EFFECTS OF DIFFERENT LAND USE INTENSITIES ON THE SUCCESSION OF SECONDARY FOREST IN THE PROTECTED FOREST SUMACO, ECUADOR

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Abstract

Studies on site and forest history provide useful insights into the effects of human activities on neotropical forest structure and functions. However, there is still a lack of knowledge regarding how land use history influences tropical forest structure and succession. The purpose of the present study is to enhance our ability both to predict and to manage tropical forest succession. Three research areas (Rukullacta, Villano and Wawa Sumaco) with different colonization dates and use intensity were selected for the study. The age of the forests ranged from 3 to 22 years. At each site, plots of 500 m^2 (20 x 25 m) were installed with four repetitions and compared with a 2000 m^2 research plot of primary forest. Within the plots, all trees above 5 cm were identified and the diameter at breast height (d.b.h.) was measured. An analysis of covariance (ANCOVA) was performed in order to investigate the driving factors of secondary forest succession. The analysis revealed that the number of occurring species depended on sample area, stand age and land use intensity. The species number-area curves at the different sites differed significantly; a correlation between land use intensity and species richness could be observed. A correspondence analysis (CA) was used to determine the patterns of species replacement. According to the results, land use affected floristic composition following abandonment. On the intensive land use level, a noticeable floristic affinity existed between different phases of succession age. The d.b.h. distribution (Weibull function) of the forests was influenced by the grade of anthropogenic disturbance. The potential timber production of the secondary forest was also analysed with a correspondence analysis (CA). On the middle- and low-intensity land use level, forest succession plots exhibit 38% more species of commercial value compared to forests that were highly used.

1. Introduction

Early in 1980, the Central Bank of Ecuador initiated a development project in the area of the Archidona tropical rain forest within the integrated rural development program FODERUMA (Fondo de Desarrollo Rural Marginal) in co-operation with the department of Rural Development within the Ministry of Agriculture (MAG). After the push towards cattle production, the project was aided by a rural development program initiated by the National Development Bank (Banco Nacional de Fomento) in 1985 and founded by the Inter-American Development Bank. This project was aimed at modernizing the agricultural sector and furthermore at integrating the rural population in the national economic development due to increased marketable agricultural production. Accordingly, each Mondayacu and Rukullacta 'socio' (member of the community) was encouraged by the project staff to purchase one bull, three cows, and three calves (PERREAULT, 2000). Under this program, FODERUMA loaned money to Mondayacu and Rukullacta communities at 6% interest and the communities in turn loaned money to the individual 'socios' at 9% interest. This procedure should provide a source of income for the program administration, thereby promoting institutional stability. In 1983, the total cattle herd in Rukullacta was 2000 and at the end of 1987 this number had tripled (BARRAL, 1987). At this time, the agrarian reform legislation, enforced by IERAC (Instituto Ecuatoriano de Reforma Agraria y Colonización), stipulated that 50% of the land must be cleared and put to 'productive use' if a person wanted to claim it. International programs of rural development and agricultural modernization also followed this aim. This meant that the region's forest cover transformed into pasture and its farmers into full-time cattle men who were dependent on unreliable foreign market forces. Thus, cattle-breeding was attractive only as long as credits were cheap and easily available. When the large cattle-breeding projects had expired and subsidies had been reduced in the mid-1990s, and with the declaration of the Protected Forest Sumaco, cattle volumes decreased dramatically in the communities. In the Protected Forest, a pasture system of different intensities was established. Due to soil degradation or fluctuations in socio-economic conditions, these pastures were abandoned after a few years. However, a number of factors retarded forest succession on the degraded pastures and the establishment of woody plants, for instance competition from exotic grasses and ferns, soil compaction, loss of soil nutrients and seed banks due to erosion and deflation, as well as harsh microclimatic conditions (UHL, 1987). In studies in the Venezuelan Amazonian, correlation was found between decreasing recover capacity in tropical forests and increasing disturbance intensity. These studies included investigations of forest biomass, productivity, nutrient cycling and species composition (e.g. HOLL, 1999).

To date, only a few studies have focused on processes of forest recovery on land hat has been used as pasture and with different intensities of colonization. Although land use in the tropics creates extensive agricultural areas and early forest succession patches, it is still rather unknown how the structure and species composition of these forest successions differ from primary forest. The present study compares tree species diversity, diameter distribution, and economic potential in 13 secondary forests aged from 3 to 22 years as well as one virgin forest in the Protected Forest Sumaco, located in the Amazonian region of Ecuador.

2. Material and Methods

In the Protected Forest Sumaco, three different research regions were selected within Holdrige's Tropical Wet Forest life zone (CAÑADAS, 1983) at 450 to 990 m above sea level. The mean annual precipitation and temperature is about 4000 mm and 28°C, respectively. 13 sample blocks of 20m x 25m with four replications (n = 52 plots) for each succession age were established (Table 1). In each plot, species of all trees ≥5 cm were recorded and d.b.h. of these trees was measured and compared with a 2000 m^2 research plot of primary forest in order to determinate the structure change of each succession in the secondary forest.

Table 1. Location, succession age and land use history of 13 selected sample plots.

Research region	Land use intensity	Succession age (yrs)	Duration and form of previous land use
Rukullacta	high	4	22 years under pasture after agriculture
		7	25 years under pasture after agriculture
		11	20 years under pasture after agriculture
Villano	medium	3	Agriculture 2 years and 12 years under pasture
		6	Agriculture 1 year and 10 years under pasture
		10	Agriculture 1.5 years and 8 years under pasture
		15	Agriculture 1.5 years and 11 years under pasture
		18	Agriculture 3 years and 12 years under pasture
Wawa Sumaco	low	3	Agriculture 1.5 years and 4 years under pasture
		5	Agriculture 2 years and 5 years under pasture
		10	Agriculture 1 year and 4 years under pasture
		15	Agriculture 1.5 years and 6 years under pasture
		22	Agriculture 1 year and 5 years under pasture

It was investigated how location and succession age affects the number of species using an analysis of covariance (ANCOVA) and the software R version 2.0.0 (2004):

$$Y_{ij} = \mu + \alpha_i + \theta_1(X_{1ij} - \overline{X_1}) + \theta_2(X_{2ij} - \overline{X_2}) + e_{ij} \quad (1)$$

With: Y_{ij} = Number of species (52 total observations)
X_{1ij}: = Δ Area in m^2
X_{2ij} = Succession age
α_i = Region (Rukullacta, Villano and Wawa Sumaco)
Θ_1, Θ_2 = Slope parameters

This relation (eq. 1) has mainly been used to compare different biotypes and for surface-sized application (ZACHARIAS and BRANDES, 1990). It was applied in its linear form eq. 2 using logarithms of dependent and independent parameters, primarily to make a comparison on a higher spatial aggregation level.

$$\log(Y_{ij}) = \log(c) + \theta_{1i} \log(x_{1ij}),\ \theta_{1i} \text{ (Slope)} \qquad (2)$$

This parameter was used to compare the different relationships between species number and increment of area for each region and succession age.

The Shanon–Wiener–Index (*H'*, eq. 3) was calculated in order to assess the species diversity in populations. *H'* considers the species number and the individual's distribution among the species (MAGURRAN, 1988). This index attained its maximum for a given species number if all species occur with the same number of individuals.

$$H' = -\sum p_i * \ln(p_i);\ \text{Where } p_i = n_i/N \qquad (3)$$

Where: H' = Diversity index
n_i: = Individual number of the i-ten species
N = Age of the succession

The Evenness J' (or moderateness, eq. 4) was introduced by PIELOU (1969) and this index relates *H'* to the maximum value of *H'* which can be attained for a given species number (S_p). *J'* indicates the degree of maximum population's diversity in percent, regardless of species number. Thus, contrary to the Shanon-Wiener-Index, populations with different species numbers can be compared using *J'*.

$$H_{\max} = \ln(S_p);\ \text{where } S_p = \text{Total number of species}$$

$$J' = H' / H_{\max} \qquad (4)$$

The Weibull distribution was used to describe the changes of diameter distribution in location and shape for each succession phase in the secondary forest (eq. 5). The three-parametrical density function of the Weibull distribution is:

$$f(x) = \frac{c}{b} \cdot \left[\frac{x-a}{b}\right]^{c-1} \cdot e^{-\left(\frac{x-a}{b}\right)^c} \qquad (5)$$

Where a = The scale parameter a, which is related to the distribution range
b = The location parameter b, which denotes the distribution's minimum value
c = The shape parameter c, which determines the distribution's skewness

The scale parameter b and the shape parameter c of the Weibull function were estimated using the Maximum-Likelihood method.

The absolute discrepancy of the diameter distribution can be defined through the following equation (6) (POMMERENING, 2002),

$$rDD = \frac{1}{2} \cdot \sum_{i=1}^{n} \left| D_{1i} - D_{2i} \right| \qquad (6)$$

Where D_{1i} = The relative frequency of the i th diameter class in population 1
D_{2i} = The relative frequency of the i th diameter class in population 2
n = The number of diameter classes

A value of $rDD = 1$ means that both distributions are entirely different, whereas $rDD = 0$ signifies that the distributions are absolutely identical. This parameter was calculated to compare the diameter distributions in different secondary forests.

An affinity index between two stands was applied in order to compare two communities regarding their similarity of species composition (JACCARD, 1928). The Jaccard index is defined as equation (7):

$$JZ = \frac{G * 100}{A + B - G} \qquad (7)$$

Where JZ = Jaccard number (Species similarity)
G = Number of species present in both habitats
A, B = Number of species present in Habitat A and Habitat B respectively

A Correspondence Analysis (CA) was applied in order to analyse the relationships between tree species composition, succession age and research regions, and to determinate the potential for timber production in secondary forests. The species in the succession of secondary forests were divided into four classes of timber value: G = low value, M = middle value, High = high value and O = other uses.

3. Results and Discussion

3.1 Influence of research regions, age and sampling area on species distribution

A high statistical significance for differences in species number between research regions, ages and sample areas (P<0.001) was detected using ANCOVA (eq. 1, Table 2). The species number of each research region responded to the different intensities of colonization time (i.e. the time period when the land was used as pasture). The mean species number in the Villano (30.1 species) area and the Wawa Sumaco (26.5 species) area differed significantly from the Rukullacta (17.5 species) area according to a Tukey's Test (P<0.05). The high statistical significance of the effect of succession age on species number can be explained by the aggregation of species during the secondary forest's succession course. In addition, the sampling area was different for each research region and this may influence the species number (Table 2). According to the results, the time of colonization and therefore the intensity of cattle ranching is an important factor to the succession of secondary forest. Similar results were found by PURATA (1986) in Veracruz, Mexico, where the extent of the crop period (i.e., the intensity of land use) and not the land use type per se (maize, coffee and pasture) appear to have a strong influence on vegetation structure.

Table 2. An analysis of covariance results for different effects of research regions (land use intensities), ages and sampling areas on species number in the Protected Forest Sumaco; Df: degree of freedom, Sum Sq: sum of squares, Mean sq: mean of squares, F value: F statistics (F-test), Pr (>F): Rejecting probability for the hypothesized different effects.

	Df	Sum Sq	Mean sq	F value	Pr (>F)
Research regions	2	1207.69	603.85	32.42	418e-09 ***
Succession age	1	961.65	961.65	51.64	274e-09 ***
Sampling area	1	2668.80	2668.80	143.30	073e-16 ***
Residuum	47	875.30	18.62		

3.2 Species number/area relationships

In addition, the species number/area relationships between different research regions and succession ages were compared with an Analysis of Covariance (ANCOVA) using linear relationships after a logarithmic transformation of both independent and dependent variables (eq. 2, Figure 1.) The null hypothesis that all slopes of the species number/area curves were equal was rejected. Significant differences existed between the curve slopes of each research region and indicate a decrease in species number with an increase of land use intensity under cattle ranching from Wawa Sumaco and Villano to Rukullacta. According to KREBS (1985), low slope deviations (≤ 30) indicate widely homogenized growth conditions between different sites. This can be observed for the different succession ages in Rukullacta, where confidence intervals for the obtained slopes were between 0.22 and 0.74 of the slope value. By contrast, the two regions Villano and Wawa Sumaco exhibited confidence intervals greater then 0.30 (with 99% provability) in a comparison of different succession ages. Widely homogenized growth and, more importantly, slower recovery of the species richness was found in the region of Rukullacta. This may be due to the fact that higher intensity levels in previous land use have increased soil compaction and fire occurrence (NEPSTAD *et al.*, 1996).

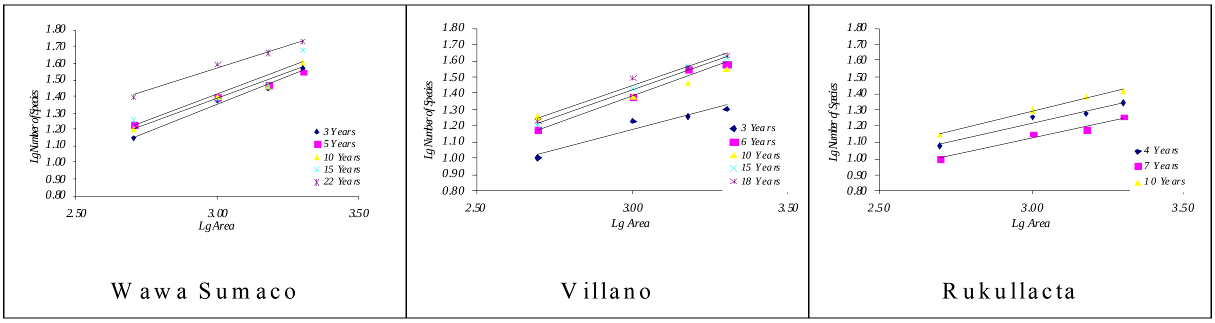


Figure 1. Transformed species number – area curves (double logarithm) of the tree research regions in the Protected Forest Sumaco.

3.3 Diversity, number of species and evenness

Tree species diversity in the different regions and in one primary forest was compared using the Shanon-Wiener diversity index (*H*') for diversity and number of species (logarithmic transformation, Figure 2). Additional isolines of evenness (*J*') that are not influenced by varying species number enhance the diversity assessments for the different successions ages. Trajectories (dashed lines) connect the succession plots of different age in temporal order (Figure 2). The primary forest had the highest number of species and the highest diversity (*H*'); among the occurring tree species, individuals were evenly distributed. The forests in the three research regions had very similar structures and remained relatively constant over time. Compared to the primary forest, all secondary forests were less diverse and less evenly structured (*J*'= 95%). The aggregation and desegregation of species and structure for each individual research region can be recognized in the course of the succession.

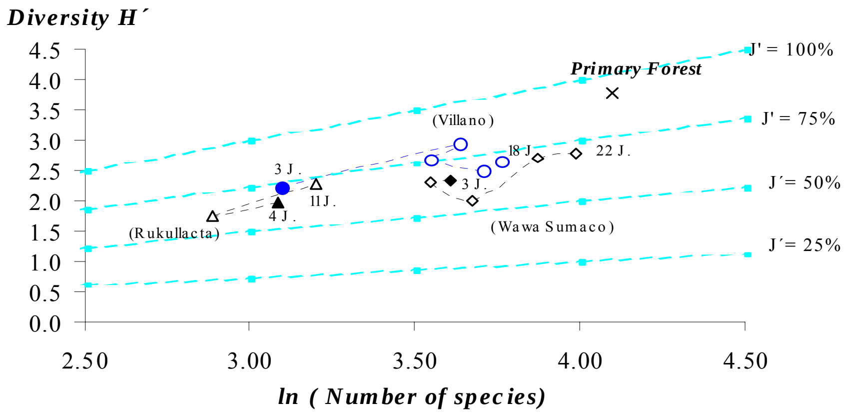


Figure 2. Diversity (H') vs. binary logarithm of the number of species for the research regions. J': Lines of the same evenness according to Schulze et al., (2000). Dashed lines (Trajectories) connecting points represent the development in temporal order (black point) due to succession ages.

According to VANDERMEER (1977), intensive competition should result in low diversity among competing species; thus, high diversity may be correlated to weak competition. Therefore, it seems reasonable to relate competition inversely to diversity. In our study, this would point to lower competition intensity on sites with lower land use intensity and higher succession age. Species 'competition' concerning resource and space sequestration, caused e.g. by different tree height, crown form, and phenology (KELTY, 1992), may decrease interspecific competition with an increase of tree species diversity in forest ecosystems.

3.4 Patterns of floristic recovery and affinity between early stages of succession

A Correspondence Analysis (CA) was performed in order to analyze whether the factors research region (land use intensity) and succession age corresponded to a specific species composition. The CA was aimed at representing a maximum amount of variance information (inertia) along in the first axis. The second axis accounts for a maximum of the remaining inertia, and so on. The total proportion (70.6%) of the inertia is displayed in four axes. The inertia can be interpreted as the weighted average of squared X distances between the average species composition and the species composition in different research regions and ages. The small proportion of the inertia displayed in each axis confirmed the low influence of region and succession age on species composition (Figure 3). Therefore, the patterns of floristic recovery can not be predicted due to both interacting factors.

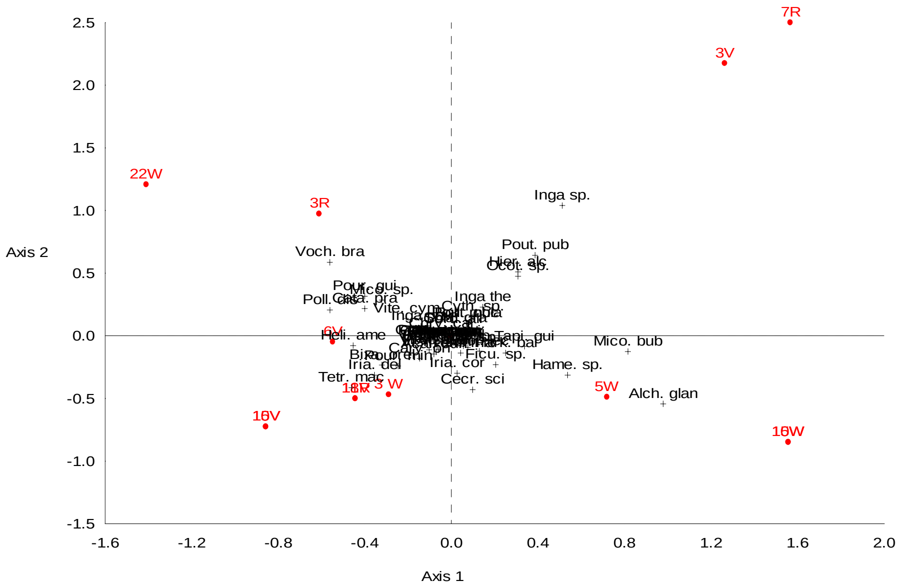


Figure 3. Biplot of results of the Correspondence Analysis (CA) considering species composition, age and region.

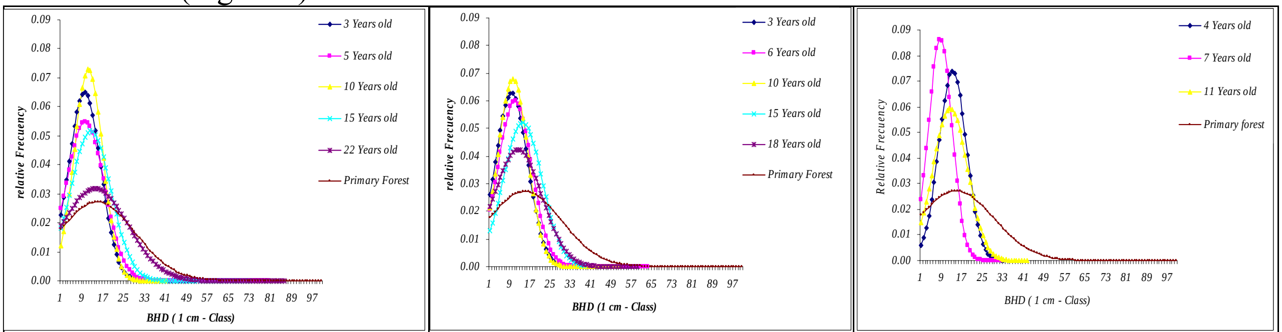
A noticeable higher floristic affinity existed between the different secondary forests of varying succession age in the region of Rukullacta in comparison with the other areas in this study. In extensive abandoned cattle pastures, or severely degraded areas, the successional courses are likely to differ from less degraded areas and the recovery of ecosystem structure and function is expected to be much slower (UHL *et al*., 1988). The presence of remaining vegetation can strongly influence the rate of initial colonization due to its effects on seed dispersal (HOLL, 1999).

Table 2. Floristic affinity between different secondary forests in Protected Forest Sumaco old (W = Forest site Wawa Sumaco. V = Forest site Villano. R = Forest site Rukullacta).

Age	**3 Y. W**	**5 Y. W**	**10 Y. W**	**3 Y. V**	**6 Y. V**	**10 J. V**	**4 Y. R**	**7 Y. R**	**11 Y. R**
3 Y. W									
5 Y. W	35.7								
10 Y. W	28.81	25.42							
3 Y. V	14.55	12.96	12.92						
6 Y. V	22.22	31.57	27.19	34.78					
10 Y. V	10.60	24.56	18.33	23.40	41.18				
4 Y. R	8.00	7.54	14.00	24.88	20.83	14.86			
7 Y. R	9.26	10.64	11.76	18.92	42.86	17.39	**42.86**		
11 Y. R	9.83	18.18	12.07	47.14	33.08	51.22	**33.08**	**30.00**	

3.5 Diameter distribution

Self-thinning and mortality cause considerable changes in the diameter distributions which effectively used to compare secondary and primary forests. (Figure 3). During the succession of the secondary forest, the scale parameter b is related to the distribution range. In this paper it was also used as a synonym of the density function. Thus, the parameter b of the Weibull function increases or decreases with stand age and stand density (Figure 3). The parameter b attained the greatest values in the stands with the lowest stock. This emphasizes the extremely high density of the Rukullacta forest succession at the age of 4 years (compare blue line in Figure 3). By contrast, it is possible to observe extremely high values of the parameter b in the Rukullacta forest at the ages of 7 and 11 years. This is related to the low density of the forest stand compared to the other forests. The shape parameter c of the Weibull function determines the distributions' skewness. In most cases, parameter c was smaller than 1. This means that the distribution is descending to (reversed J-shape). It is evident that great diametrical classes have been lost from the right to the left through the primary forest to Rukullacta. It is related to a gradient of the time during colonization (Figure 3).



Wawa Sumaco	Villano	Rukullacta

Figure 3. Diameter distribution (1-cm classes) of the succession of secondary forest stands arranged in age sequences and parameters of the Weibull function for each age of the Primary Forest in the research regions Wawa Sumaco, Villano and Rukullacta.

The difference between the diameter distributions in Wawa Sumaco and Villano was relatively small, but much greater when Rukullacta was compared to one of the other research regions. Therefore, Rukullacta showed differences in the pattern of diameter distributions (Table 3).

Table 3. Matrix of discrepancies between the diameter distributions of different forest sites for the succession of the secondary forest between 3 and 11 years old (W = Research area Wawa Sumaco. V = Research area Villano. R = Research area Rukullacta).

Age	**3 Y. W**	**5 Y. W**	**10 Y. W**	**3 Y. V**	**6 Y. V**	**10 Y. V**	**4 Y. R**	**7 Y. R**	**11 Y. R**
3 Y. W									
5 Y. W	**0.12**								
10 Y. W	**0.18**	**0.19**							
3 Y. V	0.23	0.12	0.29						
6 Y. V	0.20	0.18	0.22	0.26					
10 Y. V	0.20	0.18	0.24	0.29	0.20				
4 Y. R	**0.24**	**0.26**	**0.33**	**0.18**	**0.27**	**0.24**			
7 Y. R	**0.34**	**0.35**	**0.23**	**0.44**	**0.36**	**0.31**	**0.48**		
11 Y. R	**0.31**	**0.35**	**0.24**	**0.32**	**0.32**	**0.31**	**0.33**	**0.32**	

3.6 Value wood production in the secondary forest stands

Figure 4 shows the asymmetric CA map of four timber species' values in relation to the age of succession in the three research regions in standard coordinates. A large proportion (76.7%) of inertia is displayed along the first axis, showing high and low quality concentrated to the left, middle quality and other uses to the right. On the left side, some succession ages of Wawa Sumaco (5, 10, 22 years) can be found. On the right side, the other ages are displayed with the young Rukullacta successions (4, 7, 11 years) in the centre (Figure 4). This shows that the low quality timber species are accumulated in Wawa Sumaco and the lowest basal area in the young Rukullacta stages. The second axis captures a more subtle feature, which accounts for 17.7% of the variance and opposes middle quality and other uses. Middle quality is relatively high in the Villano regions that are 15 and 18 years old.

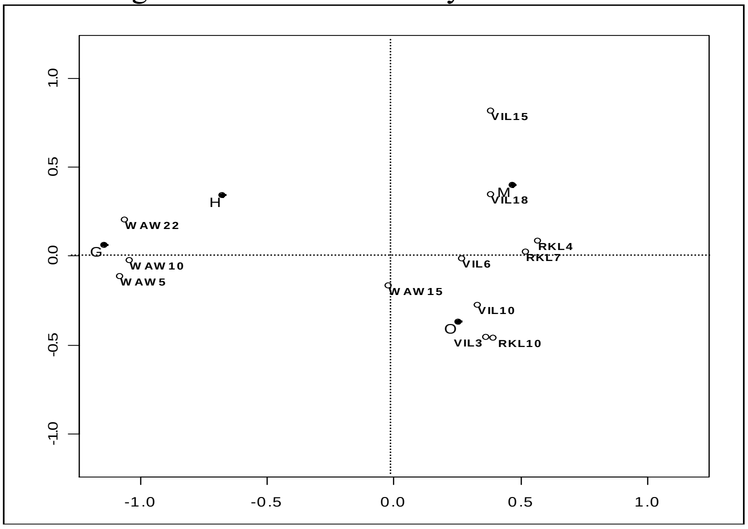


Figure 4. An asymmetric map showing the profiles of the four quality timbers (G = low value, M = middle value, High = high value and O = other uses) and 13 stages of succession of secondary forest.

The forest management in the Rukullacta region often produces short-term yields and, intentionally or not, creates ecosystems that are less variable and diverse over space and time. The secondary forest production is oriented towards the softwood used to produce wooden boxes. The purpose of any abundance of trees with other uses, like the production of fruit, is to attract wild animals for hunting. This indicates that the forest management is closely related to the needs of the local human population.

4. Conclusion

We are not able to determinate the time it takes for different successions of secondary forest to return to the previous rates of desired ecosystem services found in primary forest. But we are able to develop a deterministic model on how land use history and cattle ranching intensities affect the tropical forest of the Protected Forest Sumaco. Throughout the structure analysis in this study, we have shown how far the structure of the different secondary forests is from primary forest. These questions are important not only to people trying to restore tropical forests, but could also be interesting for production proposes. Our analysis and the characterization of the succession of secondary forest should enhance the ability both to predict and manage succession forest ecosystems in the Protected Forest Sumaco.

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