of the same species (Garrido-Pérez *et al*. in prep.) were in a gallery forest along a river, covering ~2% of our plot's surface. Other remnant trees included *Albizia guachapele* (Kunth) Dugand (Mimosoideae) and the edible mango (*M. indica*); both species are commonly used in Panama for shading cows in meadows according to the more than 40 years of independent, personal observations by EIG-P and informant 6. The concentration of shade and fruit trees in Coi 3 was much lower than for plot Coi-7, but there were several remaining *Citrus spp* with DBH < 10 cm.

The architecture, colors, and materials of our found infrastructures in Coi 3, plus artifacts like mayonnaise empty flasks, insecticide spray-cans for domestic use Appendix 2(c), shoes, and even deodorant tubes point to the mid-1980s for finding the most plausible date for a land-use change. The change consisted in a switch from pasture to Agricultural Festivals for ~40% of current plot's surface (Bastidas, in prep.). Such complex for festivals (*Feria Agropecuaria* in Spanish) were simply known as *La Feria*. During the 1980s Panama's military used to organize such festivals in different provinces for soldiers practicing agriculture across the country to meet once a year (EIG-P, pers. obs.). Therefore, the Coiba officers-in-chief built the infrastructures of their own "feria" to annually make an exhibition for choosing which produced plants and animals were going to represent them in the national *feria*. Coiba's feria conditioning included the addition of cement, and gravel to some 40% of the soil surface inside plot Coi3 (pers. obs., Appendix 1c, 2c).

Moreover, on 1985 Panama's Stanley Heckadon-Moreno and Jaime Espinosa-Gonazález published their still influential edited book *Agonía de la Naturaleza* (Agony of Nature; Heckadon-Moreno and Espinosa-González, 1985). In such a book, a plethora of scientists documented how deforestation was able to put the Nation into an environmental and socioeconomic crisis. Then, Panama´s military directly appointed Colonel Rogelio Alba as the Director of the National Institute of Natural Resources (1985-1986; Spanish acronym INRENARE; MiAmbiente, 2023). Alba took and executed two major decisions all over Panama: (a) banning to cut any tree, and (b) a vigorous "institutional reforestation" (EIG-P., pers. obs., 1985 TV-news). Alba's experience for the execution of ambitious tree-planting plans in few months is well documented (e.g. Todd 2015). Planted tree species included *Tabebuia rosea* (Bertol.) A. DC., *Handroanthus guayacan* (Seem.) (Bignoniaceae), and *Citrus spp*. During our Coiba field survey we found many similarly sized and aligned *T. rosea* / *H. guayacan* covering some 18% of current plot's surface (Garrido-Pérez *et al*. in prep.) We also found lemon and orange (*Citrus spp*). Thus, given the decisions vertically executed by the Panamanian military, we consider 1985~1986 as the most plausible date for human-made planting of such trees in plot Coi 3 for both reforesting the area and providing embellishment to the *feria* terrains (Fig. 2-c). Plot Coi 3 (as well as plot Coi 7, see further) became a fallow since January 1990 because no more ferias were made after December

1989 (Bastidas in prep.). Yet the declined population of Coiba island may have sporadically harvested fruits from some of the remaining, previously planted trees (e.g. *M. indica*, *I. edulis, Citrus spp*). On 2004 the penal was finally closed, but still the cattle and horses remained freely moving across the vast, old pastures and open areas of the Coiba Island (Garrido-Pérez and Bastidas, in prep.). While the later suggests that some fertilization by manure should have taken place in Coi 3, we consider that was diffuse due to a comparatively lower density of cows and horses per area unit respect to Coi 7 (Appendix 1c, and g).

Some species planted during reforestation in Coi 3 produce air-dispersed seeds (*T. rosea* and *H. guayacan*), but their flowers are pollinated by bees. On another hand, edible fruit-species (e.g. *M. indica*, *I. edulis*) are attractive for-and consumed by rodents (*Dasyprocta coibae*), capuchin monkeys (*Cebus capucinus*), and macaws and parrots as well (Psittacidae). Thus, after reforestation by men vertebrates living in the mature forest may have contributed to secondary succession by transporting seeds from the old-grown forest into plot Coi 3 during their visits for feeding and perching on human-planted trees. Meanwhile, bees attracted by the planted *T. rosea*, *H. guayacan*, *I. edulis*, and *Citrus spp* ensured vigorous pollination inside Coi 3. As mentioned earlier, cowboys kept large shade-and-fruit trees like *A. guachapele* and *M. indica* remaining from the 1941-1984 period. Yet it is worth to consider the institutional reforestation of 1985-1986 as the main reason explaining why plot Coi 3 reached 80.8% of the AGB compared to the old-grown forest after only 33 years of secondary succession (Table 2).

3.1.4. Plot Coi 4: El Aserradero (The Penal's Sawmill, Appendix 1d, 2d)

Traditionally known as *El Aserradero* (The Sawmill), we translate its name into "The Penal's Sawmill" because there was another, private sawmill not included in this paper (Berbey de Quijano, 1972; Bastidas, 2019). 1984's satellite imagery shows our current plot embedded into a completely open area. Satellite images from 1990 onwards show the progressive occupation of the area by forest (Google Timelapse © 2023). The average distance from Coi 4 to nearest old-grown forest is just 70 m, and such an old-grown forest was always a narrow "woods peninsula" (~50 m width in satellite images) surrounded by meadow. That contrasts with the massive, larger old-grown stand near Coi 2, or even Coi 6 (see further).

Photos by Berbey de Quijano (1972) demonstrate there were no trees inside current Coi 4. That was because such trees would have affected the dangerous maneuvers of arrival, movement, and cutting of the huge logs (saw radius = 85 cm after our direct measurements; Appendix 2d. Coi 4 is on alluvial soil, so it has received nutrient inputs transported from the fully forested hills transported by the *Quebrada de la Represa* river located near the plot. Beyond our studied sites, such a river has a dam built on 1919 (in Spanish *represa*) from which the drinkable water for the Central Camp was- and is still taken (Berbey de Quijano, 1972). The river does not cross Coi 4 so sawyers' maneuvers were not affected by the river.

Worth to say, the same river is related to plots Coi 6, and Coi 8 (see further).

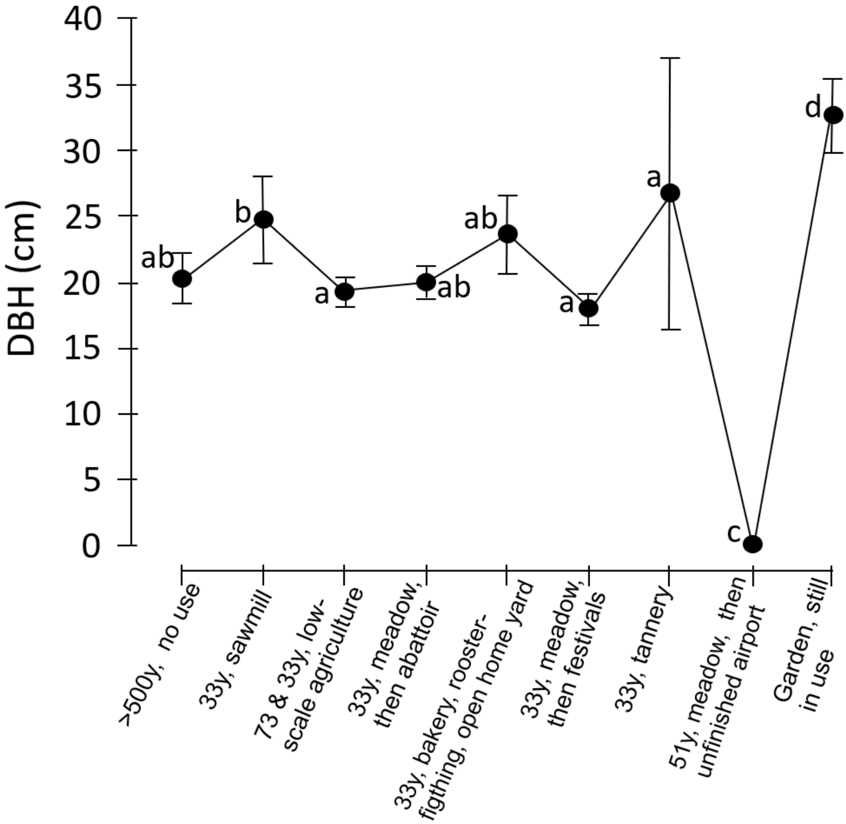

Figure 2. Average diameter at breast height (DBH = 1.30 m above ground level) for all tree stems inside nine plots ≥ 0.25 ha with different land-use histories on the Coiba Island, Panama. Characters in low captions show plots with similar DBH after Kruskall-Wallis (KW = 177.78, df = 8), and Tukey post-hoc comparison tests. Error lines are 95% confidence intervals. See Table 2 for sample sizes (n). Source: this study.

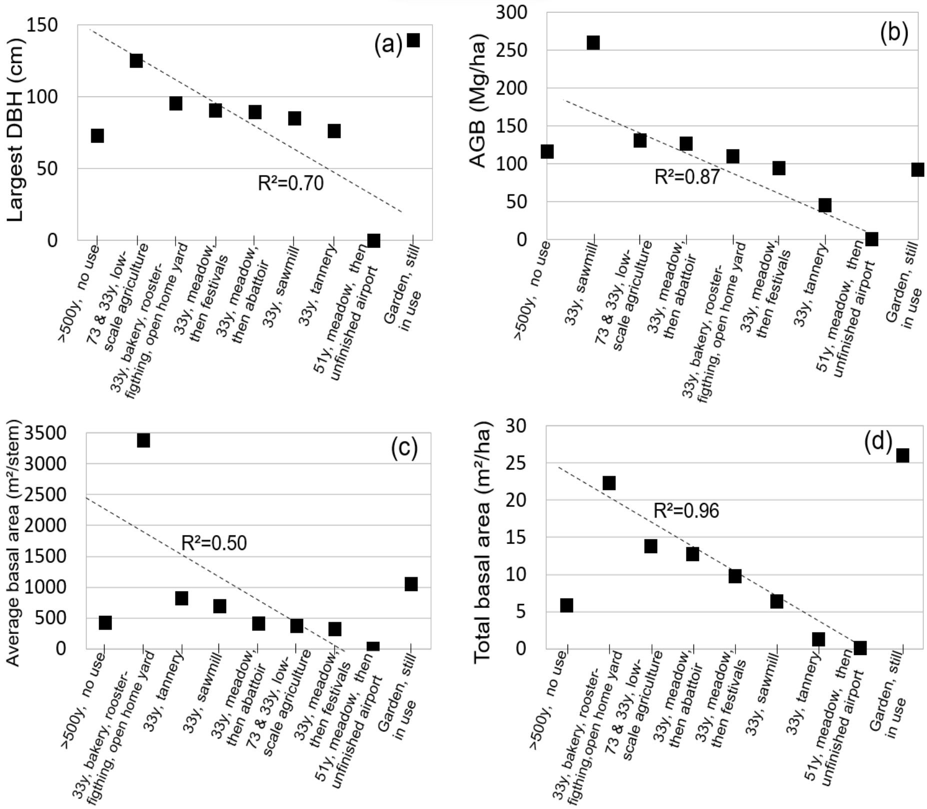

Figure 3. Four vegetation structure properties of tree communities for nine forest plots along land-use gradients ranging from > 500 y-old forest (no use, Control I) until a garden with > 104 years under cultivation still in use (Control II) for all trees ≥ 10 cm diameter at breast height (DBH = 1.3 m above ground level) on the Coiba Island, Panama. AGB = Estimated Aboveground Biomass. Dashed lines and R^2 show trends for the n = 7 plots within each gradient. Horizontal axis terms are hints to each plot land-use history; see Appendix 1 for summaries of the full land-use history of each plot and its surroundings. Source: this study.

We were attracted by the idea of dating the start of the operations' of the Penal's Sawmill in 1919 or few years afterwards based on the following, circumstantial information. Firstly, an old, human-muscle-powered saw some 3 m length is still conserved by the guards as a "silent witness" of hard-work during Coiba's earlier History. Secondly, grand-grandparents and uncles of one of us (EIG-P, age 53) conserved some XIX century wooden-furniture including banks made of tables from single logs c.a. 1.20 m width. The later suggest that the capabilities of sawing large logs in Panama is older than the arrival of engine-powered saws. Thirdly, one Panamanian realistic writer born on 1905 and working for the Health Ministry in logging areas wrote a book describing logging and saw-milling as a compulsive practice during the first ~30 years of the XX century in Panama (Candanedo, 1957). Such ~30 years were long before the introduction of engine-powered saws. However, the earliest large-scale engine-powered saw in Coiba is documented for 1941 (Bastidas, 2019, Bastidas in prep.). Moreover, the Penal's Sawmill is just some 150 m away of the cement-made penitentiary. That suggests it was easy to supply both diesel and manpower for milling the logs. Therefore, without rejecting a previous period of muscle-powered saw-milling, we dated the full start of the operations of the Penal's Sawmill on year 1941 (Appendix 1d). Such activities remained as time went by so Berbey de Quijano (1972), as well as Bastidas (in prep.) document engine-powered saw-milling for the early 1970s and throughout the 1980s. All saw-milling operations stopped from January 1990 to date and the land became a fallow since then (Bastidas, 2019; Appendix 1d).

From the last two paragraphs we deduce the following. (a) The relative importance of any edge effect from the old-grown forest for speeding secondary succession was low for Coi 4 compared to Coi 2 or Coi 6 which were at the old-grown forest. (b) The ≥ 49 years of sawmill activity compacted the soil by means of heavy logs and machinery. That reduced the chances of any previously existing seed bank to play a major role during further succession. However, (c) the alluvial income of soil nutrients had to keep a high intrinsic soil fertility (see 3.1.6 too). Also (d) the accumulation of sawdust may have contributed to amend soil characteristics like cation exchange capacity (El Halim and El Baroudy, 2014; Sotelo *et al.*, 2023, but see Eusufzai *et al.*, 2007). Thus, incoming seeds transported by rodents, monkeys, birds, or bats during the fallow period (1990-to date) should have found a porous mantle of sawdust enabling early root-growth, then facilitating the further root's penetration into the dense, yet fertile soil below de sawdust. Noteworthy, the current average tree-diameter for Coi 4 was like the old-grown forest (Fig. 2) after 33 years fallowing. This is consistent with both the absence of trees during land-use and the rapid recovery of forest functions respect to the old-grown forest (Table 1).

On another hand, (e) the seed arrival, germination, survivorship, and growth of seedlings is ought to have been vigorous, as expressed by the high stem density (368 stems ha^{-1}, Table 2). (f) The larger trees we found included some edible *M. indica*, *Spondias mombin* L. (Anacardiaceae), and *Inga edulis* Mart. (Faboideae). They are not as large as remnant trees kept on other plots like Coi 3 and Coi 7 (Fig. 3a) so they seem to have arrived after the start of the fallow (1990 onward). That presumably occurred due to seed dispersal by humans eating a few fruits and then throwing the seeds. In fact, the plot is in a cozy place, not so far away of the Central Camp where prisoners used to have lunch and dinner for some privacy, being fruits a usual dessert (Berbey de Quijano, 1972, Bastidas, pers. obs.). Therefore, (g) the human-dispersed early arrival of fruit trees widened current diameters' variance (Fig. 2). All these explain why AGB became higher for Coi 4 compared to other plots (Fig. 3b).

3.1.5. Plot Coi 5: Unfinished Airport (Appendix 1e, 2e)

Interestingly, plot Coi 5 was part of the same pasture including Coi 3, and Coi 7 thereby sharing similar histories from 1919 to 1972 (Appendix 1 c, e, g). Therefore, Coi 5 is located far away from the old-grown forest edge (average distance = 1.49 km). Still the closest part of that forest is only ~74 m away from Coi 5. All these imply that seeds arrival from the old-grown forest was not significantly different for Coi 5 compared to Coi 3 and Coi 7. However, we found Coi 5 being a novel ecosystem holding virtually zero AGB (Fig. 3a, Appendix 2). Coi 5's plants are few, sparse individuals belonging to no more than six species (Garrido-Pérez *et al*., in prep.), and no-individual stem reached the minimum diameter for this study (Figs. 2 and 3b-c; Appendix 2e. The red-clayish (sub)soil had no organic layer and no-horizons, but it had rainfall-made channels showing its degradation Appendix 2e.

Berbey de Quijano (1972) visited the site, and reported it as subjected to the construction (with bulldozers) of a field for the landing of jets. She indicated that the construction was interrupted, and the land abandoned since July 1972. Satellite images (1984 onwards, Google Timelapse © 2023), photos (ANAM 2009), reports (Ibáñez, 2011), and Bastidas' direct observations (1988 to date; Bastidas, in prep.) confirm the stand remained both abandoned and with the red subsoil exposed until today. Thus, plot Coi 5 became a novel ecosystem which functions have not started to significantly recover after 51 years abandonment (see also Martínez-Ramos and García-Orth, 2007). Most of the few tree species include bird-dispersed *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), and *Miconia argentea* Sw. DC. (Melastomataceae). That suggests seed dispersal processes on Coi 5 should have not been so different respect to Coi 3 and Coi 7. Hence, we attribute Coi 5's severe hindering of secondary succession to the mechanical removal of deep-soil and subsoil without any amendment or restoring practice.

3.1.6. Plot Coi 6: Panadería, Gallera y Traspatio de los Aserraderos (Bakery, Rooster-fighting arena, and Sawyers Home-backyard, Appendix 1f, 2f)

Site located just at the tip of a ~50 m width, old-grown forest-peninsula belonging to the large > 500 y-old forest near the *Central* Camp. Some 60% of Coi 6's perimeter remained at the edge of such a forest-peninsula (satellite images from 1984 to date). Since the largest tree we found (DBH = 53.6 cm) was smaller than other plots' largest trees (Fig. 3b), we do not think remnant trees of Coi 6 to be very old. No fruit-trees were present. Nevertheless, some coconut palms were near the meander of the ~1.8 m-width *Quebrada de la Represa* river gently crossing the plot (the same river is related to plots Coi 4 and Coi 8). The soil is alluvial receiving nutrients from the upper lands. About 45% of Coi 6's surface was used as a rooster-fighting arena (Bastidas, 2019; Berbey de Quijano, 1972). However, the infrastructure was made from wood and palm-leaves so there are no visible ruins. Still, we knew that until at least 1972 there was no-infrastructure but only the arena (Berbey de Quijano, 1972). Plot Coi 6 is located < 100 m behind the 1919's inaugurated penal. The trail leading to the *Punta Damas* Camp (settled in 1919) is nearby too. *Punta Damas* was inhabited by prisoners who were farmers from the *Los Santos* province (Panama's countryside, Bastidas, 2019). Installing rooster-fighting arenas near trails and (cross)roads is a long-standing practice in both rural and urban Panama (EIG-P's personal observation per > 40 years; independently confirmed by informant 6).

During our > 40 y-lives in both rural and urban Panama we have observed non-formal cockfights, and even meetings for roosters to "practice" at first. Throughout time, such fights attract more men, so the fights become more formal, for finally getting converted into a well-established and ruled business. Cockfighting businessmen function as "banks" for bets, referees, and operate in infrastructures (confirmed by informant 6). Thus, the deep Panama's rooster-fighting tradition, plus the fluent connection between the *Central*- and *Punta Damas* Camps point to two stages of rooster-fighting as a land-use in plot Coi 6. The first stage was an early, non-formal cockfighting place without an arena, shaded by the edge of the nearby old-grown forest peninsula, just like somewhere else outside Coiba (informant 6). The second stage corresponded to a formally established, built-up arena. Berbey de Quijano (1972) reported the second stage; for dating the first one we only found circumstantial evidence. In concrete, infrastructural expansion occurred in the *Central* Camp on 1941 (date written in cement by constructors themselves; Captain Peñalba was the officer-in-chief). For a similar date (1947) another large gally for prisoners was finished as far-away as the *Catival* Camp (inscription on such a gally under the administration of Lieutenant Souza). Indeed, both the number and spatial expansion of Coiba's penal population was dramatically high for 1941. Such prisoners were chiefly countrymen occupying places surrounded by open areas interconnected by a well-established network of rustic roads and trails (visible in Wetmore, 1959 and mentioned in Blades, 1974). Thus, by joining this circumstance to the fact that cockfighting is an ancient, widespread tradition in Panama, we felt tempted to date the first period of rooster fights in 1919. However, we preferred to conservatively date the semi-formal start of cock-fighting for 1941. As a norm, Coiba's rooster-fights were made every Sunday and – like in all Panamanian arenas, men were copiously drinking fermented beverages, particularly *chicha fuerte* (a fermented beverage made from corn; Bastidas, 2019). Yet nobody let his roosters sleeping near the arena for avoid robbery or sabotage. Instead, Bastidas (in prep.) and Berbey de Quijano (1972) document that some prisoners used to keep their personal hence – and therefore roosters near their homes – which is still a common practice all over Panama (EIG-P, pers. obs.; informant 6). Our personal observation, corroborated by informant 6 is that middle-class, moderately successful men racing fighting-cocks use to have eight of such birds, while wealthy rural citizens use to have tens of such animals.

We propose that penal's population expansion during the 1940s increased the demand of bread. Still Berbey de Quijano (1972) suggests that the bakery near the arena in Coi 6 was not there during her time in Coiba. Only Bastidas (2019) reports the bakery there during the second half of the 1980's. Yet the terrain of the bakery seemed to be part of the open area for the traffic of logs being transported towards the sawmill prior Bastidas time in Coiba (photo in Berbey de Quijano, 1972). This supports the dating of Coi 6's bakery after 1972. Finally, some 10% of our plot corresponds to part of the backyard of the house of 2-4 sawyers working full time in the penal's sawmill. They planted no-trees in their home's backyard (Bastidas, in prep.). All these activities were abruptly interrupted on late December 1989, so plot Coi 6 is fallowing since January 1990.

Synthesizing, we deduce the following for plot Coi 6. (1) The plot had no significant remnant trees but was always in direct contact with the old-grown forest. The later (2) facilitated the arrival of seeds belonging to wild tree-species (e.g. transported by monkeys, rodents, and birds during fallow). (3) Such plants found fertile soils formed by the alluvial inputs transported by the river, and the deposition of flour and other organic material from the bakery. Also, a moderate, yet persistent fertilization by roosters' fecal and human's urine from 1941 to 1989 is ought to have occurred. As a combined legacy of all three aspects, plot Coi 6 achieved 94.7% of the AGB respect to the old-grown forest in only 33 years after abandonment. On average, individual trees of Coi 6 became as thick as the ones of Coi 4 (Fig. 2). Still AGB of the later was 2.3 times higher than for Coi 6 (Table 2). Interestingly, despite its direct contact with the old-grown forest peninsula, stem density in Coi 6 is lower compared to Coi 4 which was always some 70 m away of the same peninsula (Table 2). That reinforces our deduction that the high density in Coi 4 was more a result of low mortality of newly coming plants than a consequence of a more vigorous seed rainfall there.

3.1.7. Plot Coi 7: El Matadero; also known as Los Establos (Abattoir Appendix 1g, 2g)

This plot was surrounded by a meadow at least from 1947. Current average distance from this plot to the old grown forest is 2.02 km. After clear-cutting and burning – but before settling any pasture, Panamanians traditionally plant fast-growing, mixed crops like corn (*Zea mays* L., Poaceae), beans (e.g. *Phaseolus vulgaris* L., Faboideae), chiricano beans (*Vigna unguiculata* (L.) Walp.), Faboideae), manihoc (*Manihoc esculenta* Crantz, Euphorbiaceae), and otoe (*Xanthosoma spp*., Araceae) per three years. Then the pasture is let to grow, and cows occupy the area (pers. obs.). For the large extension of the old-meadow (ANAM, 2009; Wetmore, 1956; Berbey de Quijano, 1972) we estimated the clear-cutting, burning, and planting-process to have been progressively, yet rapidly applied from 1941 to 1947. Indeed, we estimate the introduction of cows to have occurred from 1947 onwards. We found big trees, yet they were not as large as the ones of Coi 2. Also, average tree-diameter is like Coi 3 which is another plot settled on the same old meadow (Fig. 3-b, c). Therefore, there is no reason to expect that large trees of Coi 7 (and Coi 3) were unlashed individuals remaining after the original clear-cutting or earlier. Many of the large trees produce edible fruits (Garrido-Pérez *et al*., in prep.) not belonging to the old-grown forest flora (Ibáñez, 2011). Indeed, we attribute such trees' arrival to the intervention of Coiba's cowboys who were prisoners from the countryside where people throw seeds and keep fruit-and-shade trees in meadows (Bastidas, 2019). Such a practice is common for the mango *M. indica*, the jobo (*S. mombin*, and the guaba (*I. edulis*)). For Coi 7, the later plausibly explains the concentrated location of the trees around a house-and-abattoir built-up during the late 1970's – early 1980's. Berbey de Quijano (1972) photographed another rustic, wooden, cabin-like abattoir near the old *Central* Camp so she suggested to make a new, more hygienic one. The Panamanian military seemingly followed her suggestion by settling the new abattoir in the stand now occupied by our plot Coi 7. The infrastructures, including its walls, tiles, colors, inner distribution of cement-made stands, and stable nearby resemble what we saw during 1978-1989 in Panama City's *Abattoir Nacional* while living nearby. Indeed, we date the construction of Coi 7's abattoir during late 1970's (at last 1981; Bastidas in prep.).

For plot Coi 7, fertilization by manure and urine should have occurred between 1947-1982, still in low intensities due to a relatively low density of cows. In contrast, during the Abattoir land-use period (1982-1989, Appendix 1g) the whole plot was segregated from the rest of the large meadow by means of a fence. During these ~8 years the weekly mode number of scarified cows was three (generally between 2 and 6, Bastidas, in prep.). The stable's drinking-and-feeding place was designed for 10 cows, as we detected by looking into the ruins (see also Appendix 2g). Therefore, we estimated that every 2-3 weeks the number of cows living in our plot was reset to 10 individuals. Consequently, an organic fertilization by manure, urine, blood, plasma, and other fluids from the abattoir is ought to have occurred (1981-1989). That is ought to have contributed to the fast growth of both cowboys-introduced trees, and trees growing during the single fallow-period of the stand (1990- onwards, Fig. 2g). Nowadays, tree-diameters on Coi 7 average a similar value respect to old-grown forest, and the stand has the second highest AGB of our experimental plots (108 % respect to old-grown forest, Fig. 3a-b, Table 2).

3.1.8. Plot Coi 8: La Curtiembre (The Tannery, Appendix 1h, 2h)

As well as Coi 4 and Coi 6, plot Coi 8 was located just along the *Quebrada de la Represa* river. Recall that such a location is not far away of the *Central* Camp. Since the river was a key source of water, a considerable part of gallery forest was permanently kept on the ridge on both sides of the river near the Tannery. Satellite images (1984-onwards) show that such an old-grown forest stayed as a kind of "belt" only ~60 m width. The forest belt connected to the rest of the old forest. On its side, the forest belt was surrounded by a section of the Coiba meadow, plausibly clear-cut a bit after 1919 due its proximity to the meadows of the *Punta Damas* Camp (Bastidas in prep.).

Chemicals for leather-tanning were all natural, mainly coming from mangroves (*Rhizophora mangle* L., Rizophoraceae) near the *Catival* River. Animal skins were coming from the cattle occupying the pastures and hunted crocodiles and snakes. The skins were salted, and pre-dried under the sun outside Coi 8 (Bastidas, pers. obs.; presumably near the abattoir). While being embedded into the old-grown forest belt, the total surface of plot Coi 8 was 0.30 ha. The tannery was located directly on the small, flat terrain facing the river because tanning demands large amounts of fluent water (Zapata, 2008). Large trees were rarely cut, but some 85% of plot's surface was cemented. Indeed, the tannery-generated fluids went directly to the river instead of being deposited on the soil. The remaining ~15% of Coi 8's surface was kept as soil and includes a few edible fruit tree species like *I. edulis* and *S. mombin*. Therefore, some thinning is ought to have occurred for planting such trees and not only for building-up the infrastructure.

We were tempted to date tannery's settlement close to 1919 based on the following. (1) Per much more than 2000 years leather was a world-wide used, multi-purpose material to the extent of being industrialized by some countries during the first Industrial Revolution (Schlottau, 1993: 1-40). (2) Coiba's penal was planned and established following direct orders from Panama's President Belisario Porras, a rural-born man from the same province where many of the first prisoners came from. Porras himself used leader-made objects for personal, home, and even war activities when he rode his horse as a civil-war leader during the late xix-early xx century. Porras was also a liberal, positivist-oriented thinker whose sense of order and progress included well organized, industrial labor (like in Schlottau, 1993; Castro, 2000: 6-25). Therefore, it is feasible that an important industry like tanning and manufacturing leather was introduced in Coiba by the same, progressive administration establishing a dam for ensuring water (another progressive decision taken by Porras). (3) By being cowboys from the countryside (Bastidas, 2019), many of the prisoners were ought to be familiar with tanning. (4) According to the same source, Coiba started to produce cattle from the very start of its penal history so both skins and mangroves for tanning were available.

However, by decision of President Porras the first Coiba prisoners only spent up to six months there. Thus, Coiba's demand of leather had to be low-and-unstable enough for not needing a formal tannery. We are still lacking information on the date of the construction of the tannery, but photos by Wetmore (1959) already show leather-made objects. Also, Berbey de Quijano (1972) shows a fully developed production of leather, and leather-made artifacts, handcraft, and arts. Thus, we conservatively date the construction of the tannery on 1941 (Appendix 1-h) when, Coiba's population was already large. We propose the original tannery was a rustic, wood-and palm-leaves-made cabin, then replaced (tentatively during the early 1970s) by the cement infrastructures which ruins are now being covered by newly growing forest. The tannery suddenly ended its operations on late December 1989, so it became abandoned since January 1990 after at least 49 years operating (Appendix 1h). Indeed, newly coming trees started to grow 33 years ago. We warn our used word "fallow" in Fig. 4 does not fully describe what occurred after men's departure. In concrete, there was virtually no-clearcut but some thinning, so the "fallowing" process was completely different in Coi 8 respect to other plots.

From the just described history we deduce that the wide variation of tree-diameters on Coi 3 (Fig. 2) emerged as follows. In the beginning, large trees were kept by non-clearcutting the old-grown trees. Then, tanners planted fruit trees contributing to re-fill the thinned terrain. Finally, narrower trees were added by seed germination after the abandonment of the terrain since late December 1989. Consequently, all three processes are represented by the current variance of tree diameters. On another hand, cementation, and the direct disposal of tannery's fluids to the river outside the terrain should have neutralized any major chemical influence of the tannery on the further growth of trees. Therefore, most of this plot's current AGB is ought to have resulted from the keeping, planting, and arrival of new trees during both land-use and "fallow" period, without any significant biogeochemical influence excerpted by the tannery inside the plot.

3.1.9. Plot Coi 9 (Control II): Jardines de La Central (Central Camp Gardens, Appendix 1i, 2i)

Plot Coi 9 is a stand averaging 1.17 km distance from the old-grown forest. Most of this site was clear-cut during the construction of the *Central* Camp, then inaugurated in 1919, and remains in use until today. Thus, land-use here started ≥ 104 years ago while keeping essentially the same dimensions – currently 2.58 ha (Berbey de Quijano, 1972; Bastidas, 2019, satellite imagery from 1984 onwards in Google Timelapse © 2023). Many planted trees and palms appear in old photos (e.g. Wetmore, 1956; Berbey de Quijano, 1972) and include coconuts (*Cocos nucifera* L. Arecaceae), the ornamental palm *Roystonea regia* (Kunth) O.F. Cook (Arecaceae), and Caribbean pine (*Pinus caribaea* Morelet, Pinaceae). Besides all these, there are lemon and oranges (*Citrus spp*.) avocados (*Persea americana* Mill., Lauraceae), mangos (*M. indica*), jobos (*S. mombin*), nance (*B. crasifolia*), among other fruit species consumed by humans (Garrido-Pérez *et al*., in prep.). Many of such trees were not present for 1956 (Wetmore, 1956, 1957), but they were planted afterwards and became large and productive towards 1988 (Bastidas, pers. obs.; see also Berbey de Quijano, 1972). The largest tree is a *Switenia macrophyla* King (Meliaceae) which is also the biggest one of this study. That tree already had a considerable size in historical pictures (e.g. Wetmore, 1956); yet it's not clear whether it was kept as remnant tree after clearcutting or planted when the penal started to function. Other, more recently established trees in plot Coi 9 were planted during late 1980s-early 1990s. That includes the hard-wood, alien teak (*Tectona grandis* L., Verbenaceae, covering some 4% of plot's surface), plus native fruit-trees guanábana (*Annonna muricata* L., Annonaceae), papaya (*Carica papaya* L., Caricaceae), and even the alien fruit species noni (*Morinda citrifolia* L., Rubiaceae; Garrido-Pérez *et al*., in prep.). Additionally, plantains (*Musa* × *cavendishi*), and manihoc (*M. esculenta* Kranz., Euphorbiaceae) were produced as starch sources (Bastidas, in prep.). The trees are sparse (only 82.82 stems per hectare, Table

2), and we did not find significant branch-or-trunk scars made with any cutter. Thus, we deduce that weeding rather than pruning was a major management technique. Until the closure of the penal (2004) the gardening work was made by prisoners. From 2004-to-date, gardening became part of the tasks of the garrison of the Panamanian Aero-Naval Service.

From the just described land-use history, we deduce that the large sizes of trees (Fig. 3b, c) mainly resulted from the following three processes. First, a highly fertile soil thanks to the geological youth of the island (Solano, 2022). Second, the location of the *Central* Camp on the lowlands of Coiba where the soil has been millenary receiving nutrients from the higher lands (Garrido-Pérez *et al*., in prep.). Finally, the intervention of humans favoring trees by clear-cutting, planting, weeding, and by fertilizing some areas by throwing organic material from the kitchen (deduced from Bastidas, 2019, and Moncada Luna Vargas, 1989). Thus, planting is ought to have made most individual trees to arrive, weeding kept them free of competitors, and the low density reduced the chances of both tree-tree competition and pathogen's transmission due to tree-tree contact. Thus, everything humans made to the planted trees was explicitly thought for the benefit of such trees. After its ≥ 104 years of continuous land-use, Coi 9 holds almost 80% of AGB – and 4.5 higher total basal area respect to the old-grown forest (Table 2). That reflects a high per capita capture of CO_2 by individual trees due to a centennial human intervention.

3.2. Relationships among land-use histories

After looking at all plot's land-use histories along a single timeline, a cladogram showing diverging land-use histories and potential secondary succession pathways emerged (Fig. 4). Plot Coi 2 started secondary succession earlier than the others but had two fallowing events. Meanwhile, the other plots had only one fallowing period, and a more recent start of secondary succession as well (Fig. 4). Plots Coi 3, Coi 5, and Coi 7 shared a roughly similar land-use from ~1941. The land-uses of these three plots started to diverge in 1972 leading to Coi 5, then in 1978~1982 leading to Coi 7, and then the remaining stand changed in 1985 leading to Coi 3. Recall that both Coi 3 and Coi 7 started fallowing in January 1990 (Fig. 4). Such departures occurred late respect to Coi 2 (Fig. 4). Meanwhile, three stands had successional pathways based on human activities spatially related to one single river (*Quebrada de la Represa*). Such stands were inside- (Coi 8), or at the old-grown forest belt (plots Coi 4, and Coi 6; Fig. 4). Land uses among these stands started to diverge ~1941, but they shared the same date for the start of its current, single fallowing period (January 1990). Fallowing for plots Coi 3, Coi 7, and the second fallow of Coi 2 started in January 1990 too (Fig. 4). While all these was occurring, the old-grown forest (Coi 1) remained as a mature forest, so its tempo of change was slower than for all other plots, and its mode of change (e.g. by gap dynamics or by interspecific interactions) barely included human intervention. Yet the forest in plot Coi 1 currently is > 500 y-old so it was roughly 100 years younger when the whole land-use histories of our studied plots begun in 1919. Thus, due to differential land-use all current Coiba forests diverged from an original, impossible to survey forest existing some 100 years before present (Fig. 4).

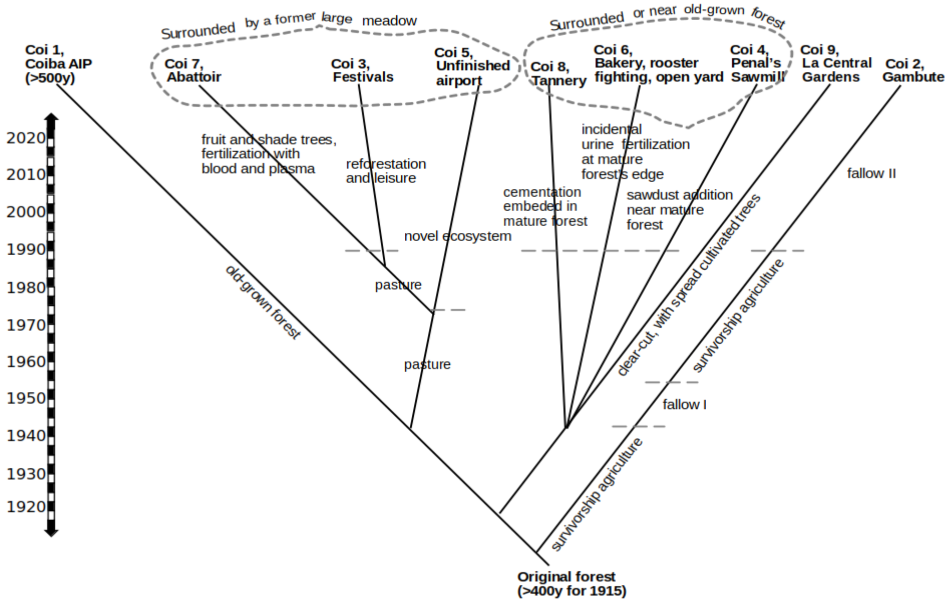

Figure 4. Cladogram synthesizing the (land-use) histories of nine forest plots on the Coiba Island, Panama, made by representing major land-use events of nine secondary forest plots along one single timeline. Each vertex represents a date of differentiation of one land-use respect to the previous ones. The old-grown forest (> 500 y-old) remains as a direct proxy of what had been the status of all other stands in the absence of land-use by humans, not as a representative of the original "primary" forest. Horizontal dashed lines represent moments of land abandonment. Descriptions near each branch provide hints on major land-uses occurring. See results, and Appendix 1 for the full land-use histories of each plot.
Source: this study.

4. DISCUSSION

One study analyzing chronosequences all over the Tropics found that AGB-recovery can take some 120 years after agriculture and pasture (Poorter *et al.*, 2021). Our results suggest a faster recovery for Coiba: most of our experimental plots needed ~30 years for reaching > 79% of mature forest's AGB. Our reported AGB-absolute values were roughly like the ones reported for 5-to-25 y-old wet forests in Manaus (Brazil), Chajul (Mexico), and Sarapiquí (Costa Rica, Rozendaal et al. 2017). The same is valid when comparing Coiba with the pattern for ~35 y-old evergreen tropical forests across México (Casiano-Domínguez *et al.*, 2018).

Moreover, such authors found that Mexican ~73 y-old forests surpassed the AGB of our Coiba 73 y-old forest in 130 Mg ha^{-1} (Casiano-Domínguez *et al*., 2018). Other sites with absolute values of AGB > Coiba are Sinnamay (Chave *et al*., 2020), and the Barro Colorado Natural Monument (BCNM, Panama Canal, Mascaro *et al*., 2012). The later was valid for forests with ages being both equal and younger than ours. All these, besides the high percentage of recovery of our plots respect to neighboring old-grown forest, confirm that secondary forests are major sinks of Carbon Dioxide (Letcher and Chazdon, 2009). Local processes making trees to grow fast in Coiba are worth for further experimental studies.

4.1. Nothing in secondary succession makes sense except in the light of Land-use History

This subtitle paraphrases Theodosius Dobzhansky (1973) who affirmed that "Nothing in Biology makes sense except in the light of Evolution". According to him, the Evolutionary Synthesis is a historical reconstruction of the relationships among living beings. Such a reconstruction of evolutionary relations contributed to surpass discussions by joining biological information thought to be dispersed and contradictory (Dobzhansky, 1973). We affirm that long-standing, controversial positions marking Ecology can be simplified and synthesized thanks to Land-use History too. Here we focus on the usefulness of chronosequences, the intermediate peak, the organismic-vs-individualistic forest concept, and the chance-vs-determinism discussions.

4.1.1. Usefulness of chronosequences, and the intermediate peak

Chronosequences assume that current secondary forests will converge towards current "primary" forests (Clements, 1916). The arrangements of our experimental plots into land-use gradients points to a reliable convergence of secondary forests towards the structural properties of neighboring mature ones and this is consistent with Poorter *et al*. (2021), and Clements (1916). However, we consider such a convergence as barely informative because all secondary forests of an area are embedded into the biogeographical, climatological, pedological and historical realm where the original old-grown forest was present. More informative are the departures from the general trends due to differential land-use legacies generating multiple successional paths as has been recognized by authors like Chazdon (2014) and Gleason (1917), provided that thorough land-use histories are reconstructed for discovering the causes of the departures (this study).

At the same time, our results suggest that intermediate peaks like the one in Mascaro *et al*. (2012) are a legacy from land-use history. Specifically, land-users of our plot Coi 2 made it to currently have both a 73 year- and a 33-year-old zones in a single stand. Land-users were also planting and caring old fruit trees in Coi 2 earlier than in other plots. By doing all these, land-users enhanced the demographic, and structural complexity of Coi 2. Consequently, the DBH of the largest tree, and the basal area as well became higher for Coi 2 respect to all other forests in our study (Fig. 3a, c, and d).

4.1.2. Organismic vs individualistic forest-concepts

Secondary succession is considered a series of steps by which abandoned stands with no-soil removal converge towards the properties of old-gown forests (Clements, 1916; Chazdon, 2008). This has been considered analogous to the development of organisms like humans from a "baby-like" stage towards a mature stage. Ecologists name that the *organismic concept* (Clements, 1916) which applicability and realism have marked debates among scholars per more than one century (Gleason, 1917; Chazdon, 2014). An alternative to the organismic concept is the *individualistic* one. According to this, the same diversity of physiological adaptations, microenvironmental mosaics, and their dynamics during succession do not lead to a single climax forest stage, but to a plurality of different, *individual* forests (Gleason, 1926). For instance, sunlight reaching the understory range from small sun flecks to medium and large tree-fell gaps which distribution changes in space and time. The same is valid for soil resources, pollinators, pathogens, root symbionts, and so on (Denslow, 1987; Schnitzer and Bongers, 2002; Silvertown, 2004). Thus, according to the individualistic concept the properties of any secondary forest will rarely be the same respect to other forests.

The land-use history approach passes over these two schools of thought. Land-use history reveals which combinations of events of the past determined the tempo (uneven rates of succession) and mode (successional pathways) generating both similarities (organismic trends) and differences (individualistic trends) among current forests (Mesquita *et al.*, 2015). Thus, some of our plots converged to high AGB because humans kept remnant trees there, others because humans planted fruit trees further attracting seed dispersers, others because humans massively reforested meadows, others because humans incidentally fertilized or amended the soil, and so on. As mentioned above, among-plots convergent trends come out of their common history: all secondary forests in Coiba resulted from the clear-cutting of a single, original forest some 120 years ago, on a single island with essentially the same bio-climatic and biogeographic background. Besides that, divergent trends resulted from history, particularly from the different degrees and modes of human-intervention. Thus, our Historical Ecology approach helps to bypass the sempiternal discussion of organismic-vs-individualistic secondary succession by integrating both convergence and divergence as part of forest history. That provides unity to the otherwise contradictory processes belonging to forest succession.

4.1.3. Chance vs determinism, or chance AND determinism?

Divergent successional pathways are considered a consequence of numerous, virtually unpredictable combinations among biological processes like the following (Chazdon, 2014; Guariguata and Ostertag, 2002; Gleason, 1917, 1926). (a) Differential adaptation of species and functional groups to the dynamics of water availability, soil resources, incident light, competitors, pollinators, predators, pathogens, and other factors which are conversely altered by a wide range of land-use manipulations (Silvertown, 2004; Bazzaz, 1979). (b) Among-stand differential constraints to the arrival of seeds, and permanence of seed banks ultimately resulting from seed dispersal in the past. All these related to the widely changing species composition of the surrounding metacommunity, and the temporal changes of seed production among species at the metacommunity level (Rosindell *et al*., 2011; Garrido-Pérez *et al*., 2018). (c) Highly changing disturbances made by both humans and Nature throughout space and time (Guariguata and Ostertag, 2002). Not surprisingly, such a wide variety of factors and processes led ecologists to consider secondary succession as a highly stochastic process (Chazdon, 2008; see also Mesquita *et al*., 2015).

Thorough Land-use History simplifies that discussion (Mesquita et al. 2015). Since most of our Coiba stands had the same successional age, their different structures were smoothly explained by each plot's history. For stands with different successional ages respect to the others, Land-use History detected the mechanisms by which they got different ages (Appendix 1, Fig. 4). Thus, the tempo and mode of (secondary) succession reject neither chance, nor determinism. For instance, current lognormal relative abundance distributions can result from random-and-symmetric arrival, birth, and death of tree-species in the past (Garrido-Pérez *et al*., 2017; Rosindell *et al*., 2011). Meanwhile, other properties of the same forests are legacies from human activities altering the outputs of herbivory, soil properties, or even seed dispersal (this study). Thorough land-use histories detect where, when, and for which forest characteristics chance has been more relevant than determinism.

4.2. Towards land-use history-based conservation initiatives

4.2.1. Human-tree mutualisms enhance secondary succession

In Coiba, *H. sapiens* certainly played our proposed multiple ecological roles (Garrido-Pérez and Glasnović, 2014): the species predated trees and formed gaps (by selective logging), made major disturbance (by clearcutting), was an ecological engineer (removing soil for making airports), etc. From all human behaviors occurring in Coiba, human-tree mutualisms were the ones enhancing secondary succession. In plot Coi 2, humans kept remnant trees, planted fruit trees, and kept old-grown forest near their worked stand for producing food and prevent landslides. In plot Coi 6, humans did not cut the old-grown forest, but used its fresh border for comfortably looking rooster-fights, then paid the trees by urinating near them after drinking a fermented beverage. The abattoir was settled on its position in the 1980s because during previous decades other humans kept and cared shade-and-fruit trees there. Such trees supplied comfort and fruits for both the cows and the cowboys of the abattoir, who literally paid with blood, manure, and other fluids fertilizing the soil. In plot Coi 3, *H. sapiens* perceived tree-coverage was not enough for making cozy festivals, so during the 1980s the men reforested the stand and nursed trees in exchange for their aesthetic-and-fruit services. In plot Coi 8, the tanners understood the river stream was an ally by supplying water for tanning, but also a threat for their living-and-working place by means of flood. Therefore, land-users decided to "respect" the forest by thinning a small area instead of clearcutting, and mitigated flood risks thanks to such a decision. Tanners also added cement for avoiding soil erosion and planted fruit trees on the remaining impacted area for both eating the fruits and compensate human-made disturbance. In the *Central* Camp (plot Coi 9), land-users planted and are still nursing trees which pay them back by producing fruits, shade, and a beautiful scenario. All these practices were made by the prisoners (often countrymen), following instructions of well-informed agronomists (other countrymen) (Berbey de Quijano, 1972). If all these are true, then countrymen display a wide range of mutualistic behaviors with trees and such mutualisms are to be incentivized.

The only plot where land-users had an antagonistic relationship with trees was the penal's sawmill – Coi 4 where no tree was allowed to stay. Letting trees to grow there implied a threat for sawyers' lives by impeding men's maneuvers with heavy logs and tables during milling. After land abandonment – however, the accumulated sawdust is ought to have performed a surface easy to be penetrated by the roots of plants which seeds came to the plot during succession. In contrast, no soil amendment occurred for the unfinished airport (plot Coi 5) after the removal of soil and part of the subsoil. Thus, one moral of our set of land-use histories is that Conservation and Restoration strategies should promote traditional human-tree mutualisms, and design amendment programs for compacted and depleted soils.

4.2.2. Boosting conservation and restoration plans by joining local traditions

All our described human-tree mutualisms belong to the traditions of many rural areas. Indeed, no scholarly exuberant discourses should be needed to convince people to care trees. The following is a proposed, easy-to-accept guideline towards a conservation strategy based on our results from Coiba.

I. Reforest near (cross) roads. If a clearcut area has a soil, then use native and fruit trees to reforest some areas like the ones near (cross)roads where people can see and take part of the reforestation process (see further). Consider adding sawdust, biochar, compost, or other soil amendment if the soil is compacted.

II. Settle places for public leisure just at reforested areas / forest-fragments. Do it under hygienic conditions and safe atmosphere for both children and adults. Take advantage of the fact that semi-open areas of the countryside – usually near (cross)roads are traditionally used for dancing, folk-music concerts, singing, poetry, open-air theatre, and festivals attracting many people. Some examples of such places are Panamanian *jorones*, *jardines*, but also fairs and carnivals as well as Mexican *palenques*, and Austro-German *Biergarten* (see also Pinzón, 2010). Such an author warns that the lack of diverse, open-air activities can lead to alcoholism, so we propose the State to offer a wide range of activities like the aforementioned. Take advantage of your "reforestation parties" for enhancing positive behaviors of people. Ask the reputable voice of invited artists to encourage the audience to stay in good mood and good relations with Nature while supporting activities like these festivals and concerts.

III. Sell beer, juice, and other beverages for getting fertilizer. Do it in re-usable jars paying deposit for avoiding trash accumulation. Let women or families to organize and sell good-prized, fresh cooked, creole food under State supervision also with deposit-paid dishes so plastic and disposables are avoided. The sooner or the later people will need to urinate, and such a urine can be collected, and used for fertilizing your reforested site (see IV). Both large beer companies and small food entrepreneurs are expected to enthusiastically participate as they are already doing in public events.

IV. Collect, distribute, and control the dosage of fertilizer. Use non-permanent toilets connected to plastic tubes transmitting urine for being collected, then dissolve the urine if necessary and re-distribute it for fertilizing the trees mentioned in I. Do not hesitate to ask Health Ministry inspectors and agronomists to strictly supervise the whole process. Consider the convenience of tolerating, or even facilitate some people to continue their custom of not always using the toilet but the bush or tree-planted areas for urinating.

V. Keep going during the lifespan of trees. Your planted trees and forest fragments will need decades for reverting deforestation, ask biologists and agronomists to join decision makers for spatially distributing decisions I-IV on a map of your country. Then apply the decisions during decades applying periodical monitoring and updating practices with the help of biologists, agronomists. Notice that steps I-IV are designed to be commercially and economically profitable to ensure its long-term permanence giving time for trees to grow and forests to be restored.

5. CONCLUSION

Global Change and secondary succession have generated a world of secondary forests impossible to be fully understood without Land-use History. Land-use History detects the tempo and mode producing the complexity, disparities, and general patterns of forest succession. That provides coherence to Ecology, and easy-to-apply suggestions for Conservation. Thorough land-use histories unveil why some forests holistically converge (or not) to the characteristics of others, what explains the intermediate peak, where the relative importance of seed dispersal was higher respect to local interactions, and for which forest patches stochastic processes prevailed over deterministic ones. By quantitatively discovering which land-use histories generated better secondary forests, Historical Ecology detects good land-use practices to be supported by decision makers.

Land-use History reconstructions demand Ecology to learn from Social Science to get informed about the origins of current forest status. By neglecting such a transdisciplinary interaction, Ecology entangled itself in a kind of "wise agnosticism" where the recognition of the myriads of biological processes making each secondary forests different to the others made Ecologists to conclude that we effectively ignore the main drivers of secondary succession. Historical Ecology provides a way out of such "enlightened ignorance" by smoothly identifying what processes of the past determined current forest characteristics. In a world composed by secondary forests, land-use history reconstructions became mandatory for understanding a planet in risks of collapse due to human-generated Global Change.

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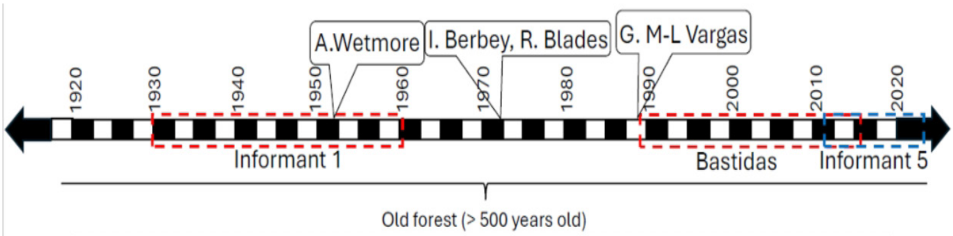
APPENDIX 1: THE LAND-USE HISTORIES OF NINE FOREST PLOTS ON THE COIBA ISLAND, PANAMA

a) Plot Coi 1: Coiba AIP (> 500 years)



Notice the absence of human-made manipulations of this one-hectare terrain plot.

We take advantage of the simplicity of this land-use history for introducing the time spans covered by three major informants living or workin in Coiba during the penal (red-dotted rectangles) and post-penal times (blue-dotted rectangle). We also present the surenames of four key authors who visited Coiba and registered their personal observations of the every-day life:A. Wetmore (1956, 1957), I. Berbey de Quijano (1972), R. Blades (1973, 1974), and G. A. Moncada-Luna Vargas (1988). Because of space limitations, both bubles and dotted-line squares do not appear in the rest of the figures of this appendix.

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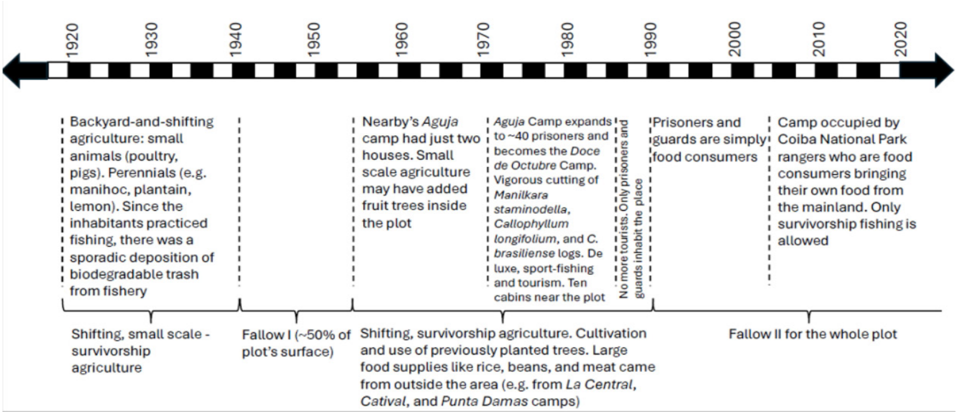
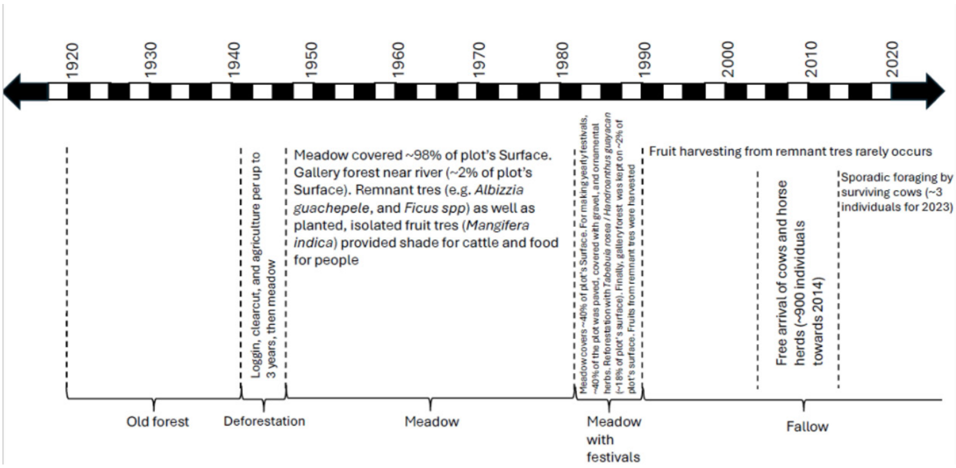
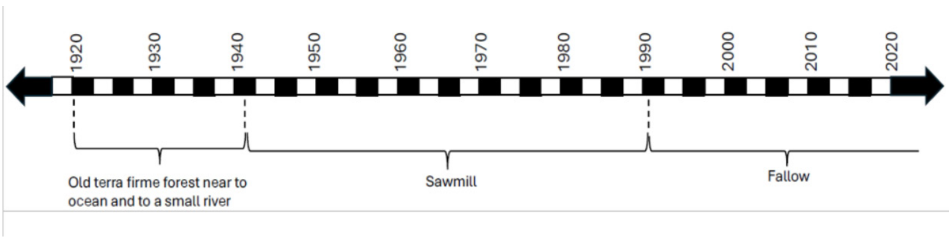
b) Plot Coi 2: Gambute (73, and 33 years)



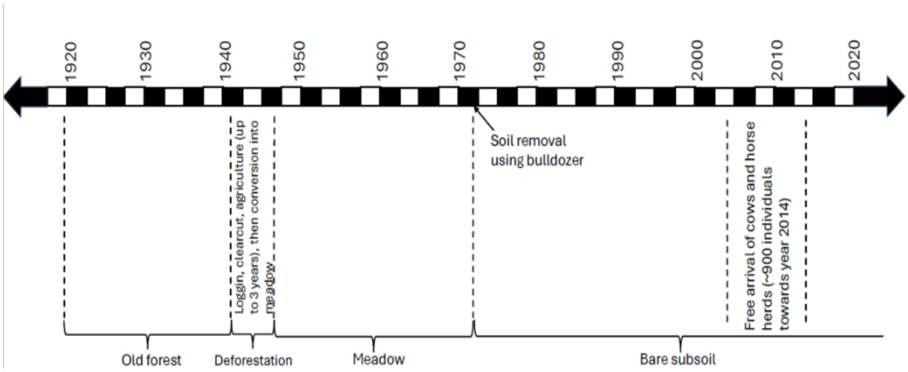
c) Plot Coi 3: La Feria (33 years)



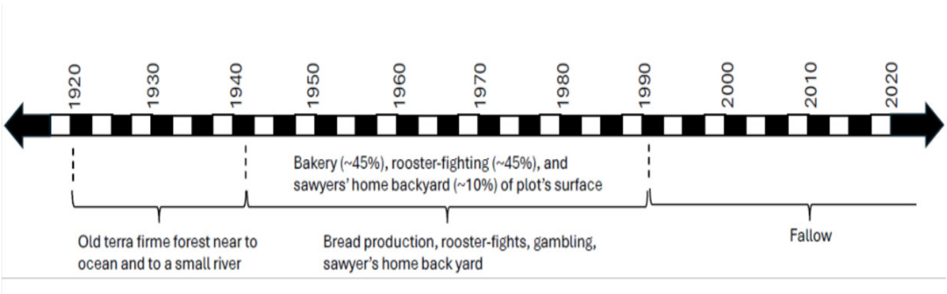
d) Plot Coi 4: Penal's sawmill (33 years)



e) Plot Coi 5: Unfinished airport (51 years).



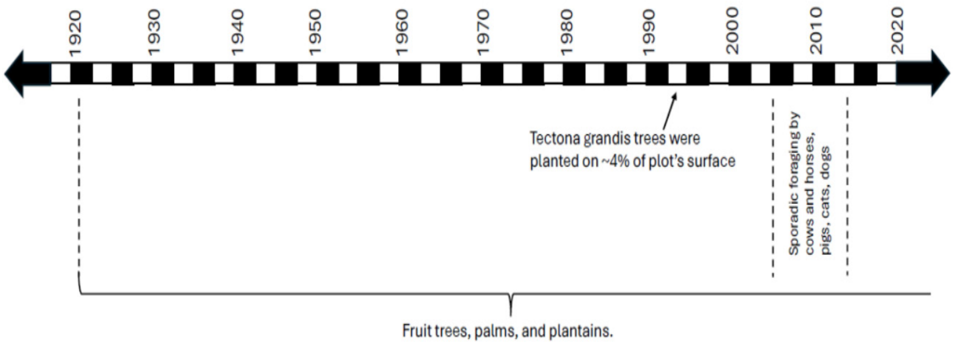
f) Plot Coi 6: Bakery, rooster-figthing arena, and sawyers' home yard (33 years).



g) Plot Coi 7: Abattoir (33 years).

h) Plot Coi 8: Tannery (33 years)

i) Plot Coi 9: Central Camp Gardens (0 years; still in use)



APPENDIX 2: PHOTOS OF NINE PLOTS ON THE COIBA ISLAND

a) Plot Coi 1, Coiba AIP Station. > 500 y-old forest

Structural characteristics
Number of stems: 137
Surface: 0.5 ha
Density: 274 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 20.23 cm (±14.50 cm)
Largest tree DBH: 72.77cm
Total Basal Area: 5.79 m^2 ha^{-1}
Average Basal Area: 419.49 m^2 $stem^{-1}$
Estimated Above-Ground Biomass: 116.41 Mg ha^{-1}

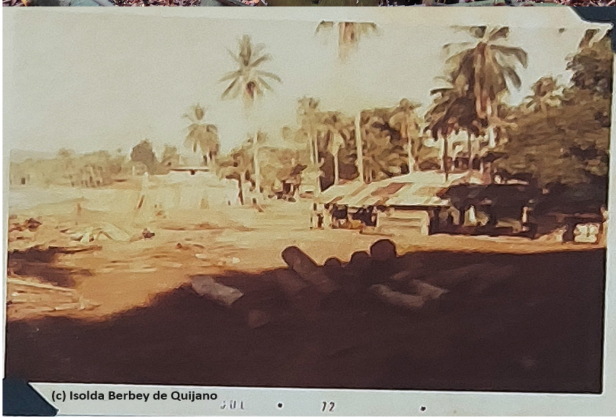
b) Plot Coi 2, *Gambute* (also known as *Doce de Octubre*, and *Aguja*). 73 y-old forest mixed with 33 y-old forest

Structural characteristics
Number of stems: 373
Surface: 1 ha
Density: 370 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 19.21 cm (±10.68 cm)
Largest tree DBH: 124.84cm
Total Basal Area: 13.80 m^2 ha^{-1}
Average Basal Area: 338.00 m^2 $stem^{-1}$
Estimated Above-Ground Biomass: 130.51 Mg ha^{-1}

c) Plot Coi 3, *La Feria*. 33 y-old forest

Structural characteristics
Number of stems: 323
Surface: 1 ha
Density: 323 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 17.98 cm (±9.86 cm)
Largest tree DBH: 90.25cm
Total Basal Area: 9.75 m^2 ha^{-1}
Average Basal Area: 321.88 m^2 $stem^{-1}$
Estimated Above-Ground Biomass: 94.10 Mg ha^{-1}
Additional comments: the knife with yellow ribbon was put as a size-scale reference for the photo.

d) Plot Coi 4, *Aserradero del penal*. 33 y-old forest



Structural characteristics
Number of stems: 92
Surface: 0.25 ha
Density: 368 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 24.75 cm (±9.86 cm)
Largest tree DBH: 84.78 cm
Total Basal Area: 6.28 m^2 ha^{-1}
Average Basal Area: 690.61 m^2 $stem^{-1}$
Estimated Above-Ground Biomass: 259.62 Mg ha^{-1}
Additional comment: The saw radius = 85 cm after direct measurement provides an idea of how large the milled logs were.

e) Plot Coi 5, Unfinished Airport. 51 y abandonment

Structural characteristics
Number of stems: 0
Surface: 1 ha
Density: 0 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 0 cm
Largest tree DBH: non applicable
Total Basal Area: 0 m^2 ha^{-1}
Average Basal Area: 0 m^2 stem^{-1}
Estimated Above-Ground Biomass: 0 Mg ha^{-1}

f) Plot Coi 6, *Panadería, gallera y patio de los aserraderos*. 33 y-old forest

Structural characteristics
Number of stems: 0
Surface: 1 ha
Density: 0 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 0 cm
Largest tree DBH: non applicable
Total Basal Area: 0 m^2 ha^{-1}
Average Basal Area: 0 m^2 stem^{-1}
Estimated Above-Ground Biomass: 0 Mg ha^{-1}
Additional comment: The white-colored circle shows part of our currently studied plot near the gallery forest-belt. Picture shot in the crossroad between the Punta Damas and the Central Camp trails. The panel at right hand shows the alluvial soil of our plot near the Quebrada de la Represa river. Photos made by Alexander Wetmore (1956).

g) Plot Coi 7, *El Matadero*; also known as *Los establos*. 33 y-old forest

Structural characteristics.
Number of stems: 308
Surface: 1 ha
Density: 308 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 20.00 cm (±9.86 cm)
Largest tree DBH: 89.17cm
Total Basal Area: 12.80 m^2 ha^{-1}
Average Basal Area: 418.94 m^2 $stem^{-1}$
Estimated Above-Ground Biomass: 126.23 Mg ha^{-1}

h) Plot Coi 8, *La Curtiembre*. 33 y-old forest

Structural characteristics
Number of stems: 15
Surface: 0.30 ha
Density: 50.50 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 26.72 cm (±18.74 cm)
Largest tree DBH: 76.24 cm
Total Basal Area: 1.23 m^2 ha^{-1}
Average Basal Area: 817.82 m^2 $stem^{-1}$
Estimated Above-Ground Biomass: 45.62 Mg ha^{-1}

i) Plot Coi 9, *Jardines de La Central*. Still in use

Structural characteristics.
Number of stems: 22
Surface: 2.58 ha
Density: 86.82 stems ha^{-1}
Diameter at Breast Height (DBH ±SD): 32.65 cm (±21.01 cm)
Largest tree DBH: 151.90 cm
Total Basal Area: 26.09 m^{2} ha^{-1}
Average Basal Area: 1052.17 m^{2} stem^{-1}
Estimated Above-Ground Biomass: 92.37 Mg ha^{-1}.