Land Cover Change in Colombia: Surprising Forest Recovery Trends between 2001 and 2010

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Abstract

Background: Monitoring land change at multiple spatial scales is essential for identifying hotspots of change, and for developing and implementing policies for conserving biodiversity and habitats. In the high diversity country of Colombia, these types of analyses are difficult because there is no consistent wall-to-wall, multi-temporal dataset for land-use and land-cover change.

Methodology/Principal Findings: To address this problem, we mapped annual land-use and land-cover from 2001 to 2010 in Colombia using MODIS (250 m) products coupled with reference data from high spatial resolution imagery (QuickBird) in Google Earth. We used QuickBird imagery to visually interpret percent cover of eight land cover classes used for classifier training and accuracy assessment. Based on these maps we evaluated land cover change at four spatial scales country, biome, ecoregion, and municipality. Of the 1,117 municipalities, 820 had a net gain in woody vegetation (28,092 km2) while 264 had a net loss (11,129 km2), which resulted in a net gain of 16,963 km2 in woody vegetation at the national scale. Woody regrowth mainly occurred in areas previously classified as mixed woody/plantation rather than agriculture/herbaceous. The majority of this gain occurred in the Moist Forest biome, within the montane forest ecoregions, while the greatest loss of woody vegetation occurred in the Llanos and Apure-Villavicencio ecoregions.

Conclusions: The unexpected forest recovery trend, particularly in the Andes, provides an opportunity to expand current protected areas and to promote habitat connectivity. Furthermore, ecoregions with intense land conversion (e.g. Northern Andean Páramo) and ecoregions under-represented in the protected area network (e.g. Llanos, Apure-Villavicencio Dry forest, and Magdalena-Urabaí Moist forest ecoregions) should be considered for new protected areas.

Introduction

Land cover change is the main cause of deterioration in ecological systems at local to global scales [1,2]. Land-use/land-cover (LULC) research has mainly focused on forest conversion (deforestation) because of its impacts on global and regional climate change [2–5], soil degradation [6], loss of biodiversity [7,8], and goods and services provided by natural systems [9,10]. Consequently, knowledge of drivers, patterns, and rates of deforestation has been increasing rapidly, yet many information gaps still exist. For example, the extent of deforestation in many tropical countries is not based on current assessments, most lagging 5–10 years. Furthermore, LULC research has not fully considered other land transitions such as forest regrowth (reforestation) despite gathering evidence that there is a worldwide reforestation trend [1,11–14]. According to The Food and Agriculture Organization of the United Nations (FAO), many areas of secondary forest are projected to increase, especially in the tropics [15]. In contrast, in many other areas deforestation is expected to increase (e.g. arc of deforestation in Brazil) due to regional and global factors, such as population growth and demand for food and commodities [16]. However, little is known about the spatial distribution and interactions of the process of reforestation and deforestation across tropical countries. It is important that LULC research focuses on joint analysis of gains and losses of forest area, because both processes can occur at broad spatial scales that encompass a range of environmental and socioeconomic conditions; and ultimately, the dynamics and type of forests undergoing change have serious implications for carbon sequestration, reduction in carbon dioxide emissions, biodiversity, and soil conservation.

Monitoring forest cover at the national level is essential for developing and implementing appropriate biodiversity conservation and carbon emission reduction policies [17]. The successful design and execution of these policies depends on the accuracy of forest cover estimates through consistent methodologies that follow a comparable classification scheme [17,18]. Typically, forest cover assessments have been made using sensors with spatial resolution between 300 and 1,000 m and mostly at larger extents [19,20]. There have also been efforts to map forest cover using sensors (e.g. Landsat, CBERS, and SPOT HVR) with finer spatial resolution (less than 100 m) [17,21,22] but these analyses are typically for...
Figure 1. Map of the 13 ecoregions and 1117 municipalities in Colombia. Insert shows the distribution of the six biomes, and the five regions.
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sub-national regions. Nevertheless, land cover mapping at the national scale using higher resolution data has major limitations because of difficulties in getting cloud-free images, low temporal resolution, or high cost, and image gaps in the case of Landsat 7 [23]. Some developing countries have produced regional forest monitoring programs (e.g. India and Brazil), including data from their own national satellites with high resolution images from 20 to 70 m (see [21,24]). However, implementing systematic forest assessments such as those in India and Brazil in other developing countries is difficult because of the limitations in technical infrastructure, expertise, and data collection costs [17]. The Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data products are reliable and useful tools for monitoring land change in developing countries. Although MODIS has a minimum spatial resolution of 250 m, advantages include: high temporal resolution (i.e., daily) of imagery which can be composited to reduce cloud coverage and rapid data availability at no cost. These characteristics allow a complete LULC mapping composites to reduce cloud coverage and rapid data availability at no cost. These characteristics allow a complete LULC mapping at no cost. These characteristics allow a complete LULC mapping not only at the global and national scales, but regional and sub-regional scales as well [18,19,25]. Colombia is one of the most biodiverse countries on Earth [26] especially in the categories of plants, mammals, reptiles, amphibians, and birds [27,28]. Colombia also has one of the largest continuous forest areas in the tropics, covering at least 49% of the national land territory [25]. Despite its high biodiversity and natural resources, there is no consistent multi-temporal dataset of LULC change for Colombia. Forest cover assessments are mainly done by two official organizations, the IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales) and the IIAV (Instituto de Investigación de Recursos Biológicos Alexander von Humboldt). These organizations provide maps and reports at regional to national scales based on remote sensing products from MODIS and Landsat sensors, but ground-based forest inventories have not been made at the national scale. Another source of information is FAO, which estimates forest cover every five to ten years. The most recent FAO estimates in 2010 are based on 2002 maps provided by IDEAM [29], but FAO adjusts IDEAM data with their own methodology to standardized forest assessment in multiple countries. At regional and local scales, government agencies (e.g. Corporaciones Autónomas Regionales), non-government organizations (e.g. Fundación Natura), and local and foreign universities also have collected LULC data. Unfortunately, each organization uses their own mapping approaches and different spatio-temporal scales, which makes it difficult to compare LULC data among studies, regions, and years.

Land transformation is not homogeneous in Colombia, but rather varies greatly among its different ecological and political regions [26] (Figure 1). The Andes and the Caribbean regions have been the most impacted as part of the early colonization process (after 1500 AD; [30]) that severely affected its biodiversity and natural resources. However, since 1900 forest clearing has concentrated in the eastern lowlands, mainly in the Amazon and Orinoco regions [31]. Forest cover transformation in Colombia usually begins with the clearing of small areas used for subsistence agriculture, later these areas are often replaced by pastures for livestock grazing; and many of these areas are transformed in to mechanized agriculture (e.g. rice; [32]). Over the years, many such areas have been abandoned due to loss of soil productivity [32,33], rural-urban migration, technology improvement, and globalization of markets [34]; these processes promote forest recovery, but in some cases these abandoned lands continue in a degraded state [35]. Nevertheless, there is a lack of recent information about how LULC varies across the country and its regions, and between different ecosystems. Thus, there is a need for evaluating land change at multiple spatio-temporal scales using a consistent methodology across the various ecological and socioeconomic gradients of Colombia.

The purpose of the present study is to assess land change from 2001 to 2010 in Colombia, with a focus on three objectives: (1) determine how land change varies at the country, biome, ecoregion, and municipality scales; (2) identify and analyze the spatial distribution of areas experiencing significant land change; and, (3) discuss the implications of our findings for land use and conservation planning in Colombia. This research was based on a novel method for mapping LULC annually, which coupled MODIS (250 m) products with reference data interpreted from high spatial resolution imagery (QuickBird) in Google Earth that allows us to quantify land change at multiple spatial scales.

**Methods**

**Study Area**

Colombia is located in the northwestern part of South America, bordered by the Caribbean Sea to the north and the Pacific Ocean to the west, and occupying an area of 1.1 million km². Colombia has about 45.4 million people and an average population density of 40.1 people per km2 (see http://www.dane.gov.co). Differences in elevation and latitude produce large climatic variation across the country. For example, there are dramatic differences in annual precipitation, ranging from 330 mm (Guajira peninsula) to 12,000 mm (Pacific lowlands). Consequently, the combination of different climates, elevation ranges, and geographic location have allowed the development of a high diversity of habitats and species richness in Colombia, as well as an array of land uses.

Colombia can be divided into five continental regions (Andean, Caribbean, Pacific, Orinoco, and Amazon; Figure 1), 26 ecoregions, and 63 ecosystems [26]. These regions have remarkable biogeographic, socio-cultural, economic, and demographic differences. Consequently, LULC across the country has undergone distinct land transitions in the different regions. The Andean region is composed of three mountain ranges (Western, Central, and Eastern) that sustain montane ecosystems with multiple vegetation types. Pasturelands are the dominant land cover in the region (24%) compared with croplands (19%). The Caribbean region is characterized by xerophytic and subxerophytic vegetation types that correspond to arid and semiarid lowland areas. Lands in the Caribbean are mainly used for cattle ranching (48%) and another considerable fraction for agriculture (14%). The Pacific region contains a dense coastal lowland rain forest, where croplands cover a greatest area (10%) compared with pasturelands which cover less than 2%. In the Orinoco region (usually referred to as the Llanos), pasturelands (86%) and croplands (3%) have increased rapidly since the 1980’s. Finally, the Amazon, the largest and least transformed region of the country, is mostly covered by tropical rainforests; however, previous studies have estimated that deforestation has converted about 6% of forests into pasturelands, and less than 1% into legal and illegal croplands [36].

In this study, municipalities (second administrative level) were the main unit of analysis. According to the National Administrative Department of Statistics (DANE) data, the number of municipalities in Colombia was 1,100 in 2007. However, we included 1,097 municipalities instead of 1,100 because three municipalities were created after the last census in 2005. We also included 20 áreas no municipalizadas or corregimientos (name of the third administrative level in Colombia) because they occupied a large area (almost 190,000 km²) in the southern portion of the country (Amazonas, Guainía and Vaupés departments). All
analyses were thus performed on 1,117 municipalities or study units.

**Land-use/land-cover Mapping**

Our LULC classification methodology generally follows those first outlined by [18] and modified for continental-scale mapping in [37]. Here we summarize the three main steps that pertain to the Colombian national maps used in our analysis:

1. **Google Earth reference data collection** (≥10,000 samples): reference data for classifier training and accuracy assessment were collected with human interpretation of high-resolution imagery in Google Earth (GE, http://earth.google.com) mainly from Digital Globe’s QuickBird satellite (http://www.digitalglobe.com) spanning 2001 to 2010 [38]. Visual interpretation methods followed those in [18,38] and were performed by the authors (AMSC, M.A, and M.C) and student technicians. Samples were 250×250-m areas placed manually across the tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, and tropical and subtropical grasslands, savannas and shrublands biomes [39], which covered Colombia and extended into neighboring countries [38] (Figure S1). Samples were located with both random sampling and stratified random sampling, which included areas with mixed cover types, and samples well within patches of homogeneous cover, and no two samples were closer than 1,000 m apart [38]. Prior to interpretation, sample centers were snapped to the closest satellite image pixel (MODIS). Each sample class was assigned the year of the image and the percent cover of seven cover classes was visually interpreted: woody (woody vegetation including trees and shrubs); herb (herbaceous vegetation); ag (agriculture); plant (plantations); built (built-up areas); bare (bare areas); and water. If two interpreters agreed on the majority cover and GE image year of a sample, then their percent cover estimates were averaged. If the interpreters disagreed on the majority cover or year (mostly cover), then an “expert” (author) estimated the final class cover and recorded the year [38]. Samples were assigned to a class if the cover in this class was ≥80%, Samples with 20–80% woody, with a bare, herb or ag component <80% were assigned to a mixed woody class.

2. **Satellite imagery used in classification**: we used the MODIS MOD13Q1 Vegetation Indices 250 m product (Collection 5) for LULC classification [18,37]. The product is a 16-day composite of the highest-quality pixels from daily images and includes the Enhanced Vegetation Index (EVI), red, near infrared (NIR), and mid-infrared (MIR) reflectance and pixel reliability [40]. Twenty-three samples were available per year, with data available from 2001 to present. All MODIS scenes were reprojected from their native Sinusoidal projection to the Interrupted Goode Homolosine projection (sphere radius of 6,378,137.0 m) using nearest-neighbor resampling. The original cell size of 231.7 meters was maintained in the reprojection. For each pixel, we calculated the mean, standard deviation, minimum, maximum, and range statistics for EVI, and red, NIR and MIR reflectance values for calendar years 2001 to 2010. Statistics were calculated for all 12 months, 2 six-month periods, and 3 four-month periods. The MOD13Q1 pixel reliability layer was used to remove all unreliable samples (value = 3) prior to calculating statistics. If fewer than three samples were available for a statistics temporal window for a given year, then the statistics for that window were given null values.

3. **Mapping LULC with the Random Forest classifier**: we mapped LULC with the Random Forests (RF) tree-based classifier [41] following methods in [37]. An advantage of the RF classifier is that it provides an assessment of error with “out-of-bag” (OOB) samples, a form of multi-fold cross-validation [18,41]. These data can be used to calculate an error matrix, an unbiased estimate of accuracy, rather than withholding samples in an independent test dataset [18,41]. RF classifier was implemented using R v. 2.12.2. [42] and the randomForest package (v. 4.6-2; [43]) with 1000 decision trees, a minimum of 5 samples in terminal nodes (node-size = 5), and sqrt(p) as number of variables randomly sampled as candidates at each split, where p is number of variables (mtry = default). Predictor variables were MODIS-based 4-, 6- and 12-month statistics for EVI, red, NIR and MIR, and were extracted for the year corresponding to the QuickBird image year (range 2001 to 2010 [38]) for each GE reference sample. We trained four separate RF based on samples in separate biomes with boundaries defined by municipalities. The tropical and subtropical moist broadleaf forests biome was split to include an Amazon basin section and a coastal lowlands section, while the desert and xeric shrublands biome was combined with the tropical and subtropical dry broadleaf forest biome [37,38] (Figure S1). An initial RF for a biome was generated with the reference data class and MODIS predictor variables from that biome. The outlier function in randomForest was used to eliminate samples with an outlier metric greater than 10, and a final RF was generated from the remaining samples, leaving 10,143 of 10,622 (96%) samples for training the final RF (Table 1). We used R and the RGDAL library to apply the RF objects to every pixel in MODIS tiles covering the zone-biome region for each year, 2001 to 2010. For a given year, if a pixel had valid 4-, 6- and 12-month statistics, then the class was assigned based on the initial RF; a secondary RF based on just 12-month statistics was applied to pixels that had only valid 12-month statistics; and, the pixel was assigned a No Data value if it had no valid predictor variables (e.g., areas with persistent cloud cover, beach/water interfaces along coasts). On average each annual map had 0.14%±0.09% of the area covering Colombia mapped as No Data. Pixels with ≤ 4 No Data values over 10 years were set to a null value and excluded from our maps, as these were unreliable areas for mapping – mostly coastal areas in Colombia. The four separate maps were then mosaicked and reclassified (post-classification) by grouping ag and herb, mixed woody and plant, and built and bare. The combining of classes into a five-class scheme helped reduce inter-class confusion and increase map accuracy while still allowing us to focus on major trajectories of change in woody vegetation. Based on the OOB statistics, the final five-class maps had an average overall accuracy of 87.4% (±4.3%), with non-water average producer’s accuracies ranging from 36.3% (mixed woody/plant) to 96.9% (woody) and user’s accuracies ranging from 72.5% (mixed woody/plant) to 89.4% (woody) (Table 2). The five-class LULC map was then summarized for the 1,117 municipalities.

**Land Change Dynamics**

To describe the patterns of land change, for the three most important vegetation classes (woody, mixed woody/plant, and ag/herb) within each municipality, we analyzed the trends performing a linear regression of cover area (dependent variable) against time (independent variable, each of the 10 years between 2001 and
If more than 1% of the total municipality area had pixels mapped as No Data for a given year, then the land cover data for that year were removed from the regression. To determine the strength of this linear relationship we used Pearson’s correlation coefficient ($R$), where positive values of $R$ represent an increase in a LULC cover and negative values of $R$ represent a decrease. We used this approach to standardize land change through time due to outliers or missing data in any given year, and the use of $R$ for trends allows us to compare municipalities, which can vary in size from 17.6 km$^2$ to 65.568 km$^2$. In addition, this trend analysis takes advantage of the ten years of data, and it is not based on just two points in time. Municipalities with significant changes in any cover had $p \leq 0.05$. All analyses incorporating absolute area were performed using estimates based on the each municipality’s regression model, rather than the raw area data used to fit the model.

We calculated the net change in cover (km$^2$) of the three classes between 2001 and 2010 considering four scales: country, biome, ecoregion, and municipality. Biome and ecoregion scales were established following the World Wildlife Fund biome and ecoregion framework [39]. We clustered municipalities into the six major biomes and 25 ecoregions that were described for Colombia (Table S1). Municipalities present in more than one biome and ecoregion were classified as the unit with the greatest area in each municipality. We included tropical and subtropical moist broadleaf forest (Moist Forest), tropical and subtropical dry broadleaf forest (Dry Forest), tropical and subtropical grassland, savanna and shrubland (Grassland), Montane Grassland and Shrubland (Montane Grassland), Desert and Xeric Shrubland (Desert), and Mangrove (Mangrove) biomes. We reduced the 25 ecoregions to 13 because some ecoregions were represented by only one or a few municipalities (Figure 1). For example, Western Ecuador Moist Forest (NT0176) was present in only one municipality (Tumaco). Therefore, this municipality was aggregated to the largest and closest ecoregion (Choco´-Darien Moist Forest/NT0115), which also contained similar environmental characteristics. We performed a Mann-Whitney test in R (v. 2.12.2; [42]) to determine if there was a significant difference in the size of municipalities that gained or lost woody vegetation.

### Results

#### Land-use/land-cover Change from 2001 to 2010

At the country level, woody vegetation was the most predominant land cover (Figure 2). Woody cover increased from 580,420 km$^2$ in 2001 to 597,383 km$^2$ in 2010, with a net gain of 16,963 km$^2$. Ag/herb class also increased from 383,097 km$^2$ to 397,741 km$^2$ with a net gain of 14,644 km$^2$. In contrast, mixed woody/plant decreased from 151,930 km$^2$ in 2001 to 122,648 km$^2$ in 2010, with a net loss of 29,282 km$^2$.

At the biome level, woody cover only decreased in the Grasslands biome (1,636 km$^2$), while it increased in the other five biomes, from 16,077 km$^2$ in the Moist Forest to 57 km$^2$ in the Montane Grassland.

### Table 1. Mapping regions and total sample counts used in each separate Random Forest (n = 4).

| Geographic region                      | Ag  | Bare | Built | Herb | Mixed woody | Plant | Woody | Water | Total |
|----------------------------------------|-----|------|-------|------|-------------|-------|-------|-------|-------|
| Tropical and Subtropical Moist Broadleaf Forests (TSMBF) |     |      |       |      |             |       |       |       |       |
| Amazon/Chocó                           | 44  | 75   | 58    | 792  | 379         | 86    | 2,794 | 823   | 5,051 |
|                                        | 334 | 9    | 131   | 327  | 151         | 77    | 797   | 309   | 2,135 |
| Tropical and Subtropical Dry Broadleaf Forests (TSDBF) |     |      |       |      |             |       |       |       |       |
| Northern S. America                    | 279 | 75   | 147   | 380  | 187         | 96    | 422   | 239   | 1,825 |
| Tropical and Subtropical Grasslands, Savannas, Shrublands (TSGSS) |     |      |       |      |             |       |       |       |       |
| Llanos                                 | 201 | 32   | 42    | 378  | 116         | 42    | 167   | 154   | 1,132 |

These include only samples filtered by the Random Forest outlier removal step (Biomes follow Olson et al. 2001).

### Table 2. Classification accuracy assessment.

| Biomes                  | Samples | Overall (%) | Ag/Herb | Bare/Built | Mixed woody/plant | Woody | Water | Ag/Herb | Bare/Built | Mixed woody/plant | Woody | Water |
|-------------------------|---------|-------------|---------|------------|-------------------|-------|-------|---------|------------|-------------------|-------|-------|
| Moist Forest$^1$         | 5,051   | 92.2        | 86.5    | 64.7       | 49.7              | 100   | 99.9  | 78.7    | 86.9       | 73.6              | 97.7  | 95.8  |
| Moist Forest$^2$         | 2,135   | 89.2        | 90.5    | 91.4       | 33.3              | 99.6  | 100.0 | 83.5    | 89.5       | 71.0              | 92.6  | 99.0  |
| Dry Forest$^3$           | 1,825   | 82.0        | 87.3    | 90.1       | 32.5              | 92.4  | 100.0 | 78.6    | 82.6       | 68.7              | 81.6  | 100.0 |
| Grasslands$^4$           | 1,132   | 86.1        | 97.4    | 67.6       | 29.7              | 95.8  | 100.0 | 83.9    | 89.3       | 77.0              | 86.0  | 98.1  |
| Total/Avg               | 10,143  | 87.4        | 90.4    | 78.4       | 36.3              | 96.9  | 99.9  | 81.1    | 87.0       | 72.5              | 89.4  | 98.2  |

**Biome description:**
- $^1$Tropical and Subtropical Moist Broadleaf Forest (Amazon basin section).
- $^2$Tropical and Subtropical Moist Broadleaf Forest (Coastal lowlands section).
- $^3$Tropical and Subtropical Dry Broadleaf Forest.
- $^4$Tropical and Subtropical Grasslands, Savannas and Shrublands.

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Grasslands (Figure 2). The mixed woody/plant class in turn, increased only in the Desert biome (621 km²), while there was a large decrease in the Moist Forest biome (27,181 km²). The ag/Herb cover only decreased slightly in Mangroves (21 km²), while increasing in the rest of biomes from 10,652 km² in the Moist Forest to 58 km² in the Dry Forest.

In 2001 and 2010, woody vegetation was the dominant cover in four ecoregions, while ag/Herb vegetation was the dominant cover in nine ecoregions (Figure 2). Land cover change varied greatly among ecoregions. Woody vegetation decreased only in Apure-Villavicencio and Llanos ecoregions with a reduction of 691 km² and 1,636 km², respectively. In the other eleven ecoregions woody vegetation increased, seven of which had a net gain of more than 1,200 km². The net gain varied from 4,535 km² in the Northern Andean forests to 63 km² in the Northern Páramo ecoregions. The Caquetá Moist forest ecoregion, the largest ecoregion in Colombia (472,066 km²) also had a small increase in woody cover (144 km²) when compared with the rest of the ecoregions. Mixed

Figure 2. Absolute area of woody vegetation (W), mixed woody/plant (MWP), and ag/herb (AH) from 2001 to 2010 at the country, biome (B) and ecoregion (E) scales. These estimates are based on estimates from municipality-scale regression models and include all municipalities.
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woody/plant class increased only in the Guajira Xeric ecoregion (532 km²), and decreased in more than 1,500 km² in eight ecoregions. Mixed woody/plant net loss varied between 7,147 km² in the Magdalena-Uraba Moist forest and 9 km² in the Magdalena Valley Dry forest ecoregions. The ag/herb vegetation mainly decreased in the Sinú-Valley Dry forest (1,347 km²), the Northwestern Andean (869 km²), and the Cauca-Valley Montane forest (310 km²). The net gain in ag/herb vegetation varied between 5,236 km² in the Caquetá Moist forest and 25 km² in the Magdalena-Valley Dry forest.

At the municipality level, woody vegetation increased in 73% (820) of the municipalities with a net gain of 26,092 km², and decreased in 24% (264) of the municipalities with a net loss of 11,129 km² (Table S2). In contrast, the mixed woody/plant class increased in 91% (347) of the municipalities with a net gain of 5,199 km², while it decreased in 68% (762) of municipalities with a net loss of 34,461 km². For the ag/herb class, the number of municipalities gaining (53%; 387) and losing (47%; 526) cover was similar, but the area gained was almost double (28,345 km²) of that lost (13,701 km²). We also found that 21% (232) of the municipalities showed significant change in woody vegetation during the last decade. This percentage was similar for mixed woody/plant (23%; 254) and for ag/herb (20%; 225). If we only considered municipalities with significant changes during the last decade, we detected a close correspondence between loss and gain of woody vegetation, mixed woody/plant, and ag/herb classes (Figure 3). Examples of this dynamic include: i) areas where woody vegetation was transformed into ag/herb in the southern part of the Magdalena Medio and the Llanos piedmont regions; ii) transitions from ag/herb vegetation to woody vegetation were located in western Cundiboyacense highplain, and between Nudo de los Pastos and the Macizo Colombiano (Figure 3A); iii) transitions from mixed woody/plant to ag/herb vegetation appeared in the Magdalena Medio and the Alto Caquetá regions; iv) transitions from ag/herb vegetation to mixed woody/plant were located only in the north of the Cundiboyacense highplain (Figure 3B); v) transitions from woody to mixed woody/plant was not common; and, v) transitions from mixed woody/plant to woody vegetation were concentrated in the Catatumbo and to the north of the Magdalena Medio, as well as to the north of the central and western Andean mountain ranges (Figure 3C). The average size of the municipalities that significantly gained or lost woody vegetation was 608 km² and 3,113 km², respectively, and this difference was significant (Mann-Whitney U = 3.6, p = 0.0003).

Finally, to determine the hotspots of woody vegetation change we selected the top 10 municipalities with the greatest net gain or loss in woody cover (Table 3). The top 10 municipalities with the greatest woody vegetation gain account for 14% of the total woody increase, and 42% of the increase when only considering municipalities with a significant change in woody vegetation. Interestingly, Cumaribo, the largest municipality in Colombia, accounted for almost 4% of total increase in woody vegetation and 11% considering municipalities with a significant gain. The 10 municipalities with the greatest woody vegetation loss account for 27% of total decrease, and 91% of municipalities with a significant loss in woody cover. Municipalities showing the greatest net gain were located primarily in the Magdalena-Uraba Moist forest and Chocó-Darién Moist forest, while those with the greatest net loss were located mainly in the Llanos, Apure-Villavicencio, and Northern Andes.

**Discussion**

**Patterns of Land Cover Change at the Country Level**

Our results show that during the last decade, land change in Colombia has been characterized by an unexpected net gain in woody cover, increasing by 16,963 km² or 3% of its initial area in 2001. In contrast, previous literature has highlighted dramatic forest loss at the national [22] and regional scales [32,44]. Woody cover as well as ag/herb classes expanded mostly at the expense of the mixed woody/plant class at the national and municipality levels. At first glance, it appears that woody regrowth results from secondary forest/shrub recovery rather than recently abandoned agricultural areas. Forest regrowth at the national scale is consistent with the general reforestation trends in Europe, the U.S.A. [45], and in other Latin American countries such as Ecuador, the Dominican Republic, Puerto Rico, Costa Rica [11–14]. However, secondary vegetation regrowth in Colombia might be the effect of land abandonment resulting from armed conflicts and economic development experienced during the last 10–20 years [46]. Land abandonment of rural areas began in the early 1990s when the Colombian government implemented an economic liberalization model, and it continued in the late 1990s as a result of the intensification of internal conflicts. The effects of these conflicts and the associated political decisions have been documented for the Caquetá region [47]. Although the amount of woody vegetation gained was almost three times higher than the amount of forest lost, it is clear that deforestation continues. Extensive woody cover losses occurred in municipalities principally to the southwest of Magdalena Medio (e.g. Segovia and Remedios) and in the Llanos regions (e.g. San Luis de Palenque, Tame), where 3,000 km² of woody vegetation were converted to croplands and pastures. Deforestation in these areas is related to gold mining and oil exploitation activities, and agricultural expansion. For example, in the Magdalena Medio region woody vegetation has been cleared for small-scale agriculture and timber extraction by miners since the 1990s [48]. In the Llanos, the construction of the Villanueva-Yopal road and the road infrastructure to aid oil exploration has stimulated the expansion of trading, cattle, and agriculture. For example, rice cultivation has increased from 1,300 km² in 2001 to 1,800 km² in 2009 [49]. The decrease in woody vegetation in these regions affects areas of global importance for biodiversity such as Serranía de San Lucas located to the south of Magdalena Medio [48] and along the Andean foothills in the Llanos.

Overall, we report a forest area of 580,420 km² in 2001 which is lower than the 617,328 km² and 615,090 km² (for the year 2000) reported by IDEAM and FAO, respectively (Table 4). Additionally, we reported an increase in 2005 and 2010, which contrasts with the large forest decrease reported by IDEAM and the slight decrease reported by FAO. In contrast, our estimates are in agreement with MOD44B Vegetation Continuous Field (VCF—using an 80% forest crown cover; [50]) results which also reported a forest area increase. However, we estimated a net gain (16,963 km² from 2001 to 2010) which is much more conservative than the gains (83,515 km² from 2000 to 2005) estimated by MOD44B (VCF). These differences can be attributed to the use of different MODIS image inputs, spatial resolution (ours 250 m vs. VCF 500 m) and processing methods, as well as differences in forest (woody vegetation) definition. For example, VCF includes plantations in forest cover. FAO defines “forest” as lands of more than 0.5 ha covered by trees over 5-m height, 10% crown cover, and include areas with native and plantation trees [29]. IDEAM classifies “forest” as lands more than 1 ha, trees over 5-m height, with 30% crown cover, that
also includes shrubs, palms, and bamboo, but not tree plantation [22]. In contrast, our definition of forest or “woody” vegetation differs from the former definitions because we include trees and shrubs, i.e., no height requirement with ≥80% cover. Consequently, our definition of mixed woody vegetation (20–80% woody) combined with plantations is more comparable to FAO’s and IDEAM’s definition of “forest”. In addition, FAO and IDEAM estimates showed the same deforestation trend because their definitions of forest are somewhat similar and FAO results are typically based on existing maps provided by IDEAM [29]. Nevertheless, IDEAM maps in 2000, 2005, and 2010 lacked information for approximately 8% of Colombia due to cloud coverage. Thus, conclusions drawn from these maps could be misleading in either direction with regard to forest cover. These areas without information from IDEAM were scattered across the country, particularly in the north portion of the Pacific region and areas spread throughout the Andes and the Amazon regions where cloud cover is high, and where at the same time we found the largest net gain in woody vegetation.

In general, our methodology to map annual LULC in Colombia, which combined MODIS products, Google Earth reference data, and Random Forest classifier [37], provides a consistent classification scheme at multiple spatial-temporal scales. The high accuracy values we obtained demonstrate the robustness of the mapping method and the reliability of our LULC maps.
which have several advantages with respect to previous maps, including: (1) quantification of both deforestation and reforestation patterns across the country at multiple spatial scales; (2) using Google Earth reference data collection for classifier training and accuracy assessment (rather than ground-based reference data collection) which provides us a fast and inexpensive way to acquire reference data across the whole country, a large part of which is difficult to access; (3) use of temporally-composited MODIS data, which greatly reduces the amount of pixels adversely affected by cloud coverage and thus allows wall-to-wall LULC change monitoring; and, (4) leveraging 10 years of annual LULC area at municipality level to better estimate 2001 to 2010 net change, thus reducing the influence of climate fluctuations or other factors that could bias analyses based on just two years of data, and to determine which municipalities had significant increases or decreases in area while normalizing differences in municipality area.

Table 3. Top ten municipalities with the greatest net gain (+) and net loss (−) of woody vegetation between 2001 and 2010.

| Municipality   | State      | Ecoregion       | Municipality Area (km²) | Net Change (km²) | Woody (R) | (p-value) | % Change |
|----------------|------------|-----------------|-------------------------|------------------|-----------|-----------|----------|
| Cumaribo       | Vichada    | Caquetá Moist   | 65,568                  | +1,065           | 0.79      | 0.005     | 3        |
| Tibú           | N. Santander | Mag-Urbá Moist | 2,680                   | +638             | 0.87      | 0.0008    | 45       |
| Uribe          | La Guajira | Guajira Xeric   | 7,890                   | +589             | 0.67      | 0.03      | 2,148    |
| Magui          | Nariño     | Chocó-Darién Moist | 1,634                | +394             | 0.66      | 0.03      | 62       |
| Medio Baudó    | Chocó      | Chocó-Darién Moist | 1,428              | +344             | 0.63      | 0.04      | 56       |
| Lloró          | Chocó      | Chocó-Darién Moist | 802                 | +322             | 0.74      | 0.05      | 108      |
| Sardinata      | N. Santander | Mag-Urbá Moist | 1,454                   | +211             | 0.78      | 0.007     | 26       |
| Rovioje       | Bolivar    | Mag-Urbá Moist | 1,284                   | +178             | 0.64      | 0.04      | 40       |
| San Benito Abad | Sucre   | Mag-Urbá Moist | 1,520                   | +164             | 0.83      | 0.002     | 447      |
| Tiquisio       | Bolivar    | Mag-Urbá Moist | 773                    | +134             | 0.62      | 0.05      | 52       |
| La Macarena    | Meta       | Caquetá Moist   | 10,756                  | −712             | −0.62     | 0.05      | −17      |
| Arauquita      | Arauca     | Apure-Villavicencio | 3,218              | −471            | −0.63     | 0.04      | −29      |
| Tame           | Arauca     | Apure-Villavicencio | 5,433            | −409            | −0.74     | 0.01      | −17      |
| Remedios       | Antioquia  | Northern Andean | 2,045                  | −384             | −0.87     | 0.001     | −27      |
| Mapiripán      | Meta       | Llanos          | 12,018                  | −359             | −0.75     | 0.01      | −5       |
| Puerto Gaitán  | Meta       | Llanos          | 17,397                  | −199             | −0.83     | 0.002     | −10      |
| Fortul         | Arauca     | Cordillera Oriental | 1,067            | −126            | −0.84     | 0.03      | −24      |
| Trinidad       | Casanare   | Llanos          | 2,973                   | −121             | −0.74     | 0.01      | −26      |
| San Luis de Palenque | Casanare | Llanos          | 3,005                  | −104             | −0.61     | 0.05      | −27      |
| Segovia        | Antioquia  | Northern Andean | 1,154                  | −103             | −0.83     | 0.002     | −10      |

Columns show area, net change, correlation coefficient (R), p-value, and the percentage of change of the top ten municipalities with greatest net gain and loss between 2001 and 2010.

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Table 4. A comparison of four estimates of woody vegetation class at the national scale.

| Year | Woody vegetation area (km²) |
|------|-----------------------------|
|      | This study (W) | This study (W+MWP) | IDEAM¹ | FAO² | MOD44B² (VCF 500 m) | MOD44B³ (VCF 500 m) |
| 2000 | n.a.              | n.a.               | 617,328 | 615,090 | 269,195 | 820,392 |
| 2001 | 580,420           | 732,350            | n.a.   | n.a.   | 298,170 | 839,487 |
| 2005 | 587,953           | 726,817            | 602,063 | 610,040 | 352,710 | 832,261 |
| 2008 | 593,611           | 722,723            | n.a.   | n.a.   | n.a.   | n.a.   |
| 2010 | 597,383           | 720,031            | 586,336 | 604,990 | n.a.   | n.a.   |

¹Data including only woody vegetation.
²Data including woody vegetation+mixed woody/plant.
³Forest cover (80 crown cover).
²Forest cover (25 crown cover).

Sources:
¹Cabrera E, Vargas DM, Galindo G, García MC, Ordoñez MF, et al. (2011).
²FAO (2010) Global Forest Resources Assessment 2010.
³Hansen M, DeFries R, Townshend JR, Carroll M, Dimiceli C, et al. (2006).

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We acknowledge that there are two potential caveats to our study. First, MODIS pixels will not detect small-scale changes (e.g., slash and burn agriculture, <5 ha) due to its lower spatial resolution. However, the accumulative change from the small-scale conversion can be captured by our 10-year trend analysis based on the aggregation of all pixels within a municipality. Although Landsat provides higher spatial resolution which facilitates detection of small-changes, there are major gaps due to clouds cover that make it difficult to map the whole country using Landsat imagery. Second, using reference data from QuickBird imagery in Google Earth could include interpretation and spatial error. For example, visual interpretation of some land cover classes in Google Earth is difficult, and therefore, our cover classes were very general. Even though our classes were relatively easy to identify, interpreters sometimes disagreed on ag and herb samples for which an expert determined the final class label. Additionally, spatial error can be the result of terrain distortions especially in QuickBird images that have not been orthorectified. However, it has been shown that QuickBird scenes are very accurate with an average error of 10 m of disagreement between ground control points and GE QuickBird images [18].

Potential Factors Explaining Woody Vegetation Recovery

There are three potential factors that could explain the increase in woody vegetation observed in our LU/LC maps. First, the possible explanation could be an increase in oil palm plantations. Oil palm plantations have expanded rapidly since the 1990s when Colombia initiated its economic liberalization model [51]. According to The National Federation of Oil Palm Growers (Fedepalma), palm plantations for oil extraction increased from 180 km² in the 1960s to almost 3,600 km² in 2010–mainly in the Meta, Casanare, Cesar, Magdalena, Bolivar, Cundinamarca, Santander, Norte de Santander, and Nariño departments. Nevertheless, we do not believe that oil palm plantations are an important component of the woody recovery we described. First, we classified plantations separate from woody vegetation. Second, municipalities identified by IGAC [52] as having large areas of oil palm plantations do not coincide with the municipalities we identified as important areas of reforestation. In fact, our results showed that from 2006 to 2008, 76% of the municipalities had net gain in woody vegetation (total of 4,740 km²). However, during the same period of time, only 7% of the municipalities had a net gain in palm oil plantations (362 km²; [52]). In addition, taking into account the ten municipalities with the greatest net gain in woody vegetation from 2006 to 2008, only Tibú (net gain of 142 km²) and Riohacha (net gain of 81 km²) have oil palm plantations (net gain of 50 and 3 km², respectively; [52]).

A second factor that could explain woody recovery is coca crops eradication programs. At the national scale, coca cultivation area dropped from 1,448 km² in 2001 to 618 km² in 2010 [53]. Eradication programs, both manually and by aerial spraying, have been implemented intensively in several localized areas of lowland forests in the Moist Forest biome. Eight of the top 10 municipalities with the greatest net gain in woody vegetation cultivated coca in 2001 (189 km²; [53]). By 2010, the area of coca in these municipalities declined to 58 km². The majority of this decline occurred in Cumaribo and Tibú municipalities, which lost 128 km² of coca plantations between 2001 and 2010. It is possible that we are detecting the first stages of natural regeneration (i.e., shrubs) following the eradication of these illicit crops.

The third potential factor that could explain the increase in woody cover, particularly in seasonal forests (i.e., dry forests), is related to the inter-annual variation in precipitation. In these areas, anomalous rainfall years (e.g., La Niña events) could change the vegetation greenness trends detected by MODIS sensors. This phenomenon could change woody vegetation to mixed woody and vice versa, especially for pixels near the 80% decision threshold. However, we attempted to minimize this effect using regression models by municipality, capturing 10-years of real trends in vegetation dynamics. It would be desirable to use high resolution data such as Landsat to evaluate the accuracy in our LU/LC maps and to verify observed land change; however, on an annual basis it is difficult to obtain the necessary temporal data for the entire country for detecting any climatic anomalies.

In summary, the national assessment of land cover change in Colombia indicates that woody vegetation gains occur in small municipalities and exceed woody vegetation losses occurring in large municipalities. This scale of analysis gives a valuable general overview of current land change, but it can mask woody vegetation losses in some areas. National scale analysis does not take into account intrinsic differences (e.g., socioeconomic, demographic, and biophysical) among regions which can promote different land cover patterns and dynamics. Therefore, by examining data at the biome and ecoregion scales it is possible to decipher where and to what extent changes in woody vegetation are occurring, and to better understand the underlying environmental and social drivers of this change.

Patterns of Land Cover Change at the Biome and Ecoregion Scales

**Moist forest biome.** This biome accounts for 86% of the total increase in woody cover. It is the largest biome in Colombia (Table S1) consisting of seven ecoregions which contain both montane forest (4 ecoregions) and tropical forest (3 ecoregions). This recovery occurred mostly from mixed woody/plant, generated in previous periods and less directly from ag/herb vegetation (Figure 2). The net gain in woody vegetation was located especially in the montane forest of the Andes mountain ranges (70%) and in the tropical forest in the Amazon and the Pacific regions (30%). Other studies have quantified forest regeneration in Colombia from secondary vegetation and abandoned pastures, particularly in the Amazon [54] and in the Andes regions [22]. This pattern of forest regrowth in the Moist Forest Biome has also been reported for Venezuela and Costa Rica [55] but, deforestation continues to be the major trend in this biome. These contrasting dynamics are driven by multiple factors including an increase in the global demand for meat (deforestation), as well as the abandonment of marginal agriculture lands and changing patterns of precipitation [55–57].

The four montane forest ecoregions (in the Moist Forest biome) located in the Andes mountain ranges contributed 65% of the total net gain in woody vegetation in Colombia, particularly in the Northern Andean (27%), the Northwestern Andean (22%), and Cauca-Valley (11%) Montane Forest ecoregions. Woody vegetation increases are likely explained by human causes such as the abandonment of traditional productive systems in the 1990s due to harsh environmental conditions (e.g., arid areas) and globalization processes which have promoted strong rural migration in many municipalities [58]. For example, 43% of municipalities located in the Chichamocha region (Northern Andean ecoregion) lost population between 1993 and 2005 (see http://www.dane.gov.co), and the area is now experiencing significant change from mixed woody/plant class to woody vegetation (mostly shrubland cover; Figure 3C). Similar abandonment patterns can be observed in the Cundiboyacense highplains (Northern Andean ecoregion) where many municipalities are transitioning primarily from ag/herb to woody vegetation. However, reforestation programs to protect watersheds [59] and to restore degraded areas [60] could also
explain part of the woody increase in this area. These factors have also facilitated a significant reforestation (transitioned from ag/herb to woody) of large expanses of montane forest to the south of the Northwestern Andean (between the Macizo Colombiano and Nudo de los Pastos) and to the north of the Cauca-Valley Montane forest ecoregions as well. This reforestation trend has been seen in both developed and developing countries, supporting the idea that the abandonment of less productive lands and the globalization of markets may lead to the regrowth of secondary forest [61,62].

All three ecoregions in the Moist Forest biome experienced gains in woody and ag/herb vegetation, which transitioned from the mixed woody/plant vegetation class. For instance, the Magdalena-Urahá Mois Forest ecoregion showed a remarkable decrease in mixed woody/plant class, particularly in the Magdalena Medio region where 46% transitioned to woody vegetation and 44% transitioned to ag/herb vegetation, the remaining area transitioned to other classes (i.e. built-up and bare soil). Woody vegetation in the Caquetá Mois forest ecoregion seems to be stable, contributing only 0.8% of the total net gain in woody vegetation in Colombia. These results coincide with data from the Amazon forest, which showed forest regrowth transitioned primarily from previous croplands [44]. However, our findings contrast with the IDEAM results that include the Amazon region as one of the deforestation hotspots of the country [22]. But, if we combine our woody vegetation and mixed woody/plant classes, which is more comparable with the definition of forest used by IDEAM, we detect a loss of >5,000 km². Virtually all of this change is from mixed woody/plant to ag/herb. These losses in the Caquetá Mois forest are the result of small-scale subsistence agriculture (driven by rural-rural migration [63] and illicit crops, particularly in the Alto Caquetá in the Caquetá department.

Grasslands biome. This is the second largest biome in Colombia and includes only the Llanos ecoregion. The Llanos is increasingly being considered as the new agricultural frontier of Colombia (see: http://webapp.ciat.cgiar.org/es/descargar/pdf/convenio_colombia_ciat.pdf). Large woody vegetation losses were located mainly in the central area of Casanare and the eastern area of Meta departments where an intense land conversion is associated with human population change and investments in infrastructure to support an important oil exploration activity and agricultural intensification. High rates of land conversion (towards mechanized agriculture and cattle grazing) corresponding with urban population growth and migration have been registered since the 1980s [64], a pattern that appears to continue today. Between 1993 and 2005, 92% of the municipalities gained people (see http://www.dane.gov.co) and 85% gained ag/herb vegetation, implying that agriculture (e.g. rice) and pastures are still expanding, as in many other regions [65,66]. Nevertheless, the transformation of savannas in the Orinoco region, which is steadily increasing and currently a major land use change in Colombia [67], cannot be quantified with our method as it will be a transition from herbaceous vegetation to agriculture, which are both contain in our combined ag/herb class. Changes are only detected when the change is to perennial plantations.

Dry forest biome. This is the third largest biome and includes three ecoregions: Magdalena Valley, Sinú Valley, and Apure-Villavicencio Dry forest. This biome accounts for 4% of the total increase in woody vegetation and its recovery was the result of a transition mostly from ag/herb vegetation in the Sinú Valley Dry forest. From 1990 to 2003, the cotton industry decreased in the Sinú valley due to changes in pricing policies and competition with the subsidized international markets that significantly affected its area and production. Consequently, this crop had an annual loss rate of 13% of cultivated land between 1990 and 2003 [68]. The Apure-Villavicencio Dry forest ecoregion showed a decrease in woody vegetation as a result of agriculture and pastures expansion (as in the Llanos ecoregion). This expansion was located particularly in the foothills of the Arauca department where the majority of the population is located. According to the DANE censuses, 93% of the municipalities in the Apure-Villavicencio Dry Forest ecoregion gained people between 1993 and 2005 and 87% gained ag/herb vegetation. We believe that the expansion of intensive agriculture and cattle pasture will continue as a major driver of deforestation in this region.

Desert and mangroves biomes. These biomes only include the Guajira Xeric ecoregion which had a net gain in woody vegetation. These biomes account for 9% and 0.7% of the national increase in woody vegetation, respectively. The increase in woody vegetation in the Desert biome was concentrated in three municipalities that alone account for 73% of the total increase in this biome. The gain in woody in these municipalities could be related to a precipitation anomaly (e.g. 2009) or perhaps a problem in the classification given that the Desert biome was classified as part of the Dry Forest biome (Table 2). Woody regrowth (mostly shrubland cover) in the Deserts have been reported in Mexico and U.S as a result of the increase in annual precipitation and the decrease of fire and grazing, respectively [57,69]. On the other hand, in the Mangrove biome, woody gains are likely the result of the implementation of conservation and management strategies of mangrove ecosystems across the country [70]. For example, the increase in woody vegetation was located in two municipalities (98% of the total increase in this biome) that contain the Via Parque Isla de Salamanca protected area, which was declared a Ramsar Site in 1998 and Reserve for Humankind and the Biosphere by UNESCO in 2000 (see http://www.parquesnacionales.gov.co).

Montane grasslands biome. This biome includes the Northern Andean Páramo ecoregion which had a slight increase in woody vegetation, accounting for only 0.3% of the national increase in woody vegetation. The gain could be the result of regrowth in areas previously occupied by Papaver somniferum (poppy) plantations. Between 1993 and 2008, the area in poppy fields decreased from 75 km² to 4 km² across Colombia [71]. This biome has also experienced a significant increase in ag/herb vegetation. The gains in ag/herb cover were located mainly in municipalities in the Santiago and Boyacá departments where potato farming and cattle grazing are important activities. In these departments, the cultivated area of potato increased from 380 km² to 482 km² between 2006 and 2008 [32] in response to the national and international demand for potato products. Since the potato is the agricultural product with highest consumption per capita in Colombia [72], its cultivation is expected to expand in the near future, adding more pressure on the Páramo ecosystems.

Implications for Conservation Planning

The implementation of protected areas is an important mechanism to reduce forest conversion and subsequent loss of species [73]. In Colombia, 56 protected areas (12% of the national's territory) are effectively reducing the probability of forest clearing [44]. Nevertheless, many protected areas are located in places with lower forest conversion risks [74]. Therefore, to increase the impact of conservation efforts, the Colombian protected area network should target areas with low levels of protection and high rates of land transformation. For instance, the Llanos and the Apure-Villavicencio ecoregions are underrepresented in the protected area network (see http://www.parquesnacionales.gov.co), and this is where we detected the
highest rates of woody vegetation loss. These areas have had extensive areas of natural savanna vegetation transformed to crops and pastures during the past 20 years [64,67]. We suggest that a primary conservation goal in Colombia should be the implementation of protected areas in these regions. The Llanos ecoregion is particularly important given its heterogeneous landscapes, its high diversity of vegetation types, and its large numbers of plants, amphibians, reptiles, and fish [75]. Not surprisingly, this ecoregion has been cataloged within the Global 200, which is a set of the most outstanding ecoregions for global conservation [75]. In addition, the Apure-Villavicencio dry forest should be taken into account in the protected areas network because it represents the transition zone between the Andean foothills and the llanos savannas where a relatively high number of plant, reptile, and bird species (including several endemics) coexist (See http://www.worldwildlife.org/wildworld/profiles/terrestrial nt.html# trop-grass). We also documented a large decrease in mixed woody/plant in the Magdalena-Uraba Moist forest ecoregion, particularly in the Magdalena Medio region. The increase in agriculture and pastures combined with ongoing illegal logging activities [70,76] have endangered a great number of native timber species (e.g. Libidibia ebano, Cariniana pyriformis). This region should be considered for the protected area network given that there is only one reserve (Serranía de los Yariguíes national park) in this region.

On the other hand, the recovery of woody vegetation in the Andes Mountain Ranges is an excellent opportunity to complement, expand and interconnect the protected areas to create a conservation network across the rural landscape mosaics in the region. A relevant area for conservation is the Northern Andean Montane Forest ecoregion, which is also included in the Global 200 [75]. In this ecoregion, the Cundiboyacense highplain had a substantial and significant gain of woody vegetation between 2001 and 2010. Other authors have stressed the importance of this region as a priority area for conservation due to its large areas of land transformation and large number of species at risk [74]. We also highlight that even though the Northern Andean Páramo ecoregion gained slight amounts of woody vegetation, the gains in the ag/ herb class were almost three times higher than woody cover gains, and therefore, the Andean Páramos remains a threatened ecosystem.

Overall, the present study indicates that at the national scale, woody vegetation gains exceed losses between 2001 and 2010. The majority of woody gains occurred in the Moist Forest biome. Analysis at the ecoregion scale showed that montane forest ecoregions contributed substantially to woody vegetation regrowth in Colombia, while the Llanos and Apure-Villavicencio ecoregions experienced the largest woody losses. The gain of woody vegetation does not necessarily imply the recovery of the high biodiversity characteristic of the original forests in many of these regions. If these “new forests” are allowed to grow, they are likely to recover a large proportion of their biodiversity in the next 40–50 years [77]. Guiding efficient conservation actions requires a better understanding of land cover change and its drivers. Consequently, our maps and land cover trends are a baseline to evaluate the effects of environmental, socioeconomic, and demographic factors on land cover change in Colombia.

Supporting Information
Figure S1 Distribution of reference data points collected from Google Earth within each of the three biomes which covered Colombia and neighboring countries. Biome description: 1. Tropical and Subtropical Moist Broadleaf Forest (Amazon basin section) 2. Tropical and Subtropical Moist Broadleaf Forest (Coastal lowlands section) 3. Tropical and Subtropical Dry Broadleaf Forest 4. Tropical and Subtropical Grasslands, Savannas and Shrublands (TFF)

Table S1 Major biomes and ecoregions in Colombia. The names and area of the 6 major biomes and the 25 ecoregions in Colombia according to Olson et al. (2001). Note that the original 25 ecoregions were grouped into 13 ecoregions because some ecoregions only include one or a few municipalities. The name of the largest ecoregion was used as the name of the aggregation.

Table S2 Woody vegetation net gain and loss for all municipalities in Colombia. Thirty three municipalities were not included because they did not have any woody vegetation.

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Author Contributions
Conceived and designed the experiments: MLC TMA. Performed the experiments: ASC MLC TMA. Analyzed the data: ASC MLC TMA. Contributed reagents/materials/analysis tools: MLC TMA ASC AE. Wrote the paper: ASC MLC TMA AE.

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