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Illegal logging, landscape structure and the variation of tree species richness across North Andean forest remnants

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Abstract

We explored the influence of a common practice in tropical countries, namely illegal logging for household consumption (ILHC), as well as that of characteristics of habitat structure on the variation of tree species richness across 10 cloud forest remnants of a Colombian Andean landscape. We estimated species richness for total, early and late successional tree species for each forest fragment. We also generated a binomial ILHC variable and six quantitative habitat descriptors related to patch size, shape and isolation. The data were analyzed with generalized linear models (GLMs) and model selection techniques based on Information Theory, complemented with partial regression analyses. We found that the presence of ILHC decreased the number of species for all tree groups, being this variable the major driver of richness variation across forest remnants. Our analyses also indicated that landscape characteristics played secondary roles in determining tree richness in all cases. Additionally, stronger negative impacts of ILHC on late successional tree species suggest that these logging activities are likely to move back ecological succession towards earlier stages of this process. As far as we know, this is the first study documenting the relative importance of ILHC practices against landscape structure for tree species richness. Our results strongly emphasize the need to consider ILHC in investigations and conservation initiatives involving tree species richness in fragmented tropical landscapes.

Keywords: Fragmentation; Landscape ecology; Anthropogenic disturbance; Plant richness; Cloud forest

1. Introduction

Forest clearing by legal or illegal logging is a major ecological problem worldwide and, particularly, in South America due to the high current rates of deforestation that are taking place in regions such as the Andes and Amazonia (Bilsborrow and Ogengo, 1992; Skole et al., 1994; Laurance, 1999; Etter et al., 2006). This reduction of forested areas often leads to both habitat insularization, which in turn affects local and regional patterns of biodiversity by altering dispersal and migration processes, and degradation or loss of unique habitats such as the Andean forests (Soule and Kohm, 1989; Laurance and Bierregaard, 1997; Scariot, 1999; Armenteras et al., 2003; Etter et al., 2006). Andean forests are recognized as a prime world hotspot (Orme et al., 2005), and represent a major priority for conservation because of their extraordinary species richness and endemicity, and because many of their constituent species are severely threatened (Olson and Dinerstein, 1997). Yet, Andean forests remain among the less studied ecosystems of the planet (Stadtmuller, 1987; Killeen et al., 2007).

Colombia constitutes a paradigmatic example. Indeed, being a megadiverse country (Myers, 1988), had lost over 73% of its continuous montane forests by the late 1980s (Cavelier and Etter, 1995) and, as a consequence of this historic deforestation, the Colombian government declared nearly 2,900,000 ha of forests and other ecosystems as protected to restrain this process. Still, the conversion of forests into ecologically simplified introduced grasslands and cropping areas keeps to be undertaken at very high rates (Alvarez, 2002; Etter et al., 2005), a process that has been predicted to intensify, especially in the Andean region (Etter et al., 2006).

This strong pressure on forest ecosystems coexists with an activity that is common to most rural areas of Latin America

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and other developing regions: the extraction of fuel-wood for household consumption (Masera and Navia, 1997; Geist and Lambin, 2001; Bishwa, 2007). Although we are not aware of any formal account of the extent of this logging activity in Colombia – possibly because it is nowadays performed illegally in most instances –, it is generally known that, historically, it has been the primary source of fuel for cooking and heating for most Andean rural families, and still continues to be key for many of them, which very often use fuel-wood as a way to lowering their electricity bills. From a biodiversity conservation point of view, this widespread illegal logging for household consumption (hereafter ILHC) can be expected to aggravate the effects of other sources of habitat loss and fragmentation on the biotas of forested landscapes (see below). However, to what extent this is the case cannot be established since, to our knowledge, no empirical forest fragmentation studies exist that had also investigated the ecological consequences of ILHC, neither in Andean regions, nor in any other forested areas.

In this context, the present study was carried out in a Colombian Andean landscape of 11,431 ha in which forest clearing and fragmentation had been intense more than 50 years ago, and is aimed at documenting the relationships of tree species richness with current ILHC and major habitat characteristics (estimated through landscape variables of patch area, shape and isolation). Because reactions to these factors might differ amongst plant species (Macarthur and Wilson, 1967; Bierregaard et al., 1992; Taylor et al., 1993; Forman, 1995; Laurance et al., 1998; Brown and Lomolino, 2000), we generated three richness variables, one including all species, and the others involving early and late succession species. We ask two questions. First, what are the effects, if any, of ILHC on tree species richness? Second, what are those of landscape characteristics?

Another widespread and frequently illegal logging activity performed at small-scale by peasants of developing countries pursues to sell the cut trees in the timber market (Geist and Lambin, 2001; Tacconi, 2007). This generally consists in a highly selective harvest (‘‘highgrading’’) of the larger (and older) trees of species with elevated marketable values (see Geist and Lambin, 2001 and references therein), which has been shown to modify the species composition and structure of the affected forests (Pollmann, 2002; Echeverría et al., 2007), and to translate them to earlier successional stages (e.g. Pollmann, 2002; Staus et al., 2002; Echeverría et al., 2007). However, based on our previous experience in the study area, this market-driven logging is absent there, while most existing tree species appear to be affected by ILHC, which would exert a different kind of tree extraction. Indeed, possibly because of its illegal nature, coupled with the fact that the cut wood is carried on foot or, less often, with the help of mules or horses, ILHC appears not to differentiate among species, although it does concentrate on tree saplings as these can be rapidly cut and transported. Given the lack of previous research, our expectations on the effects that this illegal logging activity may have on within patch tree species richness were rooted on basic ecological ideas.

First, a long-standing tenet of community ecology is that multispecies assemblages are typically composed by a few abundant species, some intermediately abundant species, and a majority of species that are represented by a reduced number of individuals (e.g. Hanski, 1982). This latter characteristic means that species extinctions are very likely under recurrent extirpations of individuals, even if these were all small (i.e. a reduced number of individuals is removed each time) and completely species-unspecific. Accordingly, we hypothesized that the ILHC-affected forest patches will exhibit less species richness than the unaffected ones in the studied landscape. Second, because a common characteristic to early successional species is to posses good dispersal capabilities, we expected smaller effects of ILHC on the species richness of this group than on that of late successional trees, which would be less capable of recolonizing the patches from which they have been driven extinct by this activity (see e.g. Kammesheidt et al., 2002). Finally, we also investigated whether landscape attributes such as patch size, shape and connectivity affected within patch tree species richness, albeit these aspects have been previously found not to be as important for tree richness variation as tree cutting in studies involving other small-scale, market-driven logging activities (Echeverría, 2005; Ingram et al., 2005; Echeverría et al., 2007).

To our knowledge, this is the first investigation of its kind carried out in cloud Andean forests, however variables of patch shape, isolation and, specially, area have been frequently shown to condition plant species richness variation in fragmented forests located elsewhere in the world (Laurance et al., 1998; Honnay et al., 1999; Hill and Curran, 2003). Additionally, we are not aware of any study that had compared the relative importance of habitat loss and fragmentation with that of ILHC for plant species richness, so the results of our study have the potential of generating insights of general interest. On the other hand, the studied landscape comprises some of the scarce remnants of cloud forests that are left in the area, and is currently under evaluation by the Medellín City Environmental Office for being converted into a regional conservation area. Therefore, our results have also the potential of being used by initiatives and policies aimed at persevering and restoring the forests of this region.

2. Methods

2.1. Study area and sampling procedures

The studied landscape is located in the Central Andean Mountains, in the province of Antioquia, Colombia (Fig. 1), and was initially delimited following a topographic criterion that took into account the altitudinal distribution of the Andean Oak (*Quercus humboldtii*) dominated forests in the area; that is between 1800 and 2700 m (see Gentry, 1982). The distribution of forest fragments across this latitudinal band is very sparse, but we concentrated on an area that is being considered to be converted into a regional conservation park by the City Council of Medellin because of the comparatively well preserved characteristics of the forest patches it comprises. Despite this,

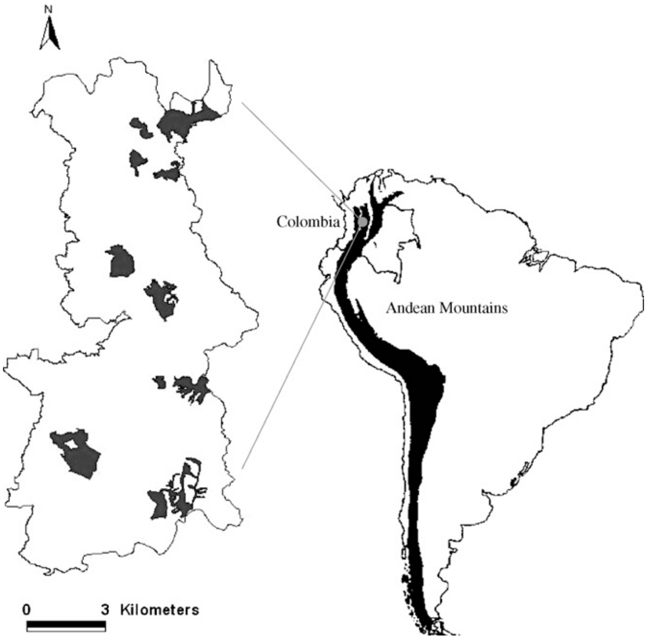

Fig. 1. Study area in the central Andes of Colombia, showing locations of forest fragments used in the study (dark patches on the left).

we also took into account the forest fragments and other landcover types laying in the vicinity of this area for the calculation of the landscape variables (see below). The topography consists in low hills occurring at the center of the area, and high elevations in its surroundings. Mean annual temperature is 14.9 °C, and mean monthly maximum and minimum temperatures are 20 °C and 5 °C, respectively. Mean annual rainfall varies from 1500 to 2200 mm and exhibits a bimodal pattern with wet periods occurring in March–May and October–November. The soils are acidic and poor in nutrients, although with high organic matter content. Potential vegetation is the characteristic high-Andean tropical forest, also known as cloud forest (see Toro, 2000 for a more detailed description of the area).

To map the forest fragments, we used a detailed cartography elaborated by a conservation project carried out by two public institutions, the Corporación Autónoma Regional del Centro de Antioquia and the Universidad Nacional (UN) (Corantioquia-UN, 2002). This cartography differentiates 10 landcover types from which we first recognized 18 potential fragments for the study. We used the Spatial Analysis module of ArcView 3.2 to pin point the fragments that had both, an edge area (i.e., a forest strip 100 m wide), and a core area (i.e. that located at a distance of ≥100 m apart from the fragment edge) (Forman, 1995). Only 10 patches met this criterion, so we excluded the remaining fragments from the study because they lack the interior habitat that characterizes natural forests.

The tree layer of the selected fragments was characterized by six plant families, which contributed 32% of the species; namely, Lauraceae – the dominant tree species group in the altitudinal band occupied by Andean forests (Gentry, 1982) –, Rubiaceae, Orchidiaceae, Melastomataceae, Asteraceae and Solanaceae (Aubad, 2005). According to their tree species composition, this author classified the fragments as being representative of high-Andean tropical forest dominated by Andean oak (*Quercus humboldtii*), in which *Hyeronima antioquensis*, *Hedyosmum bonplandianum*, *Myrcia popayanensis*, *Myrcia splendens*, *Weinmannia pubescens*, *Viburnum cornifolium and Piper cabellense* are also common; as well as characteristic species of secondary forests such as *Clethra fagifolia*, *Clusia multiflora*, *Clusia cuneifolia*, *Hedyosmum bomplandianum*, *Cavendishia pubescens and Cavendhisia bracteata*, *Befaria aestuans*, *Miconia theaezans*, *Miconia resima*, *Meriania nobilis and Viburnum anabaptista*. Additionally, using Principal Components Analysis and abundance data of the tree species present in at least three fragments, this author also found no compositional differences between fragments that experience ILHC and fragments that do not (see below), supporting that the aforementioned basic compositional structure is common to all them (Aubad, 2005).

We sampled these fragments between October 2003 and June 2005 within the framework of the Corantioquia-UN conservation project. In all cases, we included all individuals of woody and palm species (hereafter regarded as tree species for brevity) with a diameter at breast height >2.5 cm, so we are confident that differences in sampling dates did not cause any important bias in our richness estimates. The sampling involved five 50 m × 4 m rectangular plots randomly located throughout each fragment. All individuals meeting the abovementioned criteria were noted and identified at the species level. Samples of all doubtful specimens were collected and identified with the help of the specialists of the Joaquin Antonio Uribe Botanical Garden.

2.2. *Response variables*

We generated three species richness variables which included total, early and late successional species. We assigned successional stages to species by checking the primary botanical literature and electronic databases, which allowed us to classify 85% of the species. This means that the richness variables we generated for early and late successional species do not include some species (15%) and, hence, have to be interpreted with caution.

2.3. *Explanatory variables*

We generated a ILHC variable indicating the presence or absence of this activity in the patch. We verified (through numerous informal interviews with local people and personal observations) that what made a difference on ILHC pressure was the existence or not of surveillance in each forest fragment. So our variable differentiated fragments that had some kind of surveillance (either by private owners or by forest rangers in the case of fragments with some kind of public protection) from those that had not. According to this, we catalogued six forest fragments as relatively protected (i.e., Aguada, Asturias, Chorrillos, Comfenalco, La Eca and Silletero) and four as not protected (Espiritu Santo, El 14, La Parra and Vásquez). We did not take into account other possibilities to estimate ILHC pressure (such as human population density, distances to villages or roads, or other accessibility metrics), particularly because virtually all the ILHC carried out in the study area is illegal and, in consequence, can be even more intense in more isolated areas. Additionally, we used the Corantioquia-UN (2002) cartography and ArcView 3.2 combined with FRAGSTATS 3.3 (Mcgarigal et al., 2002) to generate six landscape variables. Patch size metrics were area and core area, the first variable including the total area of each fragment, and the second variable resulting after discarding a strip of forest 100 m wide from the edge of the fragment (Forman, 1995; Turner et al., 2001). Isolation variables were edge-to-edge nearest neighbor distance (NND) and the edge contrast index developed by Mcgarigal and Marks (1995), both of which were calculated taken into account the studied landscape as well as the forest fragments and other landcover types surrounding it. NND represents the shortest distance between the focal fragment and its nearest fragment. Edge contrast index has into account the habitats that are in contact with the perimeter of each forest fragment and the relative length of this contact. To do that we verified that forest patches were surrounded by four landcover types; namely, timber plantations, grasslands, brushes, and thickets. Although the tree species contribution of these habitats to the forest patches is expected to be weak (specially in those in which virtually no native trees are found, such as in forest plantations and grasslands) their different nature might be a relevant determinant of the potential of tree dispersers to reach the forests. Shape metrics included the perimeter of each fragment, and the Patton's shape index (see Mcgarigal and Marks, 1995 for details). The latter is a dimensionless circularity metrics, that is both theoretically and empirically independent of area.

2.4. *Statistical analyses*

We used generalized linear models (GLMs) by specifying a Poisson distribution and a log-link term because all response variables (species richnesses) were in the form of counts (Mccullagh and Nelder, 1989). Since all models were initially run with more than two predictors, ''best models'' (i.e. those providing maximum fits with fewer predictors) were identified with model selection techniques based on Information Theory (Stephens et al., 2007). Modelization consisted in two phases. First, to avoid including highly collinear variables in the modeling process, we calculated the Pearson correlations among explanatory variables to look for highly redundant variables ($r > 0.8$). Provided that two variables were highly correlated, we discarded the one describing a lower proportion of deviance of the richness variables for further analysis (see Mccullagh and Nelder, 1989; Teixeira et al., 2001; Quinn and Keough, 2005). Second, with the remaining variables, we generated all possible models (resulting from all possible combinations of predictors) and then evaluated their relative support. Specifically, we used the Akaike Information Criterion (AIC) combined with ΔAIC indexes (i.e. the difference between the AIC of the model being analyzed and the minimum AIC found) to compare the performance of the models by using the rule that ΔAICs > 10 indicate poor fits relative to the best model, while ΔAICs $\leq$ 2 correspond to good models (Burnham and Anderson, 2002). We also used the ΔAICs to calculate the Akaike's weighting of each model (w_i), a value that can be interpreted as the probability that model i is actually the best explanatory model (Anderson et al., 2000; Burnham and Anderson, 2002; Olalla-Tárraga et al., 2006). We complemented these techniques with partial regression analysis, which we used to partition the deviance explained by landscape effects and ILHC into independent and covarying components (see Hawkins et al., 2003). Additionally, we used the Wald statistic with Poisson errors and a log-link function to detect differences in total, early and late successional species richness values between logged and unlogged patches. *P*-Values from these analyses were Bonferroni-corrected to minimize Type I error rates (Quinn and Keough, 2005).

3. Results

The number of tree species recorded in the study area was 232, with a mean (±S.D.) number of species per fragment of 72.3 (±18.4). Of these, the proportions of early and late successional tree species (generated taking into account the subset of species for which it was possible to establish these attributes; see Section 2) were 60.4% and 39.6% in the landscape, with mean proportions of 69.2% and 30.8% in the patches, respectively.

ILHC had significant effects on total, early and late successional tree species richnesses which were lower in the patches encompassing this activity (Table 1). In addition, most of the deviance of total tree richness (92%) was described by this variable, thus indicating the overwhelming importance of ILHC for tree species persistence in the studied landscape (Table 2). ILHC was also the best single predictor of early and late successional tree species richnesses, albeit the percentages of described deviance were not so high in these cases, particularly in that of early succession tree species, a result which is in agreement with the usually large capabilities of recovery after disturbance of early successional organisms. With regard to the six landscape structure variables, all species richnesses were, in general, much weakly associated with them, as indicated by the relatively low percentages of deviance they described ($\leq$31.3%). Of these, edge contrast index was the best landscape predictor for total and late successional species, and the second best for early successional species, being these

Table 1
Mean and standard error richness values for all, early and late successional tree species in logged (ILHC) and unlogged (no ILHC) Andean forest patches

Richness	Logging		No logging		Wald	*P*
	Mean	S.E.	Mean	S.E.		
Total	51.75	2.75	86.00	2.25	38.11	<0.0001
Early succession	32.00	3.20	44.67	2.61	9.63	0.0019
Late succession	11.25	1.93	21.83	1.58	14.72	0.0001

The Bonferroni value for three interrelated analyses and an $\alpha = 0.05$ is 0.01666 which, according to the *P*-values resulted in the analyses, means that all comparisons were statistically significant.

Table 2
Association of total, early and late successional tree species richness with ILHC and six landscape structure variables in Andean forest patches

Attribute	Variable	Tree species richness		
		Total	Early succession	Late succession
Illegal logging	Logging	92.4 (−)	55.9 (−)	71.3 (−)
Area	Total area	23.9 (−)	20.8 (−)	9.5 (−)
	Core area	17.9 (−)	10.1 (−)	2.8 (−)
Shape	Shape index	6.9 (+)	19.2 (−)	14.9 (−)
	Perimeter	18.6 (−)	29.8 (−)	19.5 (−)
Isolation	Edge contrast	30.9 (+)	27.3 (+)	31.3 (+)
	NND	2.0 (−)	1.02 (+)	0.7 (−)

The percentage of deviance described by each variable, and the sign of each relationship generated through simple correlation (in brackets) are provided for each species richness estimate. ($N = 10$). NND: nearest neighbor distance.

relationships positive in all cases (Table 2). In opposition, nearest neighbour distance was the poorest descriptor of richness in all cases, indicating that distance between forest patches has weak or no effects on richness in this landscape. Finally, the variables of area and shape were intermediate predictors of richness in general, albeit late succession species richness appeared to be less affected by area size.

Strong correlations between the two variables of area, and between those of shape (see Table 3) led us to exclude core area and shape index (i.e. the variable less associated with species richness in each case; see Table 2) from multiple regression analyses to minimize collinearity. The model selection process rendered five good models (i.e. with ΔAICs ≤ 2) which were identical for all three species richness variables; namely, a single-factor model including ILHC, and four two-factor models including this variable and a landscape variable (Table 4). Although in all cases the models including ILHC only were the best ones, their relatively low support (w-values = ~ 0.24) did not allow to discard any of the other models; suggesting that landscape structure might play some secondary role after ILHC in determining tree richness.

To further explore this, we used partial regression to compute the percentage of independent and shared deviances between ILHC and a full landscape model (i.e. one including all four landscape variables involved in the modeling process). The proportions of deviance independently explained by ILHC were similar for total and late succession tree richnesses (43% and 46%, respectively), while that corresponding to early successional richnesses was substantially lower (21%) (Fig. 2). This reinforced the suggestion that the presence of early successional tree species in the patches was less affected by ILHC than that of late successional species. On the other hand, the deviance independently explained by landscape was lower for total and early successional richnesses (4% and 3%, respectively), than for late successional richnesses (12%), suggesting that the effects of landscape structure augment with the progress of the successional process. Finally, the percentage of residual deviance that was not explained by either ILHC or landscape was lower in the case of total richness (4%), and higher in those of late and, specially, early successional richnesses (17% and 42%, respectively). These higher proportions of unexplained deviance might be related with the poorer quality of the early and late successional species richnesses variables, as they did not include 15% of the tree species for which it was not possible to establish the successional status. However, the large differences in unexplained deviance between these two richnesses, with that corresponding to early succession richnesses being substantially larger, also suggest that early successional trees might be less sensitive to both ILHC and landscape configuration than late successional ones.

Table 3
Pearson correlations among six landscape variables indicative of three attributes of Andean forest patches ($N = 10$)

Attribute	Variable	Total area	Core area	Shape index	Perimeter	Edge contrast
Area	Total area	1				
	Core area	0.893	1			
Shape	Shape index	0.399	−0.051	1		
	Perimeter	0.665	0.265	0.946	1	
Isolation	Edge contrast	−0.763	−0.558	−0.557	−0.698	1
	NND	0.463	0.615	−0.212	−0.023	−0.162

NND: Nearest neighbor distance.

Table 4
Best multiple Poisson-regression models for three tree species richness variables including (a) all species; (b) early succession species; and (c) late succession species of Andean forest fragments

Model		AIC	ΔAIC	w_i	R^2
(a) Total tree richness					
Logging		68.241	0.0	0.374	0.920
Logging	Perimeter	69.438	1.2	0.205	0.936
Logging	Edge contrast	70.136	1.9	0.145	0.923
Logging	NND	70.227	2.0	0.138	0.920
Logging	Area	70.232	2.0	0.138	0.920
(b) Early succession richness					
Logging		66.853	0.0	0.243	0.540
Logging	Perimeter	68.417	1.6	0.111	0.561
Logging	Area	68.698	1.8	0.097	0.549
Logging	Edge contrast	68.772	1.9	0.093	0.545
Logging	NND	68.843	2.0	0.090	0.541
(c) Late succession richness					
Logging		56.999	0.0	0.240	0.692
Logging	Area	58.718	1.7	0.102	0.707
Logging	NND	58.943	1.9	0.091	0.694
Logging	Edge contrast	58.944	1.9	0.091	0.695
Logging	Perimeter	58.958	2.0	0.090	0.693

Models are ranked in each case by AIC from best to worst-fitting model, and only the models with $\Delta\text{AIC} \leq 2$ are presented. The Akaike's weighting (w_i) and the coefficient of determination (R^2) of each model are also provided. ($N = 10$). NND: nearest neighbor distance.

4. Discussion

Our analyses indicated that the presence of ILHC caused a strong reduction in total and late successional tree species richnesses, and a more moderate reduction in early sucessional

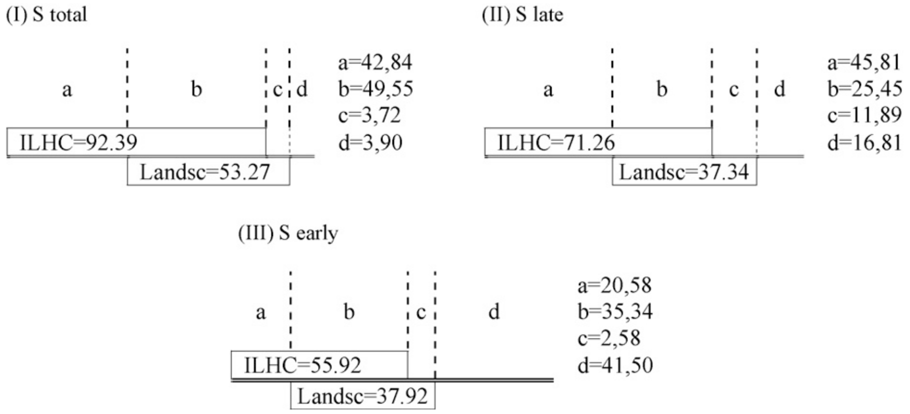

Fig. 2. Partial regressions partitioning the independent contributions of ILHC (a), landscape structure (c), the overlap between them (b) and the proportion of deviance not explained by either factor in any case (d). Variation was assessed through the proportion of deviance explained by three tree species richness variables including (i) all species; (ii) early successional species; and (iii) late successional species of Andean forest fragments. Landscape structure was defined by a four factor model including path area, perimeter, distance to nearest neighbor, and edge contrast.

tree species richness. In addition, we also detected secondary effects of landscape structure in determining species richness variation for all three plant groups, although our analyses were ineffective at identifying which aspect of the landscape was most important in any case. This may be explained by the fact that only 10 forest patches met the requirements we considered to be included in the investigation (i.e. to be true forests with a conspicuous core area), which in turn might have resulted in that the analyses had no sufficient power to differentiate amongst secondary predictors. Another likely explanation has to do with the extraordinarily high proportions of species richness deviance that were accounted for by ILHC (see Table 2), and the consequent reduced deviance that was left to be explained by the other predictors. Whatever the case, this does not undermine the importance of our most salient result; i.e. that ILHC is a major determinant of tree richness in the forest remnants of the study area.

A majority of studies of plant richness–landscape structure relationships in fragmented landscapes have found that the key factor for richness variation across forest remnants is patch area, while shape and/or isolation variables often appear playing secondary roles (e.g. Laurance et al., 1998; Honnay et al., 1999; Hill and Curran, 2003; Boutin and Hebert, 2002; Fahrig, 2003). On the contrary, some investigations have found that tree species richness is unrelated to patch size particularly in areas under a continuous human disturbance regime (Ochoa-Gaona et al., 2004; Echeverría et al., 2007). Among the landscape metrics we included in our analysis, edge contrast was the best single descriptor for total and late successional species, which might lead us to emphasize the importance of habitats types surrounding each patch for tree species richness. However, we were unable to find greater support for a particular landscape predictor, since all of them independently entered as a secondary variable in our best multiple regression models and according to an AIC difference criterion (ΔAIC) such models have to be considered equivalent (i.e. they have a $\Delta\text{AIC} \leq 2$). On the other hand, because edge contrast and other isolation measures depend on the landscapes surrounding the patch, the degree of patch isolation is strongly related to the amount of habitat remaining in the surrounding landscape. Consequently, Fahrig (2003) argued that patch isolation can be interpreted as a synonym of habitat amount in the landscape. Our results concur with this observation, since edge contrast, for example, was highly correlated with total patch size. Of course, this does not mean that tree species richness in the study area is unrelated to any landscape descriptor, but rather that we could not find greater support for one of them. Also, our results are not in contradiction with an important role of landscape on species richness in absence of logging. Furthermore, although our methodology allowed us to assess the independent contributions of logging and landscape structure, further empirical or theoretical studies are needed to examine whether these effects can interact additively or synergistically.

Generally, fragmentation studies have neglected the potential effects of human disturbances (Hobbs and Yates, 2003), by considering only sets of landscape descriptors and ignoring social and economic factors that are dynamically generating changes in the attributes of the habitat matrix (see e.g. Ochoa-Gaona et al., 2004). Even so, we can still find some examples in the literature that have taken into account human activities such as logging or cattle breeding together with landscape metrics. For example, some workers have considered a common logging activity among peasants of developing countries which basically consists in selecting and cutting the larger (and generally older) trees to shell them in the timber market (Pollmann, 2002; Echeverría et al., 2007). However, this is a highly selective and market-oriented forest logging that clearly contrasts with the non-selective nature of logging for household consumption (ILHC) we found in our study area. Therefore, both forest logging activities are not fully comparable as the expected effects clearly differ. Accordingly, to our knowledge, no study has yet jointly examined the relative importance of landscape structure and ILHC (as described in our study area) in determining tree richness, thus preventing any direct comparison with our results. The absence of ILHC in the habitat fragmentation literature is understandable in areas where this activity does not exist or is marginal (e.g. developed countries), but is surprising in regions were the rural population often take out young trees and saplings (often illegally) to obtain fuel-wood for household consumption. A possible explanation for this is the strong emphasis of the research agenda of developed countries on habitat loss and fragmentation issues and, consequently, the likely influence that this emphasis might have had in setting up similar investigation priorities in the rest of the world. Despite this, if ILHC is as widely extended as the data gathered by international agencies seem to indicate (World Bank, 2004), it might be the case that a crucial factor for tree biodiversity (i.e. ILHC) is being neglected by the habitat fragmentation research.

The situation in the study area constitutes a paradigmatic example. Although efforts have taken electricity with subsidized prices to all low-income villages of the area, some unemployed villagers consider that cooking with electricity is still expensive and, hence, have continued extracting fuel-wood from the forest patches. The fact that this is a banned activity might have aggravated its effects on tree richness. Particularly because ILHC has to be carried out quickly and, likely, without performing much selection of the tree species that are cut. This means that both early and late successional tree species might be affected by logging with similar intensities, a supposition that was supported by most of the informal interviews we made to the inhabitants of the area. Moreover, this also had a reflection in our results, as we found that the effects of ILHC on tree richness were stronger for late successional species and weaker for early successional ones. Indeed, bearing in mind ecological successional theory, the explanation for these divergences is straightforward: unless the cut tree is capable of resprouting, unspecific logging tends to create gaps that can readily be occupied by colonizing trees, but it is more likely that such gaps be occupied by early than by late successional tree species. Thus, the net outcome is that the presence of late successional trees is more strongly compromised by the effects of ILHC and, hence, late successional tree richness results more impoverished. In this respect, valuable insights could also be provided by experimentally testing the effect of logging on fragmented versus unfragmented landscapes or by applying simulated scenarios of logging and fragmentation specifically to this type of forest. For instance, results on simulated scenarios of logging and fragmentation for a neotropical landscape showed that the combined effect of logging with fragmentation can remain for long time periods because of the slower growth and later maturation of late successional species (Kammesheidt et al., 2002).

In clear contrast with the overwhelming importance of ILHC for tree richness variation in the forest remnants, the local environmental offices focus on habitat fragmentation and its potential effects on diversity, much as it typically happens in developed countries (see above). In fact, the Corantioquia-UN (2002) project – which provided much of the data used in the present study (see Section 2) – was promoted to investigate relationships between diversity and forest patch connectivity, clearly under the idea that documenting these aspects would be key for devising future conservation actions for the study area. ILHC, on the other hand, was not considered by the Corantioquia-UN (2002) project, a neglection that, in view of our results, could lead to concentrate conservation expenditures on issues of secondary importance for tree richness. In clear opposition to this, our results evidently call for the need of finding alternative and inexpensive fuel sources for household consumption and, thus, minimize ILHC. That is, if the goals are to preserve tree species richness and push ecological succession forward in the forest remnants of this landscape. From a more general point of view, our results also emphasize the need of incorporating ILHC in studies aimed at determining the factors that drive tree richness in fragmented landscapes of developing countries.

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