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Influence of distance to forest edges on natural regeneration of abandoned pastures

A case study in the tropical mountain rain forest of Southern Ecuador

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Abstract

In spite of its high diversity the forests in Southern Ecuador are highly endangered by deforestation. One of the main reasons for the loss of forests is the conversion into pastures. Due to their fast degradation, the pastures are abandoned after several years and form an increasing area of unproductive land. The remoteness from existing forest edges is discussed as one reason for the very slow natural reforestation of these areas. In this study we analyzed the regeneration of a secondary forest after approx. 38 years of succession in relation to the distance from the surrounding forest. We revealed that regeneration was rather slow. Especially larger trees with dbh > 10 cm were very scarce. Only *Dioicodendron dioicum*, *Graffenrieda emarginata* and *Clusia sp.* achieved larger diameters. The basal area of the secondary forest is still far beyond the original level in the primary forest. The number of species on plot level and the Shannon index were significantly lower in the secondary forest compared to the primary forest. The total number of species decreased from 47 to 31 with increasing distance from the forest edge and the similarity of species composition to the upper story declined to a level of 56,4 (Sörensen). *Alzatea verticillata*, *Macrocarpea revoluta* and *Palicourea andaluciana* had significantly higher abundances in the succession stages than in the natural forest. The most abundant species in all regeneration plots, *Graffenrieda emarginata* and *Purdiea nutans* seem to be generalists as they did not show preference either to natural forest or successional stages.

Keywords

Restoration, natural succession, abandoned pastures, diversity

Introduction

Fifty two percent of the world´s forests are concentrated in the tropics, which suffer the highest rate of deforestation and land conversion globally (Brown et al. 1996). In South America, the country with the highest rate of deforestation (1,7 % area/yr) is Ecuador (FAO 2006). Conversion to pastures for cattle grazing is by far the most important land use that has affected tropical forests (Hecht 1993, cit. Aide et al. 2000) and has been the main reason for deforestation in Latin America (Amelung & Diehl 1992, cit. Holl et al. 2000).

Due to their fast degradation, the pastures are abandoned after several years and form an increasing area of unproductive land. The few reforestation activities realized in Ecuador are based on plantations, mainly with introduced species like *Pinus spp.* and *Eucalyptus spp*. However, the montane forests of Latin America in general and especially in the region of Southern Ecuador and Northern Peru are focal points world wide for very high plant diversity (Barthlott et al. 1996, Henderson et al. 1991, Brummit & Lughadha 2003). Hence, plantations of exotics, usually characterized by uniform stands with low biodiversity, cannot be considered as a sustainable land use.

As the natural regeneration of abandoned pastures proceeds very slow, it is not really considered as an alternative to plantation. One reason for the very slow natural re-colonization is the remoteness from existing forest edges combined with reduced seed input caused by increasing fragmentation (Cubiña & Aide 2001, Myster 2004). However, where the distance to remaining forest edges is not too far natural regeneration could be considered at least as a valuable option for the restoration of biodiversity.

In this study we analyzed the effects of increasing distance from forest edges on the tree species diversity and the structural parameters of a secondary forest from natural regeneration. As the disturbances regime is known to have strong impacts on the regeneration of forests we will also discuss whether the regeneration patterns within the study area can by better explained by the intermediate disturbance hypothesis (Connell 1978) or the gap partititioning hypothesis (Hubbel 1999, Brokaw & Busing 2000).

The following hypotheses were tested:

H_1: Tree species and structural diversity decrease with increasing distance from the forest edge.

H_2: All species near to the edges of the surrounding forest can regenerate on the abandoned area.

H_3: Species composition of naturally regenerated areas is similar to that of the adjacent forest remnants.

H_4: We suppose that the disturbance theory of “intermediate disturbance hypothesis” (Connell 1978, Li et al 2004, Potts 2003, Sheil & Burslem 2003,) rather than the “gap partitioning hypothesis” (Hubbel 1999, Brokaw & Busing 2000) could explain the species composition and biodiversity patterns (Fig. 1).

The results can help to understand restoration processes of highly diverse ecosystem on the one hand and indicate whether the species composition, diversity and restoration velocity are suitable for contributing reforestation measures on the other hand.

Fig. 1

Methods

The study is linked with an interdisciplinary research group about “Functionality in a Tropical Mountain Rainforest: Diversity, Dynamic Processes and Utilization Potentials under

Ecosystem Perspectives”. The study area is located at 3°58´S, 79° 04´W between the province capitals Loja and Zamora in the forest of the Estacion Cientifica San Francisco (ECSF), which represents a highly diverse ecosystem of various organism groups (Braun 2001, Brehm 2002, Bussmann 2001, Homeier 2004, Matt 2001). The mean annual precipitation at 1900 m NN amounts 2200 mm but increases with the altitude. The mean temperature is 15 °C (Emck 2006). The dominant soil types of the study area are Dystrudepts, Humaquepts and Petraquepts (Schrumpf 1999). The ECSF forest is divided by pronounced ridges into watersheds of 4 to 15 hectares each. The vegetation units can be categorized into ridge-types and valley-types (Günter & Mosandl 2003). The altitudinal gradient also has a strong impact on the forest structure and species composition (Homeier et al. 2002). A detailed botanical description of species composition and zonation is given in Bussmann (2001), Homeier et al. (2002) and Paulsch (2002). The forest can be classified as a tropical montane rain forest in the lower parts and cloud forests at higher altitudes. The study site is located at an unincisive ridge at the transition zone of these main vegetation types. Mean declination is about 10-39 °.

To evaluate the effects of forest edges onto rehabilitation of abandoned pastures we studied ten transects within a patch of abandoned cattle pastures measuring 80 m x 240 m, presently covered by secondary forest. Every transect consisted of 4 plots with 25 m² each, along a gradient of increasing distance from the forest (-20 m, 0 m, 20 m and 40 m), with an additional reference plot of 400 m² inside the surrounding primary forest (Fig. 2). In the 25 m² plots all woody plants with dbh >2 cm were analysed, while in the 400 m² plot only those with dbh >10 cm. Parameters analysed were dbh, species and crown coverage (with spherical densiometer) in both plot sizes. Tree height was also measured in all plots except the reference plot.

Fig. 2

Aerial photographs proved that the pasture at 2100 m NN was abandoned approximately 38 years ago and was always surrounded by primary mountain rain forest. Thus, the study site can also be described as large gap covered by secondary forest within a matrix of undisturbed primary forest. Our area represents the same plant communities as described by Galvez et al. (2001) for altitudes of 1900-2100 m NN and those of higher altitudes of the ECSF area: At altitudes between 1900 and 2100 m *Graffenrieda emarginata*, *Alzatea verticillata* and *Hedyosmum anisodorum* were the most abundant species, at higher elevations *Purdiaea nutans*, *Myrica pubescens* and *Clusia latipes.* This coincides with our results. The study site therefore can be considered as representative for the forest at this altitude in the San Francisco Valley.

To compare the means of the structure and diversity parameters along the distance gradient from the undisturbed primary forest into the gap center, a One-Way Anova multiple comparison of means was carried out applying the Levene Test for studying homogeneity of variances. Thereafter, in order to calculate confidence intervals, the Bonferroni-Correction was used for homogene variances and Tamhane T2 in the case of inhomogeneity.

Especially in the first years of the natural succession several ecological factors vary with increasing distance, for example: light, minimum and maximum temperatures, and rainfall increase, whereas nutrient input from litterfall, seed quantity and seed diversity decrease (Cubiña & Aide 2001). If only one of these factors is the limiting factor, we should either find a strictly ascending or a descending relationship between edge distance and structure or biodiversity parameters. If a combination of positively and negatively correlated factors determines structure or diversity it is more difficult to predict the restoration processes. According to the intermediate disturbance hypothesis highest diversity should be found at the plots with medium distance to the edge, corresponding to intermediate disturbance intensity.

Results

On the reference plots in the primary forest abundance of trees and shrubs with dbh >10 cm was 685 n/ha with a mean basal area of 13,3 m²/ha. In total 47 species were registered on the total sampling area of 4000 m². The average number of species per plot was 13,1, the mean Shannon Index 2,3. In table 1 the ten species and families with the highest Importance Value Index (IVI, Lamprecht 1986) are shown. Accordingly, the most important species in the primary forest at this altitude are *Graffenrieda emarginata, Clusia sp*., *Alchornea pearcei, Myrcia sp.* and *Purdiea nutans*. It is notable that *Podocarpus oleifolius* as a ´high value timber species´ is also among the most dominant species at this altitude.

Table 1

Analysis of IVI in the 25 m^2 plots revealed that several species of the regeneration stratum show a preference for primary forest conditions (*Elaeagia sp., cf Vochysia sp., Schefflera sp., Prunus huantensis, Ocotea sp. Hyeronima sp., Nectandra reticulata, Aniba sp., Alchornea sp., Alchornea glandulosa, Siparuna sp., Hyeronima alchornoides, Weinmannia sp., Eschweilera sp., Persea subcordata*). In contrast *Palicourea andaluciana, Alzatea verticillata, Dioicodendron dioicum, Myrsine sp., Hyeronima moritziana, Bejaria aestuans, Ilex sp., Clethra revoluta and Macrocarpaea revoluta* showed strong preferences for the remote positions from the primary forest edge. In the gap, covered by secondary forest, the abundance of trees >10 cm dbh was very low. In total only 5 individuals with dbh >10 cm were found (*Graffenrieda emarginata*, *Clusia sp.* and *Dioicodendron dioicum*). This corresponds to abundances between 0 and 120 n/ha. However, number of trees <10 cm dbh was very high in all regeneration plots. (table 2) The abundance of trees >2 cm dbh did not significantly differ between gap (6560-8280 n/ha), edge (8200 n/ha) and forest plots (7300 n/ha). Also, abundances for trees >5 cm dbh were similar, though slightly lower outside the primary forest. However, regarding the structural parameters basal area and height there are significant differences between succession and forest plots which become more evident with increasing dbh. The basal area in the secondary forest varied between only 48,2 % and 54,3% of the forest level for trees with dbh >2 cm, and only 6,0 % and 7,8 % for trees with dbh >10 cm.

Table 2

It is notable that the structural parameters do not show a consistent gradient from the forest edge to the gap center. However, there are significant structural differences between forest plots on the one hand and gap or edge plots on the other hand. The number of species in the regeneration plots (dbh >2cm) was exactly the same as that of the species with dbh >10 cm in the primary forest: 47 species. However, there was a slight decline in species number from inside the forest (47) to the forest edge (39), 20 m distance (34) and 40 m distance (31), even though the Shannon Index does not show significant differences between the regeneration plots at 20 m or 40 m distance and the forest edge.(fig. 4). Similar patterns were detected for exclusive species[1]: 15 exclusive species were found in the forest, four species at the edge, six at 20 m and four species at 40 m from the edge. 85 % of all species in the upper story of the primary forest (dbh >10 cm) were also found in the regeneration plots of the primary forest.

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[1] Species that only occur at a single position along the gradient from the forest to the gap center, for example only inside the forest but nowhere else

Only *Macrocarpea revoluta, Hyeronima moritziana, Clethra revoluta, Tecoma stans, Myrcia sp.* and two *Clusia* species did not regenerate in the primary forest. The proportion of upper story species declined with increasing distance from the edge (63 % at the edge, 53% at 20 m and 47 % at 40 m from the edge).

Table 3

The distribution of the Sörensen indices confirms the observed patterns (table 3). The most similar plant communities are the upper story trees in the forest and the regeneration in the forest (Sörensen of 85,1). High similarity can be observed, but to a lesser extent between the communities at 20 and 40 m from the forest edge (Sörensen of 73,8). The lowest congruence could be found for the successional plant communities in the secondary forest and those inside the natural forest.

Two tailed T-test for paired samples (n=10) showed that several species and families of the regeneration stratum had significant higher abundances in the primary than in the secondary forest: *Clusia sp. 2*[2] (p <0,01), *Myrcia sp.* 3 (p <0,05), *cf Vochysia sp.* (p <0,05). *Alchornea sp.*, *Hyeronima sp.*, *Miconia sp.* 3, *Nectandra reticulata*, and *Prunus huantensis* were significant at a lower level (p<0,1). The species from the botanical family *Clusiaceae* (p <0,01) had significant higher abundances in the forest compared to the gap plots, and at a lower significance level (p<0,1). This was also noticeable for *Araliaceae, Lauraceae, Rosaceae* and *Vochysiaceae*. The families *Alzateaceae, Cloranthaceae* and *Gentianaceae* (all p <0,05) significantly favored positions at 20 to 40 m from the forest edge. The species with significantly higher abundances (p < 0,05) in successional stages than in the old growth forest were *Alzatea verticillata*, *Macrocarpea revoluta* and *Palicourea andaluciana*. The

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[2] Different numbers indicate different morphospecies

abundances of *Clethra revoluta*, *Dioicodenron dioicum*, *Hedyosmum anisodorum*, *Miconia sp. 1*, *Myrcia sp. 2* and *Palicourea sp*. were also higher but at a lower confidence level (p < 0,1).

Fig. 3

Relative and absolute abundances were calculated for all families and species according to the habitats forest, forest edge and gap (all positions 20 m and 40 m from forest edge). Fig. 3 shows all families in the descending order of their abundance in the gap. Accordingly, three different groups can be distinguished. Group one is represented by six families with relative abundances at 20 to 40 m in the gap higher than 66,6 %: *Asteraceae, Aquifoliaceae, Gentianaceae, Myrsinaceae, Alzateaceae and Clethraceae*. The 2nd group contains eight families with abundances lower than 33,3% in these positions: *Monimiaceae, Cunnoniaceae, Araliaceae, Lauraceae, Piperaceae, Podocarpaceae, Rosaceae and Clusiaceae*. The families of the third group did show neither preference for secondary forest nor for the primary forest and therefore can be considered as transition families from forest to earlier successional stages. It is notable that those transition families generally had higher abundances (mean 348 n/ha) than secondary forest families (191 n/ha) and especially than primary forest families (102 n/ha).

Fig. 4

The analysis at species level (mean abundances >50 n/ha) revealed *Clethra revoluta, Macrocarpea revoluta, Miconia sp., Alzatea verticillata, Palicourea sp*. and *Roupala sp*. as species with high relative abundances in the secondary forest, whereas three *Clusia* species, three *Myrcia* species, *Hyeronima sp., Schefflera sp., Piper sp., Alchornea sp., Podocarpus oleifolius* and *Prunus huantensis* had the lowest relative abundances. The number of species was lowest for intermediate relative abundances in the gaps (n = 13), whereas species number for relative abundances >66 % in gaps (n =20) and especially those with abundances lower than 33% (n = 35), were very high. Two species can be considered as generalists with very high absolute and relative abundances in the natural forest as well as at the forest edge or in the secondary forest plots: *Graffenrieda emarginata* and *Purdiaea nutans*.

Discussion

Seed recruitment

The two most important barriers to the restoration of tropical montane forest on abandoned pastures are the lack of dispersal of forest seeds and seedling competition with pasture grasses (Holl et al. 2000). This could be the reason for relatively uniform diversity and structure parameters on the regeneration plots of the study area. Several authors confirm the strong impact of distance from forest edges on seed rain, which could have caused the observed patterns in our study, too (Cubiña & Aide 2001, Holl et al. 2000). Zimmermann et al. (2000) also confirm the pattern observed in our investigation with similar abundances at different distances from the forest edge but with a reduced number of species and changes in species composition. One of the major reasons for the low rates of seed arrival in pastures is that most tropical shrubs and trees are animal dispersed, and many frugivorous birds and bats avoid large open areas that could expose them to predators, particularly if there are no perches or fruits (Engel & Parrotta 2001, Howe & Smallwood 1982, cit. Cubiña & Aide 2001, Zimmermann et al. 2001). Nangendo et al. (2002) attributed high biodiversity in regeneration to the proximity of forest edges and single tree remnants in the grassland that contributed to seed dispersal. Consequently, establishment of seed trees or bird perches could be a valuable option to increase diversity in reforestations (see section management).

Species composition

In many tropical forests, the upper story species do not regenerate in the same locations in which the adults occur (Swaine & Hall 1988). From this point of view it is surprising that almost 85 % of the upper story species at the study site could regenerate in the forest. Many species can be maintained when a forest contains a variety of successional stages and species are able to migrate among patches (Connell 1979, cit. Sheil & Burslem 2003). From that it could be concluded that in the past large and small scale disturbances took place at the study area, leading to the coexistence of successional species (*Alzatea verticillata*, *Clethra sp.*), forest species (*Podocarpus oleifolius*), and generalists (*Graffenrieda emarginata*, *Purdiaea nutans*) as dominant members of the upper story.

Zimmermann et al. (1995) for example found an effect of a temporal gradient on species composition but not on woody plant diversity. These findings correspond to our results of similar diversity indizes but decreasing similarity in species composition along a *spatial* gradient (increasing distance from the forest edge). Surprisingly, the IVI-values of primary forest species are relatively high also in the secondary forest plots (table 1). However, at larger distances from the edge (>40 m), the proportion may decrease in favour to pioneer species. This is confirmed by Finegan & Delgado (2000) who found that species composition of the dominating trees in a 30 year old secondary forest in Costa Rica consisted of a mixture of species from the old-growth and adventives colonizing from agricultural land.

Diversity

We observed an abrupt decline of diversity and structural parameters at the forest edge compared to the primary forest. However, from the forest edge to the gap center, there was only a slight change in diversity and composition. According to the ´intermediate disturbance hypothesis´ (IDH) (Connell 1978, cit. Sheil & Burslem 2003) we should not expect a soft decline from the edge to the center, but an increase and only after a certain distance a decrease.

According to IDH the highest diversity of tropical rain forest trees should occur at the intermediate stage in succession either after a large disturbance or with smaller disturbances that occur not extremely frequent or infrequent; both situations represent an open non-equilibrium. Consequently, following this hypothesis highest diversity would be expected on the center plots. Hubbel et al. (1999) present contrasting conclusions to IDH. They formulated the ´gap-partitioning hypothesis´ (GPH), which differentiates among gap sizes, location within a gap, gap shape, orientation, type and time of creation. All these factors are considered to have an impact on regeneration processes and species composition. A modificated GPH theory has been presented by Poorter & Arets (2003). They found evidence for the so called ´light partitioning hypothesis´ (LPH) in moist forests of Bolivia. Grau (2002) contradicts the IDH, too. Some authors recommend modifications of IDH. Sheil & Burslem (2003) stress that one difficulty with applying the IDH to forests is the relationship between internal tree-fall dynamics and external drivers of disturbance (eg. storms, fire and drought). Our results rather support the GPH than the IDH (Fig. 5): Schwilk et al. 1997 confirm that intermediate disturbance hypothesis may not hold true where fire is the disturbance, which also was part of the landuse history of our study site.

(Fig. 5)

Also we found evidence of differentiated adaption of species and families to certain positions in the patch of abandoned pasture, which would support the GPH (Fig. 3). In contradiction to both the GPH and the LPH we could not find significant differences of species richness along the gradient of increasing distance from the forest edge for sample sizes of 25 m², but differences in species number were notable if all plots of one distance category are combined (total sample area 250 m²). Molino & Sabatier (2001) revealed that species richness corrected for stem density was similar to that of surrounding forest and varied little with gap size. Considering the height of the upper story at the study site of approximately 10 to 15 m (Homeier et al. 2002), we can expect reduced light incidence at the forest edge but not at distances of 20 and 40 m from the edge. According to Muuß 1997 and Günter 2001 the impact of shading in those distances from the edge should be very low. It is more likely that other factors, e.g. seed recruitment could have caused the decline in species number and species composition in comparison to the natural forest.

Management

As our results show 38 years of natural development were not enough to regain the structure of the primary forest with regard to species composition. In contrast to our study site, structural parameters of a secondary forest in Puerto Rico and that of the old growth forest sites were similar after approximately 40 years (Aide et al. 2000). However, our study site is located on a ridge, so one of the reasons for slow development may be soil conditions which did not allow seedling establishment for all species. Homeier (pers. comm.) identified very low increment rates for the stands at ridges in the ECSF area. Against this background, it seems doubtfull if natural succession is suitable to meet economic objectives, at least for similar soil conditions.

If the seed flux into abandoned areas is not sufficient, planting of animal dispersed species like *Piper spp. or Myrica pubescens* could attract bats or birds (Almeida et al. 2004) and thus enhance the restoration processes. Enrichment plantings with valuable timber species like *Podocarpaceae* could contribute to a certain extent to additional income for small scale farmers. Some authors report from successfull enrichment planting trials (Pedraza & Williams–Linera 2003) and confirm that enrichment planting can also accelerate natural succession (Aide et al. 2000, Zimmermann et al. 2000), especially when animal-dispersed species are used (Garzia-Martinez & Howe 2003). Holl et al. 2000 stress on the other hand that bird perching structures alone are not an effective strategy, because they only serve to enhance seed dispersal but not to reduce grass cover, which is a major barrier to forest restoration. First results of a reforestation experiment in different successional stages of our study area show that native species develop rather well, when weeds are cleared chemically but not manually (Eckert 2006). But when the goal is to restore biodiversity, weeding could be counterproductive because it may remove new species that invade the stand during succession (Zimmermann et al. 2000).

Fragmentation of resources and habitats act differently on species diversity across spatial scales: ranging from positive effects on local species coexistence, to negative effects on intermediate scales, and to again positive effects on large spatial and temporal scales (Olff & Ritchie 2002). According to their studies large forest fragments contain the greatest numbers of tree species and the highest proportions of rare tree species. This coincides with our results of highest diversity and highest number of exclusive species in the forest. Hence using forest edges and forest fragments as tools for natural restoration of abandoned pastures, one must pay attention to a systematically distribution of forest fragments as well as conservation of appropriate fragment sizes.

Conclusions

According to the results we have to refuse all four postulated hypothesis.

H_1: Primary forest and abandoned pastures had pronounced differences in regeneration structure and diversity but there was no impact of distance from the forest edge on the structure and diversity at a per plot basis. However, there was a decline of total number of species, although not statistically significant.

H_2: Only a limited number of surrounding forest species could regenerate on the abandoned area. The number of species that exclusively regenerated inside the forest was higher than the number of species that exclusively regenerated in the disturbed areas.

H_3: The similarity of the species composition of natural regeneration and the surrounding mature stand declined with increasing distance between disturbed area and forest edge.

H_4: Hence our results rather support the gap partitioning hypothesis than the intermediate disturbance hypothesis.

The succession lead to a secondary forest with a high biodiversity, much higher than any anthropogenic established plantation. Thus, natural succession enhanced by forest edges can contribute to forest restoration, at least if the distance is not too much (in our case <40m). However, with increasing distance from the forest edge, the species composition changed from its original status in the primary forest. Especially scarce forest species disappeared and were replaced by more common species. Therefore, the conservation of perches and remnants of natural forests inside abandoned pastures is of high importance for the future restoration of biodiversity. Enrichment planting could be an additional measure to increase the number of forest species.

From a user´s point of view, the speed of natural restoration was not satisfying. Height and diameter growth were very low at the study site. Possibly the growth of the natural succession had already been influenced by soil degradation processes but it may also be possible that on the ridges at the ESCF area, soil conditions in general were poor for tree growth. Further studies on the impact of soil conditions on forest growth are important for developing strategies for forest restoration. Another priority would be the selection of fast growing tree species on different soil types. Our results suggest, that *Graffenrieda emarginata*, *Dioicodendron dioicum* and one species of *Clusia sp*. could possibly be candidates for reforestation of ridges in the montane region of Southern Ecuador. Unfortunately the knowledge of the propagation of the South Ecuadorian montane forest species in general is very poor. Studies in germination protocols are needed and it is necessary to develop techniques for propagation of plants on a larger scale. This is not only a challenge for science but also for applied development projects.

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Fig. 1: Model for explaining highest diversity at intermediate distances from the forest edge according to IDH (intermediate disturbance hypothesis)

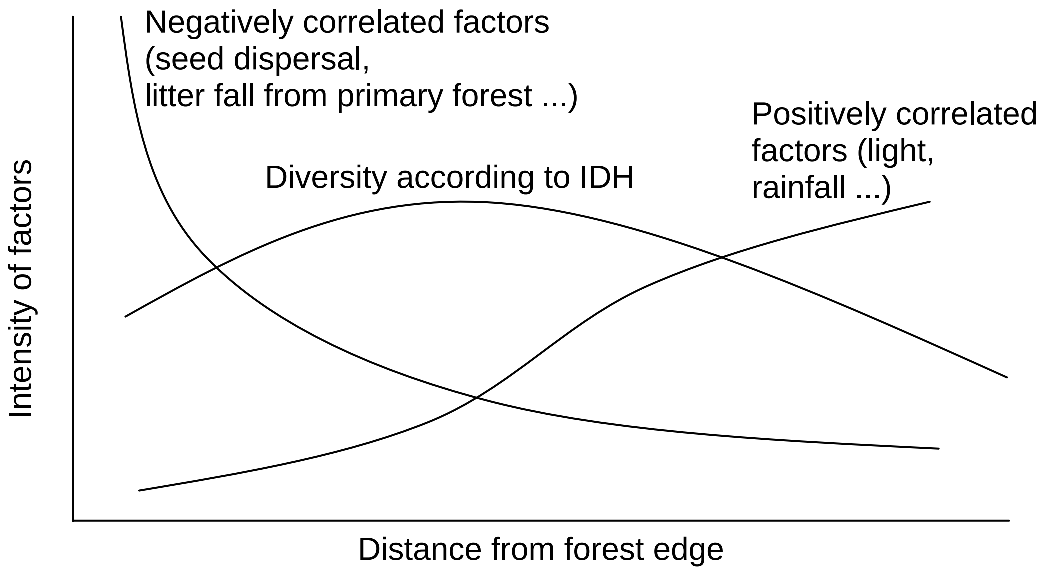

Fig. 2: Draft of the study area. The patch of abandoned pastures is surrounded by natural forest. Ten transects with 4 plots of 25 m² each were installed in the 38 year old secondary forest and one additional reference plot of 400 m² inside the natural forest.

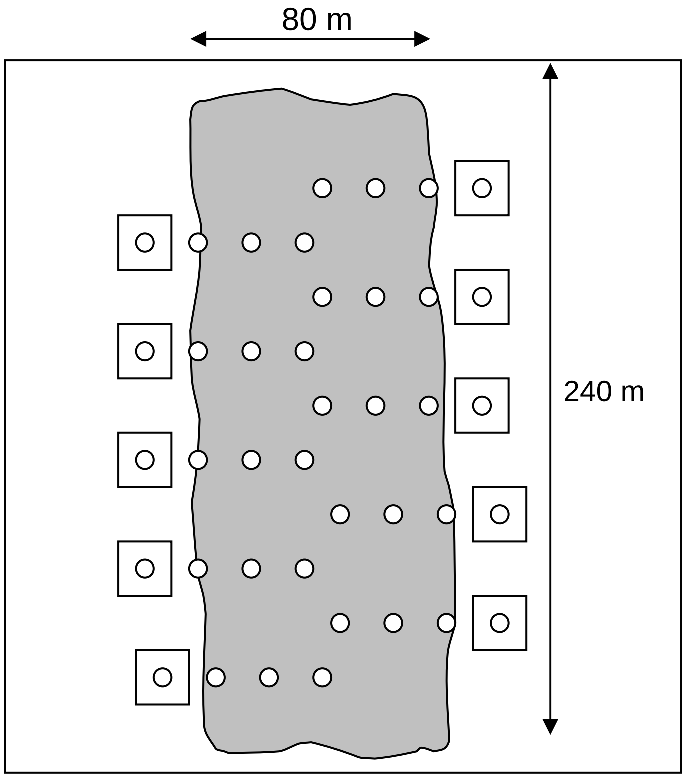

Table 1: Importance Value Index (IVI) of the most important species inside the primary forest (PF) and on the regeneration plots in the secondary forest (SF) at 20 and 40 m from the primary forest edge.

		IVI		
Species	**Family**	**PF**	**SF 20m**	**SF 40m**
Graffenrieda emarginata	*Melastomataceae*	48,52	55,9	39,4
Clusia sp.	*Clusiaceae*	31,82	20,4	10,0
Alchornea pearcei	*Euphorbiaceae*	29,34	20,6	21,3
Myrcia sp.	*Myrtaceae*	18,27	9,3	5,5
Purdiea nutans	*Cyrillaceae*	16,96	21,0	22,2
Alchornea sp.	*Euphorbiaceae*	16,89	0,0	0,0
Palicourea sp.	*Rubiaceae*	14,82	4,1	20,5
Clethra sp.	*Clethraceae*	13,37	10,6	12,5
Podocarpus oleifolius	*Podocarpaceae*	10,28	0,0	0,0
Alzatea verticillata	*Alzateaceae*	9,03	18,5	8,8
All other 37 species together		**90,7**	**139,6**	**140,2**
Total		**300**	**300**	**300**

Table 2: Impact of the distance from primary forest edge on structural parameters of trees and shrubs on the 25 m^2 plots.

Parameter	**dbh-class**	**Distance from primary forest edge (m)**			
		-20	**0**	**20**	**40**
Abundance (n/ha)	>2 cm	7320	8200	8280	6560
	>5 cm	2800	2200	2040	2240
	>10 cm	800	120	0	80
Basal Area (m^2/ha)	>2 cm	24,7 a*	12,2 b*	11,9 b*	12,4 b*
	>5 cm	21,2 a*	8,1 b*	7,0 b*	7,9 b*
	>10 cm	13,3	1,04	-	0,8
Mean Height (m)	>2 cm	5,3 a*	4,3	3,8 b*	4,4
	>5 cm	6,5 a**	5,3	4,7 b**	5,1 b*
	>10 cm	10,1	7,3	-	6,3
Max. Height (m)	>2 cm	10,5 a*	6,1 b*	5,7 b*	5,8 b*
	>5 cm	10,3a***	6,0 b***	5,4 b***	5,8 b***
	>10 cm	13,0	8,0	-	6,5
Species (n/plot)[1]	>2 cm	12,2 a**	9,2 b**	9,8	8,6 b**
	>5 cm	5,1	3,3	3,2	4,0
Shannon Index[1]	>2 cm	2,35a**	1,95 b**	2,05 b*	1,96 b**
	>5 cm	1,40	1,02	1,00	1,16
Crown Cover (%)		85,6	77,8	81,6	78,4

*different letters mean statistical differences at the level * $p < 0,05$, **$p<0,01$, ***$p<0,001$

[1] No species number per plot and Shannon index were calculated for dbh > 10 cm due to very low abundance per plot.

Table 3 : Sörensen indizes of similiarity between vegetation communities along a gradient of increasing distance from the primary forest edge

Distance	dbh	Distance from forest edge (m)			
		-20	0	20	40
		Trees with dbh >2 cm			
-20	>10 cm	85,1	69,7	61,7	56,4
-20	>2 cm		67,4	51,8	53,8
0	>2 cm			71,2	65,7
20	>2 cm				73,8

Fig. 3: Mean relative abundances (left) of the families at all regeneration plots and their distribution in forest, edge and gap (right: absolute abundances)

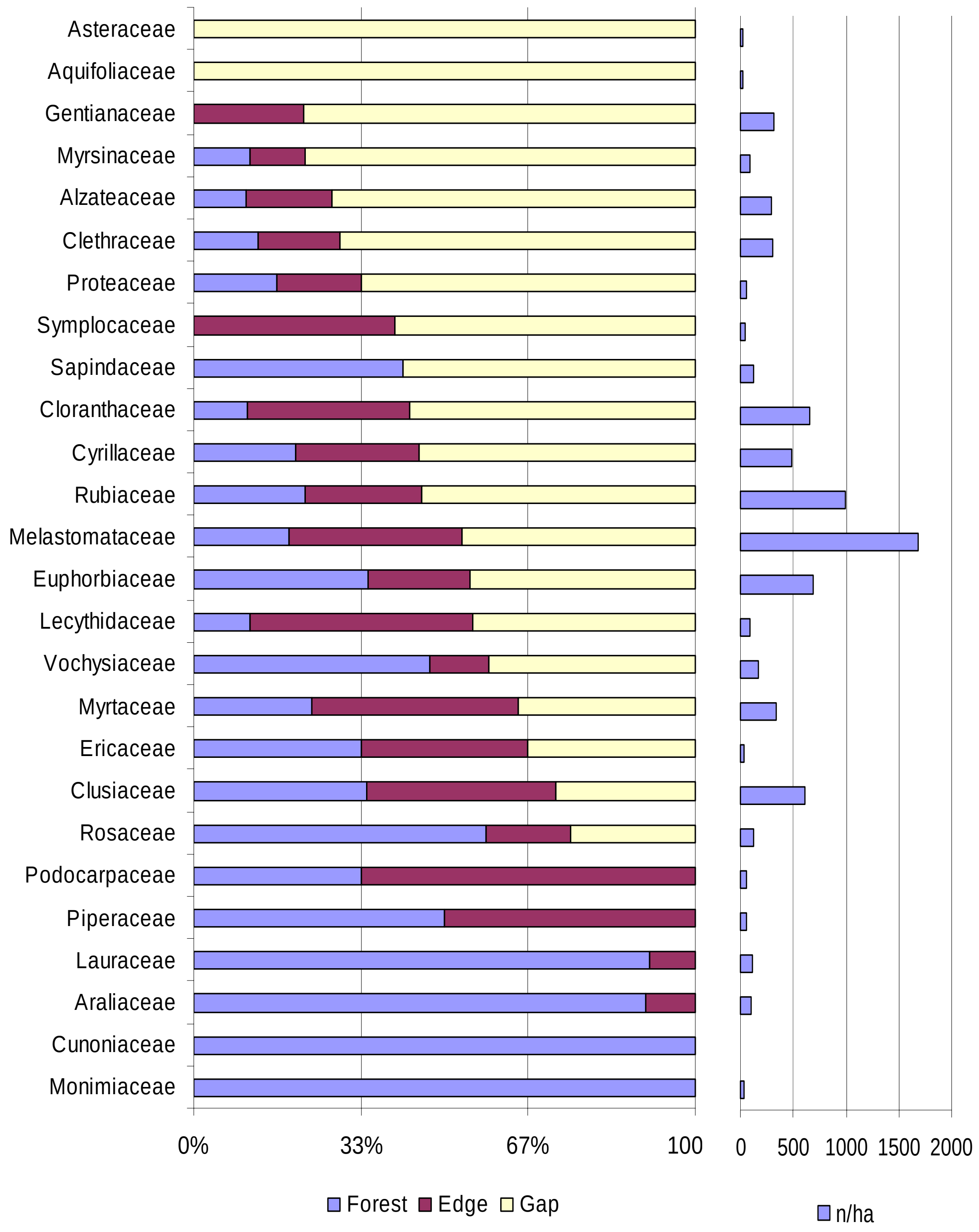

Fig. 4: Impact of distance from forest edge on diversity indizes. Species numbers were calculated for sample sizes of 250 m^2 and on plot basis 25 m^2. Equation curve for all species: y = 47,336x-0,3005, r^2 = 0,9969.

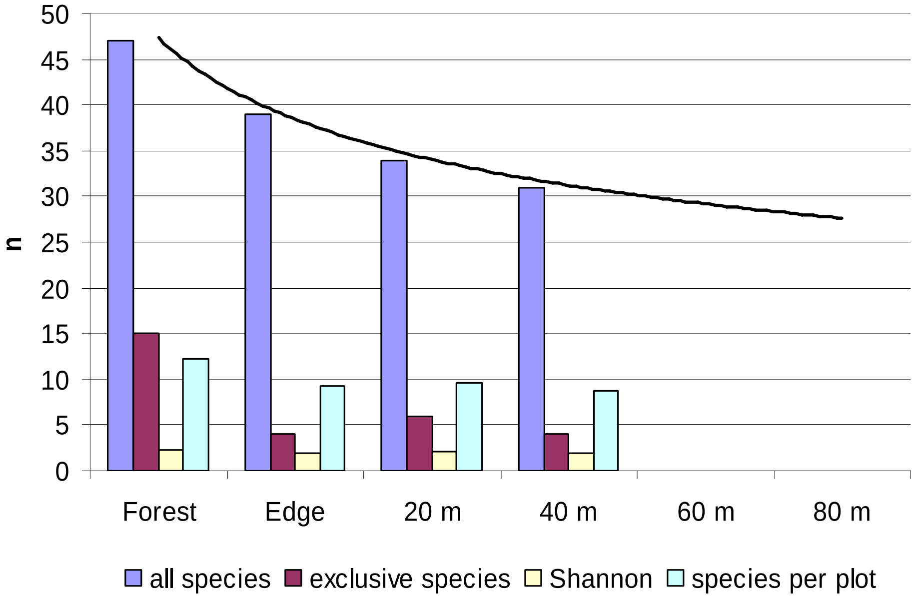

Fig. 5: Application of diversity predicted by intermediate disturbance hypothesis (IDH) and diversity patterns with increasing distance from forest edge deriving from own data