Efectos del Cambio Climático y la Deforestación en la distribución de siete especies de *Geonoma* (Arecaceae) a lo largo de un gradiente altitudinal en Colombia

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Introducción general

Colombia se encuentra ubicada en la franja intertropical contando con la cadena montañosa de los Andes como elemento fundamental que configura el medio físico, y por tanto, contando con una gran parte de la extensión total de la región más rica en plantas del mundo, los Andes Tropicales (Rangel-ch *et al.*, 1994). Esta característica hace importante entender cuáles son los factores que amenazan actualmente la permanencia de tal diversidad. El interés se centra por tanto en los procesos de cambio climático y deforestación los cuales se traducen en cambios en las temperaturas, niveles de precipitación (Feeley *et al.,* 2012) y pérdida del área efectiva de los ecosistemas (Armenteras *et al.*, 2013; IDEAM, 2014b).

Las discusiones acerca de los niveles de deforestación están ganando relevancia a nivel mundial como una de las amenazas más grandes que enfrenta la biodiversidad, debido a la rapidez y magnitud con que ocurre. Las causas del fenómeno de la deforestación pueden ser vistas desde dos ángulos. El primero es entender la deforestación como causa directa de un solo factor, el cual esta generalmente asociado a la explosión demográfica (Gibbs *et al*., 2010). El segundo, busca entenderla como consecuencia de factores interrelacionados que

crean un complejo entramado de situaciones que la originan (Gibbs *et al*., 2010). Lo cierto es que la deforestación, además de generar pérdidas en el área efectiva de los ecosistemas, también afecta la estabilidad del clima global, ya que son estos los encargados de mantener un equilibrio en los niveles de sustancias atmosféricas determinantes en los procesos de cambio climático (Zhang & Liang, 2014).

Además de la deforestación, el fenómeno de cambio climático actual también se cierne como una amenaza para la integridad de la biodiversidad tal como la conocemos. El calentamiento global presenta evidencias inequívocas, tales como el calentamiento de la atmósfera y los océanos, el derretimiento de los glaciares y el aumento del nivel del mar (IPCC, 2014). Para Colombia, se ha venido realizando un seguimiento riguroso de las variables de temperatura y precipitación, permitiendo de esta manera tener una valoración cuantitativa del proceso de cambio climático en el país. Este seguimiento lo ha venido realizando el gobierno, de la mano del Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM) entre otras instituciones, y reportando en informes periódicos a la Convención Marco de las Naciones Unidas Sobre Cambio Climático (CMNUCC). Gracias a estos reportes, es posible generar los escenarios de temperatura y precipitación bajo los lineamientos propuestos por el Panel Intergubernamental sobre Cambio Climático (IPCC).

No es sorprendente que Colombia deba hacer un seguimiento minucioso del cambio climático y demás amenazas para la biodiversidad, teniendo en cuenta su puesto privilegiado con respecto a otras regiones del planeta. Por ejemplo, en la familia de las palmas (Arecaceae), Colombia está catalogado como el tercero en el mundo en diversidad, contando con aproximadamente 262 especies (Galeano *et al*., 2015). Sin embargo, según las categorías de la Unión para la Conservación de la Naturaleza, el 20% se encuentran en peligro crítico (CR), el 37% en peligro (EN) y el 32% son vulnerables (VU) (SIB, 2014).

El género de palmas *Geonoma*, es uno de los más abundantes del Neotrópico, con 68 especies (y 140 taxones, incluyendo subespecies), de las cuales 32 se encuentran en Colombia (Galeano et al., 2015; Henderson, 2011). Su distribución va desde Haití (19º 45` N) hasta Brasil (29º 46`S) y desde México (96º 40`W) hasta Brasil (35º 04`W) (Henderson, 2011). Son representativas del sotobosque e importantes desde el punto de vista ecológico por la estrecha relación que establecen con los ecosistemas donde se desarrollan, viéndose esto representado en la interacción son sus polinizadores (abejas, moscas, viento) y con mamíferos a los cuales sirven de alimento, pero principal y fundamentalmente con las coberturas boscosas (Henderson, 2011; Roncal *et al.*, 2011). Estas palmas desarrollan su ciclo vital generalmente en el sotobosque, por lo que su detrimento está vinculado al del bosque; además, algunas tienen un nicho altitudinal, climático y biótico altamente específico, que posiblemente ha permitido que el género haya diversificado sobre otros grupos de palmas (Galeano & Bernal, 2010; Galeano et al., 2015; Henderson, 2011). En vista de lo anterior, las especies de *Geonoma* distribuidas en un gradiente altitudinal son pertinentes para entender cómo el cambio climático y la deforestación han afectado el rango de las especies y en consecuencia, el estado de conservación de las mismas y de los ecosistemas montanos.

Para la formulación y realización del presente trabajo de grado, las preguntas de investigación formuladas fueron: ¿Qué importancia relativa tienen el cambio climático (2050 – 2070) y la deforestación (2000 – 2012) en la disminución de la distribución de siete especies montanas del género *Geonoma* en Colombia? Esto se evaluó a través de la modelación de los rangos de las siete especies seleccionadas a partir de variables ecológicas.

Para cumplir con este objetivo, se articularon las preguntas dentro de un proyecto de investigación marco, titulado "*Analisis de los limitantes de las radiaciones de especies"* o POPCORN por sus siglas en inglés, el cual es una iniciativa regional internacional liderada por la Universidad de Zúrich en Suiza, y cuyo objetivo es

estudiar las radiaciones replicadas de cuatro grupo de plantas en ocho regiones montañosas de Latinoamérica, desde el punto de vista ecológico, filógenético (macroevolutivo) y de genética poblacional (microevolutivo). Las preguntas puntuales de este trabajo, contribuyeron a uno de los principales grupos de estudio, es decir, las palmas y a la perspectiva ecológica. La base del proyecto consistió en una campaña intensiva de campo, que pretendía obtener una base de datos única a nivel mundial sobre la distribucion espacial de aproximadamente 300 – 400 especies. En el componente del proyecto que se realizó en Colombia, como en las demás áreas de estudio en Latinoamerica, se estudiaron a las palmas, las bromelias, los helechos arborescentes y los helechos Polypodiaceae, produciendo el material de herbario y las muestras de laboratorio para los análisis morfológicos, filogenéticos y de genética poblacional.

Consideramos que los rangos de especies generados dentro del proyecto marco, podrían tener muchos usos, o servir para resolver una gran cantidad de preguntas. En particular, nos interesó que pudieran proporcionar insumos para los esfuerzos de conservación de los bosques montanos. Se articularon la biología de la conservación a los sistemas de información geográfica y la modelación de nicho ecológico, tomando como grupo de estudio algunas especies montanas de *Geonoma* en Colombia.

Durante la maestría, realizamos trabajo de campo en localidades de Colombia con la estudiante de doctorado del proyecto marco Ingrid Olivares y su director, el Dr. Michael Kessler, para la recolección de especies de bromelias, palmas y helechos. Se realizó una pasantía en el Instituto de Botánica Sistemática y Evolutiva de la Universidad de Zúrich en Suiza, sede principal del proyecto marco, para aprender de código en la plataforma R para la modelación de los rangos que se utilizaron durante la investigación, bajo la guía del estudiante de postdoctorado Dirk Nikolaus Karger, María José Sanín e Ingrid Olivares.

Artículo

Climate change and deforestation effects on the distribution of seven species of *Geonoma* (Arecaceae) along the elevation gradient in Colombia

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Abstract

Climate change and deforestation are two important threats that Colombian forests are currently facing, causing shifts in the distributions of plant species. Therefore, close attention is needed in order to understand the impact of both phenomena. We chose genus *Geonoma* within the palm family as an appropriate lineage to assess these impacts due to their high structural, functional, and ecological representativeness in montane forests. The species distribution models of seven species (*G. cuneata, G. deversa, G. interrupta, G. macrostachys, G. orbygniana, G. stricta,* and *G. undata*) were estimated through a machine-learning algorithm and used to assess the net effect of deforestation on the range size from 2000 to 2012, and to predict the future distribution changes due to climate change by 2050 and 2070. Our results show that the relative effect of deforestation on *Geonoma* ranges is wider and always negative, with the midlands/highlands suffering the most in terms of relative loss to deforestation, whereas the magnitude and effect of climate change is species- and elevation-specific. In conclusion, distributions along mid- and high elevations have suffered and are expected to suffer the most from both factors.

ADDITIONAL KEYWORDS: Ecological Niche, Species Distribution Models (SDMs), Neotropics, Understory palms, Mountain biodiversity.

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support during the development of the research, including data gathering, hosting the first two authors, and providing a base to which this research contributes.

Introduction

Ecosystems today are facing great challenges to ensure their ecological and biological stability, due to the ongoing processes of deforestation and climate change throughout the world. The consequences of these two phenomena are more marked in the tropics, where deforestation rates are constant and alterations in temperature and precipitation patterns are more extreme due to geographical position (Geist *et al.*, 2001; Gorte & Sheikh, 2010; Wright *et al.*, 2009) .

The tropical Andes are considered one of the global biodiversity hotspots (Alarcón *et al.*, 2002; Myers *et al.*, 2000), and harbor the highest levels of diversity for a number of organisms including vascular plants (Brehm *et al.*, 2003; McCain, 2009; Navas, 2002; Terborgh, 1997). However, they also host two-thirds of the human population of the region (Salazar, 2010). The concentration of large human settlements poses severe threats to ecosystem functioning and biodiversity conservation, and is especially concerning in view that both global climate change and deforestation will ultimately deteriorate the ecosystem services on which this human population depends.

Deforestation is critical due to its high rates and magnitude (Padit *et al.*, 2007; Vijay *et al.*, 2016). This phenomenon is especially severe in mountainous areas in view of the decrease in effective area with elevation, in conjunction with the intensity and extension of human-induced pressures (Faaborg *et al.*, 1993; Lindborg & Eriksson, 2004; King, 1998). Such assertions can be supported in the Colombian Andes with data provided by the Instituto de IDEAM (Cabrera *et al.*, IDEAM, 2011) for the period 1990 - 2010, where deforestation rate was 310,349 ha per year, with the greatest effects in the Amazon and the Andean region (40% and 32% of the area deforested in Colombia, respectively).

On the other hand, climate change is also having significant effects on the ecological and biological stability of mountain ecosystems. Topographic complexity and drastic elevation gradients favor rapid changes in climatic and physical parameters in relatively short distances (Beniston, 2003). In tropical mountains, Still *et al.*, (1999) show that scenarios of $2CO_2$ relate to the disappearance of species due to changes in cloud formation and convective rain cycles that in turn have a direct relationship with global warming. Important parameters to plant ecology such as cloud and rain cycles are significantly shifting (Beniston, 2003;

Still *et al.*, 1999), but there is still great uncertainty regarding the effects of climate and global change on tropical mountain plants. It is thus relevant to explore how the distributions of tropical organisms that cover topographic gradients will respond to deforestation and climate change.

Palms are keystone elements of Neotropical forests due to their high structural, functional, and ecological representability (Correa & Vargas, 2009), and cover most Neotropical ecosystems, from mangroves to highlands and from rainforest to xeric scrub (Galeano *et al.,* 2015). Within the palm family, the genus *Geonoma* is one of the most abundant and species-rich genera, and live from sea level up to 3200 m and reach their maximum richness and abundance on topographic gradients (Galeano *et al.*, 2015). These features pose them as a proper model group for understanding the factors underlying general diversity patterns and also those affecting survival and distribution changes in the ecosystems where *Geonoma* thrives (Roncal *et al.*, 2011).

Climate change and deforestation can affect *Geonoma* palms (and mountain forests in general), in various ways. It is expected that plant distributions will shift under climate scenarios (Hijmans & Graham, 2006; Pitelka, 1997; Rehm & Feeley, 2015), however, the feasibility of these changes is and will be restricted by the anthropological processes of deforestation that determine to a greater or lesser extent the availability of habitat for the expansion or contraction of the species distribution ranges. Therefore, climate change scenarios may predict distribution shifts but these are contingent to habitat connectivity and their absolute relevance should be considered in light of the size and magnitude of deforestation. In order to quantify to what extent each of these phenomena generate changes in the distributions of *Geonoma* mountain species, these must be analyzed as separate, although their interdependence is evident.

Species Distribution Models (SDMs) have become important tools for the quantification of the impacts generated by global change (Hijmans & Graham, 2006; Iverson & Prasad, 1998; Pearson & Dawson, 2003; Upadhyay *et al.*, 2006), as they provide a measure of species potential niches, and allow evaluating multiple species at multiple spatial and temporal scales (Cayuela *et al.*, 2009). SDMs can be used both retrospectively and prospectively; this is important as deforestation can be traced back but hardly traced forward due its miscellaneous nature, whereas climate change predictions are more reliable and also available. Since SDMs provide a quantitative record of species response when some of their ecophysiological requirements vary, they can facilitate the implementation of timely conservation efforts (Agarwal *et al.*, 2002; Peterson, 2003).

In this study we used species occurrences and climatic layers to model the effects that climate change will have and that deforestation has had over the last decades on the distribution of the selected mountain *Geonoma* species in order get a grasp on the relative importance of each. For this, future climate change (2050 – 2070) and past deforestation (2000 – 2012) effects were valued in terms of distribution changes of seven species of *Geonoma* in relation to elevation in Colombia. We also sought to elucidate which ranges within the elevation gradient are suffering the most from these two factors. Our hypotheses were that 1) not all species are suffering losses in their distribution ranges due to climate change but that all have lost important extensions due to deforestation, and 2) that climate change and deforestation will most severely affect the species and ecosystems at highest elevations, as cold refugia and total land area are scarcer.

Materials and Methods

Species Presence / Absence data

The distribution of genus *Geonoma* spans from 19°45' N (Haiti) to 29°46' S (Brazil) and from 96°40' W (Mexico) to 35°04' W (Brazil). Colombia harbors 32 out of 68 species in the genus (Henderson, 2011); these are distributed in a wide variety of elevations and ecosystems, and species richness peaks in areas with annual precipitation rates higher than 4000 mm per year, both in lowland and montane regions. *Geonoma* is ecologically important both by the high number of species and individuals and by the role they play as food for wildlife (Calderón et al., 2005; Galeano et al., 2015; Henderson, 2011).

Seven of these 32 species were here studied in view of their wide geographic but restricted elevational distributions. Thus, we selected Andean species that were common of three Cordilleras with restricted ranges on the elevation gradient (ranges: 0-1000, 1000-2000, and 2000-3200 m) (**Table 1**), broadly reflecting the lowland, midland and highland mountain forests. Here forth, we will refer to the three elevational ranges under these terms. The presence / absence locations of these seven species, *G. cuneata, G. deversa, G. interrupta, G. macrostachys, G. orbygniana, G. stricta,* and *G. undata,* came from herbarium collections (mainly from the Colombian National Herbarium and Aarhus University Herbarium), literature surveys (mainly Henderson, 2011), the Species Link webpage (splink.org.br), and ecological plots established in Brazil, Bolivia, Ecuador, Colombia, Costa Rica, and Mexico (Kessler *et al*., unpubl. data).

Table 1. Study species, their approximate altitudinal distribution, and the notation to be used for the analyses.

Species	Elevation at which the species occurs based on occurrence data (m)	Position on gradient	Assigned elevation for analysis (m)
Geonoma deversa **(Poit.) Kunth**	5-1200	Lowlands	0 - 1000
Geonoma interrupta **(Ruiz & Pav.) Mart**.	0-1500	Lowlands	0 – 1000
Geonoma stricta **(Poit.) Kunth**	5-1850	Lowlands to midlands	0 – 2000
Geonoma cuneata **H.Wendl. ex Spruce**	2-1750	Lowlands to midlands	0 – 2000
Geonoma macrostachys **Mart**.	75-1800	Lowlands to Midlands	0 - 2000
Geonoma orbygniana **Mart**.	775-2850	Midlands to highlands	1000 – 3000
Geonoma undata **Klotzsch**	550-3370	Midlands to highlands	1000 - 3000

For the niche modeling of each of the species, the total distribution range were considered in order to include all the possible implications of the variables at the regional level. However, the subsequent analyses were done just for the Colombian extent of the species ranges, due to the interest in providing information at the national level that could be used in. In total, 6100 unique records were used, with geographical location and taxonomical assignment visually quality checked, for which the following steps were carried out:

1. Geographical logic was checked between the herbarium names and Henderson (2011).
2. Elevational correspondence was checked between field GPS elevation and the ones given by the geographical coordinates (Digital Elevation Model). Outliers were sought.
3. Each specie was mapped separately and their distribution were verified with known presence and absence polygons based on Henderson (2011). Outliers were sought.

Species distribution models (SDMs)

The modeling process was based on advanced machine-learning techniques. For each species, we used four different statistical approaches: 1) Generalized Linear Models (GLM), 2) Gradient Boosting Algorithm (GBM), 3) Random Forest (RF) and 4) Multivariate Adaptive Regression Splines (MARS) with three repetitions each. The general functioning of each model is the following:

1) Flexible generalization of the ordinary linear regression. Relates the random distribution of a dependent variable (distribution function) to the systematic part (linear predictor) through a “link function” (Akbayrak, 2018; Nelder & Wedderburn, 1972).
2) Assembly technique with sequential predictors, which "learn" through the subsequent ones. Observations are chosen based on the learned errors (Grover, 2017).
3) This algorithm creates an assembly of random decision trees which are then combined to achieve a finer and stable prediction (Donges, 2018; Liaw & Wiener, 2002).
4) Algorithm that constructs the relationships among the parameters given a set of basic coefficients and functions that are entirely driven by the regression data (Friedman, 2018).

We generated two (2) different sets of 1000 random pseudo-absences, which were given the same weight as presence points (prevalence 0.5). Based on studies such the one carried out by Barbet-Massin et al. (2012), the most effective species distribution models require background (pseudo-absences) data, particularly recommending a random selection in order to reach higher predictive values. We then split the data 80/20 for testing and training. Model evaluation was done with True Skill Statistics (TSS) also known as Hanssen-Kuipers discriminant, based on Allouche *et al.* (2006) who showed that TSS improves the shortcomings identified

with Kappa (the most widely used statistic to measure the performance of the modeling processes) related to its sensitivity to prevalence while maintaining all its statistical advantages. Based on the TSS-values, a weighted ensemble model was created with the individual models that met the criteria of a TSS threshold higher than 0.80 (TSS > 0.8) (Thuiller et al., 2016). The analyses were done in R (R Core Team, 2017) based on the packages {biomod2} (Thuiller *et al.*, 2016) and {ecospat} (Broennimann *et al.*, 2017).

Once the modeling process was started, the variables entered the algorithm and their descriptive capacity with respect to the real species presences was measured individually (one variable at a time), they were given a unique weight that then was used for the construction of the ensemble models. The resulting models may not coincide exactly with the official distributions taken in the field, due to the uncertainty of computer machine learning models and the particular biological and ecosystemic relationships between them and their habitat (Elith & Graham, 2009; Sinclair et al., 2010).

We used predictors that describe the climatic species niche and their physical habitat which are listed in **Table 2**. The climatic variables used were developed by the CHELSA project (http://chelsa-climate.org) (Karger *et al.,* 2017), a high resolution (30 arc sec) climate data set for earth land surfaces that includes monthly mean temperature and precipitation patterns for the time period 1979 – 2013 (Karger *et al*., 2016).

Table 2. Climatic and topographic variables.

Bio1 – Bio11	Temperature variables
Bio12 – Bio 19	Precipitation variables
LengthGrowingSeason	Length of the growing season
MeanTempGrowth	Mean Temperature Growth
DistTreeLine	Distribution of the Tree Line
SoilGrid	Soil Grid

Climate Change Model

The future SDMs, the models described above were projected into the future variables (climate change scenarios). For the evaluation of climate change effects, we chose the MPI – ESM Model (Daniel & Correa, 2014) and within it, the 2.6 and 8.5 Representative Conservation Pathways (RCPs) along with the 2050 – 2070 temporal horizons (mean temperature). Each RCP corresponds to a specific radiative forcing pathway and emphasizes that not only the long term greenhouse gases concentration levels are of interest, but also the trajectory taken over time to reach that outcome (Moss *et al*., 2010). These were downloaded from the webpage of the Climate Change, Agriculture and Food Security Program (CCAFS). The future distribution ranges where then calculated by applying the potential niches of the species on the climate change models.

Forest Cover Data

To quantify distribution lost to deforestation, we used the Global Forest Change Dataset. This dataset was developed by The University of Maryland using the Google Earth Engine platform and embraces the time period 2000 – 2012. This study analyzed global Landsat images at a 30 m spatial resolution to classify the state of global forests, their extent, loss and gain processes (Hansen *et al*., 2013). For our analysis, we used the three main layers “loss”, “gain” and “tree cover” (**Figure 1**).

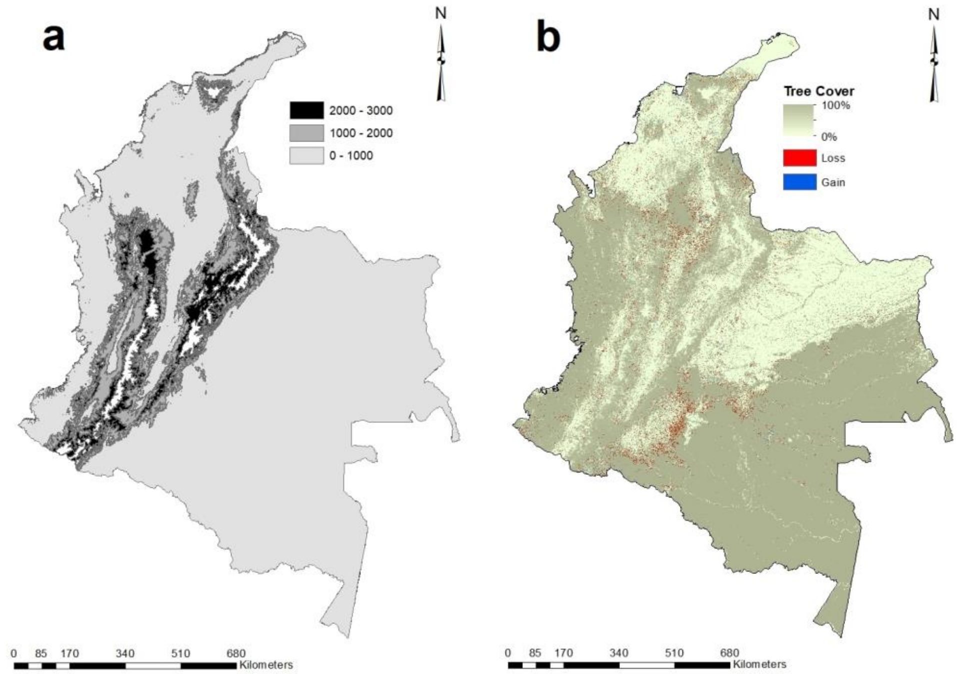


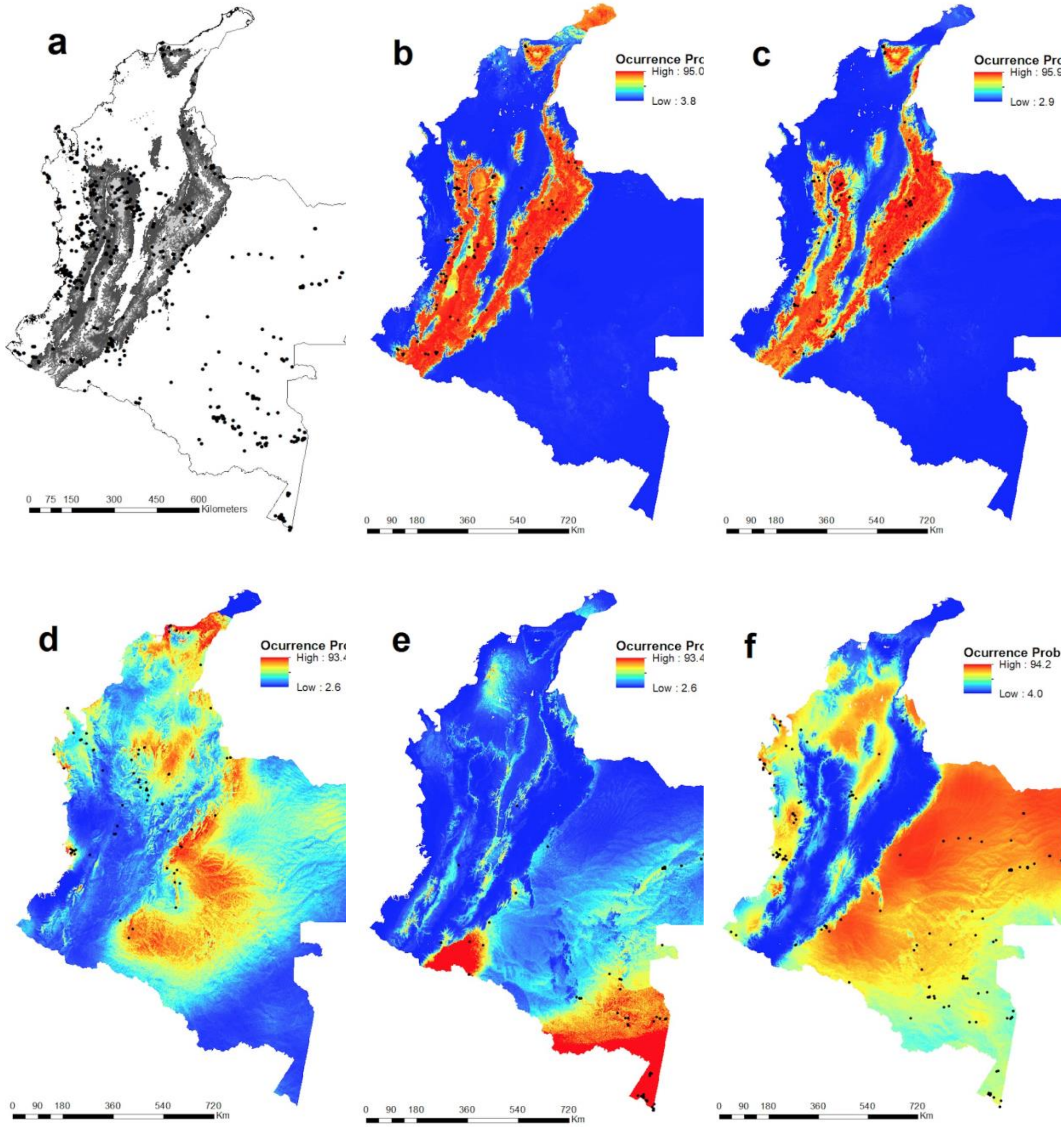
Figure 1. a) Altitudinal ranges of the mountain chains that were here studied, b) Forest cover in the year 2000; blue patches represent forest gain and red patches represent forest loss to 2012.

We then proceeded both with the SDMs based on historical variables, and those that included the climate change scenarios, to establish a threshold of presence of 0.7 for presence – absence maps of each species (**Figure S 1)**. For each species, the presence – absence map was overlaid to the deforestation layers for a measure of the effective area lost or gained.

Results

Climate change effects on the distributions of the selected species (current vs. future SDMs)

All species ensemble models (current and future) provided proper predictions with a min TSS value of 0.7 (of the chose individual models). The current ensembles managed to predict the known true presences and absences, reflecting field knowledge (**Figure 2**).


a
0 75 150 300 450 600
Kilometers
b
Ocurrence Pro
High : 95.0
Low : 3.8
0 90 180 360 540 720
Km
c
Ocurrence Pro
Low : 2.9
0 90 180 360 540 720
Km
d
Ocurrence Pro
Low : 2.6
0 90 180 360 540 720
Km
e
Ocurrence Pro
Low : 2.6
0 90 180 360 540 720
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0 90 180 360 540 720
Km

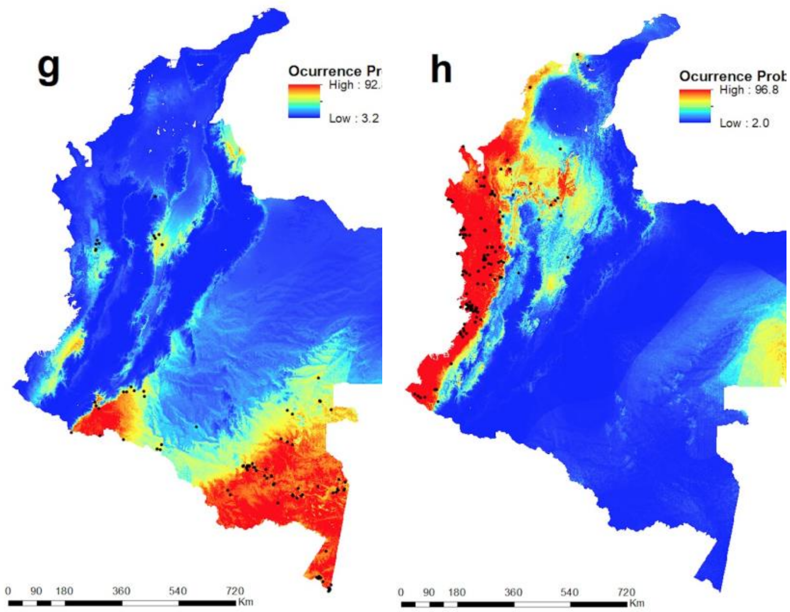


Figure 2. Species distribution models. The color scale indicates the probability of occurrence, from high (red) to low (blue); a) Species occurrences, b) Geonoma undata, c) G. orbygniana, d) G. interrupta, e) G. macrostachys, f) G. deversa, g) G. stricta, h) G. cuneata.

Changes in species distributions due to deforestation

Forest gain was five to ten times smaller than forest loss in this time period (2000 – 2012), as shown in **Figure 1** and **Table 3**. Total deforestation was more pronounced in the lowlands but was relatively higher (with respect to total forest area) in the midlands.

Table 3. Total forest loss and gain for each of the altitudinal ranges covered during 2000-2012. Forest area 2000 indicates the base year (2000) forest cover and Relative loss / Relative Gain show relative forest losses and gains in relation to the base year area.

Elevation (m)	**Forest area 2000 (Km^2)**	**Total Loss (Km^2)**	**Relative loss (%)**	**Total Gain (Km^2)**	**Relative Gain (%)**
0 - 1000	590,880	21,094	3.57	4,963	0.84
1000 - 2000	6,132	2,566	41.85	250	4.07
2000 - 3000	3,876	1,079	27.83	242	6.24

As seen in **Table 3**, the lowlands suffered the largest net deforestation with 21,094 km^2, representing 3.57% of all the country´s forest. However, in terms of relative deforestation midlands are the most affected areas with a relative loss of 41.85% of their forest cover, followed by highlands with a loss of 27.83%. In terms of forest

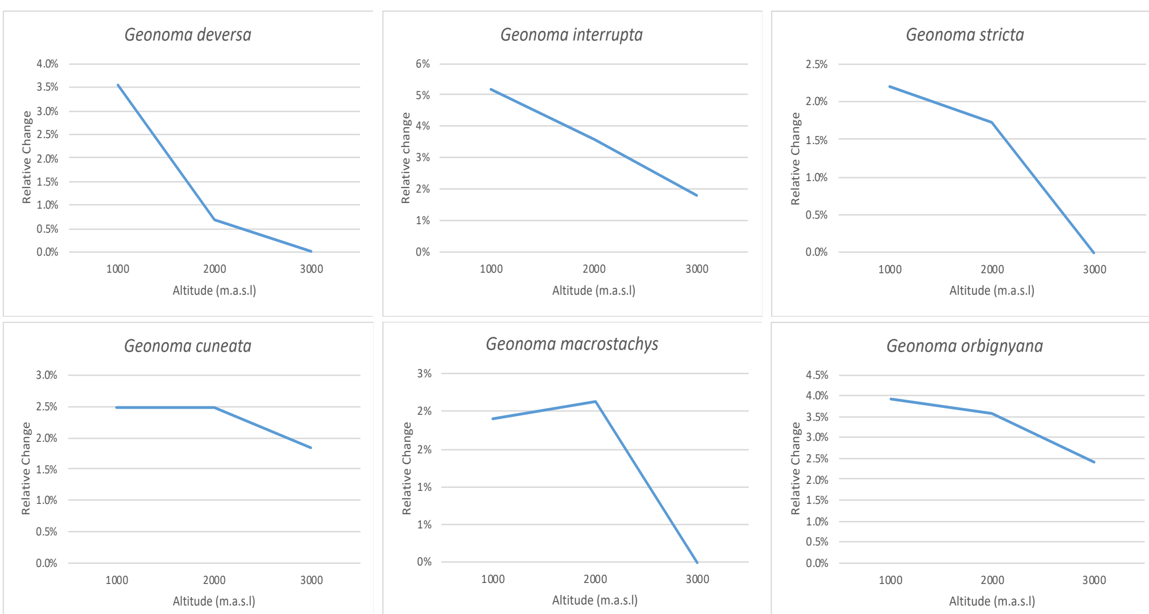
gain, there are some areas all throughout the altitudinal gradient, represented by reforested areas, forest plantations and secondary forests, which are not viable habitats for the establishment of the studied species.

The results of contrasting these deforestation values to each of the elevation ranges included in the study, as well as to each of the species, are shown in Table 4 and **Figure 3**. Table 4 shows net forest loss for each species in each elevation range. In general, the largest loss is in the lowlands for *G. cuneata, G. deversa, G. stricta, G. interrupta* and *G. macrostachys*. *G. orbignyana and G. undata*, (midland / highland species) lose the most in the midlands and highlands.

Table 4. Net loss area for each specie in each altitudinal range.

Total Loss Area (km^2)							
Altitude	***G. cuneata***	***G. deversa***	***G. stricta***	***G. interrupta***	***G. macrostachys***	***G. orbignyana***	***G. undata***
1000	3,383	20,340	4,703	9,274	2,245	791	6,378
2000	342	5	13	3,857	2	2,968	3,121
3000	9	0	0	61	0	1,458	1,459

In general, lowlands / midlands hold the highest relative area loss; however, forest was lost all throughout the gradient (and for all species) as seen in **Figure 3**. The largest differences are between *G. orbygniana* and *G. undata,* from the midlands to highlands.



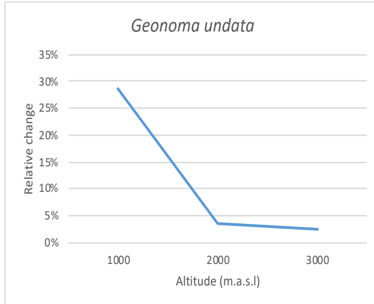


Figure 3. Relative loss due to deforestation for each of the species during the period 2000 – 2012.

Changes in species distributions due to Climate Change

The predicted effects of climate change on the presence – absence maps for all elevations, species, and scenarios are shown in **Figure 4.** The biggest changes will occur in the lowlands. With respect to relative change, the highlands will present the largest changes.

For some species such as *G. stricta* and *G. cuneata*, climate change will mean an expansion of the current species distribution ranges, especially in the lowlands and, although in a lesser proportion, in the midlands. Conversely, *G. deversa* and *G. interrupta* will visibly lose area in all elevations. It is important to note that for some species there is a significant difference in terms of the scenarios proposed by each of the RCPs, depending on the magnitude of the increase in carbon in the atmosphere, being generally the pessimistic scenarios those that generate an increase of greater magnitude, particularly in the lowlands.

Additionally, **Table 5** presents the relative area losses and gains for climate change scenarios with respect to the current distribution ranges. The highest values are presented both for relative losses and gains in midlands and highlands, being gains greater than losses. It can be note also that although the net changes in area are higher in magnitude for lowlands, it can also be observed that some species such as *G. cuneata* begin to migrate towards highlands in terms of relative areas. *G. orbignyana* and *G. undata*, the species that go higher in the elevational gradient but can also be present in the lowlands, present a much more significant range expansion in the lowlands than at higher elevations.

Figure 4. Changes in the distributions of seven species of Geonoma due to climate change. Blue bars represent the current distribution of each specie. Orange and green dotted lines represent 2050 – 2070 temporal horizons, respectively. Each RCP scenario is individually plotted.

Table 5. Relative changes in the distributions of seven species of Geonoma due to climate change. Results are presented for each RCP scenario and time horizon.

	G. deversa				***G. interrupta***				***G. stricta***				***G. cuneata***			
Alt.	**RCP 2.6**		**RCP 8.5**		**RCP 2.6**		**RCP 8.5**		**RCP 2.6**		**RCP 8.5**		**RCP 2.6**		**RCP 8.5**	
	2050	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**
1000	-100%	-100%	-100%	-100%	-99%	-98%	-100%	-100%	35%	43%	12%	1%	470%	470%	470%	470%
2000	-100%	-100%	-100%	-100%	-100%	-100%	-100%	-100%	1722%	2051%	3256%	2799%	540%	540%	540%	540%
3000	0%	0%	0%	0%	-95%	-94%	-100%	-100%	0%	0%	0%	0%	9564%	9592%	1036%	12461%

	G. macrostachys				***G. orbignyana***				***G. undata***			
Alt.	**RCP 2.6**		**RCP 8.5**		**RCP 2.6**		**RCP 8.5**		**RCP 2.6**		**RCP 8.5**	
	2050	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**
1000	-95%	-97%	-82%	-100%	3736%	116%	297%	80%	45%	12%	-17%	20%
2000	-92%	-82%	82%	-95%	6,56%	-0,54%	5,94%	0.32%	0.02%	-0.02%	-0.17%	0.02%
3000	0%	0%	0%	0%	0.%	0.04%	0.09%	0.01%	0.00%	0.00%	0.00%	0.00%

Discussion

SDMs can be used for understanding the different types of relationships that species can have with the characteristics of their environment (Elith & Leathwick, 2009). Since these characteristics can be disturbed within an SDM working framework, they can inform climate change effects on species maps. Thus, SDMs can be used to undertake strategic actions in the area of conservation, such as the development of projects aimed at facilitating the permanence of the species that presents the greatest threat (Elith et al., 2006).

However the potential applications, the SDMs can present errors that range from the algorithm statistical limitations to the errors that result from the misinterpretation of the species biotic component as seen by Fielding & Bell (1997). Although assembled methods in machine learning contributes to error reduction (obtaining highly accurate classifiers by combining less accurate ones), and advances at the mathematical and computational level generate more reliable results from the statistical point of view (Dietterich, 2000; J Elith et al., 2006), the scarcity of knowledge of the species biology and ecology remains the greatest

challenges when it comes to generating reliable SDMs. Thus, taxonomic problems, competitive relationships, species mobility, evolution and adaptation processes, or species' migration ability can be decisive for the generation of reliable results (Elith et al., 2006).

The model evaluation score used to test the models was the TSS. This statistic compares the number of correct forecasts, minus those attributable to random guessing, to that of an hypothetical set of perfect forecasts (Allouche et al., 2006). TSS scores range from -1 to +1, where +1 indicates perfect agreement and [0, -1] indicates a performance no better than random, and TSS considers both omission and commission errors. In other words, applied to this particular research, initially it was determined that 80% of the input data was going to be set as training data and the remaining 20% would be used to test the model. The TSS evaluates how well the testing data is adapted to the training data, which means, high TSS values are desirable, indicating good SDMs quality, which is a different concept of overfitting, which traditionally means that the model only adjusts to the training data, but fail to predict the testing data (Hawkins, 2004), which is not the case that is presented in the models performed. In addition to the theoretical aspects of this metric, a visual revision of the methods suggests that the models are not overfitted, and on the contrary, in some cases SDMs were overestimated, generating for some species high probabilities in the highlands where they species are not distributed (i.e. *G. cuneata, G. deversa* and *G. interrupta*).

Having these methodological considerations in mind, in general terms, we supported our initial expectations. With respect to our first hypothesis, as expected, the relative effect of deforestation on *Geonoma* ranges is wider and always negative, whereas the magnitude and effect of climate change on *Geonoma* ranges is species - and elevation - specific. With respect to our second hypothesis, the response is not generalized throughout species. First, we corroborated that *Geonoma* ranges in the highlands will suffer the most in terms of relative area lost due to deforestation, but under climatic scenarios, some species will gain area in the highlands whereas other species will lose area. Likewise, some species will lose area in the lowlands (i.e. *G. deversa*) whereas others will gain (i.e. *G. cuneata*). In a broad sense, and also as expected, climate change responses are more idiosyncratic than those to deforestation, as will be detailed below.

Habitat Loss Due to Deforestation

As discussed above, all throughout the elevation gradient, forest experienced net loss in the studied period. Consistent with the total extent of land area in the lowlands, the larger amount of forest loss took place in this range, which correspond to the tropical humid forest covering most of the Colombian territory. However, relative loss was higher in midlands and highlands, for species such as *G. stricta, G. cuneata, G. macrostachys* and *G. orbignyana,* which area typically present in midlands and highlands. This finding is also consistent with the observation that species that suffer the most are those that live at higher elevations (in relative terms). This is because highland forests are smaller, and midland forests are both small and suffering the most from deforestation (Armenteras *et al*., 2011; Bush *et al*., 2004).

Although there is some forest gain, this is always relatively small and represented by forest plantations, reforestation and secondary forest relicts that sum up to the total forested cover but that are not suitable habitats for many forest species. Hence, the loss of habitat is closely linked to the expansion of urban and rural development frontier, such as urban centers, lineal infrastructures, grazing and agriculture, which in Colombia lie within the Andean region (Rodríguez Eraso, 2011). These results are supported by other research, which show that the highest net deforestation are those located below 1000 m but the highest relative deforestation is higher in the altitudinal range, in the midlands and highlands (González *et al.*, 2011; Torrachi, 2002; Zheng *et al.*, 1997).

One of the visible effects caused by deforestation is the border effect on the stability of tropical ecosystems. Studies like the carried out by Faria *et al*. (2009) suggest that the ecosystems fragmentation, generate a change in the forest relicts structure due to the edge effect. Once the edge has been created, it is followed by a high tree rate mortality that are close to it, followed by the establishment of pioneer species - secondary forest. As seen above, secondary forests are not viable habitats for *Geonoma* species, due to the particular requirements of these palms in terms of light / shade, temperature and humidity that the forest provides for the establishment and maturation of individuals. The forest fragments clarification in the edges is possible that affects them, decreasing the population of *Geonomas* in these areas (edges) and in turn, generating an alteration of all relationships in which *Geonoma* is normally involved (Ecological relations with other species) (Kattan & Alvarez-López, 2009).

Other studies have been conducted regarding the climate change and deforestation effects on the tropical species distribution. Regarding the effects of deforestation, the studies converge on the serious consequences that the loss and fragmentation of forest areas have had and will continue to have, given the

suppression of species' habitats, the disturbance of biological and ecosystem relationships between them and with its environment and the inability that this approach imposes when it comes to generating adaptation strategies to climate change (Bonan, 2008; Etter et al., 2008; Feeley & Silman, 2010; Geist et al., 2001; Geist & Lambin, 2002; González et al., 2011; Rehm & Feeley, 2015). On the other hand, in terms of the effects of climate change, the studies agree that changes in the temperature and precipitation regimes will have consequences in the distribution ranges of the species, for most of them meaning a migration in the altitudinal gradient, generating the migration of species towards habitats that have the viable climatic conditions for its establishment (Anderson & Martínez-Meyer, 2004; Carrascal et al., 2012; Cramer et al., 2001; Feeley & Silman, 2010; Laurance & Useche, 2009; Skov & Borchsenius, 1997; ter Steege et al., 2006; Terborgh, 1997).

Changes in species distribution ranges due to Climate Change

Climate effects on the distribution of *Geonoma* species is particular both to species, scenarios, and elevation ranges considered. However, this response can be grouped by species. Pacific Ocean region distributed species – *G. cuneata* and *G. deversa* - decrease their area of distribution in all elevations. On the other hand, there are species that apparently present an upslope migration such as *G. cuneata, G. macrostachys* and *G. stricta,* this tendency being more marked in *G. stricta* and *G. cuneata*. The mentioned species are all predominantly from the lowlands and midlands.

It is also important to analyze the behavior of *G. orbignyana* and *G. undata*, which are the species distributed principally in midlands and highlands, although they are present in a portion of the lowlands. For these two species, the tendency to gain areas in lowlands is marked (where they are already present), keeping a stable area in midlands and highlands. In general terms, climate change means an expansion for the species distribution ranges, either in the three altitudes evaluated at the same time or in particular one. This trend is clearer for every specie except for *G. deversa*, it presents a significant decrease in its range of distribution in all the elevations and all the scenarios and time horizons evaluated.

Another visible climate change effect, is the possible overlap and translocation of the species distribution ranges, in the event they could migrate following the optimum climate niche. Many of them share ecological characteristics, which could generate conflict when integrating them all in the same ecosystem range. The possible difficulties can be related with their adaptation, in terms of ecological

saturation, competition for habitat and resources and the necessary synchronicity within the particular species ecology and cycles and with other species for which *Geonoma* palms provide food and stability (Dirnbdck et al, 2016; Parmesan, 2006; Rehm & Feeley, 2015).

For instance, in Colombia, *Geonoma undata* has a morphotype that is always found at the highest portion of its elevation range, many times above 2700 m. This morphotype was considered a species before Henderson's revision in 2011, under the name of *Geonoma weberbaueri*. This unit could be lost due to climate change in areas where the tree line will not be able to advance as fast as climate change. This case is not isolated or unique, as many other depend both on a specific climatic space but also on forest cover to survive.

However, despite the evidence shown in this study regarding the expanding effects that climate change could have on species ranges, none of these could be possible if there is no forest cover that supports their migration. As seen, habitat discontinuity caused by deforestation throughout the elevation gradient would hinder the migration of these understory palms (and other forest species). These results are in accordance with other studies (i.e. Pitelka 1997) reflecting on the new challenges that climate change imposes on the migration of species not only in terms of change in their distributions but also in the biological and adaptive barriers that species should overcome. At the same time, it indicates the decisive role of the fragmentation of ecosystems in terms of allowing species to make the leap to suitable spaces, given that this fragmentation reduces the ability of species to adapt to climate change.

Conclusions

The choice of *Geonoma* palms as model species for forest loss due to deforestation and climate change was informative as SDMs provided a quantitative approach of evaluating the performance of forests along an elevational gradient facing the two main threats in Colombia, which are also common among tropical megadiverse countries (Isasi-Catalá, 2011). The processes of climate change and deforestation will have both evident effects on the distributions of the analyzed species, producing significant effects in the viable areas of their distribution. In particular, it will be the deforestation processes that are and will continue to generate, in the short and medium term, the most evident impacts, due to the rapidity with which the vegetation cover is being lost and therefore the ecosystems that support the necessary conditions for the maintenance of these species.

The effects of deforestation in the country are always negative, although there are processes of forest gain, these are insignificant with respect to the magnitude of the loss, additionally, these gains usually correspond to forest plantations and secondary forests, which they are not viable habitats for the species studied. The palm species located higher in the altitudinal gradient are the ones most affected by the reduction of the effective area of the ecosystem, and since the major urban settlements are placed in the Andean region (generating a greater ecosystem fragmentation), the net effect will also be more drastic for midland and highland species.

Climate change, on the other hand, will have more idiosyncratic effects regarding the climatic scenario applied and the altitudinal range considered. However, in general terms it could be said that the areas of distribution will be expanded (except for *G. deversa*), generating an overlap between the species, with the consequent repercussions in the biological and ecosystem relationships that the species establish among themselves and with the habitat where they are found. However, the possibility that this will happen depends to a large extent on the availability of habitat and the connectivity it has with the regional and national forest matrix.

Last but not least, it is necessary to see how the processes of climate change and deforestation relate to the social situation of the country, particularly speaking of the armed conflict. This has spanned over 50 years and paradoxically aided conservation as it kept many territories void from human activities. How will scientist and legal authorities confront this newly gained threat to biodiversity is a topic of hot debate (Aguilar *et al.*, 2015; Anderson & Maldonado-Ocampo, 2013; Baptiste *et al*., 2017; Negret *et al*., 2017), and consensus indicates that governmental presence in rural environments will have to be strengthened.

Viewing also the new possibilities/challenges opened by the peace agreements, and due to the high rates of deforestation registered since the signing of these agreements, it is necessary to reinforce the efforts in the establishment of new areas under some protection figure. Additionally, is mandatory to reinforce the control made in existing ones. Particularly in the Andean zone, even though there are a considerable amount of areas under some form of protection, the total extension covered by these areas should be expanded, reducing the pressure exerted by urban settlements and the expansion of farming and livestock areas on the Andean ecosystems.

Supplementary information

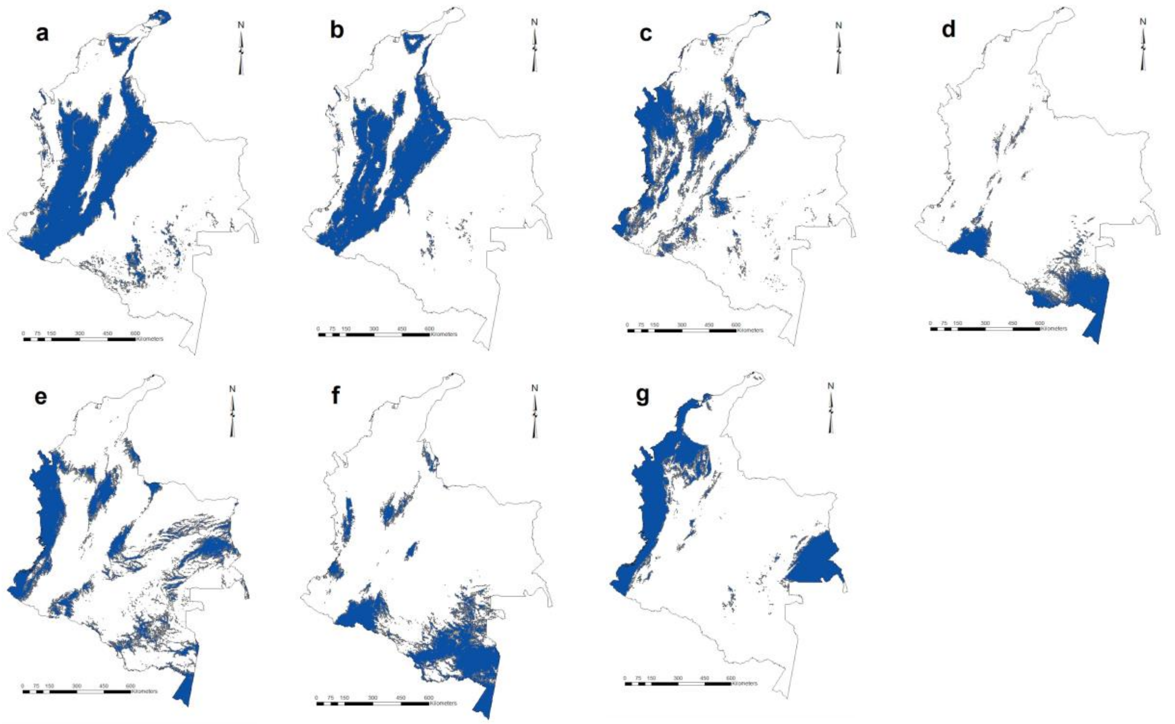


Figure S 1. Presence – Absence species maps. a) Geonoma undata, b) G. orbygniana, c) G. interrupta, d) G. macrostachys, e) G. deversa, f) G. stricta, g) G. cuneata.

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Conclusiones generales

El cambio y/o ampliación de los rangos de distribución de las especies provocados por el cambio climático, enfrentará a las especies ante nuevos retos relacionados con las barreras biológicas y adaptativas que estas deberán sobrepasar para poder establecerse de manera exitosa en las nuevas condiciones de hábitat tanto en terminos climáticos como en terminos físicos. Dichas barreras tendrán que ver con la saturación de los ecosistemas y la consiguiente lucha por un espacio en el nicho ecologico al cual aspiran.

Aunado a los procesos de cambio climático, la perdida de habitat puede llegar a potenciar de manera significativa los retos actuales para la permanencia de la biodiversdad, dada la destrucción y poca capacidad de control que se tiene de estos escenarios.

El problema climático se está integrando activamente a nivel del gobierno nacional. Aunque es un tema que puede beneficiar a algunas especies en términos de la expansión de sus rangos de distribución, los efectos y consecuencias de los procesos de deforestación y las características ecológicas de las especies y su coexistencia dentro de sus nuevos ecosistemas deberían agregarse a este panorama. Si bien las medidas que se pueden tomar al respecto se encuentran en el área de adaptación y mitigación al cambio climático, este es un fenómeno planetario donde el número de factores que lo influyen es abismal, lo más importante es desarrollar buenas estrategias de adaptación a esto, que permite mitigar los efectos negativos y mejorar las nuevas posibilidades.

El cambio climático y la deforestación están íntimamente relacionados, ya que sus efectos combinados ponen en peligro la estabilidad y la permanencia de la biodiversidad tal como la conocemos hasta ahora. La deforestación en Colombia

involucra no solo el componente biológico y ambiental sino también una serie de factores sociales, políticos y económicos, que están en constante proceso de adaptación y variación. Incluso podría decirse que la conservación de la biodiversidad es medida previamente por cuestiones políticas que están en la agenda nacional y, por lo tanto, es de gran importancia que se utilice información confiable para lograr políticas generales que verdaderamente comprendan la realidad nacional en términos ambientales. Es importante, por lo tanto, para futuras investigaciones, una comprensión detallada de los procesos de adaptación en términos ecológicos y ecosistémicos para especies indicadoras a nivel nacional.

Finalmente, los resultados presentados en este trabajo de investigación deberían idealmente ser analizados ante la perspectiva social del país y el proceso de paz que actualmente vive. Dado que los esfuerzos que se hagan por entender la biodiversidad colombiana y como esta se ve afectada por procesos de cambio locales y globales, debe estar articulada con los procesos sociales y de ocupación del territorio para que, de esta manera, se puedan generar estratégias de acción y fortalecimiento en la conservación de los bosques y en los procesos de adaptación y mitigacion ante el cambio climático.

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Anexos

Anexo 1. Código para análisis geográficos artículo 1.