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Modeling the age of tropical moist forest fragments in heavily-cleared lowland landscapes of Colombia

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Abstract

Increasingly, large areas of native tropical forests are being transformed into a mosaic of human dominated land uses with scattered mature remnants and secondary forests. In general, at the end of the land clearing process, the landscape will have two forest components: a stable component of surviving mature forests, and a dynamic component of secondary forests of different ages. As the proportion of mature forests continues to decline, secondary forests play an increasing role in the conservation and restoration of biodiversity. This paper aims to predict and explain spatial and temporal patterns in the age of remnant mature and secondary forests in lowland Colombian landscapes. We analyse the age distributions of forest fragments, using detailed temporal land cover data derived from aerial photographs. Ordinal logistic regression analysis was applied to model the spatial dynamics of mature and secondary forest patches. In particular, the effect of soil fertility, accessibility and auto-correlated neighbourhood terms on forest age and time of isolation of remnant patches was assessed. In heavily transformed landscapes, forests account for approximately 8% of the total landscape area, of which three quarters are comprised of secondary forests. Secondary forest growth adjacent to mature forest patches increases mean patch size and core area, and therefore plays an important ecological role in maintaining landscape structure. The regression models show that forest age is positively associated with the amount of neighbouring forest, and negatively associated with the amount of neighbouring secondary vegetation, so the older the forest is the less secondary vegetation there is adjacent to it. Accessibility and soil fertility also have a negative but variable influence on the age of forest remnants. The probability of future clearing if current conditions hold is higher for regenerated than mature forests. The challenge of biodiversity conservation and restoration in dynamic and spatially heterogeneous landscape mosaics composed of mature and secondary forests is discussed.

Keywords: Tropical deforestation; Forest fragment age; Land use drivers; Colombia

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1. Introduction

Increasingly, large areas of native tropical forests are being transformed into a mosaic of human dominated land uses with smaller forest fragments embedded in an agricultural and grazing matrix (Houghton, 1994; Kammesheidt, 2002). The clearing and fragmentation of tropical forests raises major ecological concerns at local, regional and global scales because of the impacts it generates, including loss of biodiversity, increased greenhouse emissions contributing to global climate change, soil erosion and deregulating hydrology (Laurance and Ferreira, 1997; Laurance et al., 1998). This has resulted in substantial changes in the structure, composition, biomass and productivity of the tropical forest pool due to an increasing proportion of secondary forests (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). In heavily transformed landscapes, larger forest remnants are commonly located on economically marginal land characterised by comparatively less fertile soils, steeper slopes and poor accessibility, while smaller, more isolated forest remnants occur in more productive and accessible landscapes (Brown and Lugo, 1990; Wilson et al., 2005).

The human induced process of change in tropical forest landscapes is characterised by the clearing of the original ecosystems followed by localised forest regeneration (Nagendra et al., 2003). This occurs at various temporal scales with different rates and spatial patterns of transformation. Pathways of change are complex as a result of the interaction of either reinforcing or opposing processes of land clearing, degradation or regeneration (Lambin, 1997). After clearing, many areas are abandoned and left to regrow, and therefore secondary forests comprise an increasing proportion of the forest resources in tropical regions (Brown and Lugo, 1990; Nepstad et al., 1991; Kammesheidt, 2002; Dunn, 2004). In general, at the end of the land clearing process, the landscape will have two forest components: a stable component of the surviving mature forests, and a dynamic component of secondary forests of different ages (Fig. 1). Following deforestation, the interaction of different land-use histories and land management practices, along with varying biophysical attributes (e.g., soil fertility), creates a dynamic landscape mosaic comprised of remnant mature and secondary forest patches of varying age and disturbance history. In these landscapes, secondary forests play an important role in the maintenance of ecosystem processes, the conservation and restoration of biodiversity (Kammesheidt, 2002; Dunn, 2004), and providing useful resources to humans (Brown and Lugo, 1990).

Regional monitoring of land cover change often overlooks the fine-scale spatial and temporal dynamics of forest regeneration due to the limitations of temporal and spatial scales of remotely sensed data, limited numbers of long-term monitoring projects (Nepstad et al., 1991; Tucker and Townshend, 2000; however, see Kimes et al., 1998; Soares-Filho et al., 2001; Nagendra et al., 2003). In general, the relatively short time spans assessed by most studies do not allow the long-term monitoring of successful regeneration of structurally complex and compositionally diverse secondary forests. Also, regeneration often occurs

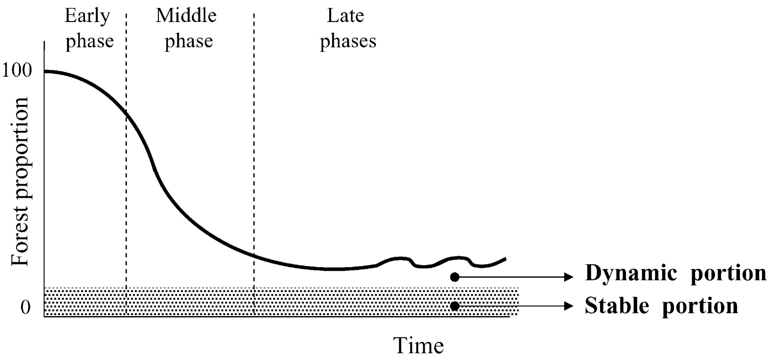

Fig. 1. Dynamics of forest cover change during the land clearing process characterised by deforestation followed by localised regeneration.

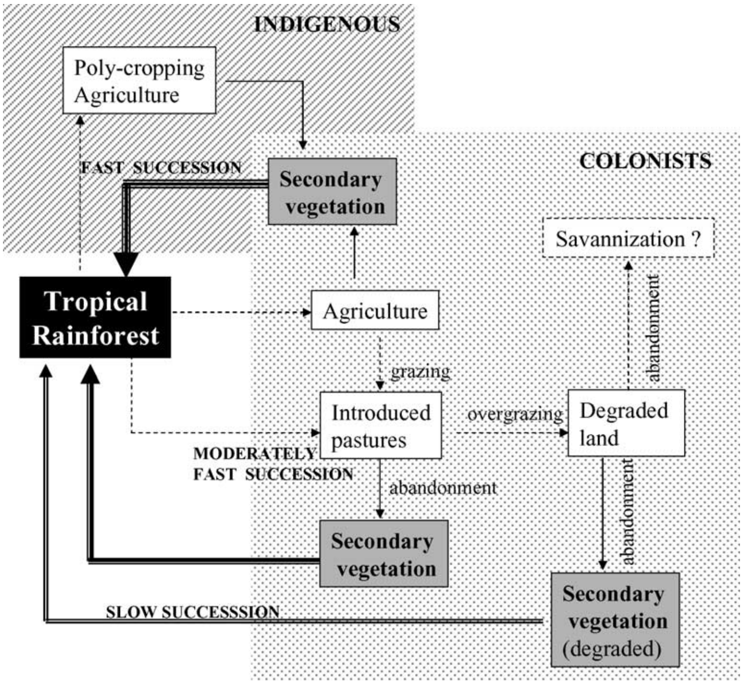

Fig. 2. Historical settlement of forested regions in tropical lowlands. Thick arrows indicate the paths of forest regeneration.

along the fringes of forest remnants and at low rates (Helmer, 2000; Moran et al., 2000), further making it difficult to monitor fine-scale changes in the amount and distribution of secondary forests due to sensor resolutions. In general, deforestation studies have dealt with land cover characteristics such as the spatial extent and proportion of remnant forest, but not with the age structure of both mature and secondary forest remnants. However, age is recognised as an important determinant of biodiversity values and the maintenance of ecological processes within forests (Brown and Lugo, 1990; Laurance and Ferreira, 1997; Guariguata and Ostertag, 2001; Lindenmayer and Franklin, 2002; Ross et al., 2002; Metzger, 2003). Therefore, secondary forests may have different biodiversity values depending on regeneration stage and hence their age structure.

In Colombia, the rates and patterns of deforestation vary regionally (Chaves and Arango, 1998). Until the early 1900s, the Andes and Caribbean regions were the focus of indigenous and European settlement and deforestation (Etter and Van Wyngaarden, 2000; Palacios, 2001). After 1920, and mainly from 1950 onwards, land clearing moved to the largely forested humid lowlands of the Amazon, the Magdalena and interior Andean foothills, with lowland moist and wet forest ecosystems the most heavily impacted (Palacios, 2001). Historically, these lowland moist forests were sparsely settled by indigenous Indian communities who practiced low-impact slash and burn agriculture (Fig. 2). At present, although the rural lowlands are settled by less than 5% of the total Colombian population, they are experiencing the highest rate of land cover change (Etter, 1998).

Over the last 10–20 years, colonisation in Colombia has been focussed on the tropical lowland moist and wet forests, resulting in an increased loss of mature forests accompanied by the regeneration of secondary forests of varying quality (Fig. 2). Most of these processes are occurring in a spontaneous, unplanned way, driven by the need for agricultural land. Colonisation usually begins with small-scale subsistence agriculture, but often terminates with cattle grazing on introduced pastures as a way of keeping land cleared. In an intermediate stage, large areas of forest are cleared for pasture and the establishment of semi-intensive cattle grazing farms. As observed in other areas of the Colombian Amazon (Etter and Andrade, 1987; Moran et al., 2000), pastures tend to deteriorate due to overgrazing and soil compaction, leading to abandonment and forest regeneration. In a final stage, as infrastructure improves and accessibility to markets and land prices increase, there is a shift to intensive mechanised agriculture of perennial tree crops such as oil palm and citrus, and annuals such as rice and soybean. The clearing of forests often follows a sigmoid pattern, with rapid rates of clearing in the mid-transformation phase, followed by a relatively stable terminal landscape structure with low levels of forest cover (Etter et al., 2005).

From the 1980s, traditional agricultural crops have been partially replaced by illegal cash crops, especially coca (*Erythroxylum coca*), particularly in the more remote areas of the colonisation fronts and often associated with armed conflict. This has had important consequences for patterns of landscape transformation by spatially redirecting colonisation patterns, and even forcing land abandonment in certain areas (Davalos, 2001).

This paper aims to predict and explain spatial and temporal patterns in the age of remnant and secondary forests in lowland Colombian landscapes. Specifically we focus on: (i) the proportion and spatial distribution of mature and secondary forest patches of different age structures; (ii) spatial and biophysical factors that might explain and predict the observed patterns; and (iii) the relationship between the age of secondary forest patches and the probability of their persistence in the landscape. We conduct a comparative study of six heavily cleared tropical forest landscapes in the Colombian lowlands by applying ordinal logistic regression to analyse the relationship between the distribution and persistence of forest age classes and soil fertility, accessibility, and the presence of remnant and secondary forest neighbours. We conclude that forest age dynamics must be explicitly dealt with to assist conservation planning in these heavily transformed landscapes.

2. Material and methods

2.1. Study area

The study focuses on six landscapes located in the humid lowlands (>2000 mm mean annual rainfall) of the central (Magdalena) and eastern (Orinoco, Amazon and Catatumbo) regions of Colombia. The landscapes comprise areas ranging from 68 to 128 km^2, which have been subjected to substantial land clearing during the last 30–60 years (Fig. 3, Table 1). Currently, cattle grazing (national herd size $\sim$ 30 million head) is the most widespread land use, as it is in many other areas of Colombia. Of the total national human population of over 40 million, less than 2 million people currently live in the rural lowlands. In general, rural population density varies from less than 5 to 20 inhabitants/km^2, with lowest densities occurring in the extensive cattle grazing landscapes.

Fig. 3. Location of the six study areas in humid lowland regions of Colombia.

2.2. Land cover data and mapping

Changes in land cover for the six landscapes were mapped for four to seven time periods between 1938 and 2002 using geo-referenced black and white aerial photographs at spatial scales ranging from 1:20 000 to

Table 1
General biophysical characteristics and data sets available for the study areas

Study area	Area (km^2)	Region	Dates of air-photo coverage	Mean altitude (m)	Mean annual rainfall (mm)/Nr. dry months (<100 mm)	Original vegetation in landscape
La Balsa	128	Orinoco	1938, 1961, 1979, 1987, 1992, 2001	250	2500/4	Forest–Savanna mosaic
Guamal	140	Orinoco	1938, 1961, 1979, 1987, 1992, 1997, 2001	300	3000/3	Forest–Savanna mosaic
Caquetá	100	Amazon	1946, 1975, 1985, 1992, 2000	200	3100/2	Forest
Opón	68	Magdalena	1971, 1985, 1996, 2002	200	3200/1	Forest
Berrío	82	Magdalena	1950, 1961, 1977, 1985, 1996, 2002	120	3000/3	Forest
Tibú	74	Catatumbo	1961, 1975, 1985, 2000	150	2700/3	Forest

1:35 000 (Table 1). Multi-spectral Landsat ETM imagery was used after 1998, as aerial photographs were not available for this period. The Landsat imagery was mapped by visual interpretation and then digitised using ArcView3.2 GIS. A uniform land cover classification comprised of seven classes was applied to all areas: remnant forests, secondary forests, savannas, introduced pastures, crops, water and urban. The classification of remnant "undisturbed" mature forest for each study area was calibrated from interior forest areas with similar structural features and canopy characteristics that were remote from disturbance areas as observed in the pre 1950 aerial photographs. For satellite imagery, forests were classified as remnant mature forests when spectral and textural characteristics matched those of known undisturbed forest areas with similar physiographic conditions, often located outside the analysis window. The final land cover maps were converted to a scale of 1:50 000 for comparability.

A forest age-class map was developed for the final land cover data set by overlaying multi-temporal forest cover (forest–non forest) maps using ArcView3.2 GIS. Because the temporal resolution and extent of the land cover maps varied for the different study areas (Table 1) and the impossibility to establish the exact age of regeneration, forest age classes were reclassified according to the following ordinal scale (Table 2):

- A5: Remnant mature forests (never cleared during the study period);
- A4: Secondary forests > 40 years of age;
- A3: Secondary forests 30–40 years of age;
- A2: Secondary forests 20–30 years of age;
- A1: Secondary forests 10–20 years of age.

2.3. Explanatory variables

To evaluate the effects of physical and economic factors on the spatial distribution of the forest age classes, data on soils, accessibility and neighbouring land cover were derived (Fig. 4). Other important drivers such as climate and topography were not analysed as they do not vary within the selected study area. Soil fertility maps, classified into three broad classes (low, moderate, high), were derived from existing soil maps obtained from the Colombian National Geographic Institute (IGAC). These were adjusted for each study area according to physiographic properties as interpreted from stereo pairs of aerial photographs. A cost–distance map of the relative physical and economic accessibility of each study area for each time period was produced using ArcView3.2 GIS. This was achieved by applying relative friction values of the cost–distance of accessing rivers, roads and surrounding human settlements plus topographic constraints on human movement. The soil fertility and

Table 2
Examples of the definition of the ordinal age classes (1 = forest present), for the La Balsa study area

1938	1961	1979	1987	1992	2001	Age class
1	1	1	1	1	1	A5
0	1	1	1	1	1	A4
0	0	1	1	1	1	A3
1	0	1	1	1	1	A3
0	0	0	1	1	1	A2
1	0	0	1	1	1	A2
1	1	0	1	1	1	A2
0	0	0	0	1	1	A1
1	0	0	0	1	1	A1
1	1	0	0	1	1	A1
1	1	1	0	1	1	A1

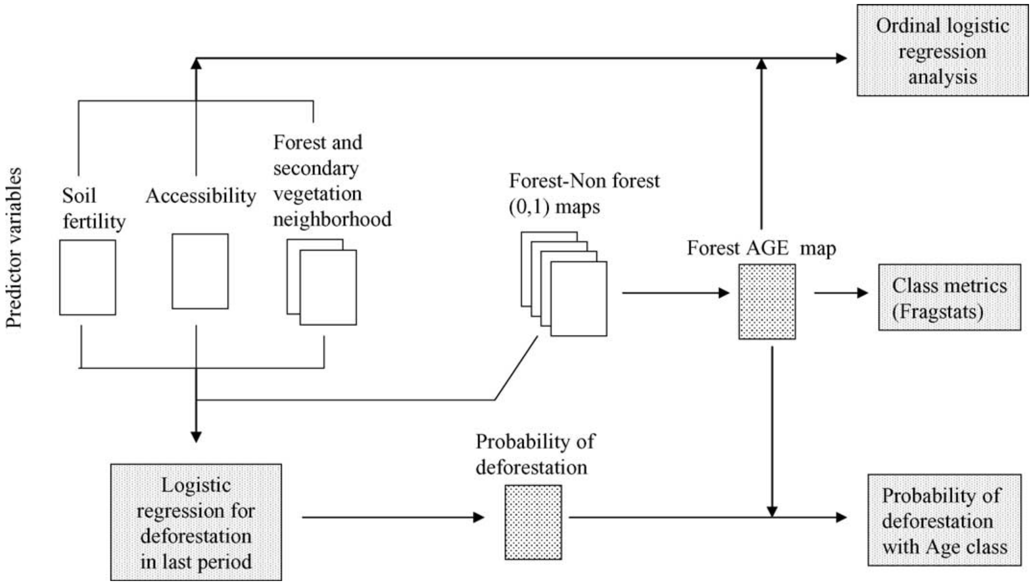

Fig. 4. Methodological procedure.

accessibility maps were scaled to 1:50,000 and converted to 1 ha raster GIS layer. The neighbourhood proportion of mature and secondary forest was calculated for each 25 ha grid for each time period. The average historical neighbourhood influence was calculated for each grid cell by averaging the neighbourhood values for all time periods.

2.4. Spatial analysis

The spatial patterning of total forest cover was quantified using FRAGSTATS version 3 (McGarigal et al., 2002). Mean patch size, amount of core area (100 m internal buffer distance to account for edge effects) and connectivity (500 m distance threshold) were calculated. Landscape metrics were computed at the class level for mature forests (A5) alone and for total forest cover (A1–A5) for the final time period. This allowed an evaluation of the contribution of secondary forests to the total spatial cohesion of forest cover in the landscape (Opdam et al., 2003).

2.5. Statistical analysis

The dependent variable, forest age class, was categorical rather than continuous. Therefore, an ordinal logistic regression model (Harrell, 2001) was applied using the S-Plus statistical software package (Insightful-Corporation, 2002). Explanatory variables for each location included soil fertility, accessibility, the area of neighbouring forest and secondary vegetation neighbours. The explanatory variables were standardized using the SCALE function in S-Plus by dividing values by their root-mean-square. The analysis was first conducted with all the variables included, and then with only soil fertility and cost–distance. For both analyses, the relative importance of the explanatory variables was assessed according to the standardised parameter estimates of the regression:

$$\gamma_j(x) = P(Y \geq j)|X = x) = \pi_j(x) + \ldots + \pi_k(x),\quad j = 1, \ldots, k$$

where Y is the categorical response variable with $k + 1$ ordered categories, and X the explanatory variables (soil fertility, accessibility, neighbourhood of forest and secondary vegetation).

To quantify the persistence of remnant and secondary forests of different ages in the landscape, we developed probability maps of deforestation (that is, forest to non-forest transitions). For this analysis, deforestation in the last time period was used as the dependent variable, where forest to non forest = 1 and forest to forest = 0.

$$\log\text{it}(y) = \beta_0 + \beta_1 X_1 + \ldots + \beta_{k+1} X_{k+1}$$

Table 3
Mature and secondary forest remnants, and total forest cover in the study areas in 2000

Study area	Mature forest (A5) (%)	Secondary forest (A1–A4) (%)	Total proportion of forest in landscape (%)
Berrío	20	80	14
La Balsa	35	65	4
Caquetá	26	74	3
Guamal	27	73	23
Opón	19	81	17
Tibú	42	58	6
Average	28.2	71.8	11.2

The average probability of deforestation was then calculated for each forest age class, by cross-tabulating the maps of age and probability of deforestation.

3. Results

3.1. General characteristics of the remnant forest cover

For the six study landscapes, the total proportion of remnant (mature and secondary) forest in the year 2000 ranged from 3% to 23% of the total pre-cleared forest cover, with an average of 11.2% (Fig. 1, Table 3). Of the remaining forest cover, an average of only 28.2% corresponded to the original forests, while the largest proportion (71.8%) corresponded to secondary forests that have regenerated during the last 60 years. We also found that individual forest fragments often consisted of a mosaic of different ages, including mature forests, as well as secondary forests (Fig. 5). The spatial patterns and distribution of the remnant forest fragments in the landscape varied between study areas depending on the physical characteristics of the landscape, such as soil fertility and accessibility (Table 4).

When forest age was plotted against the proportion of remnant forest for all study areas, a clear pattern emerged. The largest part (28.2%) of the remaining forests belong either to the older ‘‘original’’ forest cover, or to the younger secondary forests that regenerated during the last 10–20 years (42.5%, Fig. 6a). When only the regenerated forests (A1–A4) were considered, there was a negative relationship between age and proportion of remnants, suggesting that the regeneration process increases during the last phase of transformation when the clearing in absolute terms had almost stopped.

The average patch size of the remaining forests across all landscapes was 15.4 (±9.2) ha. However,

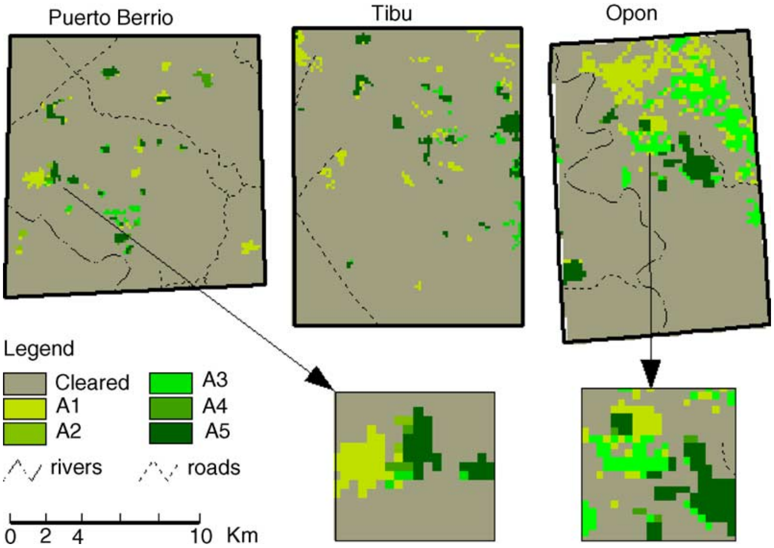

Fig. 5. Forest cover maps of three study areas showing spatial pattern of forest age. Note how remaining forest patches are largely built from regenerated secondary forests.

Table 4
Results of the standardized ordinal regression analysis showing: (a) the effect of soil fertility, accessibility and forest and secondary vegetation cover neighbourhood on the age of forest fragments and (b) considering only soil fertility and accessibility

Study area	Soil fertility	Cost distance	Average forest neighbours	Average secondary vegetation neighbours	R^2
Part (a)					
Berrio	**0.67** (0.14)	**0.52** (0.14)	**1.53** (0.18)	−**1.69** (0.21)	0.55
La Balsa	−**1.02** (0.18)	−**1.31** (0.18)	**1.46** (0.19)	−**1.86** (0.34)	0.71
Caqueta	−**0.51** (0.24)	−0.06 (0.20)	**2.19** (0.24)	−**0.89** (0.22)	0.64
Guamal	0.05 (0.06)	0.08 (0.06)	**1.27** (0.07)	−**0.34** (0.06)	0.35
Opon	**0.86** (0.11)	−**0.58** (0.10)	**2.63** (0.17)	−**0.51** (0.11)	0.69
Tibu	−0.18 (0.12)	0.16 (0.13)	**2.62** (0.28)	−**0.91** (0.23)	0.50
Part (b)					
Berrio	−0.03 (0.11)	−**0.36** (0.11)			0.04
La Balsa	−**0.46** (0.12)	−**1.66** (0.17)			0.44
Caqueta	−**1.01** (0.20)	−**0.26** (0.14)			0.13
Guamal	0.03 (0.06)	−**0.17** (0.05)			0.01
Opon	**0.44** (0.07)	−**0.43** (0.07)			0.09
Tibu	−**0.37** (0.11)	**0.58** (0.10)			0.11

Numbers in brackets correspond to the standard errors. (Bold numbers are statistically significant $P < 0.05$.)

there was a direct relationship between patch size and the relative proportion of forest, so that larger patches correspond to classes A1 and A5, which show higher proportions of forests in the landscape (Fig. 6a and b). Also, when considering only the regenerated forests, patch size decreased with increasing age, indicating again a higher regeneration rate in recent times.

Landscape metrics for the oldest age class (A5) compared to all age classes (A1–A5) showed the regenerated forests in the present-day landscape contributed substantially to an increase in mean patch size and core area. However, less clear was their effect on connectivity (Fig. 7).

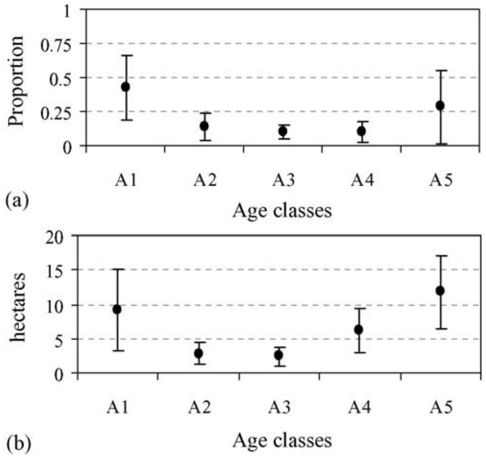

Fig. 6. Average relative forest proportions (a), and patch sizes (b), for different age classes across all landscapes.

3.2. Relation of forest age and physical variables

Overall, we found that the age class of forest fragments varied considerably between landscapes. The observed variation in age classes as explained by the model R^2 varied from 35% to 71% (Table 3a). The neighbourhood variables had greater explanatory power than the soil fertility and cost–distance factors. The relationship of the age classes with the autocorrelated neighbourhood terms is always significant and consistently positive for forest neighbours and negative for secondary vegetation. In contrast, soils and accessibility showed contradicting trends. In general, the following relationships with neighbouring forest area were identified from the results: (i) older forests were related to higher historical average neighbouring forest area, meaning they are more likely to form coherent patch structures, while (ii) younger regeneration forests were related to higher historical average of neighbouring secondary vegetation area.

When the forest and secondary vegetation neighbours were removed from the regression analysis, the proportion of the variation explained by the model

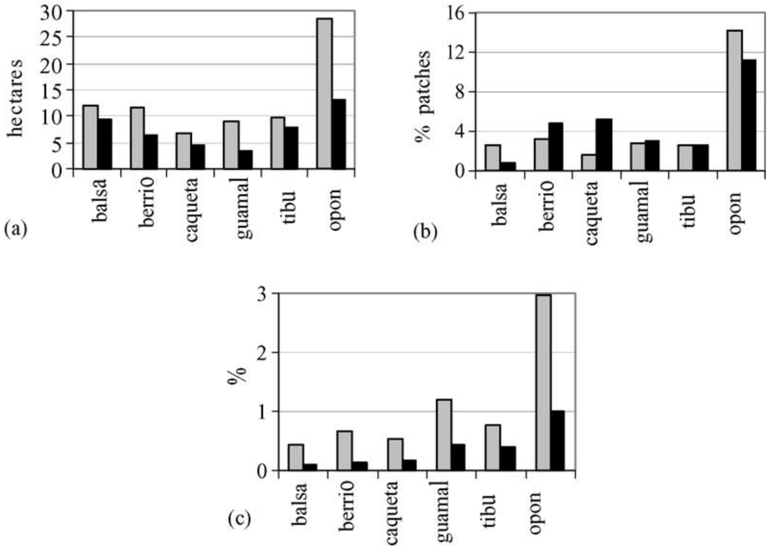

Fig. 7. Landscape metrics for mature forest remnant and all forest remnants: (a) mean patch size, (b) connectivity using a threshold of 500 m, and (c) core area as (%) of landscape (black: mature forest only (A5); grey: all remnant forest (A1–A5)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

dropped sharply in all cases (Table 3b). Accessibility showed a stronger and more consistent negative relationship with age, while soil fertility exhibited more variable relationships. These results collectively indicate that, in general, (i) mature forests have a higher probability of persistence in less accessible areas, while (ii) both older forests and regenerating forests generally occur on less fertile soils.

3.3. Probability of clearing

For most areas ($n = 4$), the probability of clearing was negatively related to the age of the forest, suggesting that mature forests were more stable (Table 5). However, for the remaining areas (La Balsa and Guamal) the probability of clearing was slightly higher for older forests. These two areas differ in that they occur in a forest-savanna mosaic landscape, where the gallery forests (not considered separately in this study) occurring in the savanna matrix, often with swampy conditions, have a high persistence probability.

4. Discussion

We have shown that forests in landscapes subject to heavy human impacts of clearing and fragmentation vary in: (i) the time since the remnant patches were isolated, and (ii) their actual successional response to

Table 5
Average probability of deforestation of remnant mature and secondary forests according to age class, calculated by the logistic regression model of the forest–non forest transitions for the 1995–2002 period

Forest age	Berrío		Caquetá		Opón		Tibú		La Balsa		Guamal	
class	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
A1	0.62	0.23	0.71	0.16	0.70	0.23	0.270	0.11	0.01	0.01	0.33	0.10
A2	0.49	0.16	0.75	0.19	0.31	0.13	0.13	0.08	0.02	0.03	0.46	0.14
A3	0.51	0.17	0.45	0.15	0.44	0.08	0.12	0.09	0.12	0.24	0.50	0.14
A4	0.43	0.18	0.52	0.21	n.a.	n.a.	n.a.	n.a.	0.06	0.14	0.50	0.14
A5	0.35	0.17	0.34	0.17	0.27	0.13	0.06	0.10	0.25	0.29	0.55	0.12

varying disturbance and regeneration processes in space and time. It is known that these aspects are important determinants of the biological and ecological values of remnant forests, impacting upon species/ecosystem richness, composition, physiognomy and structure (e.g. Guariguata and Ostertag, 2001). Therefore, land cover maps used for monitoring habitat loss and fragmentation should assess the age structure, and not just total forest cover, in highly transformed landscapes.

Our results confirm the trend of an increasing proportion of secondary forests in the highly transformed landscapes of the lowland moist forests of Colombia. Authors such as Brown and Lugo (1990) and Dunn (2004), highlight the increasing importance of secondary forests for conserving and restoring biodiversity in the tropics. But at the same time, others such as Kimes et al. (1998) question the reliability of the methods used to identify secondary forests, indicating that often secondary forests are not distinguished from mature forests between census intervals, which limits their use in assessments of carbon sequestration or biodiversity depositories.

In lowland Colombian landscapes, the spatial age structure of the fragments is best explained by the historic presence of a neighbourhood of forest and secondary vegetation, indirectly demonstrating the impact that land use history has on the transformation patterns, and in particular on age patterns (Read et al., 2001). In the Brazilian Amazon, Skole et al. (1994) in their study of tropical forest showed an increase of secondary forests up to 42% in the cleared areas, pointing to the importance of the regrowth processes and secondary vegetation during land clearing. However, differences in the size of the study area, strong land use gradients and the difficulty to refer to our clearing stages, render comparisons with our results difficult.

Guariguata and Ostertag (2001) studied sequences of forest succession after complete clearing in Costa Rica, finding that structural characteristics are restored after prolonged succession, as opposed to species composition that may take considerably longer. However, they conclude that Neotropical forests show a high regenerative power, if propagule sources are adjacent and land use intensity has not been severe. Studies of forest regeneration in the Brazilian Amazon by Nepstad et al. (1991) found that low propagule availability, increased seed and seedling predation, increased seasonal drought and root competition from grasses and forbs, collectively act as the obstacles to forest regeneration in heavily cleared areas. This also may be the case in Colombian lowland ecosystems, where remnant and regenerated fragments are spatially and functionally isolated in a matrix of exotic grasslands, which are largely hostile to recolonisation by forest species.

Although the probability of forest regeneration was predicted with reasonable accuracy, our results confirm that the prediction of the successional trajectories is difficult if based on a few physical factors such as soil fertility and accessibility. This may be due to the dependence of regeneration on more specific biophysical properties (e.g., water holding capacity) and interactions between site-specific conditions and land use history. We have shown that, with knowledge of the historical spatial patterns of the neighbourhood of forest and secondary vegetation, the age of fragments can at least partially be predicted.

The clearing process of lowland forests in Colombia was described by Etter et al. (2005) as composed of four phases that follow a negative sigmoid pattern, where the intermediate phases have very high clearing rates. The results we present here, further reinforce these trends, by showing that during the intermediate phases of fastest land clearing, very little secondary vegetation regenerates, creating a gap in the spatial mosaic and successional stages at the landscape level. In most cases, the probability of being cleared is higher for younger forests, reinforcing the conceptual model presented in Fig. 1. Contrary to the findings of Read et al. (2001) in Costa Rica, that only 1% of secondary forests had repeated disturbances, our study indicates widespread repeated disturbance regimes. However, the explanation of what processes interact and how this dynamic and more stable dichotomous behaviour is generated remains to be satisfactorily understood.

From a landscape perspective, the regenerating forests of Colombian lowland ecosystems appear to be improving the spatial structure of the remaining mature forests. Specifically, by increasing the mean patch size and core area, which might increase the chances of species recolonisation and persistence. The connectivity measured through the connectance index seems more erratic, which could be partly explained by the fact that, in some locations, secondary forests do not grow around the core areas of forest. Further research is needed to evaluate how successional dynamics affect the biodiversity values of the landscape. In particular, the contributions of heavily transformed landscapes with mosaics of scarce forest of different ages for conservation and restoration of biodiversity at the farm and landscape-level, still needs to be better understood.

Unplanned and unimpeded clearing such as those analysed here, are leading to highly degraded, heterogeneous landscapes. Forests are persisting in the economically more marginal and less productive land. Many ecosystems which are related to economically high value land for agriculture, urbanisation or mining have virtually disappeared (Wilson et al., 2005). Fortunately, many of the highly valued biodiversity hotspot areas in Colombia are still marginal to the economy, such as the Pacific lowlands and large parts of the Amazon. However, due to the social problems and expanding illicit economies that cause human migrations, these areas are becoming increasingly subject to clearing pressures and therefore more vulnerable.

As the pressure of human activities on natural ecosystems continues, biodiversity conservation will increasingly have to deal with highly transformed landscapes. Therefore, land use solutions that combine conservation with restoration are becoming increasingly important (Young, 2000; Lugo, 2002). However, for this strategy to be successful, we will need to better understand the subtle dynamics of land cover change. Conservation planning must begin to recognise that tropical forest landscapes are dynamic and that different landscapes often have differing vulnerabilities and levels of resilience (Lugo, 2002; Wilson et al., 2005). Nevertheless, improving the biological and ecological values of highly transformed landscapes in political contexts such as the one prevailing in Colombia demands that basic conservation rules on reserve selection and protection be effectively enforced.

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