Patterns and Trends of Forest Loss in the Colombian Guyana

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ABSTRACT

Spatial patterns of tropical deforestation and fragmentation are conditional upon human settlement characteristics. We analyze four different human occupation models (indigenous, colonist frontier, transition and established settlement) in the Colombian Guyana Shield at three different times: 1985, 1992 and 2002, and compared them for: (1) deforestation rates; (2) the amount of forest as classified according to a fragmentation pattern (interior forest, edge forest, perforated forest and forest patch); (3) various fragmentation metrics using repeated measures analysis of variance; and (4) potential future deforestation trends though the implementation of a spatially explicit simulation model. The indigenous and colonist frontier occupation models had low rates of deforestation (0.04%/yr), while the well-established settlement occupation model had the highest rate (3.68%/yr). Our results indicate that the four occupation models generate three deforestation patterns: diffuse, which can be subdivided into two subpatterns (indigenous and colonist); geometric (transition) and patchy (established settlement). The area with the established settlement model was highly fragmented, while in the transition occupation area, forest loss was gradual and linked to economic activities associated with the expansion of the agricultural frontier. The simulation of future trends revealed that indigenous and colonist areas had a constant, albeit small, loss of forest covers. The other models had a deforestation probability of 0.8 or more. Overall, our results highlight the need for new and urgent policies for reducing forest conversion that consider intraregional variability in human occupation linked to differences in land-use patterns.

Global deforestation is recognized as one of the core causes of global environmental change (Cassel-Ginz & Petschel-Hels 2001, Klepeis & Turner 2001). It drives species extinction and habitat destruction and affects carbon emissions and climate change on several scales (Sala et al. 2000, Houghton 2003, Foley et al. 2005). The effects of deforestation and fragmentation on forest composition, structure and function are widely known (Burke & Nol 2000, McMahon & Cuffney 2000, Laurance et al. 2002a, b), and include species mortality, changes in trophic interactions and increased susceptibility to logging, fires and invasive species (Sala et al. 2000). In addition, deforestation changes the landscape configuration thus affecting the ecological processes of an area (Skole & Tucker 1993, Turner et al. 2001, Peres et al. 2010). A close relationship between deforestation and forest fragmentation has been established, and ecosystem degradation and patch characteristics have been shown to be associated with the degree of fragmentation (Mertens & Lambin 1997, Roy & Tomar 2000).

The most common causes of deforestation are land-use change driven by increasing demand for agricultural land and timber from tropical forests (Geist & Lambin 2001, Rudel 2007, Rudel et al. 2009). The spatial patterns of deforestation and fragmentation are conditional upon human settlement characteristics and land-use history (Lambin & Ehrlich 1997, Steininger et al. 2001, Barbosa & Metzger 2006, Rudel 2007), and appropriate conservation strategies depend on the historical deforestation processes (Ferraz et al. 2009). Many land cover change models erroneously assume that changes in land cover occur in a spatially homogeneous manner across landscapes and regions (McDonald & Urban 2006). Different models have analyzed the occupation of tropical forests using ecological, economic and social variables (Perz & Skole 2003, Margulis 2004) at different spatial scales (Laurance et al. 2002a, b), and all have shown unique intraregional patterns of deforestation and land-use change.

Studies of the spatial patterns of deforestation in the Amazonian region suggest that occupation processes and the spatial configuration of the landscape are heterogeneous in both time and space (Soares-Filho et al. 2001, Armenteras et al. 2006, Arce-Nazario 2007, Fearnside 2008).

In recent years, several studies of patterns of land-use change in the Andean, Caribbean and Amazonian regions have shown that differences in biophysical characteristics can influence land-use patterns (Armenteras et al. 2003, Viña et al. 2004, Etter et al. 2005, 2006a). Few studies, however, have identified the spatial patterns of deforestation and fragmentation and analyzed the temporal dynamics of the landscape in regions such as the Guyana Shield. This region, a priority for conservation because of its highly diverse and endemic biota, has been known for its low deforestation rates (Ter Steege et al. 2000), though the extent of land-use change, deforestation and ecosystem fragmentation has increased in recent decades (Rodriguez et al. 2006). The lack of long-term information on these topics limits our knowledge of the changes in the region under different land occupation circumstances, which can greatly differ between indigenous and colonization land-use patterns.

The objective of this paper is to analyze the spatial and temporal variability of deforestation patterns among different human
occupation models associated with different land-use characteristics determined by the presence of indigenous or colonist populations in the Colombian Guyana Shield. In particular, we consider four common occupation types in the region that differ in a wide range of economic, political and demographic factors. For each model, we determine: (1) the rate and overall percentage of deforestation; (2) the pattern of fragmentation; and (3) potential future trends of deforestation. We used multi-temporal satellite images from three dates from 1985 to 1992 and 1992 to 2002. Furthermore, to estimate the amount of forest that will potentially be lost in areas in the future, we used a cellular automata approach.

**METHODS**

**STUDY SITE.**—The study area (80,527 km²) is located between the Amazon River and Orinoco basin and belongs to the western province of the Guyana phytogeographic region. It includes the department of Guaviare and portions of the Caqueta, Guainia, Vichada and Meta departments (Fig. 1). The region has an average altitude of 100–200 m with occasional isolated hills and low ‘tepuis’ (i.e., table mountains with shrub and savannas) up to 800 m in height. The climate of the area is tropical, very humid, has only one period of rainfall (2800–3500 mm/yr) and an average temperature of 24.5°C. It has high floristic and ecological complexity as a result of geological, topographical, soil and water gradients (Daly & Mitchell 2000). Vegetation types found include white sand vegetation, flooding forests and several tropical rain forest systems. The region is rich in biodiversity and the high species endemism of its associated vegetation types.

There is a west to east gradient of human settlement across the study area with the west being largely developed, leading eastwards through a colonization front to indigenous dominated regions in the eastern extremity. This region contains 30 indigenous reservations, which make up almost 31 percent of the study area. Land-use changes in the region are mainly related to the extraction of natural resources (Ariza et al. 1998) followed by the establishment of pastures and crops. The occupation process follows the course of navigable rivers and roads. Illicit crops (e.g., coca) have been one of the main economic drivers of this region in recent decades (United Nations Office on Drugs and Crime [UNODC] 2006) and have been found to be a significant factor in land-use change (Armenteras et al. 2009). Livestock grazing and pasture lands are mainly concentrated near municipalities with ongoing infrastructure and road development.

**FIGURE 1.** Location of the study area and distribution of the human occupation models.
OCCUPATION MODELS.—Based on the knowledge of regional experts regarding historical occupation processes and the influence of driving forces of landscape change (Bartel 2000), our hypothesis is that attractors (roads originating in the colonization front and rivers) influence the way occupation is undertaken in a region. From this approach, we delimited four subregions in our study area that correspond to four common occupation models: indigenous, colonist frontier, transition and established settlement. We characterized these models by a series of social, economic, demographic and historical factors following similar methodological approaches to those described by Geist and Lambin (2001). The first model, the indigenous model, corresponded to areas associated with traditional indigenous agriculture (shifting). This model is characterized by continuous rotation on small parcels near rivers, and most of the territory falls under the legal status of indigenous reserves with settlements of less than a few hundred people per site (Instituto Geográfico Agustín Codazzi [IGAC] 2008). The colonist frontier model was also associated with shifting subsistence agriculture and low densities of human settlements compared with permanently settled areas. It is composed of small properties irregularly distributed over an area with land tenure. The transition model was associated with the transition from colonist to permanent settlements, which was characterized by large livestock production; in peripheral areas, the expansion of the human frontier was influenced to a lesser extent by coca crops. Finally, the fourth subregion, established settlement, refers to large established cattle ranches with a well-developed infrastructure, roads and populated areas.

REGIONAL AND LOCAL DEFORESTATION AND FRAGMENTATION PATTERNS.—We used land cover information from supervised classification of yearly Landsat TM and ETM satellite images. Each image was registered to a base of Landsat ETM images for the year 2000, which were georegistered using 1:100,000 topographic maps of the Geographic Institute of Colombia. The RMs error was less than one pixel. Land cover was classified using ERDAS Imagine V8.7 (Erdas Inc, Atlanta, Georgia, U.S.A.). We obtained 11 classes, which were reclassified into three classes following the previously applied methodology in the area (Armenteras et al. 2009): forest (including forests and small areas with shrub and savannas), nonforest (pastures, crops and infrastructure) and water (rivers and lakes). The final accuracy, carried out only for the 2002 map, was 95 percent, calculated using the methodology described by Meidinger (2003), which is based on evaluating the quality of the map using field data and visually checking the map with aerial photographs and SPOT images. We carried out fieldwork to verify the land cover classes in two of the occupation models.

The study was carried out at the regional scale (which considers the whole area that corresponds to each occupation model) to establish the general context of the analysis and to identify intraregional differences among occupation models. Furthermore, we randomly selected seven 2500 ha (5 × 5 km) windows for each subregion, termed local scale, to analyze differences among occupation models in landscape structure.

Deforestation rates were calculated using the relationship of Puyravaud (2003):

\[
\text{Change rate} = \frac{1}{(t_2 - t_1)} \ln \left( \frac{A_2}{A_1} \right) \times 100.
\]

where \(A_1\) and \(A_2\) are the forest areas in hectares at years \(t_1\) and \(t_2\), respectively. For example, for the period from 1985 to 1992, \(A_1\) and \(A_2\) are the forest cover values in 1985 and 1992, respectively.

To evaluate fragmentation, we used the forest fragmentation model of Riitters et al. (2000) and Riitters and Coulston (2005), which classifies each pixel according to its state of fragmentation using two parameters: \(P_f\), which is the amount of forest (values between 0 and 1; 1 indicates 100% forest), and \(P_{ff}\), which is related to the probability (values between 0 and 1) that a pixel has another forested pixel as a neighbor. By resampling the land cover map to pixels of 250 × 250 m using a mobile window of 5 × 5 pixels, we obtained four categories of fragmentation: (A) interior forest (all pixels surrounding the central pixel are forested, and both \(P_f\) and \(P_{ff}\) = 1); (B) edge forest (the majority of pixels around the central pixel are forested, but the central one may be a fragment or an edge, so that \(P_f > 0.6\) and \(P_{ff} < 0\)); (C) perforated forest (the majority of pixels around the central pixel are forested, but the central one belongs to a group of patches or edges; \(P_f > 0.6\) and \(P_{ff} > 0\)); and (D) forest patch (the central pixel is part of a fragment of forest included in a matrix of nonforest, \(P_f < 0.4\)).

We also used the following metrics that were computed for the entire study area and for each of the windows separately for the three dates studied: (A) number of patches (NP), patch density (PD), mean patch size (MPS) and largest patch index (LPI) as measures of the degree of fragmentation (Barbosa & Metzger 2006, Cayuela et al. 2006); (B) Euclidean nearest neighbor distance-area-weighted mean (ENN) as a measure of proximity; and (C) cohesion (COH) and aggregation index (AI) as measures of connectivity and adjacency of the transformed matrix, respectively. These metrics were computed using Fragstats v. 3.3 (McGarigal & Marks 1995).

STATISTICAL ANALYSIS.—Differences in deforestation rates and the effects of the occupation models for each year on the extent of forest classified according to its rate of deforestation and on the various fragmentation metrics were evaluated with a repeated measures analysis of variance test. To normalize the data, the metrics PD, LPI and COH were log transformed. Statistical analyses were carried out using SPSS v. 16.0.

MODELING DEFORESTATION TRENDS.—A simulation model based on cellular automata, which analyzes land cover change relationships among neighboring areas to predict future changes (Soares-Filho et al. 2002), was implemented in Microsoft Visual Basic® 6.0.

Throughout the simulation it was assumed that: (1) deforestation is spatially autocorrelated with transportation networks and other areas of recent deforestation (i.e., attractors sensu Bürgi et al. 2004); (2) deforestation rates as a function of distance were constant during the 50-yr time period; (3) deforestation rates were calculated from the more recent 1992-2002 period only, which arguably more accurately describes the current deforestation
dynamics taking place in the area; (4) total deforested area during one 10-yr time step was the same as total deforested area during the 1992–2002 period; (5) regeneration rates were assumed to be negligible within the four regions during the 50 yr of each model run; (6) deforestation processes were bounded to each of the four regions separately; and (7) one occupation model did not change to another during the simulated time span.

The model first estimated the amount of deforestation from 1992 to 2002 as follows: (A) a map of recently deforested pixels was calculated by comparing the 1992 and 2002 maps (i.e., only pixels that had changed state were retained); (B) those pixels were then grouped into separate patches that consisted of pixels that shared one side or vertex (e.g., all pixels within one patch were in side-to-side or vertex-to-vertex contact); (C) each separate patch was inspected to see whether there were any river, road or previously deforested pixels (during the 1985–1992 period) at a distance of one or two pixels, or more, from the border of the patch; and (D) a table was created in which the complete distribution of those patch areas was stored as a function of three distance categories (e.g., one, two or more than two pixels away), creating a distance-dependent look-up table of patch areas.

Next, simulated maps were calculated every 10 yr using the previous map and the look-up table of patch areas already computed. The simulated maps were created as follows: (A) a forested pixel was chosen at random from the image, and its proximity to rivers, roads and previously deforested pixels was assessed; (B) according to that proximity, a patch area was chosen randomly from the look-up; (C) the pixels contiguous to the original forested pixel were deforested uniformly until the total area matched that of the chosen patch; and (D) the algorithm picked another forested pixel and repeated steps (A), (B) and (C) until the total deforested area in the image approximately equaled the total area deforested from 1992 to 2002 for that distance category.

One whole model run consisted of a 50-yr simulation with time steps of 10 yr. The output of the model includes maps of forested and deforested areas for each of the four occupation models and the total number of forested and deforested pixels for each distance category. Monte Carlo simulations were carried out to estimate the degree of uncertainty associated with independent model runs. Maps of mean deforestation probability in 50 yr were subsequently computed as the arithmetic average of 1000 simulations. We also evaluated future mean trends in deforestation every 10 yr. Values close to one in the final probability maps pinpoint locations that will very likely suffer deforestation during a 50-yr time interval. Values close to 0, on the other hand, indicate pixels that will probably remain forested.

RESULTS

REGIONAL AND LOCAL DEFORESTATION RATES.—Across the entire study area, there was an overall loss of 347,406 ha of forest between 1985 and 2002 (rate = 0.25%/yr). In 1985, 59.5 percent of the area classified as established settlements was covered by forests, while 82.9 percent of the area defined as transition was forested; the other two models (indigenous and colonist frontier) were 99.6 percent forested. There was substantial variability in annual deforestation rates among the four subregions across the 17 yr of the study: 0.04 percent/yr for the indigenous occupation region, 0.17 percent for the colonist frontier area, 1.99 percent for the transition subregion and 3.68 percent for the established settlement area. Higher deforestation rates were observed in the period from 1992 to 2002 (0.33%/yr) than in the period from 1985 to 1992 (0.14%/yr).

At the local scale, there were significant differences in forest loss among occupation models ($F = 8.0, P = 0.001$) and between time periods ($F = 5.7, P = 0.025$). The interaction between these two variables was also significant ($F = 3.1, P = 0.045$). Deforestation rates were lower during the first period than during the second period in all four occupation models. Both indigenous and colonist frontier subregions showed low deforestation rates (<1.3%) during both periods, while high rates (>4.5%) were observed for the transition occupation model; the area with the established settlement had a low rate of deforestation during the first period and the highest rate during the second period. Little to no forest regeneration (i.e., increase in forest) occurred in either of the two time periods and was therefore neglected in the simulation model.

REGIONAL AND LOCAL FRAGMENTATION PATTERNS.—In 1985, 87 percent of the study area was classified as interior forest, 8.7 percent as edge forest, 2.8 percent as perforated forest and 1.4 percent as forest patches. The indigenous, colonist frontier and transition occupation models had the greatest percentage of interior forest (Table 1), while the major category in the established settlement model was edge forest (37%). From 1985 to 2002, the interior forest category decreased in area by 56 percent in the established settlement occupation model and by 71 percent in the transition model (Table 1). In both the indigenous and the colonist frontier occupation subregions, interior forest decreased by between 2.5 and 12 percent. The area of edge forest decreased by almost 50 percent in all of the occupation models while the area of perforated and patch forest categories increased considerably, especially in the occupation models more associated with the presence of colonists and indigenous groups. An exception was the perforated forest category in the settlement establishment area.

At the local level (seven windows for each subregion), window analysis results indicated significant differences both for occupation model and for year. The interaction between occupation model and year was significant for all forest categories except the forest patch category (Table 2); these comparisons indicate that the variability in change rates were similar among the four occupation models in both time periods. In the interior forest category (Fig. 2A), the greatest forest loss occurred during the second period of analysis (1992–2002), with annual rates > 13 percent in the transition occupation model and the established settlement areas. Most of the forest area in the indigenous and colonist frontier consisted of edge forest in 1985 and 1992 but increased moderately (transition) or even decreased (established settlement) in 2002. Edge forest area was three times greater in the indigenous and colonist frontier models in the second time period than in the first time period (Fig. 2B). The area of perforated forest (Fig. 2C) increased over time in the indigenous and colonist frontier models and decreased.
in the two models associated with more established settlements in 2002. Finally, the forest patch category had annual change rates of < 1.7 percent, which were not significantly different among the four occupation models (Table 2).

The two factors considered, occupation model and year, showed significant differences in the various landscape metrics used (Table 3) except for NP, PD and ENN, while the interaction of the two factors was significant for all of the metrics except AI. The NP and PD metrics showed similar trends through time, increasing in the transition and established settlement models and remaining low in the indigenous and colonist frontier models (Figs. 3A and B).

The LPI was high and fairly constant in the indigenous and colonist frontier occupation models, while in the models with a more permanent population, these values were low and decreased from 1985 to 2002 (Fig. 3C). The COH decreased in the transition and established settlement models and remaining low in the indigenous and colonist frontier models (Figs. 3A and B). The ENN was highly variable among models and years, with increasing differences among models through time and higher differences between forest fragments among years in the models associated with more established settlements (Fig. 3E).

**Expected Trends in Deforestation.**—The probability maps for the indigenous and colonist frontier occupation models depict a similar pattern of deforestation that takes place mainly along rivers (Figs. S1A and B). Deforestation probabilities in pixels close to rivers and roads, however, were noticeably higher in the colonist frontier than in the indigenous models. The indigenous area showed a low deforestation probability (0.01) in 77 percent of the reserve for the next 50 yr, which suggests that the processes that shape the dynamics of the indigenous territory are markedly different from those in the other three areas. Figure S1C, on the other hand, reveals that the transition occupation model will rapidly expand into the surrounding forests; approximately 40 percent of the 2002 forest area has a deforestation probability of 0.8 or more. Finally, the probability of suffering deforestation in the next 50 yr is exactly 1 for all forest pixels in the well-established settlement regions (Fig. S1D).

From our evaluation of decadal forest change as a function of time and categorical distance to rivers, roads and previously deforested pixels, in the case of the indigenous and colonist frontier occupation models, the simulation predicts that forest loss will be more pronounced near rivers, roads and previously deforested areas. This can also be seen in the established settlement and transition areas, which show a rapid drop in deforestation probability at all distances. Remarkably, forest loss at distances shorter than 500 m reaches a plateau for this last model after 40 yr (curve marked by triangles in Fig. 4C), which is due to the complete deforestation of all locations close to rivers (e.g., rivers are surrounded by deforested areas all along their length). After 40 yr, deforestation in this distance category takes place only in forests close to previously deforested areas. Moreover, these two latter models show a more rapid decline in forested area than the other two occupation models. In fact, all simulations show no forested area remaining after 50 yr in the well-established areas, and the probability map shows 100 percent certainty of deforestation.

**DISCUSSION**

Overall, our results indicate high variability in regional deforestation rates between the occupation modes. Moreover, each spatial pattern, in addition to having its own particular geographic

### TABLE 2. Effects of human occupation model type and year (repeated measures) on the different categories of forest fragmentation. NS, not significant.

<table>
<thead>
<tr>
<th>Categories of forest fragmentation</th>
<th>Established settlement</th>
<th>Transition</th>
<th>Colonist frontier</th>
<th>Indigenous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year HOM</td>
<td>Year</td>
<td>Year HOM</td>
<td>Year</td>
<td>Year HOM</td>
</tr>
<tr>
<td>Interior forest</td>
<td>49.5</td>
<td>&lt; 0.001</td>
<td>61.29</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Edge forest</td>
<td>1.06</td>
<td>NS</td>
<td>0.13</td>
<td>NS</td>
</tr>
<tr>
<td>Perforated forest</td>
<td>1.38</td>
<td>NS</td>
<td>0.34</td>
<td>NS</td>
</tr>
<tr>
<td>Patch forest</td>
<td>21.6</td>
<td>&lt; 0.001</td>
<td>13.0</td>
<td>0.001</td>
</tr>
</tbody>
</table>
location, has unique characteristics. These patterns are similar to those proposed by Mertens and Lambin (1997) and also used by Geist and Lambin (2001), in which the indigenous and colonist frontier models are equivalent to what these authors called a diffuse pattern. Our results, however, indicate that deforestation rates and fragmentation patterns are significantly different from the coloni-
ization front to interior forest occupied by indigenous communities. The deforestation rates and pattern for the transition model fit well with the geometric pattern proposed by Mertens and Lambin (1997). Finally, the well-established population with the economic characteristics of the established settlement model fits well with the patchy deforestation pattern proposed by this classification. The highest deforestation rates for the region correspond to the geometric and patchy deforestation patterns (3.7% and 2.0%, respectively). Similar rates have been observed by other authors for the La Macarena region (0.97%, Armenteras et al. 2006), lowland forests of Colombia (1.5%, Etter et al. 2006a), and Colombian-Ecuadorian Amazonia (1.6%, Viña et al. 2004, 0.9%, Sierra 2000).

One factor that may affect deforestation rates is related to the dominant landscape matrix found in each pattern, and to the prox-
imity of a patch to a colonization front which may act as an attrac-
tor of deforestation. In diffuse patterns, the spatial arrangement is less obvious, and river access plays an important role, especially in areas occupied by indigenous populations who typically established small cultivated parcels (‘chagras’) in floodplains for subsistence ac-
tivities. Such activities will arguably not modify the diffuse spatial pattern that we observe in future years. These areas, primarily within indigenous reserves and National Natural Reserves, are buffers against deforestation, as indicated by Armenteras et al. (2009) (deforestation rates were between 3.98 and 1.49 times higher outside the borders of reserves areas than inside them).

In the colonist frontier model, characterized by a slow and dis-
persed increase in the number of small parcels, deforestation along rivers and roads is evident, and attractors of deforestation are asso-
ciated with the opening of new colonization fronts. Geographical data of the System for Illicit Crops Monitoring project for the period from 2000 to 2008 indicate that the progress of coca crops is associated with the transition and established settlement models; thus, coca becomes an important driver of deforestation in the region.

In the patchy and geometric patterns associated with the es-
established settlement and the transition models, respectively, the short distance between transformed patches can lead to accelerated changes. Gutiérrez et al. (2004) have shown that urban centers in

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**FIGURE 2.** Mean (± SE) values of the three fragmentation categories: (A) interior, (B) edge and (C) perforated, for the four human occupation models identified in the Guyana region in the three studied years (1985, 1992 and 2002). N=7 in all cases.

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**TABLE 3.** Effects of human occupation model type and year (repeated measures) on the variables used to characterize fragmentation patterns. To normalize the data, the metrics PD, LPI and COH were log transformed. AI, aggregation index; COH, cohesion; ENN, Euclidean nearest neighbor dis-
tance-area-weighted mean; LPI, largest patch index; NP, number of patches; NS, not significant; PD, patch density.

<table>
<thead>
<tr>
<th>Variable</th>
<th>HOM Year</th>
<th>HOM Year</th>
<th>HOM Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>NP</td>
<td>2.5 NS</td>
<td>0.9 NS</td>
<td>8.2 &lt; 0.001</td>
</tr>
<tr>
<td>PD</td>
<td>2.7 NS</td>
<td>1.1 NS</td>
<td>11.9 &lt; 0.001</td>
</tr>
<tr>
<td>LPI</td>
<td>44.1 &lt; 0.001</td>
<td>75.3 &lt; 0.001</td>
<td>2.7 0.023</td>
</tr>
<tr>
<td>ENN</td>
<td>1.0 NS</td>
<td>0.0 NS</td>
<td>3.1 0.046</td>
</tr>
<tr>
<td>COH</td>
<td>19.7 &lt; 0.001</td>
<td>29.9 &lt; 0.001</td>
<td>4.7 0.001</td>
</tr>
<tr>
<td>AI</td>
<td>8.7 &lt; 0.001</td>
<td>36.1 &lt; 0.001</td>
<td>0.8 NS</td>
</tr>
</tbody>
</table>

(1997).
the Colombian Amazon play a central role given their location in transitional zones between consolidated colonies and colonization fronts. Furthermore, Etter et al. (2006a) found that accessibility (roads, urban centers and rivers) were the important variables in shaping deforestation in the region. In addition, in these patterns, deforestation tends to be explained primarily by a high spatial autocorrelation coefficient (Aguiar et al. 2007). The geometric pattern shows the greatest variability during this study and has undergone the greatest changes in spatial configuration. This pattern is the result of the important front of consolidation of human colonization along the road between San Jose de Guaviare and Calamar, an axis for access to these settlements. The established settlement area constitutes a strategic zone, given that it directly connects the markets of Villavicencio and San Jose del Guaviare (Fig. 1), where most of the population growth and economic activity occurs along the road axis. In this area, consolidation of the colonization front is evident. Existing protected areas (in particular, the national protected area of the Macarena) have become important barriers to deforestation and fragmentation (Armenteras et al. 2009), which has also been described by Aguiar et al. (2007) in Brazil.

The association of fragmentation patterns with rates of deforestation shows that annual rates of deforestation > 4 percent are found in patterns with < 50 percent interior forest and > 45 percent perforated forest. This result indicates that the patchy and geometric patterns have higher fragmentation indices with an increased forest edge. These data agree with the results of Barbosa and Metzger (2006) in Brazilian Amazonia forests, who reported a decrease in the survival of interior forest species in areas with a Pf value of < 0.6 of forest and greater fragmentation and decreased connectivity at intermediate values of Pf. In the Colombian Amazonia, Etter et al. (2006b) have also shown that connectivity is lost more quickly at intermediate levels of deforestation and that this relates to the exposed forest edge.

Differences between the occupation models were significant in almost all of the categories and indices of fragmentation analyzed. Relatively small differences are evident in the structure and spatial composition through time in the indigenous model, which may be related to the fact that indigenous communities typically utilize floodplains to establish small cultivated parcels. For the colonist frontier model, occupation is consolidated along rivers (Itilla,
Unilla and Inírida), with a considerable increase of human-transformed fragments (generally illicit crops) within a dominant matrix of forests. As suggested by Arcila et al. (1999), this zone is characterized by a slow, dispersed increase in the number of small parcels in initial stages of deforestation, with a form of linear establishment following the courses of rivers and their effluents with small nuclei whose populations are of migratory origin.

Given the intraregional variability in patterns and trends in the Colombian Guyana, future policies should take these factors into consideration in view of the results obtained with transition and established settlement models. The geometric and patch patterns observed, in which the interior forest category comprises < 30 percent of the total area and the connectivity between fragments declines considerably, must be viewed under the perspective of better connectivity management and secondary ecosystem conservation alternatives. It is necessary to use subpattern divisions and to analyze the underlying drivers that generate these divisions to predict future deforestation patterns and effects for species diversity (as suggested by Ewers & Laurance 2006).

Throughout the simulations we have assumed that deforestation rates, as measured from the 1992 to 2002 period, will remain constant during the next 50 yr. Even though relevant land cover change drivers may (and some of them certainly will) change in future years, the use of the 1992–2002 rates as representative for the 2002–2052 time period will provide an approximate (and, indeed, useful) idea of what to expect in terms of average patterns of deforestation in the Colombian Amazon.

The annual deforestation rate (0.25%) found in this study indicates that this region has low deforestation rates compared with the rest of South America. The question remains whether the present regional pattern (i.e., forest loss concentrated in just one or two regions while the remaining forest is conserved) is preferable to the alternative (i.e., forest loss spread more homogeneously throughout all regions but not intensively in one particular region). Our results reveal the importance of incorporating spatial pattern projections into the strategic planning of the region, taking into account settlement characteristics. For example, in patterns that show high risks of deforestation and fragmentation through time, incentives and strategies should be oriented toward intensifying land use in the most productive regions and thereby reducing deforestation pressure elsewhere. For this reason, future plans for the region should include clear directives for social investment and deforestation reduction while promoting the use of more technological and well-capitalized agricultural enterprise. Approaches used to reduce deforestation will also need to be tailored to specific types of land occupation and land uses. In particular, reduced emissions from deforestation and degradation, or payments for environmental services, are alternatives that are being applied in South America, to provide incentives to colonists to maintain ecological processes in the region (Butler & Laurance 2008, Morse et al. 2009). For low population areas, conservation and sustainable use should be priorities, and planning schemes should avoid providing incentives for the development of enterprise-driven agricultural or large cattle ranching schemes.

ACKNOWLEDGMENTS

We sincerely thank the Departamento Administrativo de Ciencia, Tecnología e Innovación-Colciencias and the Alexander von Humboldt Biological Research Institute for their financial support of the development of the original project and of the authors’ mobility and academic cooperation. We thank Alexander Rincón, Milton Romero, Nestor Bernal and Edersson Cabrera for their participation in the original project and Carol Franco for her help in the
preparation of the figures in this work. R. Molowny-Horas acknowledges the financial support of the Spanish MICINN and the European Social Fund through the Plan Nacional de Potenciación de Recursos Humanos.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Probability maps of pixel deforestation across a 50-yr period.

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