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Conservation Implications for the Persistence of Species into the Future

Modelamiento de la Dispersión de Atelinos (Primates, Atelinae) a través de Escenarios de Cambio Climático y Fragmentación de Hábitat en Colombia

Implicaciones en la Conservación para la Persistencia de las Especies a Futuro

Jaime Burbano-Girón

Universidad Nacional de Colombia
Facultad de Ciencias
Departamento de Biología
Bogotá, Colombia
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Director:
Thomas R. Defler, PhD.
Co-Director:
Andrés Etter, PhD.

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Abstract

Prioritizing landscape connectivity is a primary objective in the conservation planning of biodiversity, since it is assumed that there will be scenarios where the dispersal of species would be necessary due to habitat fragmentation and climate change. Atelines (Primates, Atelinae) include species of Spider Monkeys (*Ateles spp*.) and Woolly monkeys (*Lagothrix spp.*); primates with great importance for the tropical forest ecosystems where they inhabit because of their role as seed dispersers. Due to habitat loss and habitat fragmentation, hunting and illegal trade, these species are increasingly endangered. The aim of this study is to identify priority areas of conservation for ateline dispersal in Colombia in order to maintain connectivity among their populations under scenarios of habitat fragmentation and climate change in the period 2000-2020. Spatiotemporal functions of habitat quality and cost flow were constructed to evaluate the probability of dispersal and the dispersal flux of each species under a graph-theoretical approach, based on the following variables: i) net primary productivity, ii) cover type, human iii) population density and iv) climatic habitat suitability. The resulting dispersal scenarios show differences between species located in different regions: i) species distributed in the Amazon (*A. belzebuth* and *L. lagothricha lagothricha*) do not show problems in terms of spatial or temporary connectivity; ii) *A. geoffroyi* distributed over the Pacific region shows a slight trend towards habitat fragmentation, however in the short term (10 years) these effects do not cause ruptures in the connectivity for the species; iii) Andean species (*A. hybridus* and *L. lagothricha lugens*) show a clear and drastic loss of habitat over time, strongly limiting their current and future dispersion possibilities. Changes in habitat climatic suitability for *A. belzebuth, A. geoffroyi* and *L. lagothricha lagothricha* are higher in moister and warmer low-land areas, responding to increases in precipitation and temperature projected in climate change scenarios. For *A. hybridus* and *L. lagothricha lugens* the climatic habitat suitability is greater in warmer regions with moderate elevations, where major process of deforestation have occurred over dry and Andean forests. Based on connectivity analysis we propose the following as conservation targets: i) source patches, ii) areas of persistence, iii) lost, iv) and regenerated habitat,

v) stepping stones, vi) the most efficient network of habitat connected patches (minimum spanning tree), vii) and the probable physical connections where species dispersal would take place. Spatial and persistent habitat representativeness in protected areas (PAs) for each species is low. The results show that larger PAs can be an effective measure for habitat conservation of species, since patches of remaining habitat under these regions are mostly conserved. We identify the Serranía de San Lucas as a priority conservation area; it is not legally protected and is the main source patch for *A. hybridus*, the ateline species treated in most detail.

Key words

Dispersal, habitat fragmentation, climate change*, Ateles, Lagothrix*

Resumen

Priorizar la conectividad del paisaje es uno de los objetivos primordiales en la planeación para la conservación de la biodiversidad, ya que se asume que existirán escenarios donde la dispersión de las especies será necesaria debido a la fragmentación de hábitat y el cambio climático. Los Atelinos (Primates, Atelinae) incluyen las especies de Monos Araña (*Ateles spp.*) y Monos Lanudos (*Lagothrix spp.*); primates de gran importancia para los ecosistemas de bosque tropical húmedo donde habitan por su rol como dispersores de semillas. Debido a la fragmentación y pérdida de hábitat, la cacería y el comercio ilegal, estas especies están cada vez más en peligro de extinción. El objetivo de este estudio es identificar áreas prioritarias de conservación para la dispersión de los atelinos en Colombia con el fin de mantener la conectividad entre sus poblaciones bajo escenarios de fragmentación de hábitat y cambio climático en el periodo 2000-2020. Se construyeron funciones de calidad de hábitat y costo de flujo espaciotemporales para evaluar la probabilidad de dispersión y el flujo de dispersión de cada una de las especies bajo un enfoque de teoría de grafos, con base en las siguientes variables: i) productividad primaria neta, ii) tipo de cobertura, iii) densidad poblacional humana e idoneidad de iv) hábitat climática. Los escenarios de dispersión resultantes muestran diferencias entre las especies localizadas en diferentes regiones: i) las especies distribuidas en la región amazónica (*A. belzebuth* and *L. lagothricha lagothricha*) no mostraron problemas en términos de conectividad espacial o temporal; ii) *A. geoffroyi* distribuido sobre la región pacífica, muestra una leve tendencia negativa hacía la fragmentación de hábitat, sin embargo a corto plazo (10 años) estos efectos no causan rupturas en la conectividad para la especie; iii) las especies Andinas (*A. hybridus and L. lagothricha lugens*) muestran una clara y drástica pérdida de hábitat a través del tiempo, limitando fuertemente sus posibilidades de dispersión actuales y futuras. Los cambios en la idoneidad de hábitat climática para *A. belzebuth, A. geoffroyi* y *L. lagothricha lagothricha* son más altos en áreas más húmedas y cálidas de tierras bajas, respondiendo a los incrementos en precipitación y temperatura proyectados en los escenarios de cambio climático. Para *A. hybridus* y *L. lagothricha lugens* la idoneidad de hábitat climática es mayor en regiones más cálidas con elevaciones moderadas, donde los procesos de deforestación más importantes han ocurrido sobre los bosques secos y andinos. Con base en el análisis de conectividad se propusieron los siguientes objetos de conservación: i) parches fuente, ii) áreas de hábitat persistente, iii) perdida iv) y regenerada, v) stepping stones, vi) la red más eficiente de los parches de hábitat conectados (minimum spanning tree), vii) y las conexiones físicas probables donde la dispersión de las especies se llevaría a cabo. La representatividad espacial y de persistencia de hábitat en las áreas protegidas para cada especie es baja. Los resultados muestran que áreas protegidas más grandes pueden ser una medida efectiva de conservación del hábitat de las especies, ya que los parches de hábitat remanente bajo estas regiones están mayormente conservados. Se identifica la Serranía de San Lucas como una zona prioritaria de conservación, ya que esta no está legalmente protegida y es el principal parche fuente para *A. hybridus*, la especie de atelinos más amenazada.

Palabras Clave

Dispersión, fragmentación de hábitat, cambio climático*, Ateles, Lagothrix*

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Introduction

Habitat fragmentation and climate change are considered two of the main threats leading to biodiversity loss (Sala et al. 2000; Stedman-Edwards 2000; Sax & Gaines 2003; Opdam & Wascher 2004; Millennium Ecosystem Assessment 2005; de Chazal & Rounsevell 2009; Pereira et al. 2010), considering species extinction as a topic of most concern (Thomas et al. 2004; Kuussaari et al. 2009; Jackson & Sax 2010). In this context, the decrease in the range of species distributions because of habitat fragmentation (Honnay et al. 2002; Fahrig 2003) and climate change in terms of potential migrations and projected shifts in the geographic range of species have received special attention (Thomas et al. 2004; del Barrio et al. 2006; Thuiller et al. 2008), particularly when some of these predictions have been modeled outside of protected areas (PAs) (Araújo 2004; Hannah et al. 2007).

In most of projections, it is expected that species will be confronted with the movement through adverse climate gradients and fragmented landscapes; hence, aspects like the extent of the PA, their spatial arrangements, the remnant vegetation, and the connectivity should be taken into account to analyze the sensitivity of PAs to species' persistence (Pearson & Dawson 2005; Moilanen et al. 2009). Consequently, this has led to the necessity of defining and prioritizing conservation areas, which would allow the dispersion of the species in space and time (Williams et al. 2005; Hannah et al. 2007; Phillips et al. 2008b; Carvalho et al. 2011; Dawson et al. 2011; Hole et al. 2011).

In this regard, the "Guidelines for Applying Protected Area Management Categories" proposed by the International Union for Conservation of Nature and Natural Resources (IUCN) (Dudley 2008), emphasizes that conservation areas will have to serve as buffers against climate change events, and provide a set of natural habitats connected to supply dispersal corridors which also permit evolution and adaptation. In Colombia, the "Unidad Administrativa Especial del Sistema de Parques Nacionales Naturales" (UAESPNN) (www.parquesnacionales.gov.co) has adopted as part of its Action Plan for 2010-2019, a proposal to ensure ecological representativeness of the National

System of Protected Areas (SINAP by its Spanish acronym) and the connectivity between them, where the formulation of selection criteria for places which increase the connectivity and viability of PAs, ecosystems, and species at different scales are a main concern.

In order to apply prioritization for conservation areas in the framework of Systematic Conservation Planning (SCP), the identification of target species that can be used as proxies for biodiversity in the planning region is necessary (Margules & Pressey 2000; Margules & Sarkar 2007). The use of species, taxa or umbrella groups in this context is frequent. Although some studies have tested the inefficiency of using single species, others have shown that birds or mammals used as a group of key species, can be useful and constitutes an effective conservation tool (Roberge & Angelstam 2004; Branton & Richardson 2011).

Primates have often been considered as umbrella species (Caro et al. 2004; Martins & Valladares-Padua 2005; Lambert 2011). In particular, the ateline group (*Ateles spp. and Lagothrix spp.*) due to their ecological role as seed dispersers, and their vulnerable/endangered conservation status, makes them a key group for prioritizing conservation areas (Strier 1992; Stevenson & Aldana 2008; Defler 2010). For these species, there is a large uncertainty on what we could expect in their distributions in response to climate change scenarios, making their study a remarkable contribution towards its conservation, even more if it is applied in the entire context described above.

This study aims to model the dispersal of the atelines through scenarios of climate change and habitat fragmentation in Colombia with a graph-theoretical approach, to select a set of areas that would need additional attention from conservation authorities in order to maintain populations of them. The proposed approach, takes into account their dispersal over suitable habitats based on the scenarios proposed, and also evaluates the representativeness of the actual PAs in terms of their size and spatial distribution, prioritizing the set of areas chosen in order to guarantee the connectivity for the species through space and time.

Objectives

Identify a set of areas that deserve additional attention in order to guarantee the dispersion of Atelines over suitable habitats based on scenarios of climate change and habitat fragmentation through time (2000-2020).

1. Analyze the differences projected in dispersal of Atelines through time (2000-2020) under scenarios of climate change and habitat fragmentation.

2. Prioritize areas for conservation of Atelines in order to retain or improve the connectivity through time (2000-2020), under scenarios of climate change and habitat fragmentation.

3. Determine if the dispersion of Atelines is guaranteed through time by the current PAs in Colombia based on scenarios of climate change and habitat fragmentation.

1. Conceptual Framework

1.1 Biodiversity Threats: Climate Change and Habitat Fragmentation

The Intergovernmental Panel on Climate Change (IPCC) (2007) has reported actual evidences of climate change continuously affecting multiple natural systems. For the next two decades a warming of about 0.2°C per decade is projected primary because of increases in: i) CO_2 due to fossil fuel use and land-use change, ii) CH_4 due to livestock and fossil fuel use, and iii) N_2O due to agriculture. As consequence, some of the following changes are expected to occur: i) a maximum warming on terrestrial ecosystems, ii) a greater thaw depth in most permafrost regions, iii) a probable increase in the frequency of hot extremes, heat waves, heavy precipitation and tropical cyclone intensity, iv) a poleward displacement of the storm paths outside the tropics developing changes in patterns of wind, precipitation and temperature, and v) an increase in precipitation at high latitudes with decreases in most subtropical land regions.

All these probable effects are expected to have negative implications on global biodiversity such as: i) changes in ecosystem structure and function, ii) alterations in species' ecological interactions; iii) shifts in species' geographical ranges; and iv) negative consequences for ecosystem goods and services such as water and food supplies (Araújo & Rahbek 2006; Thuiller 2007). In general terms, it is probable that the ecosystems will exceed their resilience by a combination of climate change, associated disturbances (e.g. flooding, drought, wildfire, insects, ocean acidification), and other drivers of global change (e.g. land-use change, pollution). Additional and major preoccupations are that probably 20 to 30% of plant and animal species will increase their risk of extinction (medium confidence), and that net carbon uptake by terrestrial ecosystems is likely to peak before mid-century and then grow weaker or even reverse, amplifying climate change (IPCC 2002).Direct climate change effects on biodiversity are not globally measurable, therefore these have been frequently studied under interactions with habitat loss/fragmentation (Opdam & Wascher 2004; de Chazal & Rounsevell 2009; Clavero et al. 2011). The studies have shown that climate change can promote the progress of transition conditions and the opening of gaps inside the vegetation (Del Barrio et al. 2006), in addition to species turnover (Thuiller 2004), shifts in the distributions and abundances of species (Parmesan & Yohe 2003; Root et al. 2003) and possible migrations (Pearson 2006). However, the effect of most concern is the possibility of species extinction (Thomas et al. 2004; Bässler et al. 2010; Jackson & Sax 2010).

Nevertheless, the relationship between habitat fragmentation and climate change is not totally understood and the actual impacts of climate change, may have been over- or under-estimated because of the lack of integrated analyses that consider their joint implications on biodiversity change (Sala et al. 2000; de Chazal & Rounsevell 2009; Pereira et al. 2010). For example, a recent study on birds at a community level, show that land use changes can reverse, hide or intensify the perception of climate change impacts, underlining the need of an explicit incorporation of the relationship between climate change and land use dynamics, to understand what climate change indicators really represent, and then identifying the actual climate change impacts (Clavero et al. 2011).

Also, current impacts of habitat fragmentation may have been underestimated. Fragmentation is a phenomenon visible from a context of change, including an evolutionary level; hence long-term impacts of fragmentation may not be seen because of the presence of confounding species factors that can mask them. Some of these traits may be specific trophic level, dispersal abilities and the degree of habitat specialization that influences the responses of the species (Ewers & Didham 2006). However, there is a general assumption in which both, climate change and habitat fragmentation in association, might cause a greater impact than either of these by themselves, particularly at the metapopulation and the species range levels (Opdam & Wascher 2004; de Chazal & Rounsevell 2009).

The process of habitat loss/fragmentation decreases the sizes of habitat patches and increases their number and isolation, transforming the properties of the remaining habitats (Fahrig 2003). Fragmentation in a landscape forces the species that survive in the habitat remnants to be confronted with a modified environment in a reduced area as well as novel ecological boundaries, with implications at different levels, given that in any landscape the number of species and organisms is high and variable, each one with different life history strategies (Ewers & Didham 2006).

Habitat fragmentation essentially acts to change the core of a species' distribution and therefore its abundance (Del Barrio et al. 2006). However, it also affects the richness and diversity of species and genes, increasing the effects of genetic drift and the probability of species extinction. Many empirical studies continue to document changes in species richness associated with habitat fragmentation, describing positive, negative and absent relationships (Fahrig 2003). These studies report that shifts in biotic and abiotic parameters at edges, make ecological processes more variable than in fragment interiors, leading to increased turnover and variability in population (Ewers & Didham 2006).

Habitat isolation both in space and time alters the distributional patterns of species causing impacts on metapopulation dynamics. Among these gene flow and individuals' movements are the most affected. In this situation the impact of the landscape matrix is a decisive factor in the effects exerted by fragmentation on populations, due to the role played in the species dispersal, associated mortality, and the pressure over microclimatic gradients present at fragment edges (Pulliam et al. 1992; Ewers & Didham 2006). Other more specifically negative effects have been found and reported by Fahrig (2003), e.g., the reduction of the trophic chain length (Komonen et al. 2000) or the change in the number of specialist species (Gibbs & Stanton 2001), and changes in aspects of animal behavior that affect breeding (Kurki et al. 2000), predation (Bergin et al. 2000), foraging (Mahan & Yahner 1999), and dispersal success (Bélisle et al. 2001).

The growing frequency of disturbances caused by large-scale climate events probably increases gaps and reduces species' distributional ranges, particularly in fragmented areas. Taking into account the effects of climate change on metapopulations, habitat distribution and on land use changes, future biodiversity research and conservation strategies will be challenged to reorient the focus and scope of such studies by integrating more dynamic aspects at the landscape level, both spatially and conceptually (Opdam & Wascher 2004).

1.2 Foraging, Species Dispersal and Connectivity in the Context of Habitat Fragmentation and Climate Change

Habitat selection for residency and movement as a behavioral process depends on the resource and habitat selection by individuals, which in turn depends on aspects like conspecific attraction, habitat imprinting, or natal home range cues at different spatial and temporal scales (Chetkiewicz et al. 2006). Organisms are motivated to move for different reasons such as foraging, evading predators or searching for breeding opportunities (Ims 1995), generating movements on a daily or regular basis, seasonal and migratory movements, dispersal movements, and range expansion (Bennett 2003).

Under habitat fragmentation and climate change scenarios the limitations for the foraging and dispersal of species determined by landscape connectivity, plays a fundamental role for their persistence (Harrison & Bruna 1999; Williams et al. 2005; Apps & McLellan 2006; Ewers & Didham 2006; Phillips et al. 2008b), and therefore in the preservation of biodiversity and its ecosystem functions (Boyer et al. 2006; Stevenson & Aldana 2008). The foraging behavior of a species responds to environmental configurations that support or constraint the search for food (Heller 1980; Hughes 1990), and it is maximized through time by natural selection (Pyke et al. 1977). According to the optimal foraging theory (Emlen 1966; MacArthur & Pianka 1966), the most favorable behavior depends on the choice of a currency, the choice of the appropriate cost-benefit functions (i.e., establishing the constraints), and by solving for the optimum behavior that maximizes the net rate of energy intake (all these subject to the various constraints) (Schoener 1971).

Main foraging aspects are: optimal diet, optimal patch choice, optimal allocation of time to patches, and optimal patterns and speed of movements (Pyke et al. 1977). These, are the base of two optimal foraging models: i) individuals forage longer when the distance between patches is longer too and the environment less profitable (Charnov 1976), and ii) the optimal time per unit area decreases with the distance from the central place (Andersson 1978). However, if an animal does not distinguish the quality of the existing patch types, then its optimal allocation of time should depend on: i) how much foraging time remains, ii) on its experience in each patch type, and iii) on any prior knowledge about the kinds of patches available (Pyke 1984). These last three aspects are a basis for understanding the notion of adaptive foraging.

Adaptive foraging refers to changes in resource or patch exploitation by the experience of consumers that give them higher fitness compared with other individuals that show other strategies, suggesting that adaptation and evolution can happen on similar time scales, where two major components can accelerate them: variations in abiotic environment, and dispersal to and from neighbor communities (conditions of changing scenarios) (Loeuille 2010). Thus, if the species can be adaptive in terms of foraging, their persistence can have a lower risk, even though it does not involve optimal use of habitat (Kokko & López-Sepulcre 2006).

Previous postulates are key concepts in the context of actual and future habitat fragmentation and climate change, where individuals are expected to experience variable negative and positive fitness in response to landscape configuration changes (the spatial arrangement of habitat patches and ecotones) and this may result, in a change of the species movements (Tischendorf & Fahrig 2000). Thinking in terms of evolutionary adaptations to warmer conditions and patchy habitats in species’ ranges (McCarty 2001), resource use and dispersal will have to evolve rapidly at the same time that range margins change (Parmesan 2006), varying the threshold between species´ foraging and dispersal (a scenario that is unlikely for long-lived ateline primates).

In the context of landscape ecology, species dispersal is usually associated with the movement of individuals from one habitat patch to another (Turner et al. 2001), or from an existing population to another since the perspective of metapopulations (Dunning et al. 1995). Thus, species dispersal has consequences for individual fitness, population dynamics, species distributions and genetics (Wiens 1997; Hanski 1999).

The optimal use of habitat patches by species depends on landscape elements and their configuration. The characteristics of the matrix between patches, corridors linking patches, and patches of preferred habitat, make the movement through the landscape mosaic different for different species (Selonen & Hanski 2003; Apps & McLellan 2006). The process of movement understood as the different ways in which animals move within landscapes, defines the patterns of distribution and related ecological processes, to the point that the probability of movement can determine the connectivity of landscapes (Chetkiewicz et al. 2006).

The concept of connectivity is used to illustrate how spatial arrangement and quality of elements in the landscape affect the movement of organisms among habitat patches (Bennett 2003). A particular landscape at the same time might provide high connectivity for some organisms and low connectivity for others. A landscape with high connectivity permits individuals to move without constraints between suitable habitats, such as vegetation types for foraging or sleep, while a landscape with low connectivity (highly fragmented) restricts moving between selected habitats (Bennett 2003).

Connectivity can be addressed from two points of view: structural connectivity, referring to the degree to which some landscape elements of interest are adjacent or physically connected to another (Tischendorf & Fahrig 2000), and functional connectivity, understood as the degree to which a landscape mosaic facilitates or impedes movement among resource patches (Taylor et al. 1993). The latter depends on how an individual recognizes and responds to landscape configuration, and so in this sense, functional connectivity varies with the species, the context, and the scale, and may not be equivalent in all directions of movement (Bélisle 2005).

In terms of habitat fragmentation and climate change the role of connectivity is essential in order to extend the geographic range of species, maintain continuity in the landscape and connect PAs (Chetkiewicz et al. 2006). As far as the extent that dispersal resource availability and environmental factors permit, species are projected to track the changing climate and habitat, and likewise shift their distributions in response (Walther et al. 2002). For this, an integrated landscape approach to conservation is necessary, including aspects like: i) plans at broad spatial scales, ii) protection of key areas of natural habitat, iii) maximization of conservation values across a variety of land tenures, iv) maintenance and restoration of connectivity, v) and the integration of conservation with surrounding land uses like agroforestry (Bennett 2003; Laurance 2004).

However, high levels of movement through a landscape cannot be associated with the functional connectivity of a landscape (Bélisle 2005). Therefore, to understand how landscape structure affects movement and, therefore, the population dynamics of a species, a clear empirical knowledge about movement patterns, and especially about the ecology of the species is needed to implement actions towards species conservation (Selonen & Hanski 2003).

1.3 Ateline Ecology and Conservation Status in Colombia

The family Atelidae is the most extensively distributed of the New World primates and includes genera: *Alouatta* (howler monkeys), *Ateles* (spider monkeys), *Brachyteles* (muriquis - woolly spider monkeys) *Lagothrix* (woolly monkeys) and *Oreonax* (yellow-tailed woolly monkey previously incorporated in *Lagothrix,* but at present considered a monospecific genera including the Peruvian endemic species *Oreonax flavicauda*) (Strier 1992; Cornejo et al. 2008; Defler 2010). However, some authors disagree with the validity of the genus *Oreonax*, and it is still debated (Matthews & Rosenberger 2008; Rosenberger & Matthews 2008).

Based on morphological, behavioral and molecular analyses of Atelid phylogenetic relationships, it is possible to distinguish between two natural groups of Atelidae: the first, subfamily Alouattinae including *Alouatta*; and the other four genera grouped in the subfamily Atelinae (Strier 1992; Rylands & Mittermeier 2009; Defler 2010). These last four genera are commonly referred as the atelines (ateline monkeys), with four species for Colombia according to Defler (2010) (Table 1).

The distribution of atelines in Colombia encompasses a large proportion of the continental territory because this group is characterized by wide geographic ranges (Ford & Davis 1992; Strier 1992; Defler 2010). However, present habitat loss for this species also has largely and significantly reduced their current distributional area, and added to the lack of knowledge of the real distribution of some of them, leads to concern for the formulation of conservation measures of these species (Defler 2010).

The natural habitat of atelines is primary forest in the different ecosystems where they are found. They prefer the highest canopy levels and move primarily between middle and upper segments (Ford & Davis 1992; Defler 2010). They descend to the ground rarely, except under specific conditions like when eating soil or rotten wood, visiting salt licks, drinking from streams during the dry season, escaping attacks (by adult females) of adult males, or as part of a chase game (Campbell et al. 2005).

Ateles belzebuth lives below 1300 m of altitude in primary rainforest, gallery forest and in seasonally flooded forests when these offer a seasonal abundance of fruits (Boubli et al. 2008; Defler 2010). *Ateles geoffroyi* has been reported for many more types of habitats than other species of *Ateles*: evergreen, semideciduous and deciduous forest, dry forest, humid forest, cloud forest, mangrove forest and at altitudes reaching 2000 – 2500 m on the western slopes of the Andean western cordillera of Colombia (Cuarón et al. 2008). *Ateles hybridus* has been frequently found in evergreen forest, tropical semi-deciduous forest, tropical coastal forest, dense evergreen forest, and at moderate elevations (280-600 m) in montane seasonal forest (Urbani et al. 2008; Defler 2010). *Lagothrix lagothricha* occurs in primary forest from lowlands up to elevations of 3000 m and occasionally in degraded forest and flooded forest. In the Llanos Orientales *Lagothrix lagothricha* inhabits primary tropical moist forest but also morichales and yarumales (Defler 2010). The species can be found in cloud forests, although the decrease in the size of the groups as they live at higher altitudes is notable (Durham 1975).

Table 1. Ateline species and subspecies present in Colombia according to Defler (2010).

Species	Species Authority	Common Names	Subspecies
Ateles belzebuth	É. Geoffroy, 1806	Long-haired Spider Monkey, White-bellied Spider Monkey, Mono Araña, Mono Araña De Vientre Amarillo, Marimonda, Marimba, Braceadora, Coatá, Maquizapa.	*Ateles belzebuth belzebuth*
Ateles geoffroyi	Kuhl, 1820	Brown-headed Spider Monkey, Black-headed Spider Monkey, Marimonda, Marimunda, Choiba, Mono Negro Mica, Zamba.	*Ateles geoffroyi rufiventris* and *Ateles geoffroyi robustus* (recognized by IUCN specialists Cuarón et al. (2008) as *Ateles fusciceps rufiventris*)
Ateles hybridus	I. Geoffroy, 1829	Variegated Or Brown Spider Monkey, Brown Spider Monkey Mono Araña, Mono Negro, Choiba.	*Ateles hybridus hybridus* and *Ateles hybridus brunneus*
Lagothrix lagothricha	Humboldt, 1812	Humboldt's Woolly Monkey, Woolly Monkey, Macaco Barrigudo, Mono Barrigudo, Mono Caparro, Mono Lanudo, Mono Choyo, Choyo, Choro, Churuco, Chuluco, Barrigudo, Mico Cholo, Mico Negro, Mico Churrusco.	*Lagothrix lagothricha lagothricha* (recognized by IUCN specialists Palacios et al. (2008) as *Lagothrix lagothricha*) and *Lagothrix lagothricha lugens* (recognized by IUCN specialists Stevenson & Link (2008) as *Lagothrix lugens*)

Spider monkeys travel and forage in the canopy and are extremely suspensory. When they move, they spend more time hanging from the branches and locomoting by brachiation, swinging or climbing. The proportion of walking or running is lower compared to the other taxa in the group (Ford & Davis 1992; Strier 1992; Defler 1999, 2010; Cuarón et al. 2008; Urbani et al. 2008). While locomoting and feeding *Lagothrix lagothricha* move quadrupedally 41% of the time, and use arm movements 1.7% of the time (they employ this type of locomotion much less than the spider monkeys).

Lagothrix also climbs over 38.8% of time and spends about 10.8% of its time moving and jumping (Defler 1999, 2010).

Results presented by Cant et al. (2003) show significant differences in the use of suspensory modes by *Ateles* and *Lagothrix*. *Ateles* implements more brachiation (using forelimbs and tail, with trunk rotation) and forelimb swing (similar to brachiation, but without trunk rotation) than *Lagothrix*, while this latter employs 20% suspensory movement using pronograde forelimb swing (similar to forelimb swing but differs due to the body position in a pronograde direction), a behavior that *Ateles* did not show in this study.

Results presented for Isler (2004), show that there are very few differences between *Ateles* and *Lagothrix* in gait parameters of climbing on small diameter trees and vertical and oblique ropes, while climbing in large diameter trees differs considerably, reflecting the higher costs of locomotion for *Lagothrix*. However at the same speed, *Ateles* takes longer strides and the support phase takes a smaller percentage of cycle duration than in *Lagothrix.* Phylogenetic differences would be the principal cause for differences in patterns of movement in *Ateles* and *Lagothrix*, however, the general pattern illustrates that these species base their use of space on rapid locomotion, that enables them to minimize travel time between different resource patches to access fruits, frequently suspending from branches with their prehensile tail, arms and legs to better and more easily reach and handle food (Strier 1992; Defler 2010).

Although the home and daily range of atelines is characterized as large, the data vary between species and even between populations because of resource availability. This means, that when the habitat provides a large amount of resources, the individuals will not have to travel large distances because resources can be easily found. On the other hand, poor habitats that do not provide enough resources for species will force the displacement of individuals to be larger in order to find resources in other habitats. Based on this, the approximate home range of *Ateles* species may vary between 100 and 400 ha, while the daily range ranges between 0.5 and 5 km. For *Lagothrix lagothricha* it may differ approximately between 100 and 800 ha for the home range, and between 1 and 3 km for the daily range (Ford & Davis 1992; Defler 2010). These conditions described above determine movement patterns of the species; therefore they are a major concern in this study.

Atelines change the proportions in their diet in order to compensate for the scarcity of resources (Mittermeier & Van Roosmalen 1981; Strier 1992; Peres 1994; Castellanos & Chanin 1996; Defler 1996; Defler & Defler 1996; Stevenson et al. 2000; Di Fiore & Rodman 2001; Di Fiore 2004; Stevenson 2004; Dew 2005; Gonzalez-Zamora 2009). These primates pass from an energy-maximizing strategy of food acquisition during times of fruit abundance to an energy-minimizing strategy that focuses on animal foods during sources scarcity (Strier 1992). This strategy permits to lay down fat reserves when ecological conditions are worsen, suggesting again that regional differences in habitat quality are extremely influential in ateline behavioral ecology, in this case as an opportunistic response in foraging strategy (Stevenson et al. 2000; Di Fiore & Rodman 2001).

Atelines are highly frugivorous and prey upon seeds of just a few species. Spider monkeys feed mostly on the mature, soft parts of a very wide variety of fruits, which comprise approximately 83% of their diet. They also can eat young leaves and flowers (both especially at times of fruit shortage during the beginning of the dry season), young seeds, floral buds, pseudobulbs, aerial roots, bark, decaying wood, and honey, and very occasionally small insects such as termites and caterpillars (Mittermeier & Van Roosmalen 1981; Castellanos & Chanin 1996; Stevenson et al. 2000; Dew 2005; Boubli et al. 2008; Cuarón et al. 2008; Urbani et al. 2008; Gonzalez-Zamora 2009; Defler 2010).

Russo et al. (2005) found for *Ateles spp*., that from the 59 most frequently consumed genera from forests in Colombia, Ecuador, Panama, and Surinam, only 4 genera: *Brosimum* (Moraceae), *Cecropia* (Cecropiaceae), *Virola* (Myristicaceae), and *Ficus*, (Moracae) were ranked within the top 20 at every forest. They also found that interforest variation in plant species composition and abundances, in addition to annual fruiting phenologies and dietary flexibility of *Ateles spp.*, explained the results in diet for each species in each forest, suggesting again that variation in plant community structure strongly influences dietary preferences.

The dietary habits of *Lagothrix lagothricha* are not very different from those found for *Ateles spp.*; these variations show differences in plant species richness, plant abundances and annual fruiting phonologies of each forest (Strier 1992; Stevenson et al. 2000; Di Fiore & Rodman 2001). However, *Lagothrix* are not hard-fruit specialists and their fruit diet is significantly more diverse than that of spider monkeys (Dew 2005). Defler (2010) describes the species as an obligate frugivore. *Lagothrix lagothricha* bases approximately 80% of its diet on fruits, complemented with immature leaves, seeds and exudates of flowers and seeds. It can consume a number of different plants (close to 200) that vary in response to forest species composition and abundance. The most important families in its diet are: Moraceae, Sapotaceae and Leguminosae (Peres 1994; Defler 1996, 2010; Defler & Defler 1996; Stevenson et al. 2000; Di Fiore 2004; Stevenson 2004; Dew 2005).

Dew (2005) reports that overlap in diet between the atelines is high; nevertheless each genus specializes to some degree on a different set of fruit resources and their foraging patterns are slightly different. *Lagothrix* visits more food resources per unit of time, feeds less in the canopy, visits more small food patches and preys on more seeds. In contrast, *Ateles* feeds on less rich food resources and are more likely to return twice to a food resource than *Lagothrix*. *Ateles* maximizes the consumption of fruit pulp, swallowing more intact seeds, while woolly monkeys minimize the amount of seeds ingested by more careful food processing. This is a principal aspect in terms of seed dispersion and a probable reason why *Ateles spp*. are not more efficient than woolly monkeys at improving plant germination rates, even though spider monkeys depend more heavily on fruits than woolly monkeys do (Stevenson et al. 2002).

Seed dispersion by atelines can be considered very effective in comparison to other primates, in terms of their effects on the seeds they eat and which rarely decrease their germination rates (Stevenson et al. 2002). Their principal ecological role as seed dispersers is extremely important in order to maintain forest diversity (Stevenson et al.

2002; Defler 2010), to the point that their absence may have negative effects on plant populations, especially large-seeded plants, that are rarely swallowed by other seed dispersers (Wunderle 1997; Peres & van Roosmalen 2002).

For example, in a comparison between a continuous and fragmented forest with floristic affinities and similar ecological characteristics in Tinigua National Park, Stevenson & Aldana (2008) found that diversity was lower in the fragmented forest where fewer large-seeded plant species lived, suggesting that forest fragmentation and local ateline extinctions affect plant communities, reducing diversity and affecting large-seeded plants. Thus, ateline conservation is not only important for the preservation of the species *per se*, but also for the conservation of their habitats, that ideally should include large continuous forest extensions with high productivity that would be able to support many other species.

Atelines are particularly susceptible to hunting and habitat fragmentation (Chapman & Peres 2001; Defler 2010), therefore, towards their conservation, priority strategies should be as follow: i) Census the species to generate information on the species´ actual distribution, densities, and their population structure. ii) Maintain the largest extension of forest in actual PAs. iii) Propose the establishment of new PAs. iv) Generate strategic alliances with indigenous communities and other groups. v) Create conservation campaigns and education plans. vi) Identify financial support for the maintenance and monitoring of all these (Defler et al. 2005; Boubli et al. 2008; Cuarón et al. 2008; Palacios et al. 2008; Stevenson & Link 2008; Urbani et al. 2008; Defler 2010; Morales 2010). Conservation status of ateline species and their specific conservation actions are presented in Table 2.

Table 2. Conservation status for ateline species present in Colombia. Based on data from: Defler et al. (2005), Boubli et al. (2008), Cuarón et al. (2008), Palacios et al. (2008), Stevenson & Link (2008), Urbani et al. (2008), Defler (2010) and Morales (2010).

	Category of Threat		**CITES Appendix**	**Major Threats**	**Conservation Actions**
Ateles belzebuth	Int. Col.	EN EN	II	Heavy subsistence and market hunting for food and habitat loss due to colonization and illicit crops	Maintain the extension of forest in actual PAs, mainly in Parque Nacional Natural Sierra de La Macarena, Tinigua Natural National Park and Cordillera de Los Picachos. Support the establishment of new PAs specially in forest area between Caguán and Yarí rivers
Ateles geoffroyi	Int. Col.	CR CR	II	One of the most threatened species with high possibility of extinction in Colombia due to hunting, habitat loss and fragmentation	Widespread censuses of *Ateles* are needed, especially in National Natural Parks Katios and Orquideas, where it is believed that populations have declined recently.
Ateles hybridus	Int. Col.	CR CR	II	One of the most threatened species in Colombia due to hunting and habitat fragmentation. *Ateles hybridus brunneus* is probably the most endangered of both due to their small range of distribution and the growing threat of colonization, which added to its long birth intervals, every 3-4 years can lead to extinction in a short time. *Ateles hybridus* is also one of The World's 25 Most Endangered Primates 2008-2010 (Mittermeier et al. 2009).	These are some more of the measures outlined in the plan of action for the conservation of this species, which is well referenced in Defler 2010. Identify conservation measures within the priority areas: Catatumbo Cocuy Quinchas, Luke and Bajo Cauca. Enact the generation of the Natural Park Serranía de San Lucas. Generation of strategic alliances with indigenous communities and other groups. Conservation campaigns. Support, strengthen and solidify nature reserves, particularly the one of La Serranía de Las Quinchas of ProAves Foundation. Recovery and reforestation in the areas of distribution. Generate a database of campaigns, research projects, outreach and conservation actions that involve the species. Community environmental diagnosis to define the risk factors for the species in each of the locations.
Lagothrix lagothricha	Int. *L.l.la*	VU	II	The major threats are hunting for food (mainly subsistence) and habitat loss due to agricultural development/expansion and illicit crops. Late maturation and long inter-birth intervals (typically around 3-4 years) makes it difficult for them to recover their populations. Also national and international pet trade affects this species	Although *L.l.lugens* is protected by law in 12 or 13 units of conservation, many of these PAs were established for the purpose of preserving other habitat, very different to that required by *Lagothrix*, while in other cases, the PA contains very little of the preferred habitat for the species, then it is expected that new areas that have a really possibility to maintain populations can be established, accompanied by financial support by government for the maintenance and monitoring of them.

∗ Int. and Col., correspond to abbreviations of International and Colombian categories of threat respectively.

1.4 Conservation Planning for Habitat Fragmentation and Climate Change: Prioritizing Conservation Areas for Species Dispersal

Definition and prioritization of conservation areas that permit the continued presence and persistence of the species in space and time is a main concern, taking into account the actual needs of conservation into the future, and the anticipation of species loss due to multiple threats to biodiversity (Hannah et al. 2007; Carvalho et al. 2011; Dawson et al. 2011; Hole et al. 2011). Major preoccupations like fragmentation and climate change (Sala et al. 2000), must be taken into consideration to ensure aspects like dispersal (Williams et al. 2005; Phillips et al. 2008b), especially in scenarios of possible migrations (Pearson et al. 2006) and unconnected habitats (Sala et al. 2000).

Climate change at all scales interacts with other disturbing global trends like deforestation and air pollution, producing combined negative effects for the environment and natural resources, which will be worse in the future if integrated measures for mitigation and adaptation are not taken into account (IPCC 2007). The IPCC (2002) proposes potential adaptation options to reduce climate change impacts on ecosystems and biodiversity, including the following: i) reduction of deforestation, ii) reforestation, iii) captive breeding of animals, iv) *ex situ* conservation of plants, v) translocation programs to increase or restore endangered or sensitive species, and iv) connect reserves with corridors that provide dispersal and migration routes for plants and animals.

In this context, the best strategy for compensating habitat fragmentation is the improvement of habitat connectivity (Tewksbury 2002; Chetkiewicz et al. 2006), as a basic concept in PAs design (Margules & Pressey 2000; Margules & Sarkar 2007). Bennett (2003) specifies three options to expand connectivity by managing landscapes: i) habitat mosaics, ii) habitat corridors and iii) stepping stones. The first one refers to act over the entire landscape mosaic, and the second and third ones to manage specific habitats for specific responses.

A common error and a strong criticism in corridor planning is the homogenization of species and scales in corridor design, when we know that functional connectivity is certainly species-specific. Thus, connectivity approaches based on corridors may not take into account all or even most of the species for which a corridor is designed. Therefore, in many cases corridor structure could be insufficient and unnecessary to support species movement and dispersal. For this reason a better integration of pattern and process is significantly important in corridor planning (Chetkiewicz et al. 2006).

To resolve this concern in conditions of large area requirements, habitat connectivity has been managed for site-specific locations of important biodiversity elements or indicators of ecosystem health (Margules et al. 2002; Margules & Sarkar 2007). Umbrella species have been used as proxies for this, assuming that a group of species (particularly birds and mammals) can represent co-occurring species that share the habitat and overlap their distributions at different uses of ecological niches (Lambeck 1997; Thorne et al. 2006). Nevertheless this concept does not have a commonly accepted methodology that permits a correct selection of the species to use, it is clear that richness and abundance are higher at sites where umbrella species are present than in those sites where they are absent (Roberge & Angelstam 2004; Branton & Richardson 2011).

The use of primates as umbrella species is not common, but its few applications have demonstrated interesting implications in terms of conservation (Caro et al. 2004; Martins & Valladares-Padua 2005; Lambert 2011). In this context the modeling of the distribution of umbrella species (Loyn et al. 2001; Kerley et al. 2003; Branton & Richardson 2011; Edman et al. 2011; Estrada et al. 2011) or their habitat (Graham et al. 2006, 2010b; Waltari et al. 2007; VanDerWal et al. 2009), commonly performed through Species Distribution Models (SDMs), have been approaches for determining key areas for conserving biodiversity.

SDMs are mostly constructed under the niche ecological concept, more commonly known as Ecological Niche Models (ENMs) (Guisan & Thuiller 2005). ENMs vary between the application of the fundamental niche concept, where the assumption is that species are distributed over all their suitable habitats, and the realized niche concept, where the assumption is that species are distributed just over part of their fundamental niche because of biotic interactions (Pulliam 2000). The first approach is the most commonly used and bases the occurrence of species on biotic predictors (Peterson et al. 2007; Elith & Leathwick 2009), while the second uses mechanistic modeling, that incorporates physiological or behavioral parameters for the species (Kearney & Porter 2004).

The projections obtained using SDMs usually illustrate the probability that a species is present in a given location, but also they can be interpreted as the suitability of the habitat for the species´ presence, with values ranging between 0 and 1, which may be useful for introducing a persistence gradient for the species (regions of high, medium, or low habitat suitability, where it is understood that conditions may or may not be given for the persistence of species) (Araújo & Williams 2000). However, the selection algorithms for defining conservation areas usually work with species occurrences and ignore the uncertainty produced by converting the probabilities of occurrence into binary maps (Carvalho et al. 2011).

Additional uncertainties are added when we use projections out of occurrence data or in hypothetical scenarios like climate change (Elith & Leathwick 2009). Calculating and describing the uncertainty implicit in the projections is thus necessary if we want to integrate climate change considerations into spatial conservation priority, since the PAs chosen may be already based on intermediate probabilities of species occurrences causing high uncertainties, and compromising their utility for conservation decisions (Araújo & New 2007; Carvalho et al. 2011).

Modeling approaches generally assume full or no dispersion (Peterson et al. 2002; Lawler et al. 2009). However, some of them recently have combined the use of dispersion corridors in order to prioritize conservation areas with climate change scenarios, using the potential distributions of species constructed with SDMs as optimal habitats for dispersion through time (Williams et al. 2005; Phillips et al. 2008b).

These, include the challenge of integrating patterns of landscape composition and configuration, and the processes of habitat selection and movement trough time (Chetkiewicz et al. 2006).

Chetkiewicz et al. (2006) reviewed different algorithms for modeling corridors that connect conservation areas. Some of them are as follow: i) Linkage zone prediction models, which predict the relative probability of movement through an area by integrating qualitative scores for a number of spatial layers. ii). Conditional logistic regression, that quantifies movement probabilities across landscapes using step selection functions. iii). Neutral models, based on percolation theory for evaluate the movements within spatially random structured systems. iv). Least-cost path analysis, that estimates movement costs between two points of a habitat in terms of their suitability. A combination of these last can be found in graph theory that offers the measurement of landscape connectivity holistically by combining the movement emphasis of percolation theory and the habitat modeling potential of least-cost path modeling.

Graph theory has evolved from transportation and computer networks (Ahuja et al. 1993) and since 2000 has been applied to assessments of landscape connectivity (Bunn et al. 2000; Urban & Keitt 2001). Graph analysis measures structural and functional connectivity, (Bunn et al. 2000; Urban & Keitt 2001; Calabrese & Fagan 2004; Proulx et al. 2005; Kent 2009; Urban et al. 2009), showing important implications for conservation planning (Minor & Urban 2007, 2008; Treml et al. 2007; Phillips et al. 2008b). Graph theoretical approaches combine landscape data (typically derived from Geographic Information Systems) with movement data, measured as either a dispersal distance (Calabrese & Fagan 2004), or a random draw from a dispersal kernel generated as a function of dispersal probability with distance (Cowen & Sponaugle 2009). For the entire network different elements can be established and diverse metrics can be used to assess the connectivity and potential dispersal for the species.

Although graph theory in general terms is based on a binary description of habitat (nodes), it is feasible to classify these nodes probabilistically with a resource selection function (RSF) used for characterizing habitats (Chetkiewicz et al. 2006). A RSF, which can be also understood as SDM (Elith & Leathwick 2009), is defined as any function that uses variables as habitat attributes to predict a layer proportional to the probability of use of a resource unit (a sampling unit of the landscape e.g., a pixel or grid cell) (Manly et al. 2002). For example a random sample of resource units could be drawn and examined for the presence or absence of an organism (Boyce & McDonald 1999).

Therefore, it is possible to identify habitat (nodes) in a graph with a SDM or a RSF, and use these to define areas where species are more likely to occur (high). These areas used to generate nodes (habitat patches) and the inverse of the RSF (i.e., 1/RSF) applied as a cost surface for modeling the movement of the individuals, can be used to generate a graph and then determine, which are the key areas for conserving the dispersal process of the species (Chetkiewicz et al. 2006).

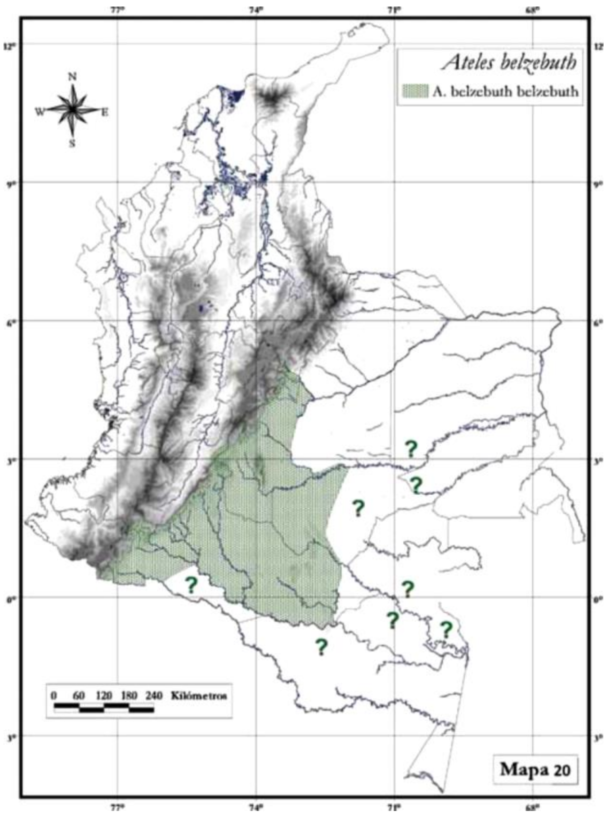
Linking graph theory with SDMs as a RSF, offers a method for quantifying connectivity at a broader scale and corridors in a more specific analysis because it explicitly combines spatial topology with resource selection (Wagner & Fortin 2005). Because graph theory summarizes the spatial relationships between landscape elements (configuration and composition) (Urban & Keitt 2001; Calabrese & Fagan 2004), it is particularly helpful to predict the impacts of adding or deleting particular landscape elements (Chetkiewicz et al. 2006), and then explore the consequences of habitat loss scenarios (Urban & Keitt 2001; Treml et al. 2007).

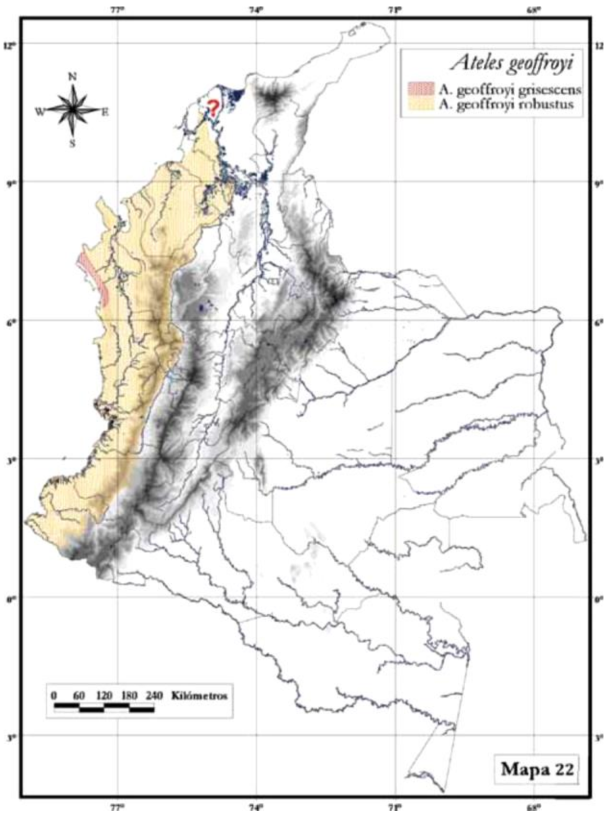
2. Materials and Methods

2.1 Study Area

Atelines distribution and dispersal compromises almost the whole of Colombia; hence, at the greatest scale this study is national. However on a regional scale, the study involves each of the distribution ranges of the four ateline species found in the country (Table 1 and Figure 1).

In addition, in order to prioritize areas for maintaining or improving species' connectivity, an analysis of the representativeness of PAs system is necessary. We briefly describe the actual representativeness of SINAP in Colombia and the context of the country in terms of land use and major socio-economic activities.





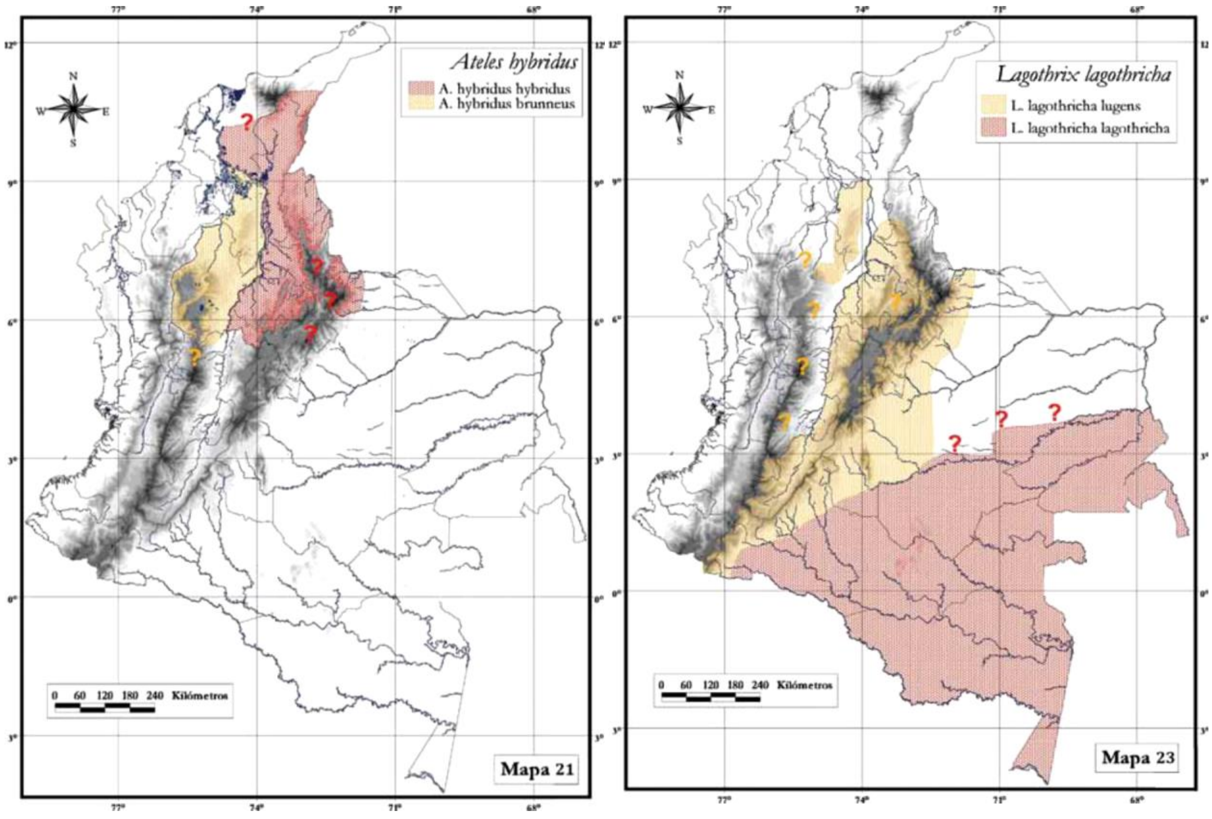


Figure 1. Distribution of ateline species present in Colombia. Source: Defler (2010).

2.1.1 Species' Distributional Ranges

The distribution of *Ateles belzebuth* is not totally clear for various reasons, particularly at the southern and eastern limits (Defler 2010). This species is found in Colombia in the piedmont of eastern Andean Cordillera southward from Río Upía basin in the department of Boyacá, including la Sierra de La Macarena from río Ariari up to piedmont of the Cordillera, eastern Caquetá and the Coehmaní rapids in the south-east of the department of Caquetá, and Yari River southwest and north of the río Caquetá, for most of the department (Boubli et al. 2008; Defler 2010). Defler (2010) reports the easternmost observation on the right bank of the river Apaporis, in the Salado de La Estrella, but generally the species is unknown in that region and hypothetically the collected female individual represents an outlier due to long-distance dispersal. Isolated records of observations from residents in remote eastern areas support the possible long-distance dispersal of females away from known populations and also the existence of not previously unknown populations (Defler, pers. com.). The species´ existence is not clear between the ríos Caquetá and Putumayo, except in the most westerly parts and the piedmont of the Cordillera (Boubli et al. 2008; Defler 2010).

Ateles geoffroyi robustus is found in the lowlands of the Colombian Pacific Region, from the southernmost parts of the Western Cordillera of the Andes, northward west of the Río Cauca, as far as the southern limit in Cabo Corrientes, Department of Chocó, where it may be replaced by *Ateles geoffroyi grisescens* (a taxon whose current presence in Colombia has not yet been confirmed). *Ateles geoffroyi rufiventris* also can be found in the Urabá region in north-western Antioquia, and departments of Córdoba, Sucre and northern Bolivar, eastward to the lower Cauca River and along its western bank to south-central Antioquia. The southernmost data corresponds to Concordia, Antioquia and the southernmost record in Colombia is from Barbacoas, department of Nariño. Historically the northern boundary was the southern bank of the Canal del Dique near Cartagena, however its distribution probably reached the Pendales region in the early part of the last century (Cuarón et al. 2008; Defler 2010).

In Colombia, *Ateles hybridus hybridus* is found from the right bank of the Río Magdalena in the departments of Magdalena, Cesar (north of the southern slopes of the Sierra Nevada de Santa Marta), the southwestern portion of the Guajira, in northernmost parts of the Serrania de Perija and in the middle valley of río Magdalena to the border of the departments of Caldas and Cundinamarca. There are two populations of this subspecies in eastern slopes of the eastern Andean Cordillera on the frontier with Venezuela: one found in the slope of Catatumbo region in the department of Norte de Santander and the other in the northern forest of the foothills in the department of Arauca. *Ateles hybridus brunneus* occupies the region of the lower basins of Cauca and Magdalena rivers in the departments of Bolivar, Antioquia and Caldas, but its southern limit is at present not well established (Urbani et al. 2008; Defler 2010).

Lagothrix lagothricha lagothricha is distributed in Colombia over the Amazon Region east of the Cordillera Oriental. *Lagothrix lagothricha lugens* is found north of the river Guayabero, ranging from the foothills and eastern slopes of the Cordillera Oriental to the Colombian-Venezuelan frontier on the banks of río Apure (Bojabá). There are abundant individuals in Serranía de La Macarena and along the foothills in the region of Uribe, between Serranía de La Macarena and the Cordillera Oriental. The subspecies is found up to 3000 m of altitude in Andean Region and is present from the upper río Magdalena Valley in Puracé National Park at least to southern Tolima, with an isolated population in the Serranía de San Lucas, in southern Bolivar (Palacios et al. 2008; Stevenson & Link 2008; Defler 2010). Apparently, there was also a population on the western slopes of the Cordillera Oriental and there is evidence that some animals still exist in the southern department of Santander. The boundaries between the two subspecies are not well defined although they seem to have a contact zone that may be located not far from the Cordillera Oriental, in the department of Caquetá, although *Lagothrix lagothricha lugens* may reach the Caguán river (Defler 2010).

2.1.2 Land Use Context in Colombia

Colombia is divided into five major biogeographic regions that are contrasting in their biophysical and land cover/use characteristics: i) Caribbean (115,400 km^2), ii) Andes (278,000 km^2), iii) Pacific (74,600 km^2), iv) Orinoco (169,200 km^2), v) Amazon (455,000 km^2), and two smaller regions: the Magdalena (37,100 km^2) and Catatumbo (7,000 km^2), commonly included in the Andean region with also two inter-Andean valleys: Cauca Valley (between Central and Western Andes) and Magdalena Valley (between Central and Eastern Andes) (Etter et al. 2006d).

Land conversion in Colombia is heterogeneous and mostly responds to socio-economic factors, with higher rates in the Caribbean and Andean regions, and lower in the Amazon, Orinoco and Pacific regions (González et al. 2011). Historically, in the Andes and the Caribbean have occurred the major changes as a result of human colonization and densification processes since prehispanic times (Etter & Van

Wyngaarden 2000), mostly affecting Andean and dry forests by a combination of agriculture (predominant in early times) and livestock grazing (predominant in recent times) (Etter et al. 2008). In lowlands of Amazon, Orinoco and Pacific regions, a recent (approximately since 1940) unplanned deforestation has been driven by colonization fronts, subsistence agriculture and illegal crops (Etter et al. 2006a), although in some areas mechanized agriculture, livestock grazing and oil extraction have shaped different (no unplanned) deforestation patterns (Etter et al. 2005; Armenteras et al. 2006).

In Figure 2 is presented an approximation of the current (2000-2003) land cover in Colombia (IDEAM et al. 2007). The Andean region shows the most heterogeneous mosaic with differences between montane and lowland forest defined by the accessibility and contrasting wealth and economic activities (Armenteras et al. 2011). Pasturelands are the most abundant land cover in the region (24%) followed by croplands (19%) (Sánchez-Cuervo et al. 2012). The Caribbean region is characterized by dry vegetation types that correspond to arid and semiarid lowland areas, with forest remnants restricted to the Sierra Nevada de Santa Martha. Land use in the Caribbean is mostly cattle ranching (48%) and agriculture (14%) (Sánchez-Cuervo et al. 2012). The Pacific region has large proportions of lowland rain forest, fragmented in small proportions over Nariño and Darien areas by croplands (10%) and pasturelands (<2%) (Sánchez-Cuervo et al. 2012). The Orinoco region has a constant dynamic of natural and induced fires in savanna ecosystems (Etter et al. 2010; Romero et al. 2010) over natural, semi-natural and artificial pasturelands (86%) (Sánchez-Cuervo et al. 2012). Land cover type in the Amazon region is primarily forest, however deforestation processes have been reported with high rates in foothills of the eastern cordillera in the zone of Caquetá and Putumayo (Etter et al. 2006a), where has been converted about 6% of forests into pasturelands, and less than 1% into legal and illegal croplands according to IDEAM et al. (2007).

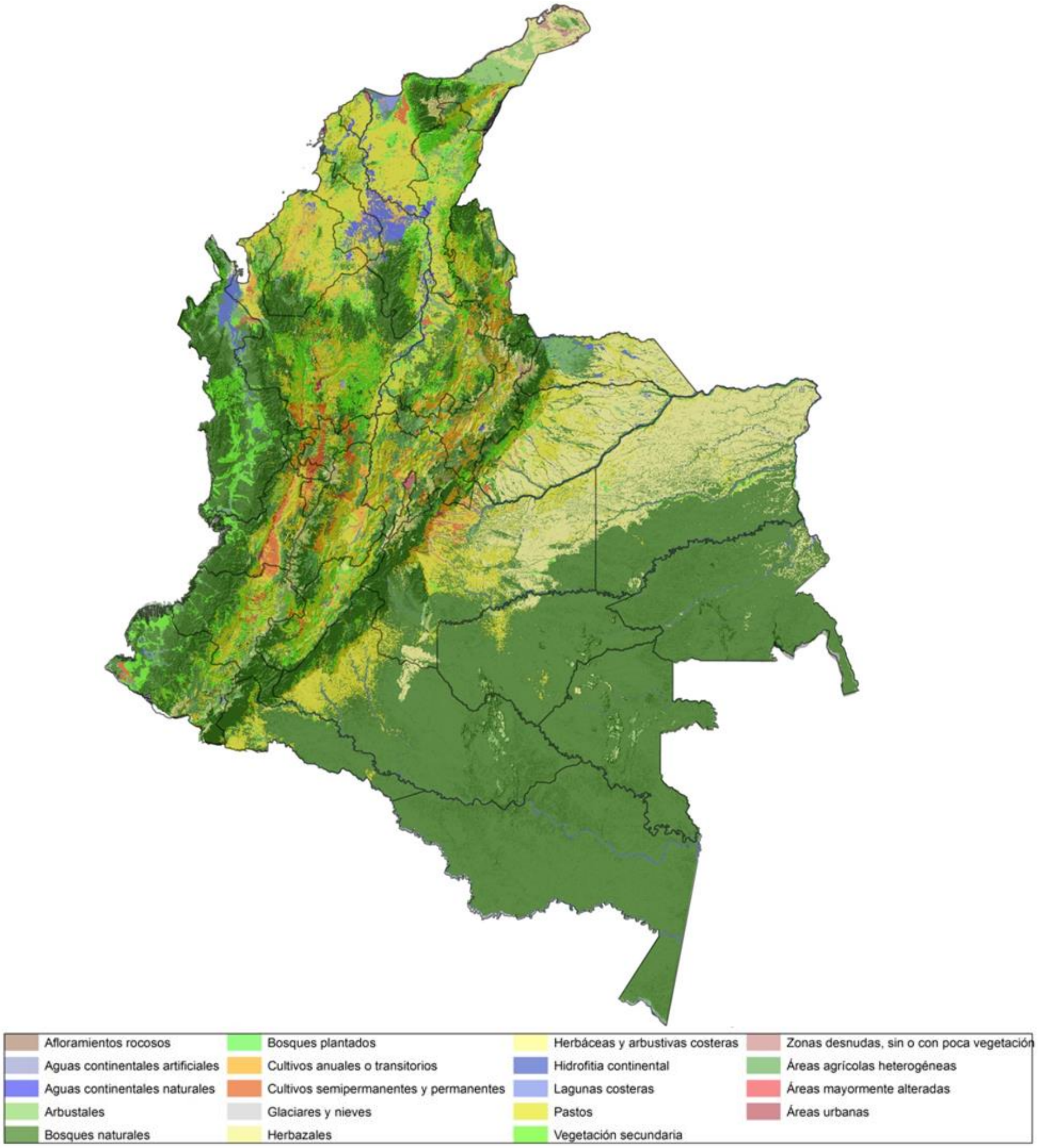


Figure 2. Map of land cover in Colombia (2000-2003). Adapted from IDEAM et al. (2007).

2.1.3 Socio-Economic Context in Colombia

Since 1900 the population of Colombia has experienced an approximate tenfold exponential increase, exceeding 44 million people (Etter et al. 2011). Since indigenous times, most of the Colombian population has been concentrated in the Andean and the Caribbean regions (70%) with a higher growth since 1950 (Etter & Van Wyngaarden 2000; Armenteras et al. 2011). On the other hand, Orinoquia and Amazonia regions (about 54% of total area) have less than 3% of the population and a density of less than one person per km^2 (DANE 2008).

Drug trade and guerilla uprising have been developed in rural and remote areas of the country during the last 20-30 years, causing further social and political instabilities for economic and public policies, with significant repercussions for the movements of rural populations to urban areas and migration outside the country (Etter et al. 2006d). The urban population in Colombia increased from 28% of the total population in 1938 to 76% in 2005, but in absolute terms the rural population increased from 6 to 10 million in that period according to DANE (2008c). These illegal activities are also contributing to an unknown degree to forest conversion and fragmentation (Etter et al. 2006a, 2006d; Armenteras et al. 2009, 2011; Rodríguez et al. 2011).

Principal economic activities in Colombia are agriculture (coffee, flowers), mining (oil, coal and nickel), cattle grazing and industrial exports (Etter et al. 2006d). Agriculture in Colombia contributed approximately 11.5% to the National Gross Domestic Product (GDP) and 22.7% of the labor force, including agriculture, livestock and fishing. Since 1990 the direction of Colombian agriculture has been changing to replace imports by export-oriented agribusiness emphasizing a group of permanent crops, including coffee, bananas, sugar cane and cocoa, as principals (DANE 2009).

In addition, new economic forces have recently appeared. Oil palm expansion and new mining and oil concessions are expected to increase in Colombia affecting other land uses (Figure 3). For example, during the period 2002-2008, of the 155,100 ha of new oil palm plantations 51% replaced pasturelands, 29.1% croplands, and 16.1% natural vegetation (forest and savannas) and regrowth forests (Castiblanco et al. 2013).

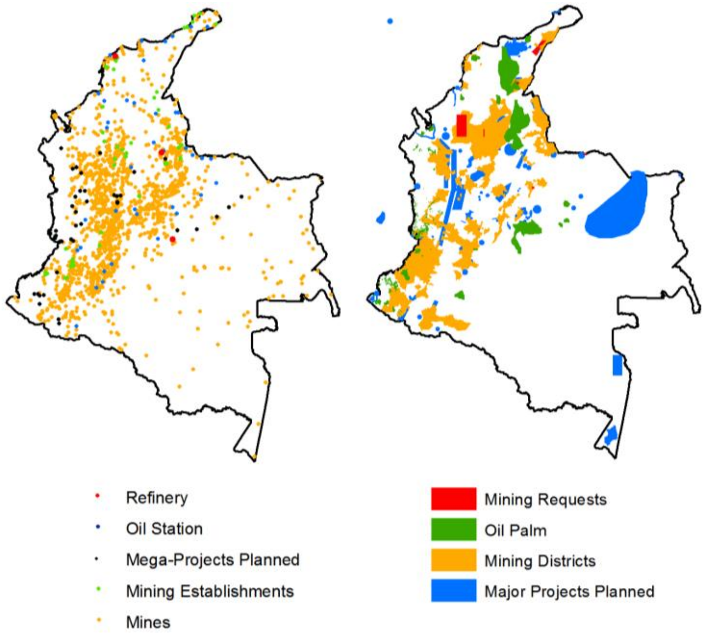


Figure 3. Location of mining and oil-Related activities, major Socio-Economical planned projects and most important places of oil palm distribution in Colombia. Constructed with data from: Instituto Geográfico Agustín Codazzi (IGAC) and Instituto Colombiano de Geología y Minería (Ingeominas)

2.1.4 Context for PAs in Colombia

The Colombian PAs (Figure 4) are grouped in the SINAP, which are managed by the UAESPNN (Unidad Administrativa Especial del sistema de Parques Nacionales Naturales), described from a political perspective as an articulated set of PAs, social stakeholders, and strategies of management towards conservation in Colombia (www.parquesnacionales.gov.co). The SINAP was created by the signing of the Convention of Biological Diversity through the Law 165 of 1994, that was based the formulation of the National Biodiversity Policy, this made a commitment to form and consolidate a National Protected Areas System, the SINAP. Currently the SINAP is formally structured by the legal designation Act 216/03 (Vásquez & Serrano 2009).

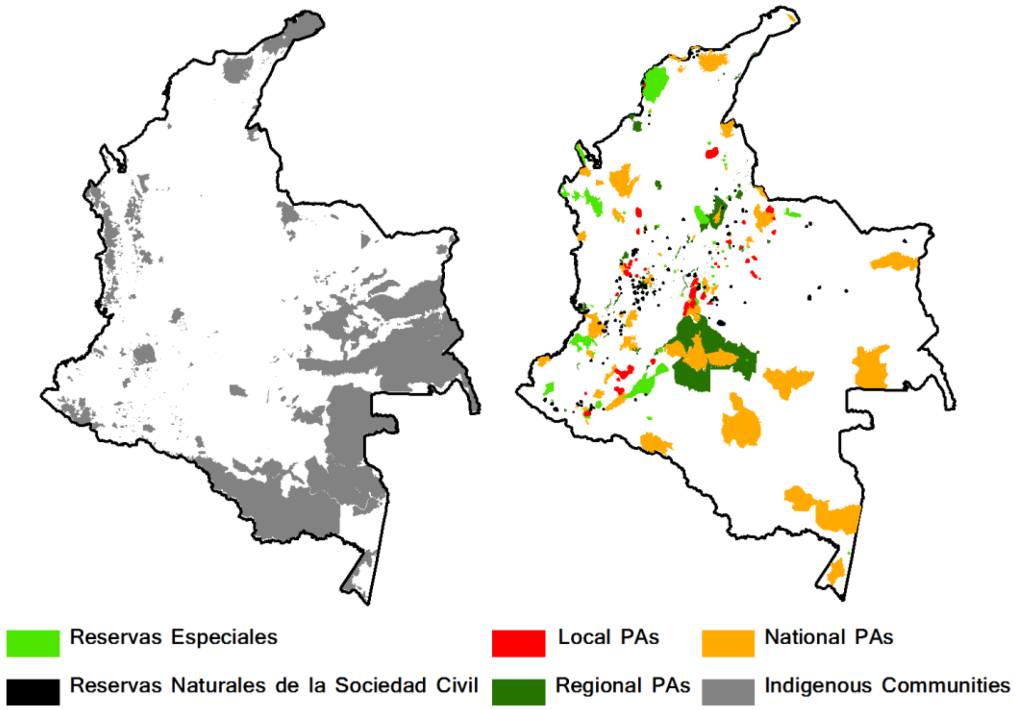


Figure 4. Location of PAs, other conservation figures in Colombia and Indigenous Communities.

According to Vásquez & Serrano (2009), in Colombia the SINAP is composed of 486 PAs including national, regional and local categories, with a total area of approximately 224 391km^2, occupying approximately 11% of the continental and maritime Colombian territory (approximately 24% when only the mainland is taken into account). From the total coverage of SINAP, 27% corresponds to the marine protected area “Sea Flower”, and 10.5% to a special figure called “Distrito de Manejo Integrado - Ariari Guayabero”, that cannot be included as a physical PA. This makes us wonder what the real protection provided by SINAP for Colombian biodiversity is.

Since PAs in Colombia are subject to the necessities and behavior of its surrounding populations, an approximation of the good or bad conservation status of PAs could be the low or high human population density, respectively. For indigenous reserves that are higher in density in the Amazon and Orinoquia regions (Figure 4) (DANE 2007), the role in terms of conservation is discussed by Armenteras et al. (2009), especially in terms of habitat fragmentation, since high rates of deforestation have been found in indigenous population areas in the Colombian Guyana Shield.

The continuing expansion of the agricultural frontier and especially ranching in the surrounding zones of PAs affect them permanently (Armenteras et al. 2009). There is ample evidence that continuing deforestation due principally to the construction of infrastructure, agriculture and cattle ranching, illicit crops, and continuing migrations due to unrest in Colombia (Cavelier & Etter 1995; Etter et al. 2006d), may have considerably affected the PAs (Armenteras et al. 2009), hence, the real representation of SINAP should be reevaluated.

2.2 Modeling the Potential Dispersion of Atelines under Climate Change and Habitat Fragmentation Scenarios for Identifying Priority Conservation Areas

A general procedure for obtaining major potential areas for the dispersion of atelines under climate change and habitat fragmentation scenarios is presented in Figure 5. All the analyses were performed for the years: 2000, 2010 and 2020 at a spatial resolution of 1 km, since it is the grain of climatic information used. Although land cover was available in a finer resolution, 1 km represents the maximum pixel data.

Procedures for selecting priority areas needing additional attention in order to ensure the dispersal of atelines over suitable habitats are as follow: i) the construction of current and future scenarios of land cover and climate, ii) the current and future potential distributions for ateline species, iii) the construction of habitat quality and cost flow functions, iv) a connectivity and dispersal corridor analysis, and finally v) a selection of priority conservation areas for ateline dispersal.

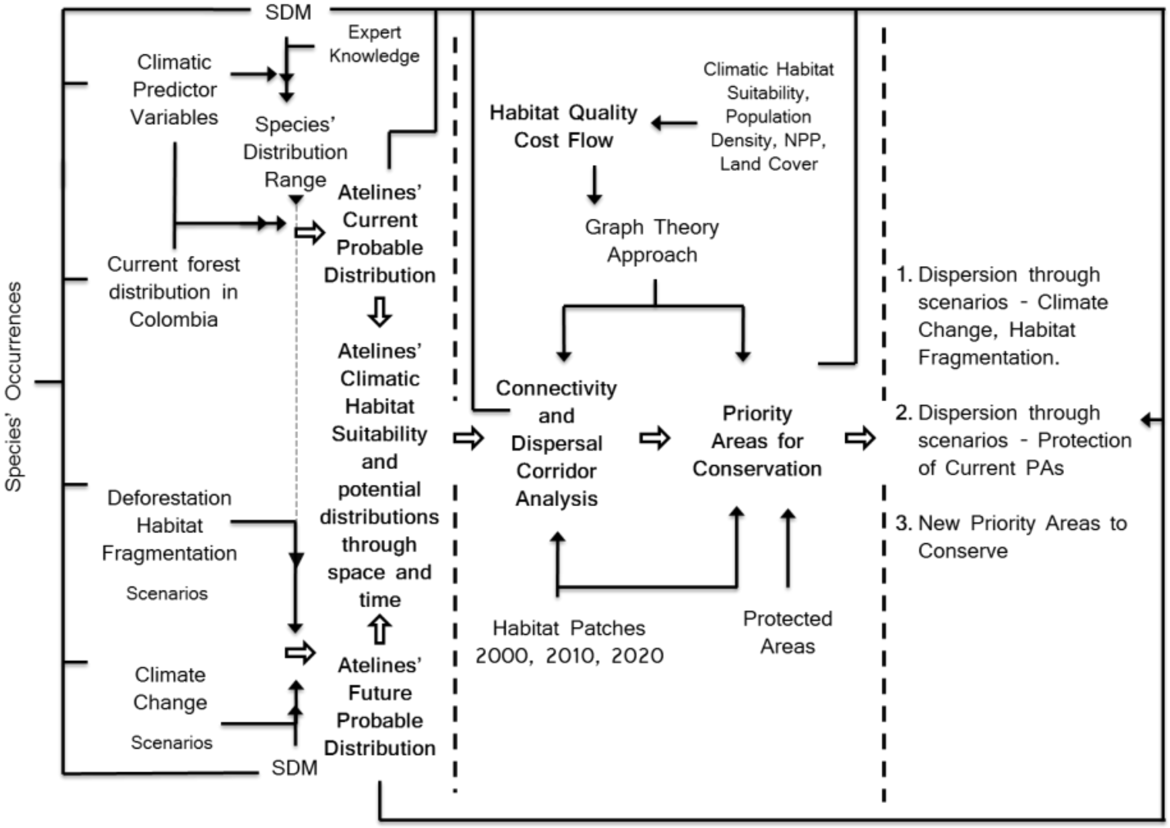


Figure 5. General procedure to identify main potential areas for the dispersion of atelines under climate change and habitat fragmentation scenarios.

2.2.1 Current and Future Scenarios of Land Cover and Climate

Figure 6 shows the process to obtain final land cover and climate layers for the years: 2000, 2010 and 2020. Because of their differences, the method used to construct each data layer is presented separately.

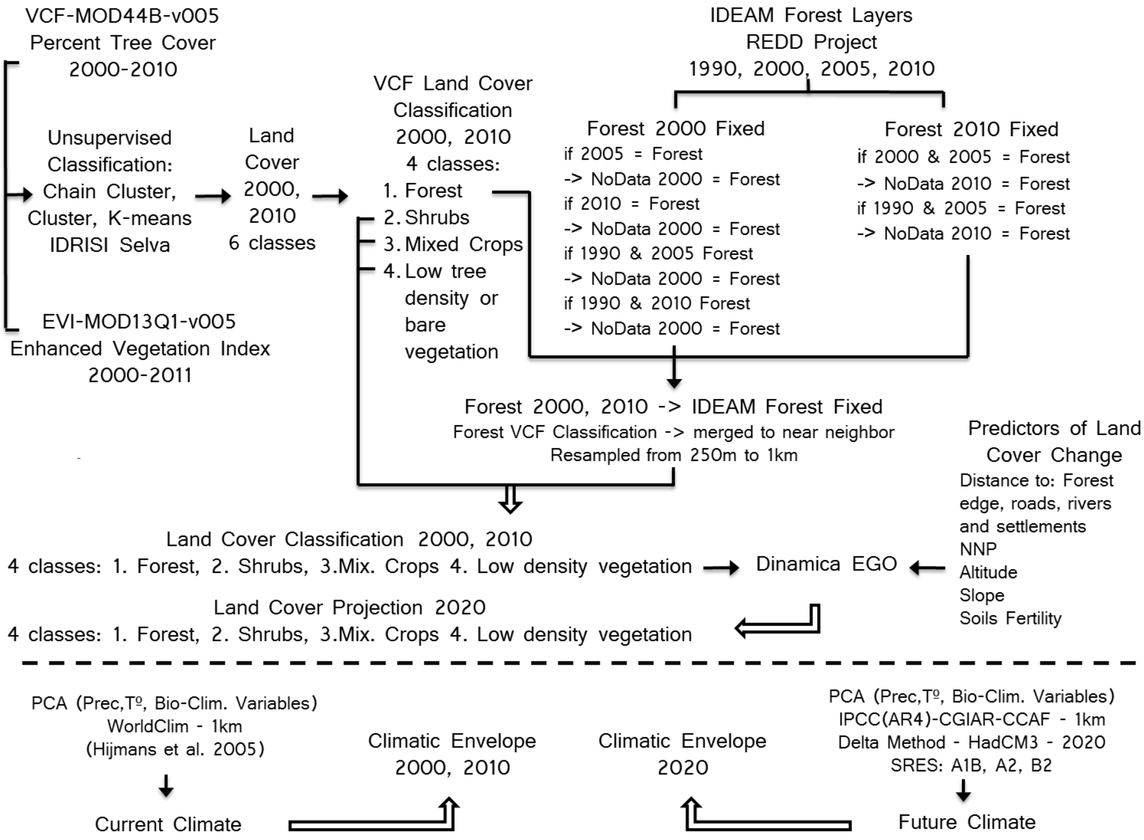


Figure 6. Detailed diagram for the construction of current and future scenarios of land cover and climate.

Land Cover Scenarios

The land cover scenarios were constructed as approximations to different cover types representing different costs for the movement of atelines. Due to the lack of comparable data for non-forest areas, procedures were developed to generate layers in these regions that serve to an input for modelling the potential dispersal of species, since landscape matrix is the most important factor affecting species dispersal.

Land cover scenarios were generated by combining two data sources: i) an unsupervised classification applied to MODIS Vegetation Continuous Fields product (VCF-MOD44B-v005); ii) and the forest layers produced by the Instituto de Hidrología, Meteorología y Estudios Ambientales (IDEAM), in the context of Reducing Emissions from Deforestation and Forest Degradation (REDD) project for Colombia (García et al. 2011). VCF layers presented NoData pixels for some areas (particularly in the Pacific region) and dates (2001-2005 and 2007), while IDEAM forest layers were only available for the years 1990, 2000, 2005 and 2010 and also had NoData pixels, as result of clouds and Landsat ETM banding.

The VCF product represents the surface vegetation cover as a proportion of basic vegetation traits. It has been generated annually (2000-2010) at 250 m of resolution, using monthly composites of Terra MODIS 250 and 500 m Land Surface Reflectance data, and Land Surface Temperature (Townshend et al. 2011). In this study we used the layer percent tree cover to classify land cover in the non-forest areas. It has a range between 0 and 100, where higher values represent a higher proportion of tree cover.

Other studies have used MODIS remote sensing data to create land cover classifications, in particular the Enhanced Vegetation Index (EVI-MOD13Q1-v005), a sub product of Normalized Difference Vegetation Index (NVDI) (Clark et al. 2010; Sánchez-Cuervo et al. 2012). These methodologies used control points, which were not available for this study. Nevertheless, we performed an unsupervised classification with both: VCF and EVI products. Using the IDRISI Selva software, we applied Cluster, Chain Cluster and K-means algorithms (Clark Labs 2012).

For each MODIS product and each date (2000-2010 for VCF and 2000-2011 for EVI), the parameters of algorithms were modified using a trial and error method to select the best performance in each case. In Figure 7 an example of the distribution of values inside each resultant class after applying unsupervised classification is presented. The comparisons performed, confirmed for each date of VCF product the best performance of K-means algorithm respect to the other ones showed by EVI product.

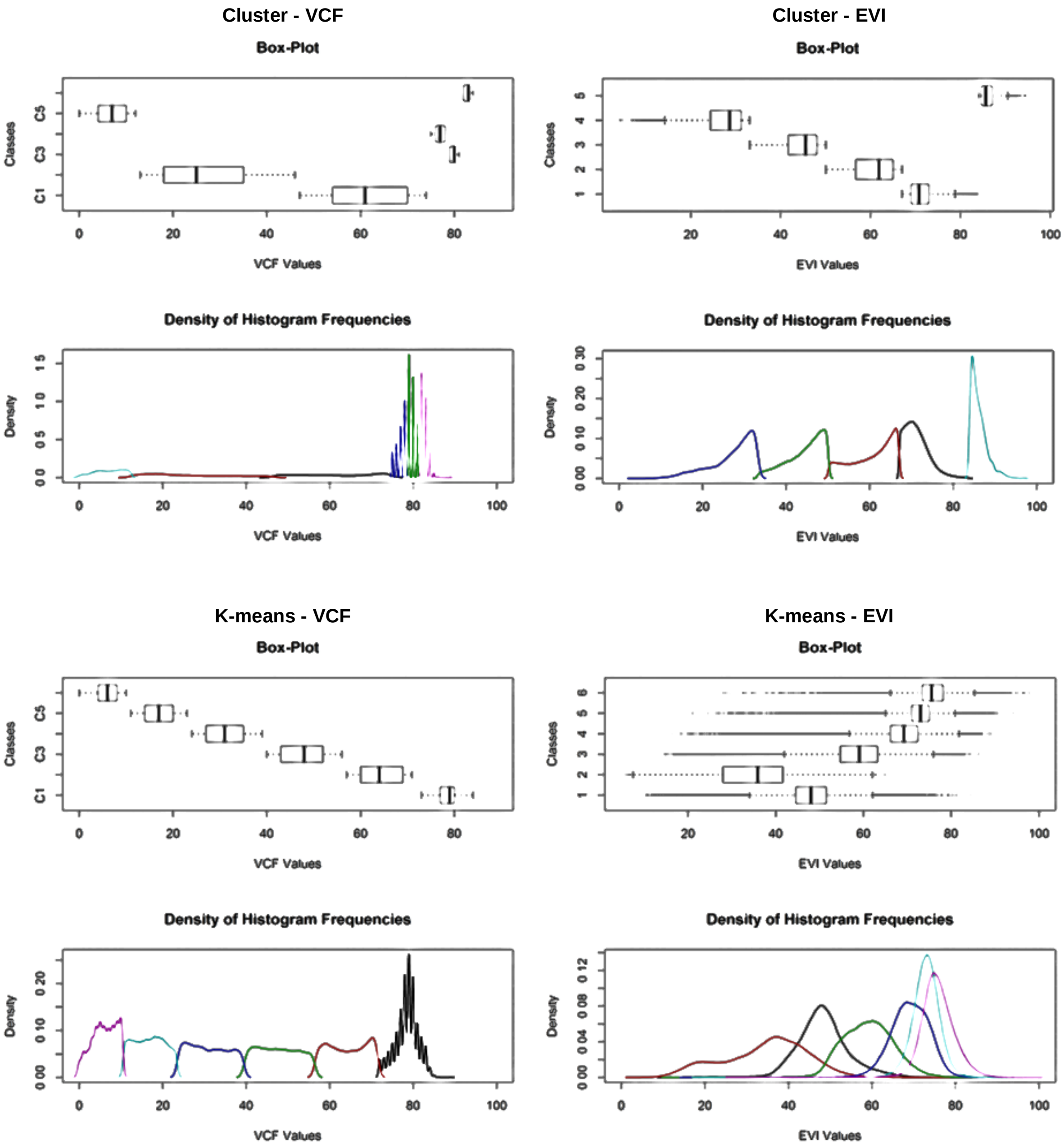


Figure 7. Distribution of classes constructed from VCF and EVI products using cluster and k-means methods for the year 2000. EVI values are normalized between 0 and 100.

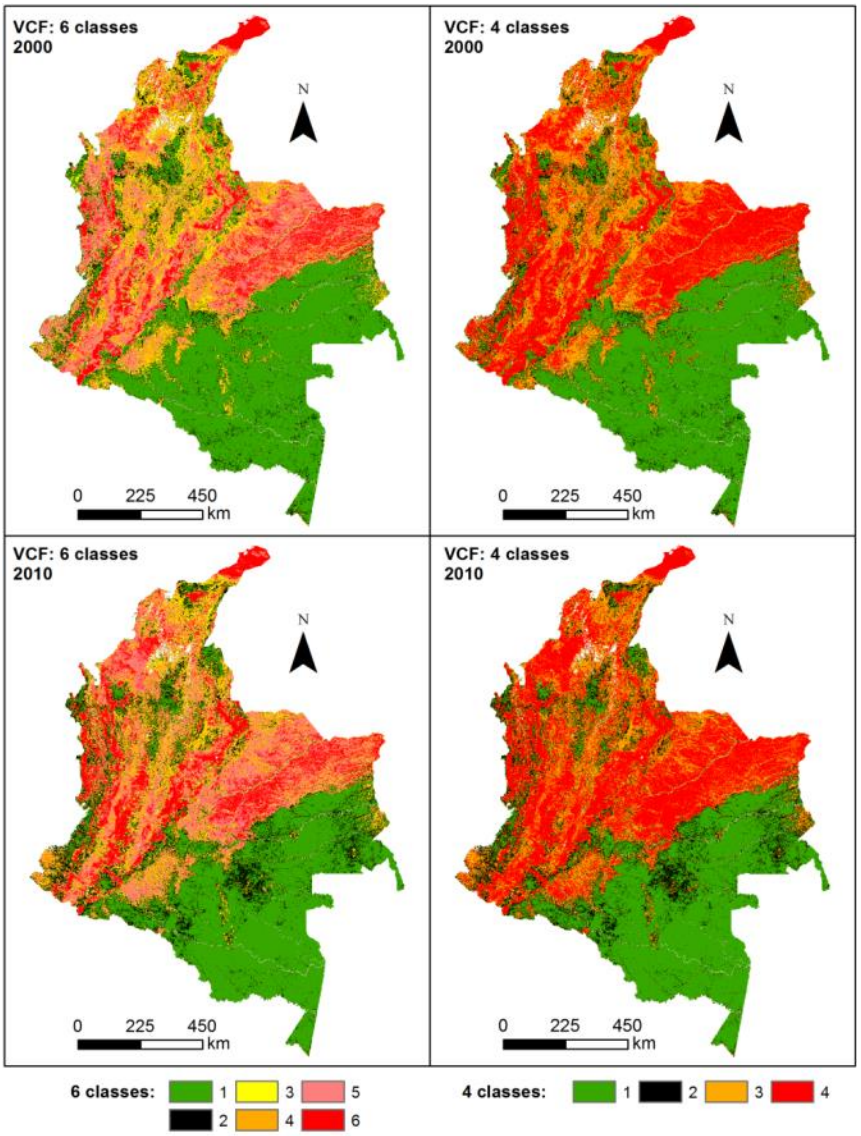


Figure 8. Reclassification of VCF K-means products. Ordinal Classes are inversely related to VCF values. Class 1 corresponds to values close to 100 (higher proportion of tree cover) and class 6 and 4 correspond to values close to 0 (lower proportion of tree cover). Intermediate classes correspond to intimidate VCF values.

The results were evaluated using expert knowledge, and particularly the concordance with the forest distribution of IDEAM layers was taken into account. The 6 classes obtained from unsupervised classification using K-means and VCF product were selected as preliminary land cover layer for years 2000 and 2010. However, VCF classification was reclassified to 4 classes merging classes: 3 with 4 and 5 with 6 (Figure 8). Classes 4 and 6 were spectrally close to classes 3 and 5 respectively (Figure 7), and are close to cover types spatially not differentiable under the unsupervised classification methodology used, therefore they could increase the uncertainty level on the land cover classification.

Since class 1 in classification does not spatially match the distribution of forest cover in Colombia (Figure 8), (especially in the Pacific region where major errors in VCF values were found due to the constant presence of clouds), the forest cover in the land cover classification was taken from IDEAM forest layers (Figure 9). Unfortunately, original IDEAM forest layers were also affected with clouds and Landsat ETM banding. Thus, IDEAM forest layers for year 2000 and 2010 were fixed by filling the NoData pixels with the information of the other dates. For this, all layers were resampled from 30 m (original spatial resolution of IDEAM layers) to 250 m to match grid size of the VCF classification. With this procedure, some of no-data pixels were combined to dominant classes (forest or no forest) using a majority algorithm as resampling technique.

Conditions created for repairing original IDEAM layers follow a major assumption: forest persistence. For year 2000, we supposed that forest existence after 5 (2005) or 10 years (2010) necessary should imply the existence in year 2000, i.e., a mature forest could not be generated in less than 5 years. If there was forest in 2005 or 2010 it was because there was forest in 2000. In this sense, if there was forest in 2005 or 2010, we assumed it as evidence of forest existence in year 2000 as well. For year 2010, a major assumption was made: the future persistence of forest. We supposed that forest persistence for 5 (2000-2005) or 15 (1990-2005) years suggested the existence of forest in 2010, i.e., if there was forest during those periods, there should also be forest after 5 years.

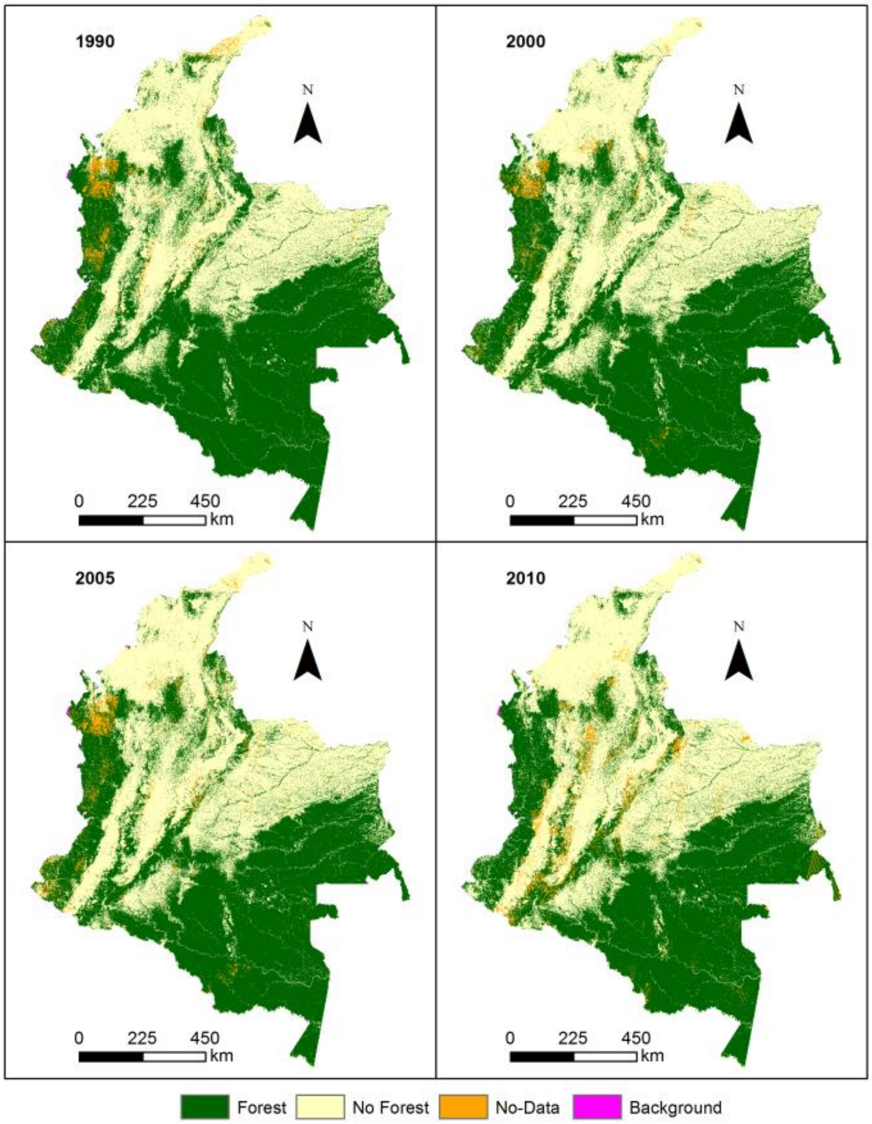


Figure 9. IDEAM forest layers. Source: García et al. (2011)

Final fixed forest of IDEAM layers was inserted in the VCF classification, replacing all pixels located over the intersection area. Class 1, equivalent to forest cover, was primarily substituted. Pixels remaining of class 1 after insertion corresponding to original VCF classification were merged to the nearest neighbor. Final layers were resampled to 1 km grid size using a majority filter, which in turn homogenize the land cover classification at a higher degree.

These land cover scenarios were constructed to respond to the cost of movement for primate species, and therefore they not directly correspond to a land cover type. Nevertheless, forest cover can be associated with class 1, shrubs or secondary vegetation mixed with stubbles with class 2, crops and mixed crops with class 3, and low tree density or bare vegetation (including savannas, urban areas and deserts) with class 4 (Figure 8).

The 2020 land cover scenario was modeled in Dinamica EGO (Soares-Filho et al. 2001, 2002, 2009; Maria de Almeida et al. 2003). Dinamica EGO is a spatially explicit model for simulating the dynamics of landscape and it has been regularly and widely used for modelling land use/cover changes (LUCC) at different scales (Soares-Filho et al. 2002, 2006, 2012; Nepstad et al. 2009; Teixeira et al. 2009; Silvestrini et al. 2010; Mas et al. 2012). An explanation of the process used to project land cover dynamics in Dinamica EGO is presented in Table 3. More detailed information can be found in Maria de Almeida et al. (2003) and Soares-Filho et al. (2009).

For the modelling process, 2000 and 2010 land cover scenarios were used to construct the land cover transitions, using 2010 as the initial land cover map to start simulation. Performance was primarily evaluated using expert knowledge of results, taking special attention in the coherence of spatial distribution for losses and persistence locations of forest. To validate the simulated 2010 map a confusion matrix was constructed between the observed (land cover scenario in 2010) and the simulated map (Congalton 1991).

Dinamica EGO uses a set of co-variables to explain the landscape dynamics in the time period of the two land cover maps. These predictor variables can be static or dynamic. All of them were considered as static except distance to forest edge, which was recalculated in Dinamica EGO at each different time step defined in the simulation. Co-variables used are described in Table 4 and their spatial distribution ranges and units are shown in Figure 10. All of them were constructed at 1 km cell size.

Table 3. Description of the processes to project land cover data in Dinamica EGO. Additional processes like analyze map correlation and validate simulation can be consulted in Soares-Filho et al. (2009).

Step	Description
1. Calculate transition matrices	A transition matrix between a pair (older and earlier) of land cover images is constructed. Each record contains the probability that each land cover category will change in every other category in the time step, according to cross tab results of the intersection between the two images.
2. Calculate ranges	Each continuous variable is categorized according to defined increments for construct ranges. For each continuous variable in Table 4 the minimum increment value was set as 5000m. Calculation of ranges follows the method adapted from Agterberg & Bonham-Carter (1990).
3. Calculate weights of evidence	The weights of evidence method taken from Bonham-Carter (1994), is applied to produce a transition probability layer, that contains the most suitable areas for a change. Weights of evidence are calculated by a Bayesian method in which the effect of a spatial variable on a transition is calculated independently of a combined solution. The weights of evidence represent each variable's influence on the spatial probability of a transition.
4. LUCC simulation model with path formation (patcher) and expansion (expander)	A local cellular automata rule uses a transition engine to simulate spatial dynamics in a landscape. It works with information about patches in two forms: patch generation (patcher) and patch expansion (expander). The first one is used to generate or form new patches through a seeding mechanism. Patcher searches for cells around a chosen location for a joint transition. The process is started by selecting the core cell of the new patch and then selecting a specific number of cells around the core cell, according to their Pij transition probabilities. The second one is used only for the expansion or contraction of previous patches of a certain class. Thus in the Expander, a new Pij spatial transition probability depends on the amount of cell type j around a cell type i. Parameters for patcher module: mean and standard deviation of patches, were derived from mean patch metrics calculated for land cover layers.

Table 4. Co-variables used to model land use changes.

Variable	Type	Original Resolution	Source
Distance to Forest Edge (DE)	Continuous	1 km	Land cover classification
Distance to Roads (DR)	Continuous	1:100 000	Roads Layer produced by Instituto Geográfico Agustin Codazzi (IGAC)
Distance to Rivers (DRi)	Continuous	1:100 000	Rivers Layer produced by IGAC
Distance to Settlements (DS)	Continuous	1:100 000	Towns Layer produced by IGAC
Altitude (A)	Continuous	1 km	Digital Elevation Model (DEM) produced by United States Geological Survey (USGS)
Slope (S)	Continuous	1 km	Derived from altitude
National Natural Parks (NNP)	Categorical	1:100 000	Registro Único Nacional de Áreas Protegidas Integrantes del SINAP (RUNAP)
Soil Fertility (SF)	Categorical	1:500 000	Soil classes layer produced by IGAC and modified for fertility by Etter et al. (2005)

These variables have been recognized as drivers of land cover change (Mertens & Lambin 1999; Lambert et al. 2001; Serneels & Lambin 2001; Geist & Lambin 2002; Lambin et al. 2003; Leemans et al. 2003; Geist et al. 2006) and have been recurrently used in LUCC models for national (Etter & Van Wyngaarden 2000; Etter et al. 2006b, 2006c, 2006d, 2008; Etter & McAlpine 2007; Armenteras et al. 2011; Rodríguez et al. 2011) and international (Lambin et al. 1999; Mertens & Lambin 1999; Southworth & Tucker 2001; Lambin & Geist 2003; Nagendra et al. 2003; Linkie et al. 2004; Lepers et al. 2005) applications at different scales.

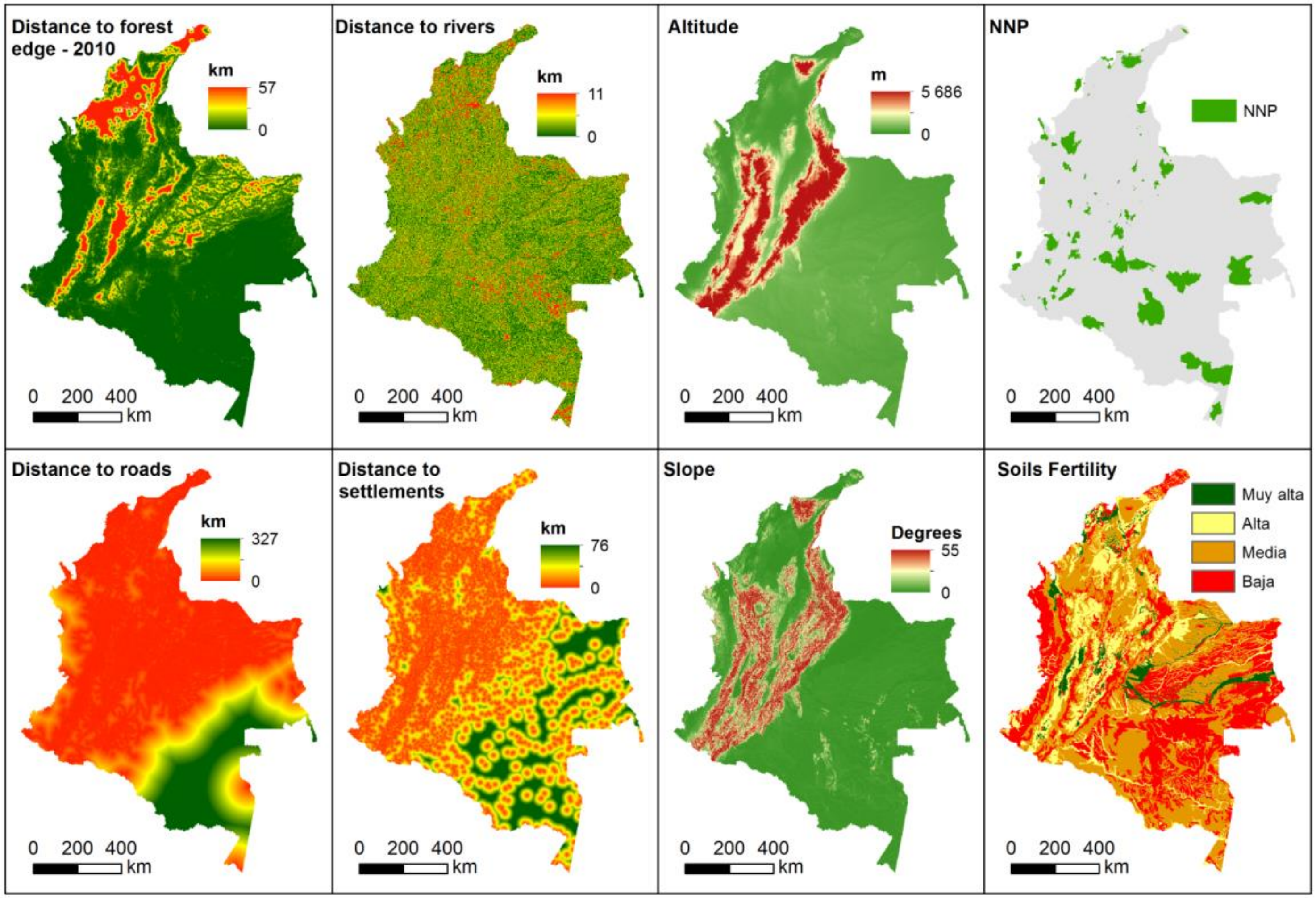


Figure 10. Co-variables used in Dinamica EGO.

Climate Scenarios

Climate can influence the movement of atelines. We used two different global climate products as climate scenarios: i) WorldClim - Global Climate Data (www.worldclim.org) for current climate (2000 and 2010) (Hijmans et al. 2005), and ii) the IPCC Fourth Assessment Report (AR4) (2007) projections downscaled by CCAFS et al. (2012) for future climate (2020).

WorldClim is probably the most widely climatic source used in ecological studies at larger scales. WorldClim is a global climate dataset including monthly total precipitation, monthly mean, minimum and maximum temperature, and 19 derived bioclimatic variables (Table 5). These were interpolated using thin-plate smoothing spline algorithm (TPS) with coordinates and elevation as co-variables in ANUSPLIN software. Average monthly climate data from weather stations with more than 10 years of time series data in the period 1950-2000 were used (Hijmans et al. 2005). Past and future projections are available in the WorldClim data base, but these were not used in this study.

Although WorldClim has the drawback to lack data after 2000, it has 4 main advantages: i) It has a global extent, allowing the use of observations within the entire distribution of atelines, which in turn promotes good performance of the SDMs used to construct the species distributions and their habitat quality (to be detailed later). ii) The resolution: 1km, that is detailed taking into account the global extent of data and also is the same of this study. iii) The method used for interpolating climate surface that is also used for downscaling climatic future projections of IPCC (AR4) (2007) (to be detailed later). v) It has been widely and consistently used for multiple spatial ecological applications related to weather, hence the results obtained are comparable with other studies.

Future Climatic layers were obtained from the Global Circulation Model (GCM) Downscaled Data Portal (www.ccafs-climate.org), which is an initiative from the International Centre for Tropical Agriculture (CIAT for its Spanish acronym) and the

Climate Change, Agriculture and Food Security program (CCAFS), both as part of the Consultative Group on International Agricultural Research (CGIAR) (CCAFS et al. 2012). Data available results from spatial disaggregation to 24 different GCMs from the IPCC (AR4) downloaded from the Earth System Grid (ESG) data portal. A total of 441 future climate scenarios were produced for the same variables included in WorldClim (Ramirez & Jarvis 2010a).

Table 5. Bioclim variables from WorldClim. Source: www.worldclim.org/bioclim.

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7*100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

IPCC (AR4) scenarios used were restricted by the availability of information on download date (September 24th, 2012) including 2 restrictions: i) the downscaling method ("Delta Method") and the resolution (1 km), and ii) the model (HadCM3). Available projected scenarios for 2020 fulfilling the above limitations were: A1B, A2 and B2; therefore, these were used as climate change scenarios for this study. The Table 6 resumes the characteristics of climate change scenarios according to the Special Report on Emissions Scenarios (SRES) (IPCC 2000).

“Delta Method” downscales (using TPS) the variables at 1km resolution, based on the sum of interpolated anomalies (a departure from a reference value or long-term average) to WorldClim layers (baseline) (Ramirez & Jarvis 2010b). The HadCM3 was the only model included through all scenarios available. HadCM3 ranks highly with respect to other models (Reichler & Kim 2008) and does not need flux adjustment to prevent large climate drifts in the simulation, i.e., it has good performance without artificial adjustments for controlling unrealistic climate states (Gregory et al. 2000).

Finally, taking into account the importance of seasonal variability of precipitation and temperature for resources, and therefore, for the movement of atelines (Defler 1996; Defler & Defler 1996; Di Fiore 2004; Dew 2005; Russo et al. 2005), a climatic envelope for including climatic variability in the SDMs and the dispersal flux function was constructed. Three kind of climatic envelopes were created as a result of the first component in a Principal Component Analysis (PCA). All layers for each of the three different sets of climatic variables in current and future scenarios (monthly total precipitation, monthly mean temperature and the 19 bioclimatic variables) were used in the PCA. A total of 12 (1 current and 3 climatic change scenarios times 3 sets of climatic variables) climatic envelopes were generated using IDRISI Selva (Clark Labs 2012) and afterwards were normalized between 0 and 100.

Table 6. Scenarios of climate change according to SRES. Modified from Beaumont et al. (2008). Source: IPCC (2000, 2007).

Synthesis	**Scenario**	**World Population**	**Economic growth**	**Land-use change**	**Primary energy use**	**Hydrocarbon resource use**
Groups: A1T, A1B, A1Fl. Global and economic focus. Rapid economic growth, a global population that peaks in mid-century and rapid introduction of new and more efficient technologies.	A1	~ 7 billion	Very high	Low	Very high	Oil: low to very high Gas: high to very high Coal: medium to very high
Regional and economic focus. High population growth, slow economic development and slow technological change.	A2	~ 15 billion	Medium	Medium	High	Oil: very low to medium Gas: low to high Coal: medium to very high
Global and environmental focus. Global population as A1, but with more rapid changes in economic structures toward a service and information economy.	B1	~ 7 billion	High	High	Low	Oil: very low to high Gas: medium to high Coal: very low to high
Regional and environmental focus. Intermediate population and economic growth, emphasizing local solutions to economic, social, and environmental sustainability.	B2	~ 10 billion	Medium	Medium	Medium	Oil: low to medium Gas: low to medium Coal: low to very high

The PCA is known to be a technique for reducing the number of variables and incorporating their variability into a minimum number of subsets (components) that adequately represent the original information with the least distortion. This method constructs each component as a lineal combination of original variables, each one of them explaining the variability found in a particular subset of initial data; hence, each component resumes a group of correlated variables, but each component is orthogonal (uncorrelated) to the others in space and time (Peña 2002). For these reasons, this method has been proposed for use in a spatial time series analysis and has been remarkably effective in establishing the underlying sources of variability in the data (Eastman 2012).

The sum of the variances of the components is equal to the sum of the variances of the original variables, then the percentage of variance explained by each component corresponds to the proportion between the variance of the component and the total variance (Peña 2002). This last value is relevant, since it represents the accuracy of one or more components chosen to represent the original data variability (Table 7).

Table 7. Values of variance explained by the first component from PCA.

Scenario	Precipitation	Temperature	Bioclim
Current	70.620	98.580	84.886
A1B	71.159	98.924	97.935
A2	71.721	98.539	97.900
B2	73.928	98.773	97.575

2.2.2 Current and Future Potential Distributions for Ateline Species

A detailed diagram to model the potential present and future distributions of atelines under climate change and land cover scenarios is presented in Figure 11. This approach is based on the SDMs, which has been widely used to depict actual, past or present species' distributions (Peterson et al. 2002; Araújo & New 2007; Pearson et al.

2007; Thuiller et al. 2008; Elith & Leathwick 2009; Graham et al. 2010b). Although the primary objective of a SDM is this last, we additionally intend to use its result as an approximation to a climatic habitat suitable over current and future climate scenarios, since climatic envelopes were used as co-variables in the SDMs.

The SDMs used for these kinds of approaches, are based on the occurrence of species and predictor variables (Peterson et al. 2007; Elith & Leathwick 2009), establishing the fundamental niche or potential distribution for the species in the first instance, and then determining its realized distribution based on the knowledge of its habitat and geographic range (Phillips et al. 2004). The fundamental niche of a species is the set of all the conditions that enable their survival over time, while its realized niche is the subset of the fundamental niche actually occupied by the species (Hutchinson 1957). The latter may be restricted by several factors such as: human influence, biotic interactions (e.g., competition, predation) or geographical barriers (Pulliam 2000). ENMs, then represent an approximation of the ecological niche of a species exclusively on the environmental dimensions examined, i.e., only over the predictor variables used for modeling.

Although SDMs describe the suitability of the environment in an ecological space, the goal is to project this suitability in geographic space, producing a geographic area of the species predicted presence. The realized niche is usually smaller than the fundamental niche; in this sense the abstraction and simplification of biotic and abiotic environments (with respect to the environmental variables being modeled), can lead to a predicted distribution smaller than the potential distribution. However, if the model tries to include the precision and complexity of the environment, its projection in geographic space will represent with a greater certain the potential distribution of the species (Phillips et al. 2006).

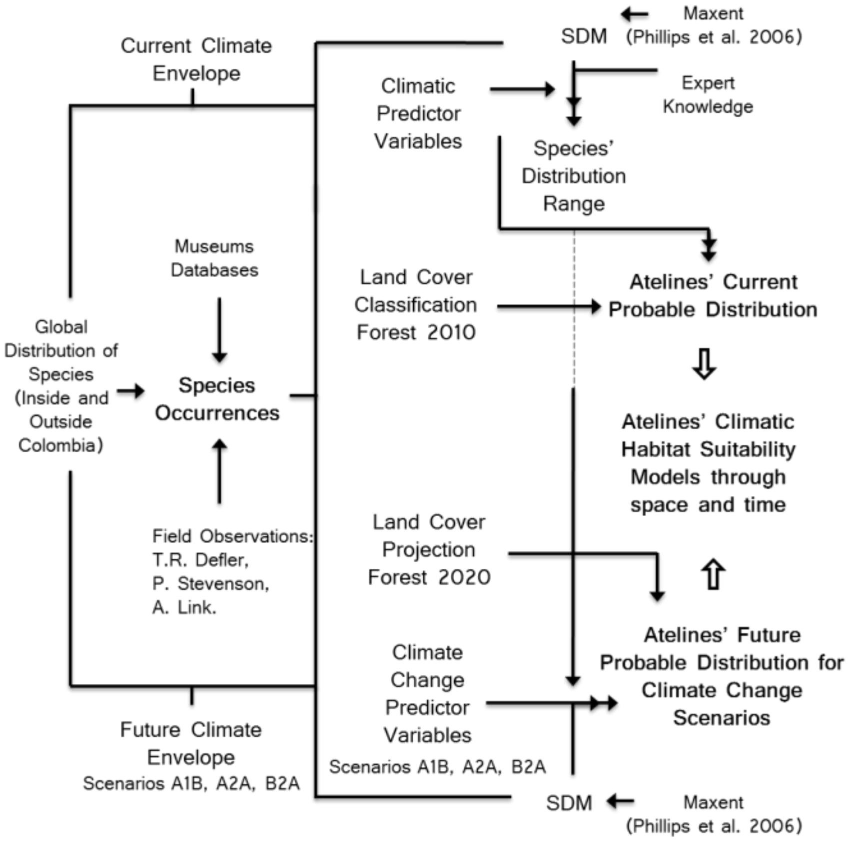


Figure 11. Detailed diagram for modeling the current and future potential distributions for atelines in Colombia.

If the realized niche and the fundamental niche do not fully coincide, the algorithm used to model will be unable to characterize the fundamental niche of the species; hence, it should be assumed that the required information is not present in the localities of occurrence, probably because they have been extracted from a small geographic area. Therefore, it is recommended that the sample universe of observations be extracted from a large study region (Elith & Leathwick 2009; Graham et al. 2011) (if possible, from the entire distributional range of the species) in order to characterize with higher confidence the ecological niche of the species, represented in the spatial variation from localities of occurrence and the environmental conditions (Peterson & Holt 2003; Phillips et al. 2006).

In this context, we used species occurrences for the entire distribution of the ateline species, i.e., with information inside and outside Colombia, obtained, verified and arranged from: i) collection databases (mostly provided by Defler (unpublished)), ii). field observations (mostly provided by A. Link, P. Stevenson and T.R. Defler), iii). the world web databases Mammal Networked Information System (MaNIS - www.manisnet.org) and The Global Biodiversity Information Facility (GBIF - www.gbif.org).

The SDMs for *L. lagothricha* were constructed separately for the two subspecies, since models using all points did not clearly define the expected limits of the species distribution ranges. Thus, for all the analyses the two subspecies are considered individually, but this does not mean we consider them as two different species; as was specified before, we are using the taxonomic information provided by Defler (2010) that considers all Colombian *Lagothrix lagothricha* as being one species rather than two.

Table 8. Number of species points occurrences used in SDM.

Species	Original	Used	% of Used	Altitudinal Range
Ateles belzebuth	60	56	93	0-1300
Ateles geoffroyi	43	43	100	0-2500
Ateles hybridus	115	92	80	0-900
Lagothrix lagothricha lagothricha	92	63	68	200-1400
Lagothrix lagothricha lugens	62	62	100	0-3000
Total	**372**	**316**	**85**	

A total of 372 records of localities for the presence of species were obtained from the different sources used, but only 316 (85%) were used in SDM (Table 8 and Figure 12). 52 observations were excluded for two reasons: i). Because they did not match spatially (Figure 12) or attitudinally (Table 8) with historical and known distribution range limits of species, or ii) because occurrences were separated less than 5km of distance. In practice it is known that occurrences grouped in specific areas tend to make the model overestimates the species occurrence in these regions, leading to underestimate the total area of the species distribution (Renjifo et al. In press).

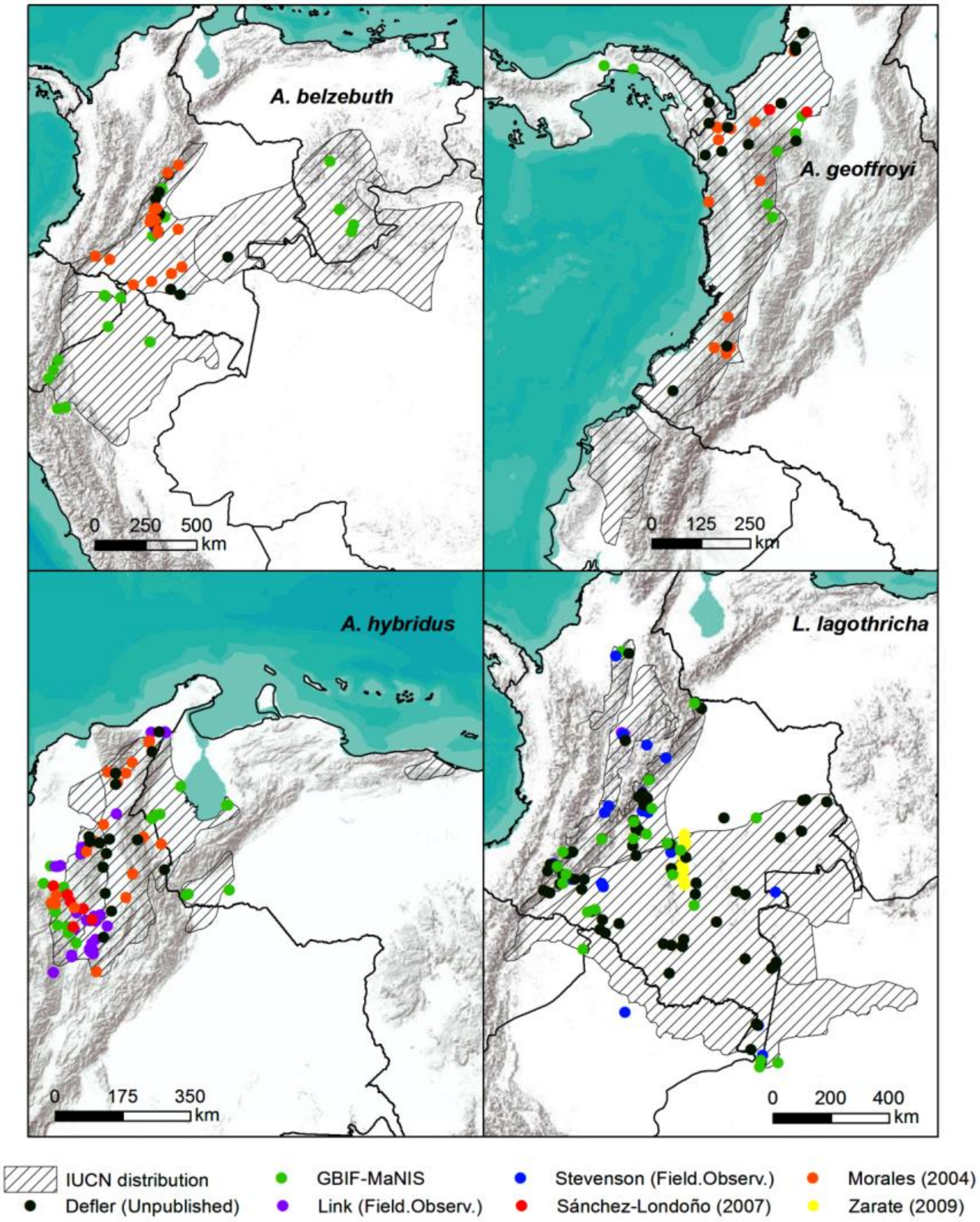


Figure 12. The 316 Presence points used in SDM by species and source.

Is known that for almost any species the distributional range is limited by altitude; and the climate is often a good predictor of species distributions because it determines some physiological characteristics of the species (Hijmans & Graham 2006). To assess the potential distribution of atelines using SDMs, we used as predictor variables the elevation and the three climatic envelopes constructed: bioclim, monthly precipitation and monthly temperature for current and future climate scenarios, in combination with occurrence points of species. Due to georeferenced localities of presence for species were distributed inside and outside Colombia, the co-variables used were prepared to spatially include all species occurrences.

The SDM MaxEnt (Phillips et al. 2004, 2006; Phillips & Dudík 2008; Elith et al. 2010), was used to model ateline distribution and their climatic habitats. MaxEnt uses the fundamental niche ecological concept and the maximum entropy approach, and has been tested continuously with good performances compared to other modeling approaches (including both SDM for presence-only data and presence-absence data) under current and future climate scenarios, and also under different sample sizes (Elith et al. 2006; Hernandez et al. 2006; Hijmans & Graham 2006; Peterson et al. 2007; Wisz et al. 2008; Elith & Graham 2009; Velásquez-Tibatá et al. 2012).

MaxEnt estimates the probability distribution of maximum entropy (i.e., the closest to a uniform distribution) of each predictor variable in the study area, subject to the condition that the expected value of the moments (e.g. mean, variance, covariance) on the estimated probability distribution, must be as close as possible to the moments generated from empirical data of the occurrence of species (Phillips et al. 2006; Elith et al. 2010). For all species and climate scenarios (current and future), the models were ran using the default regularization values which have been adjusted to perform well for different species and regions (Phillips & Dudík 2008). Models for current climates were run using 10 bootstraps with 75% of occurrence points for training and the remaining 25% for testing, while models including the climatic envelope built over climate change scenarios were performed using all records to avoid biases in distribution models following the same structure proposed by Velásquez-Tibatá et al. (2012), who modeled the distribution of 146 species of birds in Colombia.

To convert continuous scale models produced by MaxEnt to maps of presence/ absence it is necessary to apply thresholds. Several methods have been proposed to define them (Liu et al. 2005), however these have been developed mainly thinking on the presence/absence of localities information, which is rarely available. For models using only presence data, the minimum training presence value, i.e., the highest probability value where the omission rate is the lowest, is the common threshold used (Anderson et al. 2003; Pearson et al. 2007). The omission rate is equal to the fraction of the test locations falling within pixels predicted as not suitable for the species (Phillips et al. 2006). Ecologically, when we define the minimum training presence as a threshold value, we are selecting as the species' distribution, the pixels predicted as being at least as suitable as those where a species' presence has been recorded (Pearson et al. 2007).

To evaluate the actual predictive performance of SDMs independent assessment data are required. Although statics calculated over testing data do not necessarily imply the validation of the predicted distribution, bootstrapping provides a measure of internal consistency for the models (Araújo et al. 2011). Values of area under the receiver operating characteristic (ROC) curve (known as the AUC - area under the curve), were in all cases greater than 0.9, verifying good model performances (Wisz et al. 2008). However, it is known that this method is affected when only presence data are available and it has some problems as a comparative measure of accuracy between model results (Pearson et al. 2007; Lobo 2008). Therefore, we also evaluate using expert knowledge the distribution obtained for each species across different percentile omission thresholds (0-30) applied, taking as base value the minimum training presence (Renjifo et al. n.d.; Velásquez-Tibatá et al. 2012). In all cases, these were approximately concordant with the known distribution of atelines.

The application of a minimum training presence threshold to obtain species' distributions often overestimates the known species´ ranges; hence, we obtained in the evaluation of models using expert knowledge that generated distributions were not totally concordant with known range limits of atelines. To address that, we limit the potential distribution of species in Colombia using a combination of one or more of the following criteria: i) expert knowledge of natural and known limits of species' distribution, ii) existing geographic ranges proposed by Defler (2010) (Figure 1) and IUCN (Figure 12), iii) altitudinal known limits (Table 8), and iv) the available occurrence points used in SDMs (Figure 12).

For future species' distributions responding to climate scenarios, we defined the same ranges obtained for current climate, i.e., future ranges restricted to places predicted as suitable in the present (Velásquez-Tibatá et al. 2012). Thus, this study measures the exposure of species' distributions to climate changes, but it does not account for the possible migration of species to other suitable areas (Araújo et al. 2011). Additionally, all species' distributions for current and future scenarios were restricted using forest cover (the natural habitat of atelines) obtained from land cover scenarios for the years 2000, 2010 and 2020 (Phillips et al. 2004).

MaxEnt output with continuous values between 0 and 1 (when the exit option is a logistic) was used as a climatic suitability layer for current and future scenarios, since it responds accordantly to the predictor importance of each pixel (Elith et al. 2010). This product is commonly confused with the probability of occurrence of the species and represents only the probability of occurrence of the species when the average value of the predictor variables has a probability of 0.5. To obtain the conditional probability of occurrence of the species given by the predictors, it would be necessary to know the proportion of occupied sites (prevalence) in the landscape for the species that are unknown. For this reason, the default prevalence is set by MaxEnt as 0.5 (Phillips & Dudík 2008; Elith et al. 2010).

Finally, 15 different distributions (for 3 habitat layers and 5 species) and 20 climatic habitat suitability layers were combined (for 4 climatic conditions and 5 species), to produce 25 (5 species habitat each one with 4 climatic habitat suitability layers under 3 different habitat distributions) different networks for use in the connectivity and dispersal corridor analysis. Each distribution defined by habitat patches in 2000 and 2010 were associated with current climate conditions for the 5 species (a total of 10 networks), while the habitat patches in 2020 were associated with 3 different climatic conditions corresponding to 3 different climatic scenarios for the five species (a total of 15 networks).

2.2.3 Habitat Quality and Cost Flow

A detailed diagram to explain the construction of habitat quality (HQ) and cost flow (CF) functions is presented in Figure 13. These functions are the basis for the network analysis of species connectivity and dispersal. They were built from 4 sources: i) climatic habitat suitability, ii) population density, iii) net primary production (NPP) and iv) land cover.

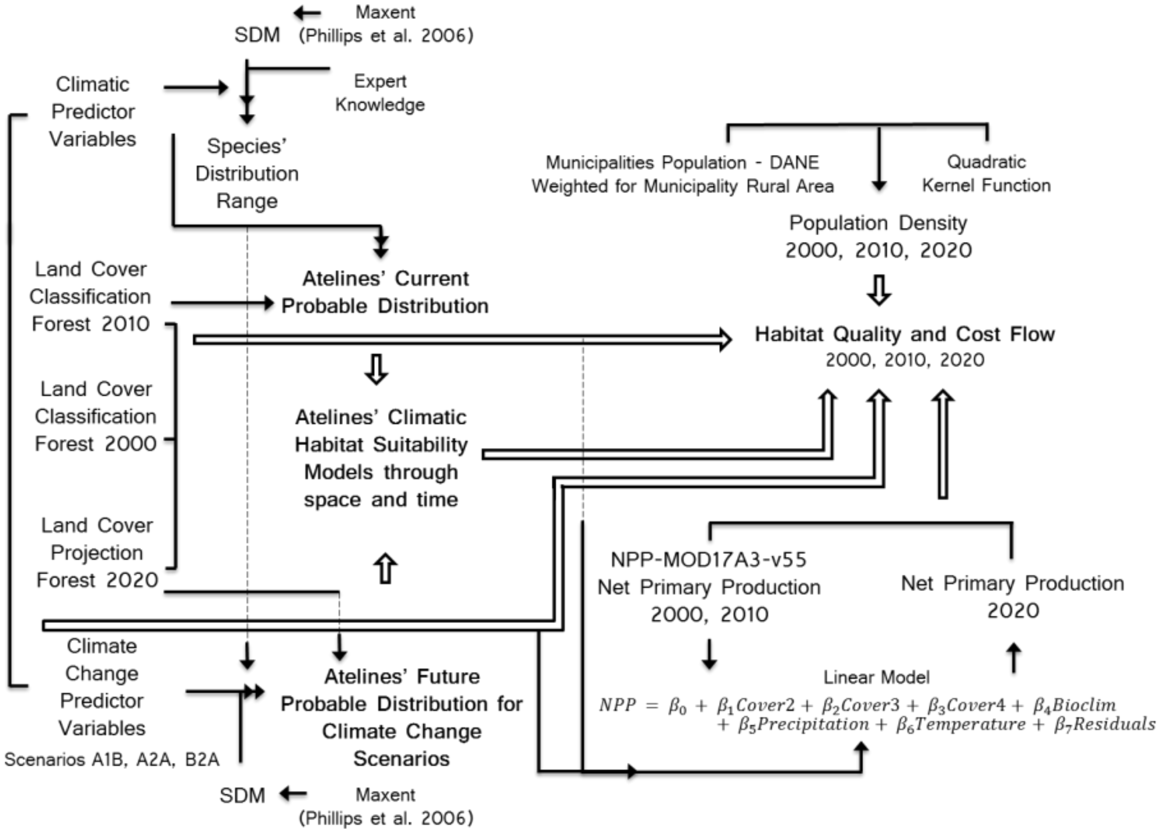


Figure 13. Detailed diagram for building the dispersal flow function.

Climatic habitat suitability layers were created using SDMs as described above. Twenty habitat suitability layers were incorporated into the analysis corresponding to 5 species times 1 current climate conditions, plus 5 species times 3 future climate scenarios($[5\ sp. \times 1\ current\ climate\ layer] + [5\ sp. \times 3\ future\ climate\ layers]$). Figures of layers are shown in the Results chapter.

For building population density layers, total population estimations for municipalities in Colombia from the years 2000, 2010 and 2020 were obtained from the Departamento Administrativo Nacional de Estadistica (DANE)[1]. For each municipality, the total population estimation was weighted by the proportion of its rural area with respect to the sum of all the municipalities' rural areas in Colombia, according to the information obtained from the Federación Colombiana de Municipios (www.fcm.org.co). The weighting proposed, gives more heft in terms of population density to municipalities with less number of habitats located in the following regions: Amazon, Orinoco and Pacific, where hunting of atelines occurs in equal or greater proportion to the other regions (Defler 2010), where population density is greater.

The weighted value of population for each municipality was assigned to its respective polygon centroid for computing population density. The latter was calculated for the years 2000, 2010 and 2020 using a quadratic kernel function, which fits a smoothly curved surface to each centroid (Yamada & Rogerson 2003). The surface value is highest at the location of the point and diminishes with increasing distance from the point. Calculations were performed using the kernel density function incorporated into spatial analyst tools extension in ArcGIS 10 (ESRI 2010). Human population density layers obtained are shown in Figure 14.

NPP corresponds to the second layer of MODIS product Net Primary Production Yearly (NPP-MOD17A3-v55), which describes the rate at which plants in an

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[1] http://www.dane.gov.co/index.php?option=com_content&view=article&id=75&Itemid=72

ecosystem produce net useful chemical energy. The rate at which light energy is converted to plant biomass is primary productivity, and the sum of total converted energy is called gross primary productivity (GPP). NPP is the difference between GPP and energy lost during plant respiration. Values of the NPP layers range between 0 and 65,500 kgC/m^2 for the entire world, in a spatial resolution of 1km (Heinsch et al. 2003). They were downloaded annually for the period 2000-2010.

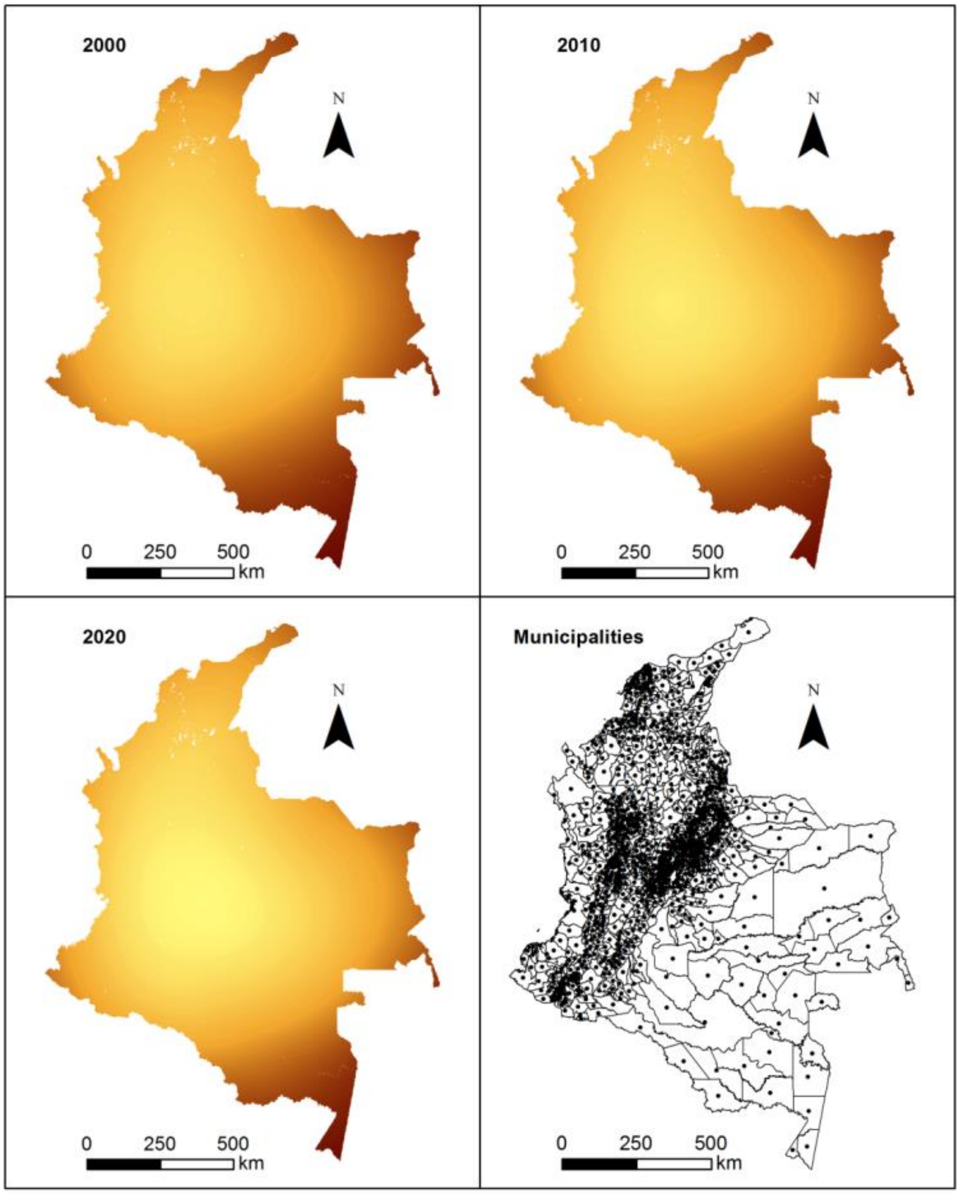


Figure 14. **Human** population density layers. Values are dimensionless because of weighting. Light colors indicate higher population density.

NPP is proportional to absorbed photosynthetically active radiation (APAR), based on the suggestion that the NPP of well-watered and fertilized annual crop plants is linearly related to the amount of solar energy they absorb (Running et al. 1999). Taking this into account, NPP is derived directly or indirectly from MODIS products as follow: i) surface reflectance (MOD09), ii) land cover dynamics (MOD12), iii) Leaf Area Index (LAI) (MOD15), iv) Fraction of Photosynthetically Active Radiation (FPAR) (MOD15), and v) GPP (MOD17) (Heinsch et al. 2003).

NPP measures the production activity or biomass of terrestrial vegetation, indirectly measuring forest production (Running et al. 1999). For this analysis we assumed that the latter is directly associated with resource availability in the forest. As was specified previously, forest productivity is a determinant factor for the atelines in terms of habitat quality and movement patterns, since resource availability determines aspects like diet composition and abundance, foraging strategy, time spent and the composition of foraging activities, and daily ranging distances (Ford & Davis 1992; Strier 1992; Stevenson et al. 2000; Di Fiore & Rodman 2001; Defler 2010).

The NPP MODIS product for the years 2000 and 2010 were incorporated in the construction of HQ, and CF, after filling few and small gaps with no information, using spline interpolation; nevertheless for the year 2020 the NPP had to be projected. In this context and with available generated information (taking into account the necessity for using data for 2020), we supposed that climate and particularly temperature and precipitation (since areas that are warm and wet generally are more productive) in combination with vegetation structure and nutrient availability are control variables for primary productivity, since these relationships have been already established (Bondeau et al. 1999; Schloss et al. 1999; Moldenhauer & Lüdeke 2002; Nemani et al. 2003; Matsushita et al. 2004).

We tried to explain the NPP observed using: climatic variables (constructed climatic envelopes), land cover (land cover layers generated) and soil fertility (co-variable included in land change projection model for 2020). Temperature and precipitation are included recurrently in NPP models for testing the relationship of NPP and climate change (Running & Coughlan 1988; Moldenhauer & Lüdeke 2002; Matsushita et al. 2004). Land cover was a proxy for vegetation structure; although LAI or NVDI are used more often to quantify this characteristic (Cramer et al. 1999; Phillips et al. 2008a), it was not possible to include them due to the limitation of available information for 2020. Soil fertility was originally used to simulate nutrient availability; however, it was not a statistically significant variable in the models, thus it was not finally included.

Although NPP is commonly constructed using combinations of mathematical and physical models (Running & Coughlan 1988; Field et al. 1995; Cramer et al. 1999; Moldenhauer & Lüdeke 2002; Matsushita et al. 2004), we used a statistical approach to project NPP for 2020. Generalized linear models (GLM) were applied, since they are flexible, efficient and common multivariate techniques that are used to predict a dependent variable that can be explained by independent (categorical and/or continuous) predictors.

We used different families and links functions for each GLM generated. Two models for each family and link function were built to explain the NPP in 2000 and 2010. The information used for models was inverted in dates to test the efficiency of the models for predicting 10 years later or 10 years before (since this projection is what we were looking for), i.e. the models used the information of 3 climatic envelopes and land cover as predictor variables. To predict NPP in 2010, land cover of 2000 was used and vice versa. In addition, we used another predictor variable to take into account the spatial autocorrelation of observations, constructed as the residuals of a polynomial linear model of second order between NPP (2000 and 2010) and the pair of coordinates (x and y) for each observation (Equation 1).

$$NPP = \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 y^2 + \beta_5 xy$$

Equation 1. *Polynomial linear model of second order between NPP and the pair of coordinates for each observation.*

Adjusted R^2 statistic, the probability value of t-statistic for coefficients of predictors, and the probability value of F-statistic for the sum of squares of GLM were considered as measures of model performance and significance. A combination of jackknife and cross-validation approaches was constructed for validating the performance of models. For each GLM run, a random sample of all observations without replacement was selected for the model. The total number of pixels from layers extracted in each case corresponded to 50% (556,639 points) of all observations. To complete this value, the number of observations was randomly selected from each different natural region proportional to its area with respect to Colombia, in order to ensure that observations were sufficiently distributed through the entire country. In this way, the sample could be considered as representative (Table 9).

Table 9. Number of observations extracted by region to run the models.

Region	**Area (%)**	**Num. Of Obs. Extracted**
Andean	28	155,859
Caribbean	10	55,664
Orinoquia	15	83,496
Pacific	7	38,965
Amazon	40	222,655
Total	**100**	**556,639**

The procedure described here was applied to each family link combination 500 times for the NPP of two years, i.e., 1000 GLMs were ran for each family link function combination: 500 predicting NPP in 2010 using climate envelope layers, land cover in 2000 and residuals of NPP for 2010 as independent variables, and 500 predicting NPP in 2000 with the same variables except land cover (land cover in 2010). In each run, the values of the coefficients for each variable and the model performance measures chosen were satisfactory evaluated (jackknife), validating in each time the model.

Also a cross-validation verification was implemented at each run in two ways: i) On the remaining 50% of points not used to construct the model, verifying the model performance to predict NPP in the same year but with a model constructed under information of 10 years before. ii). Over all observations of the inverted year of NPP model, verifying the model performance to predict NPP ten years before or latter but with a model constructed under information in the same year of prediction. The statistic used to evaluate cross-validation results was the average of the absolute relative error (ARE) applied for all the observations tested in each model run (Equation 2).

$$ARE = abs\left(\frac{observed - predicted}{observed}\right) \times 100$$

Equation 2. *Absolute relative error (ARE).*

Taking into account GLM performance measures and cross-validation results, the normal linear model had the best performance compared to other families of models. The best results among the approaches of different years was for the prediction of NPP in 2010 using as variables the three climate envelopes, land cover in 2000, and the residuals of relationship between NPP and coordinates in 2010. Mean parameters of coefficients obtained were used in the final model to predict NPP in 2020, since for 500 replicates of each model run the parameter variability was too low (Table 10). Five NPP layers were generated: 2 from MODIS product for years 2000 and 2010, and 3 more for year 2020 and each climatic scenario (Equation 3 and Figure 15). All the analyses were constructed in R (R Development Core Team 2012) and python (Python Software Foundation 2008) programming languages.

$$\begin{aligned} NPP_{2020} = {} & \beta_0 + \beta_1 Cover2_{2020} + \beta_2 Cover3_{2020} + \beta_3 Cover4_{2020} + \beta_4 Bioclim_{SRES} \\ & + \beta_5 Precipitation_{SRES} + \beta_6 Temperature_{SRES} + \beta_7 Residuals_{2010} \end{aligned}$$

Equation 3. *Linear model for prediction of NPP in 2020.*

Final source included in the analysis of HQ and CF was land cover (2000-2020) (layer figures are shown in Results chapter). With the four sources: i) climatic habitat suitability, ii) population density, iii) NPP, and iv) land cover, we construct the functions of HQ and CF for the 5 atelines species, the 3 land cover years and the 3 climate change scenarios. A total of 25 layers for the 3 functions were constructed corresponding to 5 species times 2 first land cover years, plus 5 species in last land cover year times 3 scenarios $([5\ sp.\times 2\ years\ (2000\ and\ 2010)] + [5\ sp.\times 1\ year\ (2020) \times 3\ scenarios])$.

The two functions proposed: HQ and CF, are widely used in connectivity and dispersal analysis under a graph-theoretic approach (Bunn et al. 2000; Urban & Keitt 2001; Pascual-Hortal & Saura 2006; Minor & Urban 2007; Saura & Pascual-Hortal 2007; Bodin & Saura 2010; Saura & Rubio 2010). HQ, has recently taken on special importance in terms of connectivity, since this last is looked now as a property of the habitat itself (Baranyi et al. 2011). CF, on the other hand, is considered the main alternative for assessing inter-patch flow, i.e, the value expressing a connectivity and dispersal degree between habitats, and it is based on the cost that some variables relevant to the species impose on their movement (Phillips et al. 2008b; Kupfer 2012).

Table 10. **P**arameters obtained for NPP linear model.

Parameter	Mean	Stand.Dev.	Coef.Var.	Median	Min	Max
Intercept	12558.954	9.221	0.073	12559.000	12527.000	12586.000
Cover2	-455.255	7.440	-1.634	-455.700	-475.400	-430.600
Cover3	-462.778	3.177	-0.686	-462.800	-472.300	-453.200
Cover4	-538.032	2.897	-0.538	-538.000	-547.400	-529.400
Bioclim	-162.640	0.307	-0.189	-162.600	-163.700	-161.700
Precipitation	70.126	0.150	0.214	70.130	69.500	70.560
Temperature	60.132	0.107	0.178	60.120	59.770	60.500
NPP Residuals	0.998	0.000	0.047	0.998	0.997	1.000
R^2 Adjusted	0.852	0.000	0.026	0.852	0.851	0.852
MARE 1	11.512	0.031	0.273	11.510	11.440	11.590
MARE 2	13.412	0.003	0.025	13.410	13.400	13.420

- ∗ Mean absolute relative error (MARE) 1, corresponds to cross-validation verification i, validation on the same year of prediction. MARE 2 corresponds to cross-validation verification ii, validation on ten years before the year of prediction.

HQ was constructed assuming high values for the best habitat conditions for the species based on the four source layers. Defined best conditions were as follow: i) high climatic habitat suitability, ii) less population density, iii) high NPP, and iv) low values of land cover according to 4 classes (1-Forest, 2-Shrubs, 3-Mixed Crops, 4-Low tree density or bare vegetation). All values of sources layers were normalized between 0 and 1 using Equation 4.

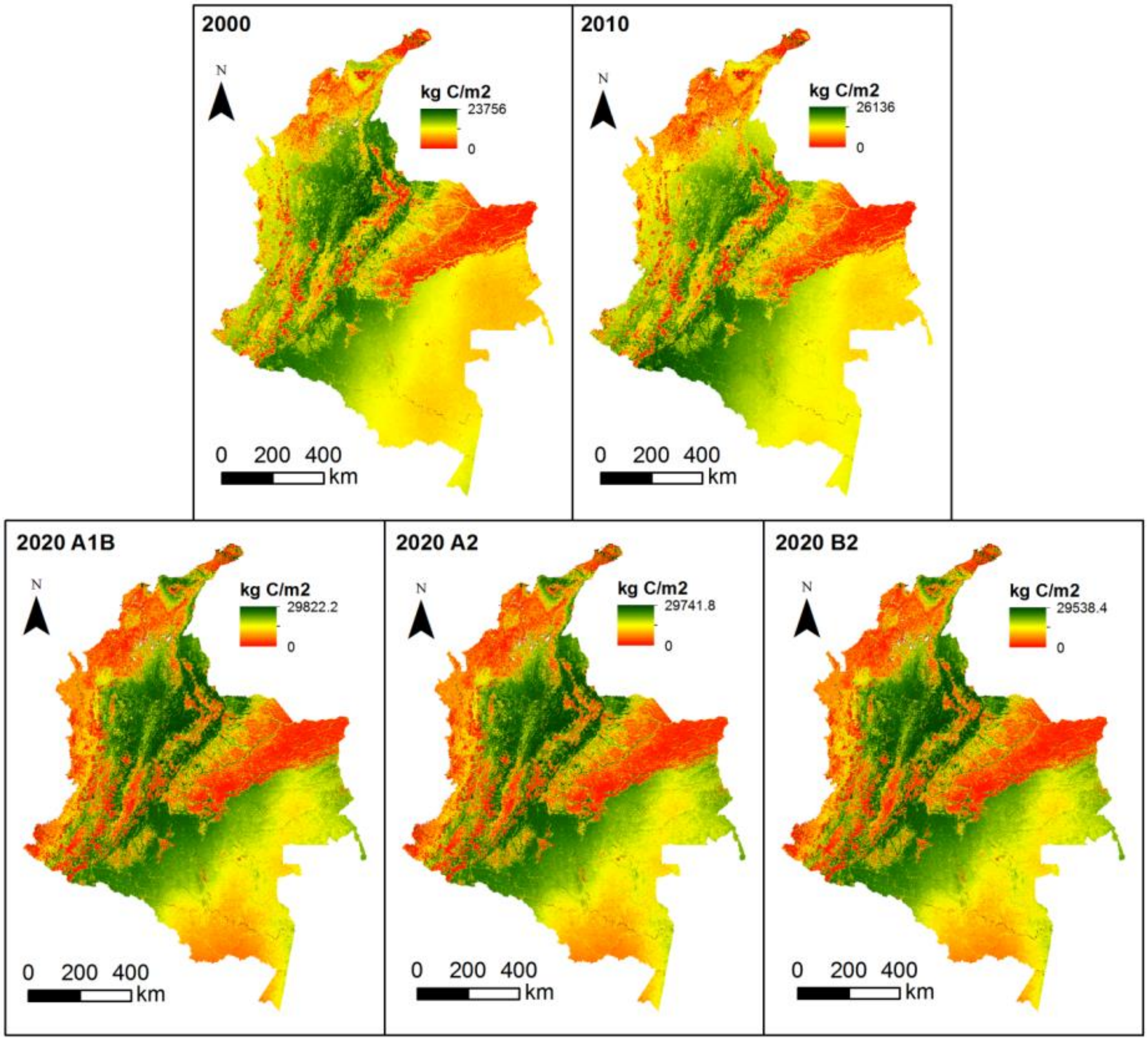


Figure 15. NPP maps for years 2000, 2010 and 2020.

$$Norm\ Variable = \frac{Value - MinValue}{MaxValue - MinValue}$$

Equation 4. *Normalization of variable values.*

Since high values should indicate better HQ, then after normalization procedure, population density and land cover were inverted using Equation 5. The final HQ habitat layer for each species, each land cover year, and each climatic scenario was calculated using Equation 6. It is divided by 4, to rank the final values between 0 and 1, due to all 4 variables were normalized into these values.

$$Inv\ Variable = Abs\ (MaxValue - Value)$$

Equation 5. *Inversion of variable values.*

$$HQ = \frac{Hab.Clim.Suit. + Pop.Dens. + NPP + LandCover}{4}$$

Equation 6. *Calculation of Habitat Quality.*

CF should be consider in the inverse sense of HQ, because it represents less favorable conditions for the species and hence, the cost for species movement. We assumed that cost flow is a function of the same 4 source variables, thus the CF layer for each species, in each year, and each climate scenarios was calculated as the inverse function of HQ (Equation 5 and Equation 6). Other important variables like density or distance to roads could be also considered in this kind of analysis; however, due to the uncertainty in building future roads, we decided not to include it in the function. All the analyses were performed using map algebra operations in R (R Development Core Team 2012) and python (Python Software Foundation 2008) programming languages.

2.2.4 Connectivity and Dispersal Corridor Analysis

A detailed diagram to perform the analysis of connectivity through corridors for ateline dispersal is shown in Figure 16. It is based on a graph-theoretical approach, that evaluates the potential dispersal for species through habitat patches according to a probability of dispersion. This probability is determined by the species habitat quality and dispersal distance that acts as a threshold to determine which habitats are connected (Calabrese & Fagan 2004; Chetkiewicz et al. 2006).

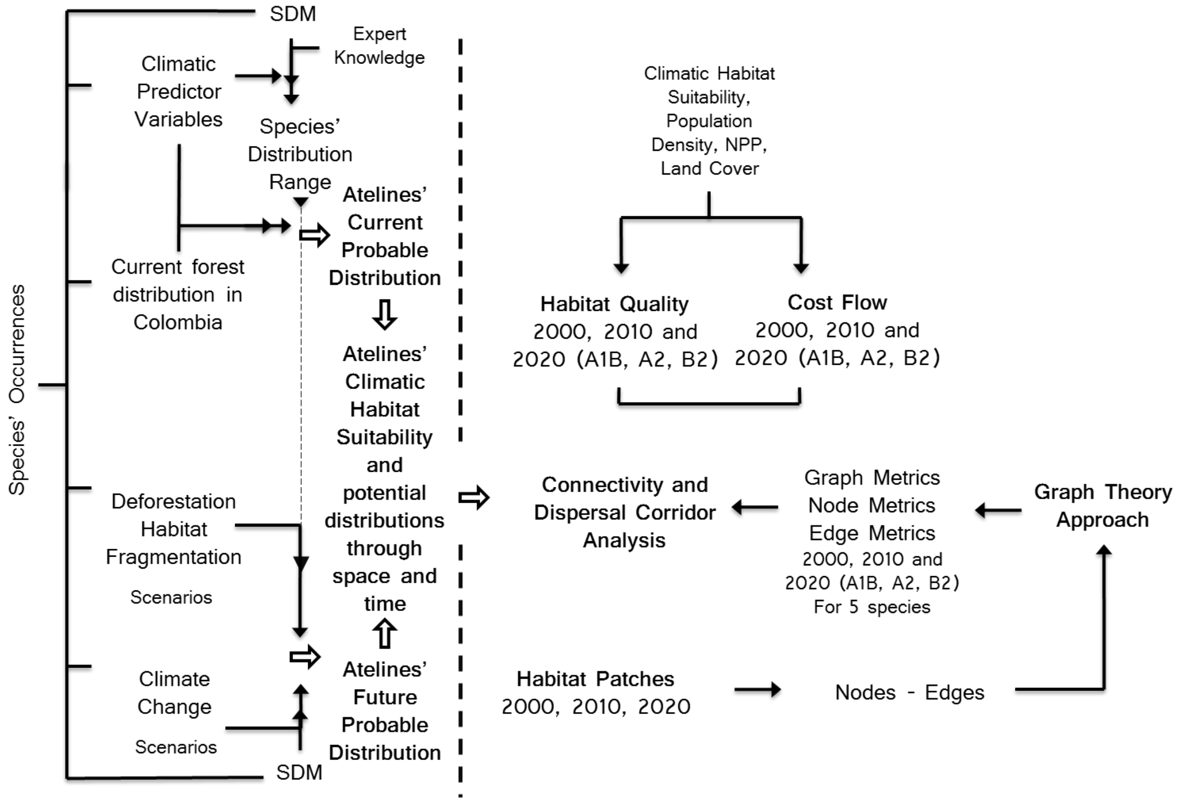


Figure 16. Detailed diagram for performing the connectivity and dispersal corridor analysis for atelines in Colombia.

All forest patches were determined using the 8-neighborrule into each atelines distribution for the years 2000, 2010 and 2020, and were assumed to be habitat patches for the species. Patches with an area larger or equal to 1 km^2 (1 cell) were taken into account, since in this range is included the theoretical home range of the species, and also atelines have been reported in habitat patches smaller than 100 ha (Alfonso 2006; Guerrero Pérez 2007; Aldana 2009; Roncancio et al. 2010). This does not necessary imply that in fact populations of species inhabit all habitat patches; however, in this case we assumed that they can live and move through all forest patches.

Dispersal distances for atelines have not yet been reviewed, in part, because the dispersion of these species through very disturbed matrices is unlikely. As was mentioned before, it is rare that ateline species move or fall to the ground; they spend most of their time on trees (Defler 2010). However, according to a review published by Estrada et al. (2012), the use of agroecosystems has been reported for *A. geoffroyi grisescens* (in Central America) and *L. lagothricha lagothricha* (in Colombia), as corridors to reach native habitat or other agroecosystems.

The movement of atelines into habitats has a wide range of response to resource availability, between 100-400 ha for home range and between 0.5-5 km for daily ranges in *Ateles spp.*, and between 100-800 ha for home range and 1-3 km for daily ranges in *Lagothrix lagothricha* (Ford & Davis 1992; Defler 2010). Although the above values are extensive and large, these are calculated essentially over locomotion on trees, not over ground movements; hence, they do not necessarily indicate that distances for atelines dispersion may occur between these ranges; then in this context, we decided to use as threshold distance for dispersal the minimum possible value, i.e., 1 km, the spatial resolution of all layers.

Network analyses based on graph theory require the definition of two elements: nodes (vertices) and edges (links). Nodes were defined by the habitat patches for the species and edges by the connections established between these. For this particular study, the edges for each species and each year were assumed to be all the links between habitat patches at a distance of 1 km from border to border. A graph (network) is a set of connected nodes and edges describing the landscape as a set of interconnected patches (Ricotta et al. 2000; Jordán et al. 2003; Chetkiewicz et al. 2006). Nodes represent patches of suitable habitat for the species with a surrounded matrix of non-habitat (non-forest) that varies its quality according to some variables affecting the movement of the species (HQ and CF) (Urban & Keitt 2001).

The existence of a link between each pair of nodes implies a potential ability of the species to disperse between them, due to established connections. Edges may have a physical correspondence in the landscape in the form of an existing corridor, but in this case edges only represent the potential (functional) connections between a pair of patches (Pascual-Hortal & Saura 2006). The existence of connections (links) between patches can be symmetric (undirected graphs) or take into consideration source/sink dynamics (directed graphs) (Proulx et al. 2005; Saura & Pascual-Hortal 2007). The first one (symmetric or undirected graphs) establishes the same probability for dispersal of species between the two connected nodes, assuming the same conditions for the species to pass from patch i to patch j and vice versa. With the second type of connection different probabilities for species dispersal can be established, depending on whether it inhabits a source patch or a sink patch according to the habitat quality of the patches (Pulliam 1988; Pulliam & Danielson 1991). Thus, probabilities for moving from source patch i to a sink patch j are lower than in the opposite case (Minor & Urban 2007, 2008). We used both cases in this analysis with the application of different nodes and edges metrics.

Some other concepts besides node and edge used in graph theory metrics are described above, according to Urban & Keitt (2001a) and Urban et al. (2009). A path is a sequence of connected nodes in which no node is visited more than once. Its length can be measured by distance units or number of links (topological distance). A path is closed if the initial node is the same than the final node. A closed path with three or more nodes is a cycle. A path that does not include cycles is a tree; and a tree that includes every node in the graph is a spanning tree (multiple spanning trees can exist in a graph). A component is a set of nodes forming a connected region (subgraph) where a path exists between every pair of nodes, hence there is no functional relation (no path) among patches grouped in different components (any isolated patch forms a component itself) (Figure 17).

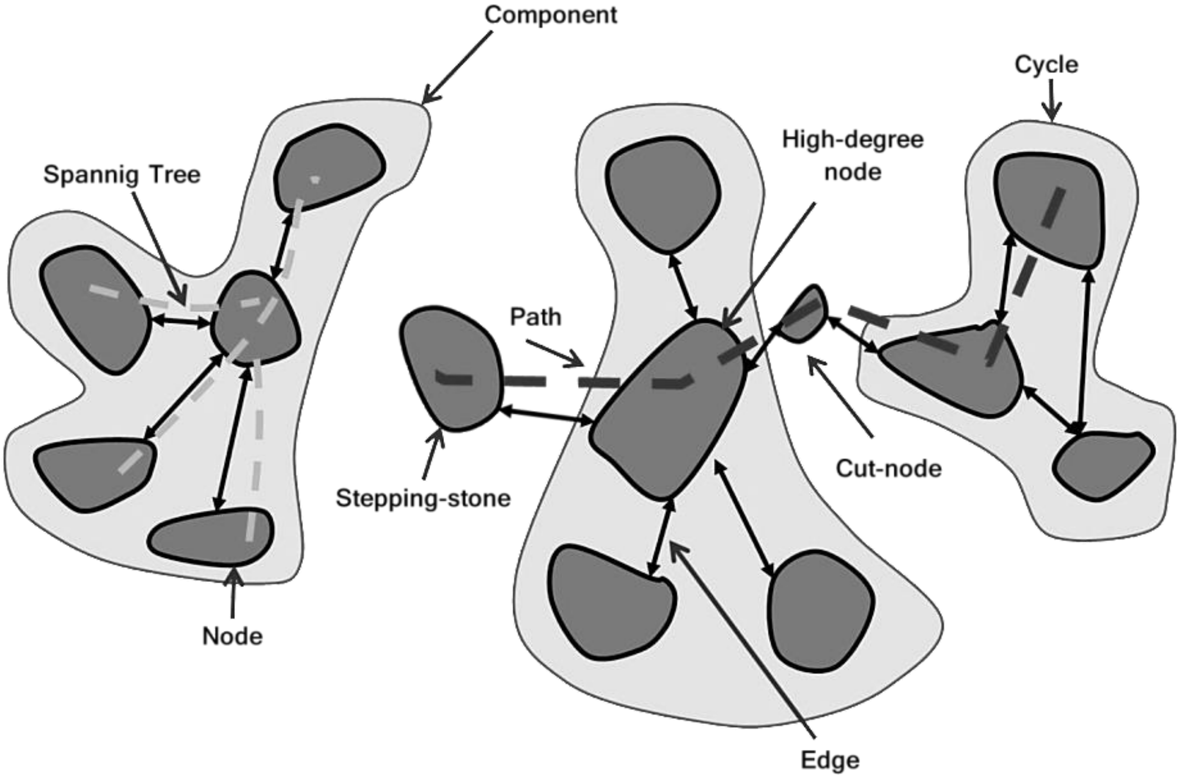


Figure 17. Example of the elements in a graph.

Differences between landscape connections assuming symmetric dispersal probabilities (the probability of dispersal from patch i to patch j being the same than from patch j to patch i), or asymmetrical and weighted probabilities (the probability of dispersal from source patch i to a sink patch j is lower than the one for dispersal from sink patch j to source patch i), were given by different proposed metrics, that in turn, correspond to different software used: Conefor Sensinode 2.6 (Saura & Torné 2009), and the igraph (http://igraph.sourceforge.net) package implemented on the platform of R (R Development Core Team 2012) (
Table 11).

For using both approaches, a matrix of probabilities of dispersal between each pair of nodes i,j was constructed, assigning a continuous value between 0 and 1 for connected nodes (patches separated by a distance equal to 1 km from border to border) and exactly 0 for non-connected nodes (patches separated by a distance greater than 1km from border to border). The connection distance was computed as a Euclidian distance using coordinates from each border pixel belonging to each patch, to all border pixels belonging to all other patches in the distribution of species. This was a very extensive computational procedure because of the use of multiple loops and the amount and size of patches; therefore it has to be parallelized to use simultaneously multiple processors for computing. It was performed on R through the “snow” package (R Development Core Team 2012).

In the event that a node could be connected to another by more than one combination of pixels, we choose the connection where cost flow was minimal, according to the CF layer created by the CF function (Equation 5 and Equation 6). Cost flow between all established connections was computed using Dijkstra’s (1959) algorithm through a costDistance function implemented in the R package “gdistance” (R Development Core Team 2012); this calculates the cost as the least-cost distance between two pairs of coordinates according to a transition layer. Cost values obtained were normalized (Equation 4) between 0 and 1 and then inverted (Equation 5), to convert them into probabilities of dispersal from patch i to patch j (P_{ij}) (a lower cost implies a higher probability to disperse and vice versa). These values were used as entries for dispersal probabilities of **symmetric** matrix.

To calculate dispersal probabilities of **asymmetric** matrix, a dispersal flux (DF) function was created. It is based on HQ and CF functions (Equation 6), and also reflects the probability for a species to move between habitats; however, this tries to take into account the preference that the species may have for moving to patches with higher HQ (Bunn et al. 2000; Saura & Pascual-Hortal 2007). For this analysis, nodes were characterized by their quality-weighted area (QA): multiplying the area (A) patch proportion with respect to the total patches´ area in the species distribution, and the habitat quality of the patch, calculated as the sum of all pixels in the patch from the HQ layer.

The DF function has been widely used analyze the dispersal of species between patches. It is constructed using the habitat quality of nodes and a probability of dispersal, although this latter is often taken as an exponential decay function of distance between nodes (Bunn et al. 2000; Urban & Keitt 2001; Minor & Urban 2007). DF (F_{ij}) from patch i to patch j was calculated as the ratio of QA between both patches (QA_{ij}), multiplied by the probability of dispersal between them P_{ij} (taken from normalization and inverting process to CF value between two patches) (Equation 7). QA_{ij} is lower when the source patch i has a greater QA than patch j (source patch is the denominator and the sink patch is the numerator), since we assumed that the probability of dispersal flux for the species is smaller if it is inhabiting a patch with high values of HQ.

$$F = QA_{ij}P_{ij}, \quad \text{where } QA = \frac{QA_j}{QA_i}, \text{ and } QA_i = \frac{A_i}{A_{total}} \sum_p^n HQ_{pi}$$

Equation 7. *Calculation of Dispersal Flux.*

A total of fifty matrices were constructed using the 5 species for the 3 land cover dates and the 5 climatic scenarios. Twenty five matrices of dispersal were constructed using probabilities of dispersal (symmetrical matrix) for metrics implemented in Conefor software (Saura & Torné 2009), and Twenty five were also constructed for dispersal flux probabilities (asymmetrical matrix), used in the calculation of metrics obtained from the igraph (http://igraph.sourceforge.net) package on R (R Development Core Team 2012).

Table 11 presents a synthesis of the most commonly used metrics in network analyses. Metrics are grouped by type (node, edge or graph) and also have a connection condition: i) binary (B), whether taking into account the connection; or ii) probabilistic (P), whether taking into account weight given to the connection through the probability of dispersal (symmetrical matrix), or the probability of dispersal flux (asymmetrical matrix). Also metrics used in this study are specified. They were selected according to their recurrent use in graph-theoretic studies evaluating connectivity and also based on the analysis of Baranyi et al. (2011), Laita et al. (2011) and (Kupfer 2012), which discuss and compare the usefulness and convenience of many of them. To depict the node and edge metrics results, two PCA were constructed for comparing graphically the results using a biplot (the first one between the three climatic scenarios for each species, and the second one between the three years for each species).

2.2.5 Prioritization of Conservation Areas for Ateline Persistence

A diagram showing the procedure to prioritize PAs is shown in Figure 18. The prioritization of conservation areas for ateline persistence was performed to optimize their dispersal under climate change and habitat fragmentation scenarios in order to guarantee the persistence of their populations. This was determined by the graph, node and edge metrics, primary based on habitat quality, dispersal probability and dispersal flux for each species. Connections between habitat patches for dispersal, the habitat patches themselves, and their surrounding areas, were considered as conservation areas to be prioritized.

We based our approach on the assumption that the presence or abundance of species can be associated with the size, quality, and connectivity of the patch as proxies for the persistence of populations (Minor & Urban 2007). Larger patches often enclose more individuals; nevertheless both area and habitat quality can affect the population sizes and thus, the density of individuals due to changes in reproductive success (Kurki et al. 2000; Fahrig 2003; McVinish & Pollett 2013). These dynamics in turn, might be affected by human factors influencing connectivity trough deforestation or regeneration patterns (Ims 1995; Clevenger & Waltho 2005). Then patches, connections and the landscape matrix should be taken into account in priority areas. Patches connected, where the potential dispersal of species is supposed to occur, are more likely to be occupied than isolated patches (Pulliam et al. 1992; Dunning et al. 1995); therefore, smaller patches that occasionally can experience local extinctions, would be recolonized from neighboring patches if they are well connected (Minor & Urban 2007).

Table 11. Common metrics used in graph-theoretic approaches measuring connectivity. See also Figure 17.

Used	Type	Metric	Description	Source	Software
Yes	Node (B)	Integral index of connectivity (IIC)	Calculated from the attributes of the patches and the topological distances between them. It takes into account the connected area existing within the patches, the estimated dispersal flux between different patches, and their contribution as stepping stones or connecting elements that uphold the connectivity between other patches.	Pascual-Hortal & Saura 2006a; Bodin & Saura 2010; Saura & Rubio 2010	Conefor
Yes	Node (P)	Probability Index (PC)	Conceptually similar to IIC but for weighted graphs. It uses the maximum product probability instead of the topological distance between patches.	Boitani et al. 2007a; Bodin & Saura 2010; Saura & Rubio 2010	Conefor
Yes	Node (B)	Landscape coincidence probability (LCP)	Probability that two points located randomly within a landscape reside in the same component.	Pascual-Hortal & Saura 2006a	Conefor
No	Node (P)	IICconn	One of the three fractions of IIC measuring the contribution of the analyzed patch to the connectivity between other patches, as a connecting element or stepping stone between them.	Saura & Rubio 2010	-
No	Node (P)	dIICconn	Analogous to IICconn but for the PC index in weighted graphs.	Saura & Rubio 2010	-
No	Node (B/P)	PCconnector / IICconnector	How much patch contributes to connectivity between other patches by serving as an intermediate stepping stone (connecting element) that cannot be fully replaced by other patches in the network. This contribution depends only on the spatial (topological) position of the patch in the landscape. A high value implies that the loss of a patch would severely reduce the connectivity between other habitat patches.	Bodin & Saura 2010; Saura & Rubio 2010	-
No	Node	PC / IIC	Loss of habitat availability caused by the removal of a patch, evaluated	Bodin & Saura 2010; Saura	-

Used	Type	Metric	Description	Source	Software
	(B/P)		as the relative decrease (%) in the PC or IIC value following the removal.	& Rubio 2010	
No	Node (P)	Harary Index	Sum of the inverse values of the topological distance (number of links in the shortest path) between every two patches. If two patches belong to different components, their topological distance is infinity	Ricotta et al. 2000; Jordán et al. 2003	-
Yes	Node (P)	Strength or weighted vertex degree	Summing up the edge weights of the adjacent edges for each vertex	Minor & Urban 2007a	Conefor
Yes	Node (P)	Weighted Habitat Quality	Habitat quality for patches weighted for proportion of patch area.	Minor & Urban 2007a	HQ func.
Yes	Node (B)	Betweenness	Number of geodesics (shortest paths) going through a vertex or an edge. Describes the frequency with which a patch falls between other pairs of patches in the network. It is calculated by finding the shortest paths between every pair of patches in the landscape, then counting the number of times those paths cross each node.	Minor & Urban 2007a; Bodin & Saura 2010; Saura & Rubio 2010	Conefor
No	Node (B)	Closeness centrality	How many steps are required to access every other vertex from a given vertex.	Baranyi et al. 2011	-
Yes	Node (B)	Cut-node	Vertices whose removal increases the number of connected components in a graph, i.e., those whose removal breaks a single graph component into several smaller ones.	Minor & Urban 2007a	igraph, R
Yes	Node (B)	Degree	The number of its adjacent edges.	Proulx et al. 2005; Minor & Urban 2007a, 2008	igraph, R
Yes	Node (B)	Minimum spanning tree (MST)	Contains the set of links of minimum total weight (summed distance or cost) that joins all nodes into a single connected cluster (i.e. where every node is accessible from every other node by following links from one node to another).	Reunanen et al. 2012	igraph, R

Used	Type	Metric	Description	Source	Software
Yes	Graph (B)	Integral index of connectivity (IIC)	Follows the same concept described for node metrics.	Uses the same sources mentioned in node metrics.	Conefor
Yes	Graph (P)	Probability Index (PC)	Follows the same concept described for node metrics.	Uses the same sources mentioned in node metrics.	Conefor
Yes	Graph (B)	Landscape coincidence probability (LCP)	Follows the same concept described for node metrics.	Uses the same sources mentioned in node metrics.	Conefor
Yes	Graph (B)	Characteristic path length or average path length (CPL)	Calculates the average length between all pairs of reachable patches in the network.	Minor & Urban 2008	igraph, R
No	Graph (B)	Compartmentalization or connectivity correlation	Correlation between node degree and average node degree of its neighbors.	Minor & Urban 2008	-
Yes	Graph (P)	Diameter	Longest shortest path joining any two nodes in the network.	Bunn et al. 2000; Minor & Urban 2008	igraph, R
Yes	Graph (B)	Number of edges	Total number of links in a graph.		igraph, R
Yes	Graph (B)	Number of nodes	Total number of habitat patches in a graph.		igraph, R
Yes	Graph (B)	Transitivity	Probability that the adjacent vertices of a vertex were connected.	Minor & Urban 2008	igraph, R
Yes	Edge (P)	Cosf Flow	Derived cost flow function.		CF func.
Yes	Edge (P)	Flux	Derived dispersal flux function. An edge attribute that indicates amount of movement between nodes.	Bunn et al. 2000; Urban & Keitt 2001a; Minor & Urban 2008	DF func.
Yes	Edge (B)	Integral index of	Follows the same concept described for node metrics. Its importance is	Uses the same sources	Conefor

		connectivity (IIC)	measured using edge removal methods.	mentioned in node metrics.	
Yes	Edge (B)	Landscape coincidence probability (LCP)	Follows the same concept described for node metrics. Its importance is measured using edge removal methods.	Uses the same sources mentioned in node metrics.	Conefor

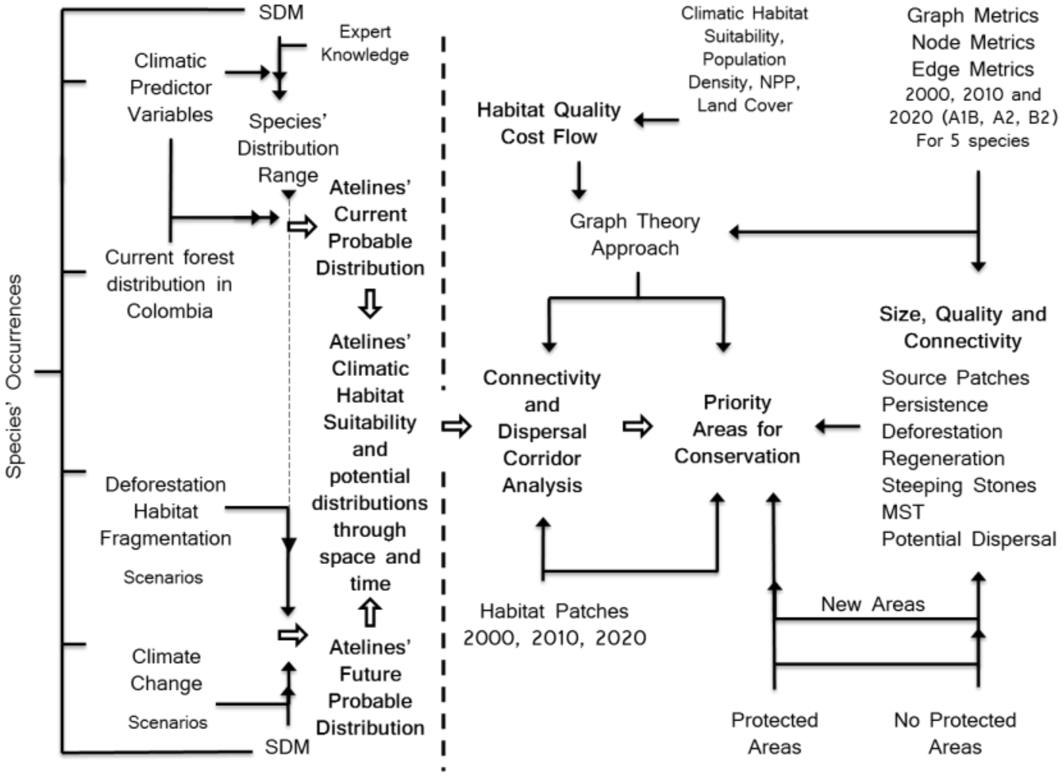


Figure 18. Diagram for Prioritization of Conservation Areas.

According to Minor & Urban (2007a), understanding the above three patch attributes (size, quality, and connectivity) the selection of priority areas for species dispersal can contribute to the construction of a protected area network. In this context, as conservation targets we analyzed: i) source patches, ii) areas of persistence, iii) lost, and iv) regeneration of habitat, v) stepping stones, vi) the most efficient network of habitat connected patches (minimum spanning tree), and vii) the probable physical connections where species dispersal would take place (Table 12). All of these metrics together were the basis for determining priority conservation areas for ateline dispersal.

High values in the first component of the PCA for node and edge metrics used in the connectivity and dispersal corridor analysis (
Table 11) were also used to identify patches and connections with high quality, capacity and connectivity (sources patches) for each species during each year. Persistence patches were calculated as the remaining habitat area spatially

intersected during the three years. In contrast, regions where habitat loss and regeneration occurred during both periods: 2000-2010 and 2010-2020 were included. The MST (
Table 11) was employed to identify the main connection network for species dispersal and the cut-nodes to represent the stepping stones connections. Finally, potential links established (border of two patches separated by 1 km) were consider as the corridors where physical dispersion of species could occur.

Priority areas were measured as the sum of conservation targets (Table 12) for each year and each species. Major priority areas were the ones with the total superposition of conservation targets; therefore, the maximum value for priority areas could be 7 and the minimum 0. In addition, areas where processes of land use change have occurred, are occurring, or are expected to occur; areas where the presence of the species should be reviewed; and areas where climate suitability in future scenarios is the highest; were identified as priority areas.

Table 12. Conservation targets for prioritizing PAs for ateline species.

Element		Conservation Target	Source
Patches	1	Sources	Values in PCA of node metrics. Normalized between 0 and 1. Values close to one were considered as source patches.
	2	Persistence	Persistence areas. Intersection of remnant habitat for species during the three years.
	3	Habitat Loss	Regions where habitat loss for species occurred in the period 2000-2020.
	4	Habitat Regeneration	Regions where regeneration of forest occurred in the period 2000-2020.
	5	Stepping Stones	Nodes identified in cut-node metrics.
Patch - Edges	6	MST	Nodes connected in MST metrics.
Edges	7	Connections	Probable physical connections where dispersal take place.

We also evaluated the representativeness of Colombian PAs for each species in terms of their intersecting area with i) the original species distribution, ii) the persistence, deforested and regenerated regions, iii) the remaining habitat in each year, and iv) the conservation targets (as the sum of values within intersecting area). To represent the results of representativeness synthetically, the PAs were grouped according to their assigned category and their size in four types: protected areas at i) national, ii) regional and iii) local scale, and iv) natural reserves of civil society (reservas naturales de la sociedad civil - RNSC) (Table 13). All the analyses were performed using map algebra operations in ArcGIS 10 (ESRI 2010).

Table 13. Groups formed by categories of PAs.

PA	Category
National	Área Marina Protegida
	Área Natural Única
	Parque Nacional Natural
	Reserva Forestal Protectora
	Reserva Forestal Protectora Productora
	Reserva Nacional Natural
	Santuario De Fauna Y Flora
	Santuario De Flora
	Via Parque
Regional	Área De Manejo Especial
	Área De Manejo Especial De Carácter Regional
	Distrito De Manejo Integrado
	Distrito De Manejo Integrado Y Área De Recreación
	Parque Natural
	Parque Natural Regional
	Parque Natural Regional Y Ecológico
	Parque Regional Natural
	Parque Regional Natural Y Ecológico
	Reserva Forestal
	Reserva Forestal Departamental
	Reserva Forestal Natural Y De Investigación
	Reserva Forestal Protectora
	Reserva Forestal Protectora Productora
	Reserva Forestal Protectora Y Bosque De Interés General
Regional	Reserva Hídrica
	Reserva Natural
	Santuario De Vida Silvestre
	Zona De Interés Cultural
	Área De Manejo Especial
Local	Área Forestal Distrital
	Parque Ecológico Distrital De Humedal
	Parque Ecológico Distrital De Montaña
	Parque Forestal Y Zoológico
	Parque Municipal
	Parque Municipal Natural
	Parque Natural Municipal
	Reserva Forestal Hidrográfica, Piscícola Y Patrimonio Ecológico
	Reserva Ecológica
	Reserva Ecológica E Hídrica
	Reserva Ecológica Y Patrimonio De La Ciudad
	Reserva Forestal
	Reserva Forestal De Interés Público Y Patrimonio Ecológico
	Parque Regional Natural
	Reserva Forestal Protectora
	Reserva Natural
	Santuario Distrital De Fauna Y Flora
	Zona De Utilidad Pública E Interés Social

3. Results

3.1 Future Scenarios of Land Cover and Climate

Land cover layers show good performances in terms of spatial distribution and the proportion of classes according to expert knowledge (Figure 19), and the approximation of land cover map in Colombia (Figure 2). Results of model performance for predicting land cover scenarios in 2020 are acceptable according to values obtained in a confusion matrix, comparing projected and constructed land cover classifications for 2010. Errors of commission and omission (overall error of 16%), in addition to Kappa index of agreement (overall value of 0.72) are shown in Table 15. Major errors in association, predicting location and proportion of pixels occur for classes 2 and 3 because of intermixing between them, but with good projections of classes 1 and 4, which are dominant categories in the landscape.

Table 14. Results of Dinamica EGO model performance for the scenario in 2020.

Classes	Errors of Commission	Errors of Omission	Kappa Index of Agreement
1	0.05	0.02	0.94
2	0.72	0.82	0.17
3	0.45	0.41	0.50
4	0.18	0.25	0.66

∗ Errors of commission and omission are expressed as proportions.

Final land cover layers are presented in Figure 19. The proportion of different classes tends to show no significant change in a broader scale, especially between the period 2010-2020. However, regional level variations in cover proportions are more evident, which would suggest the same pattern for species habitats (Figure 20 and Figure 21). Deforestation processes in all regions are evident, except for the Amazonian and Pacific regions, where forest stability is consistent throughout the entire period, with a very small proportion of reforestation between 2010 and 2020 after deforestation between 2000 and 2010 (Figure 20).

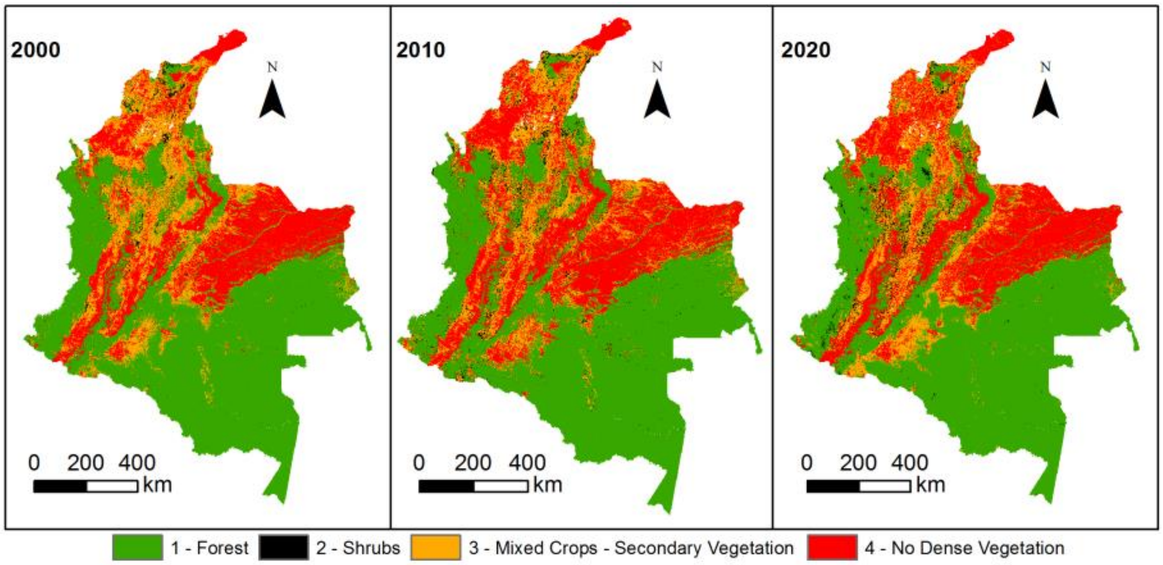


Figure 19. Final constructed land cover layers.

Strong forest conversion in the last decade is projected over the foothills of the eastern slope of the Cordillera Oriental in Putumayo region (Figure 21), which in addition to the historically advanced colonization front in Caquetá described by Etter et al. (2006a), make this a critical area with a disruptive component for *L. lagothricha* subspecies. For the Pacific region, deforestation occurs in isolated patches distributed throughout the region resulting in a fragmentation process, in addition to intense forest loss in Tumaco during the period 2000-2010. However, a similar amount of forest lost is recovered for Tumaco in the projection for 2020, with also some patches in Darien and Katios regions (Figure 21). In this context, is evident the work of the cell automata approach used by Dinamica EGO, since patches surrounding by a large area of a different class are briefly converted to the surrounding matrix in the projections for 2020.

In the Orinoquia region, the predominance of savannas is maintained over the two periods, since savannas are the dominant cover in this area. The transformation process of land cover is mainly dominated by fires, as illustrated by Romero et al. (2010), producing after the process more low tree density or bare vegetation.

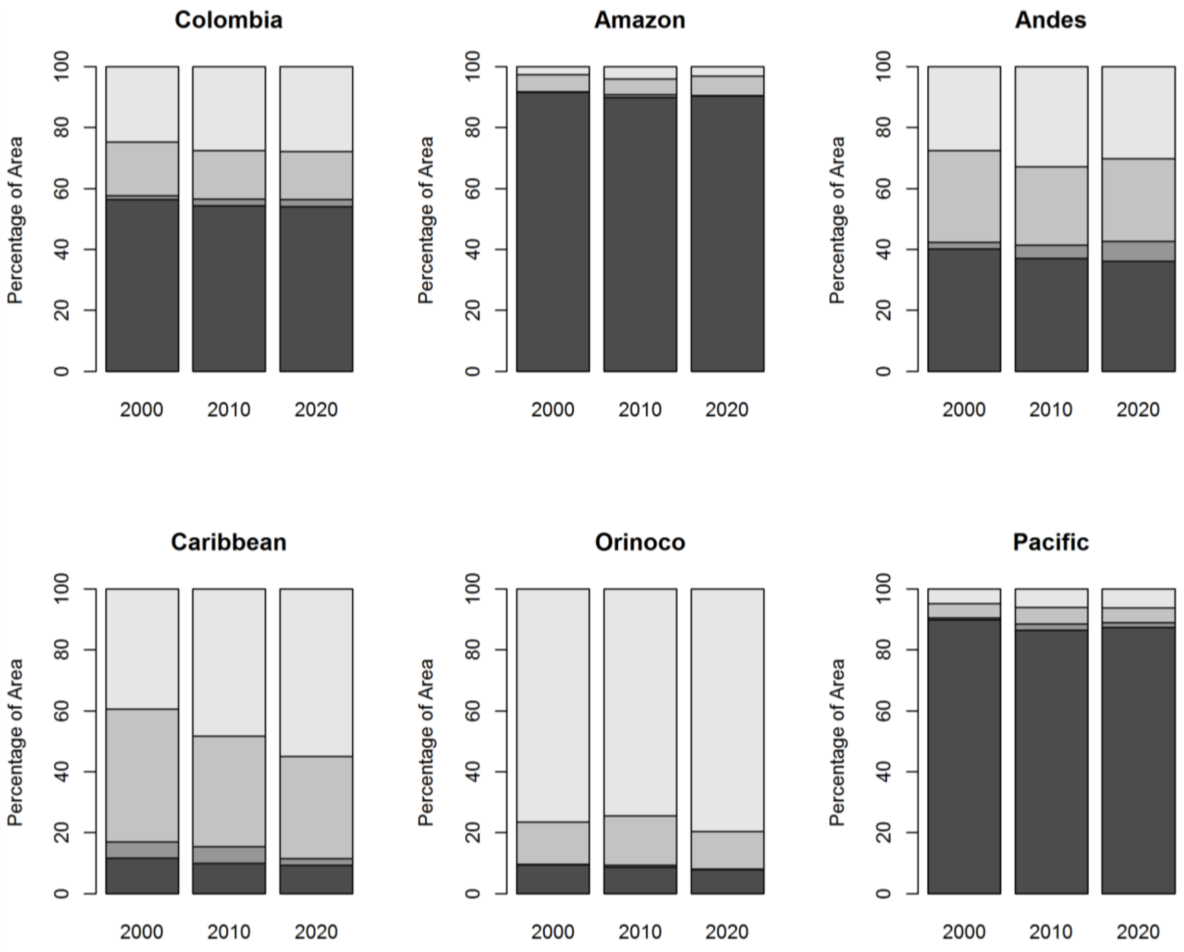


Figure 20. Proportion of land cover in Colombia for the period 2000-2020 by region. Corresponding legend is ■ Class 1 ▩ Class 2 ▨ Class 3 □ Class 4

The highest rates of deforestation are found for the Caribbean and Andean regions, where major processes of natural cover transformations have taken place in Andean and dry forests (Figure 20). Remnant forests in these regions are projected to be affected. Some fragmentation processes would occur according to scenarios projected in i) Serranía de San Lucas, ii) Catatumbo region, iii) surrounding areas of Sierra Nevada de Santa Marta, and iv) over Cordillera Central in the departments of Tolima and Valle del Cauca (Figure 21).

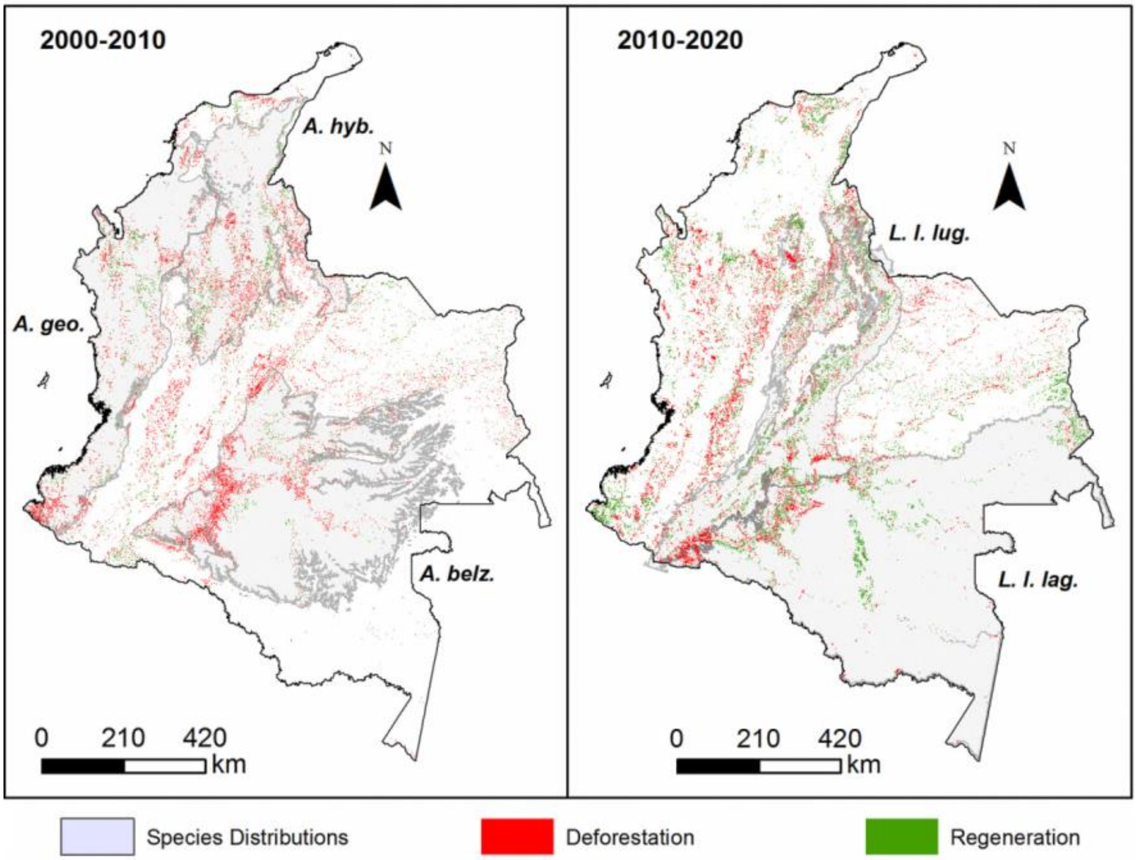
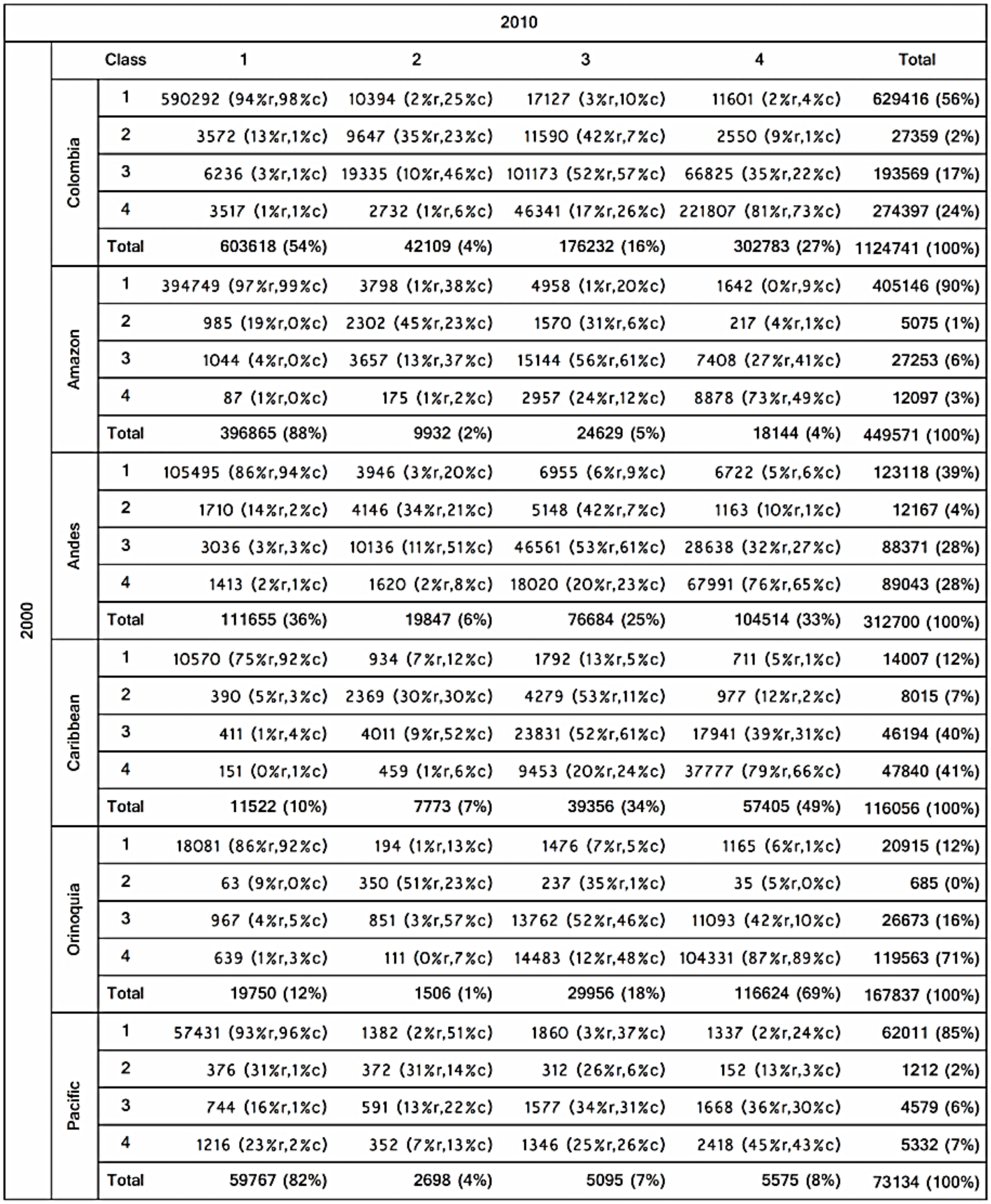


Figure 21. Areas of deforestation and regeneration during the periods 2000-2010 and 2010-2020.

Transition values for deforestation and regeneration are proportionally distributed between the other classes in different regions. Nevertheless, for both processes, the forest class has the largest contribution (class 1) (Table 15 and Table 16). This is translated into a high spatial autocorrelation pattern, i.e., if a cell is surrounded by forest the most likely cause is forest, hence the importance of PAs for conserving natural vegetation.

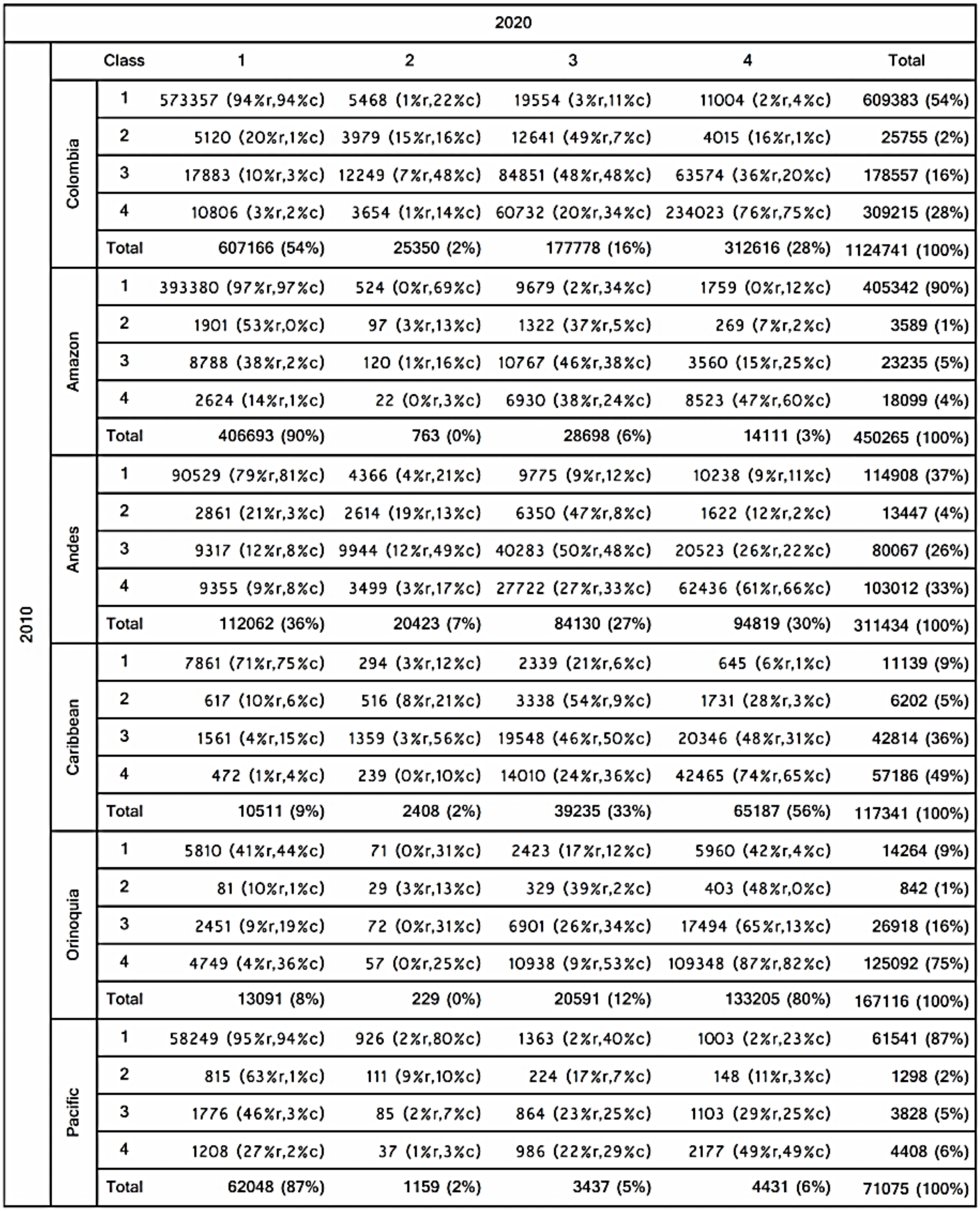
Table 15. Values for transition of land cover by regions during the period 2000-2010.



			2010				
		Class	1	2	3	4	Total
2000	Colombia	1	590292 (94%r,98%c)	10394 (2%r,25%c)	17127 (3%r,10%c)	11601 (2%r,4%c)	629416 (56%)
		2	3572 (13%r,1%c)	9647 (35%r,23%c)	11590 (42%r,7%c)	2550 (9%r,1%c)	27359 (2%)
		3	6236 (3%r,1%c)	19335 (10%r,46%c)	101173 (52%r,57%c)	66825 (35%r,22%c)	193569 (17%)
		4	3517 (1%r,1%c)	2732 (1%r,6%c)	46341 (17%r,26%c)	221807 (81%r,73%c)	274397 (24%)
		Total	603618 (54%)	42109 (4%)	176232 (16%)	302783 (27%)	1124741 (100%)
	Amazon	1	394749 (97%r,99%c)	3798 (1%r,38%c)	4958 (1%r,20%c)	1642 (0%r,9%c)	405146 (90%)
		2	985 (19%r,0%c)	2302 (45%r,23%c)	1570 (31%r,6%c)	217 (4%r,1%c)	5075 (1%)
		3	1044 (4%r,0%c)	3657 (13%r,37%c)	15144 (56%r,61%c)	7408 (27%r,41%c)	27253 (6%)
		4	87 (1%r,0%c)	175 (1%r,2%c)	2957 (24%r,12%c)	8878 (73%r,49%c)	12097 (3%)
		Total	396865 (88%)	9932 (2%)	24629 (5%)	18144 (4%)	449571 (100%)
	Andes	1	105495 (86%r,94%c)	3946 (3%r,20%c)	6955 (6%r,9%c)	6722 (5%r,6%c)	123118 (39%)
		2	1710 (14%r,2%c)	4146 (34%r,21%c)	5148 (42%r,7%c)	1163 (10%r,1%c)	12167 (4%)
		3	3036 (3%r,3%c)	10136 (11%r,51%c)	46561 (53%r,61%c)	28638 (32%r,27%c)	88371 (28%)
		4	1413 (2%r,1%c)	1620 (2%r,8%c)	18020 (20%r,23%c)	67991 (76%r,65%c)	89043 (28%)
		Total	111655 (36%)	19847 (6%)	76684 (25%)	104514 (33%)	312700 (100%)
	Caribbean	1	10570 (75%r,92%c)	934 (7%r,12%c)	1792 (13%r,5%c)	711 (5%r,1%c)	14007 (12%)
		2	390 (5%r,3%c)	2369 (30%r,30%c)	4279 (53%r,11%c)	977 (12%r,2%c)	8015 (7%)
		3	411 (1%r,4%c)	4011 (9%r,52%c)	23831 (52%r,61%c)	17941 (39%r,31%c)	46194 (40%)
		4	151 (0%r,1%c)	459 (1%r,6%c)	9453 (20%r,24%c)	37777 (79%r,66%c)	47840 (41%)
		Total	11522 (10%)	7773 (7%)	39356 (34%)	57405 (49%)	116056 (100%)
	Orinoquia	1	18081 (86%r,92%c)	194 (1%r,13%c)	1476 (7%r,5%c)	1165 (6%r,1%c)	20915 (12%)
		2	63 (9%r,0%c)	350 (51%r,23%c)	237 (35%r,1%c)	35 (5%r,0%c)	685 (0%)
		3	967 (4%r,5%c)	851 (3%r,57%c)	13762 (52%r,46%c)	11093 (42%r,10%c)	26673 (16%)
		4	639 (1%r,3%c)	111 (0%r,7%c)	14483 (12%r,48%c)	104331 (87%r,89%c)	119563 (71%)
		Total	19750 (12%)	1506 (1%)	29956 (18%)	116624 (69%)	167837 (100%)
	Pacific	1	57431 (93%r,96%c)	1382 (2%r,51%c)	1860 (3%r,37%c)	1337 (2%r,24%c)	62011 (85%)
		2	376 (31%r,1%c)	372 (31%r,14%c)	312 (26%r,6%c)	152 (13%r,3%c)	1212 (2%)
		3	744 (16%r,1%c)	591 (13%r,22%c)	1577 (34%r,31%c)	1668 (36%r,30%c)	4579 (6%)
		4	1216 (23%r,2%c)	352 (7%r,13%c)	1346 (25%r,26%c)	2418 (45%r,43%c)	5332 (7%)
		Total	59767 (82%)	2698 (4%)	5095 (7%)	5575 (8%)	73134 (100%)

∗ Percentages are calculated by rows (r) and columns (c), indicating the proportion of classes in which reference classes in row (r) were converted into 2010 and vice versa. Some percentages do not sum 100% because of rounding values.

Table 16. Values for transition of land cover by regions during the period 2010-2020.



			2020				
		Class	1	2	3	4	Total
2010	Colombia	1	573357 (94%r,94%c)	5468 (1%r,22%c)	19554 (3%r,11%c)	11004 (2%r,4%c)	609383 (54%)
		2	5120 (20%r,1%c)	3979 (15%r,16%c)	12641 (49%r,7%c)	4015 (16%r,1%c)	25755 (2%)
		3	17883 (10%r,3%c)	12249 (7%r,48%c)	84851 (48%r,48%c)	63574 (36%r,20%c)	178557 (16%)
		4	10806 (3%r,2%c)	3654 (1%r,14%c)	60732 (20%r,34%c)	234023 (76%r,75%c)	309215 (28%)
		Total	607166 (54%)	25350 (2%)	177778 (16%)	312616 (28%)	1124741 (100%)
	Amazon	1	393380 (97%r,97%c)	524 (0%r,69%c)	9679 (2%r,34%c)	1759 (0%r,12%c)	405342 (90%)
		2	1901 (53%r,0%c)	97 (3%r,13%c)	1322 (37%r,5%c)	269 (7%r,2%c)	3589 (1%)
		3	8788 (38%r,2%c)	120 (1%r,16%c)	10767 (46%r,38%c)	3560 (15%r,25%c)	23235 (5%)
		4	2624 (14%r,1%c)	22 (0%r,3%c)	6930 (38%r,24%c)	8523 (47%r,60%c)	18099 (4%)
		Total	406693 (90%)	763 (0%)	28698 (6%)	14111 (3%)	450265 (100%)
	Andes	1	90529 (79%r,81%c)	4366 (4%r,21%c)	9775 (9%r,12%c)	10238 (9%r,11%c)	114908 (37%)
		2	2861 (21%r,3%c)	2614 (19%r,13%c)	6350 (47%r,8%c)	1622 (12%r,2%c)	13447 (4%)
		3	9317 (12%r,8%c)	9944 (12%r,49%c)	40283 (50%r,48%c)	20523 (26%r,22%c)	80067 (26%)
		4	9355 (9%r,8%c)	3499 (3%r,17%c)	27722 (27%r,33%c)	62436 (61%r,66%c)	103012 (33%)
		Total	112062 (36%)	20423 (7%)	84130 (27%)	94819 (30%)	311434 (100%)
	Caribbean	1	7861 (71%r,75%c)	294 (3%r,12%c)	2339 (21%r,6%c)	645 (6%r,1%c)	11139 (9%)
		2	617 (10%r,6%c)	516 (8%r,21%c)	3338 (54%r,9%c)	1731 (28%r,3%c)	6202 (5%)
		3	1561 (4%r,15%c)	1359 (3%r,56%c)	19548 (46%r,50%c)	20346 (48%r,31%c)	42814 (36%)
		4	472 (1%r,4%c)	239 (0%r,10%c)	14010 (24%r,36%c)	42465 (74%r,65%c)	57186 (49%)
		Total	10511 (9%)	2408 (2%)	39235 (33%)	65187 (56%)	117341 (100%)
	Orinoquia	1	5810 (41%r,44%c)	71 (0%r,31%c)	2423 (17%r,12%c)	5960 (42%r,4%c)	14264 (9%)
		2	81 (10%r,1%c)	29 (3%r,13%c)	329 (39%r,2%c)	403 (48%r,0%c)	842 (1%)
		3	2451 (9%r,19%c)	72 (0%r,31%c)	6901 (26%r,34%c)	17494 (65%r,13%c)	26918 (16%)
		4	4749 (4%r,36%c)	57 (0%r,25%c)	10938 (9%r,53%c)	109348 (87%r,82%c)	125092 (75%)
		Total	13091 (8%)	229 (0%)	20591 (12%)	133205 (80%)	167116 (100%)
	Pacific	1	58249 (95%r,94%c)	926 (2%r,80%c)	1363 (2%r,40%c)	1003 (2%r,23%c)	61541 (87%)
		2	815 (63%r,1%c)	111 (9%r,10%c)	224 (17%r,7%c)	148 (11%r,3%c)	1298 (2%)
		3	1776 (46%r,3%c)	85 (2%r,7%c)	864 (23%r,25%c)	1103 (29%r,25%c)	3828 (5%)
		4	1208 (27%r,2%c)	37 (1%r,3%c)	986 (22%r,29%c)	2177 (49%r,49%c)	4408 (6%)
		Total	62048 (87%)	1159 (2%)	3437 (5%)	4431 (6%)	71075 (100%)

- ∗ Percentages are calculated by rows (r) and columns (c), indicating the proportion of classes in which reference classes in row (r) were converted into 2020 and vice versa. Some percentages do not sum 100% because of rounding values.

Constructed climate envelopes are shown in Figure 22, where climatic known regions can be observed. Humid regions, characterized by extremely high precipitation rates are clearly defined. In the Pacific region the highest values occur particularly in Chocó, in addition to the Orinoco region in the foothills of Cordillera Oriental, and the Amazon region in the Caquetá and Putumayo areas.

Humid regions are constant over climate scenarios (2020); however Orinoquia and the Amazon show a drier pattern that is not present for the current scenario (2000 and 2010). The latter, has the problem of absent climate stations in the region, therefore there is high uncertainty in WorldClim results for this area. This does not occur for future scenarios created from GCMs, where this pattern is spatially and intensity constant. The Andean region and the dry inter-Andean valleys and Caribbean are clearly visible for three climatic envelopes, where the spatial pattern of temperature does not seem to change for any scenario.

There is a slight increase in precipitation for the Orinoco and the Amazon regions, according to projections from IPCC (AR4) (2007), especially in scenarios A2 and B2 with respect to A1B. These results are not comparable with the current scenario due to the different spatial patterns generated as product from different climate models used. For this region there is a clear difference in climate scenarios showed by Bioclim envelope, where the central area is drier (green) with respect to other areas which are wetter (yellow to brown).

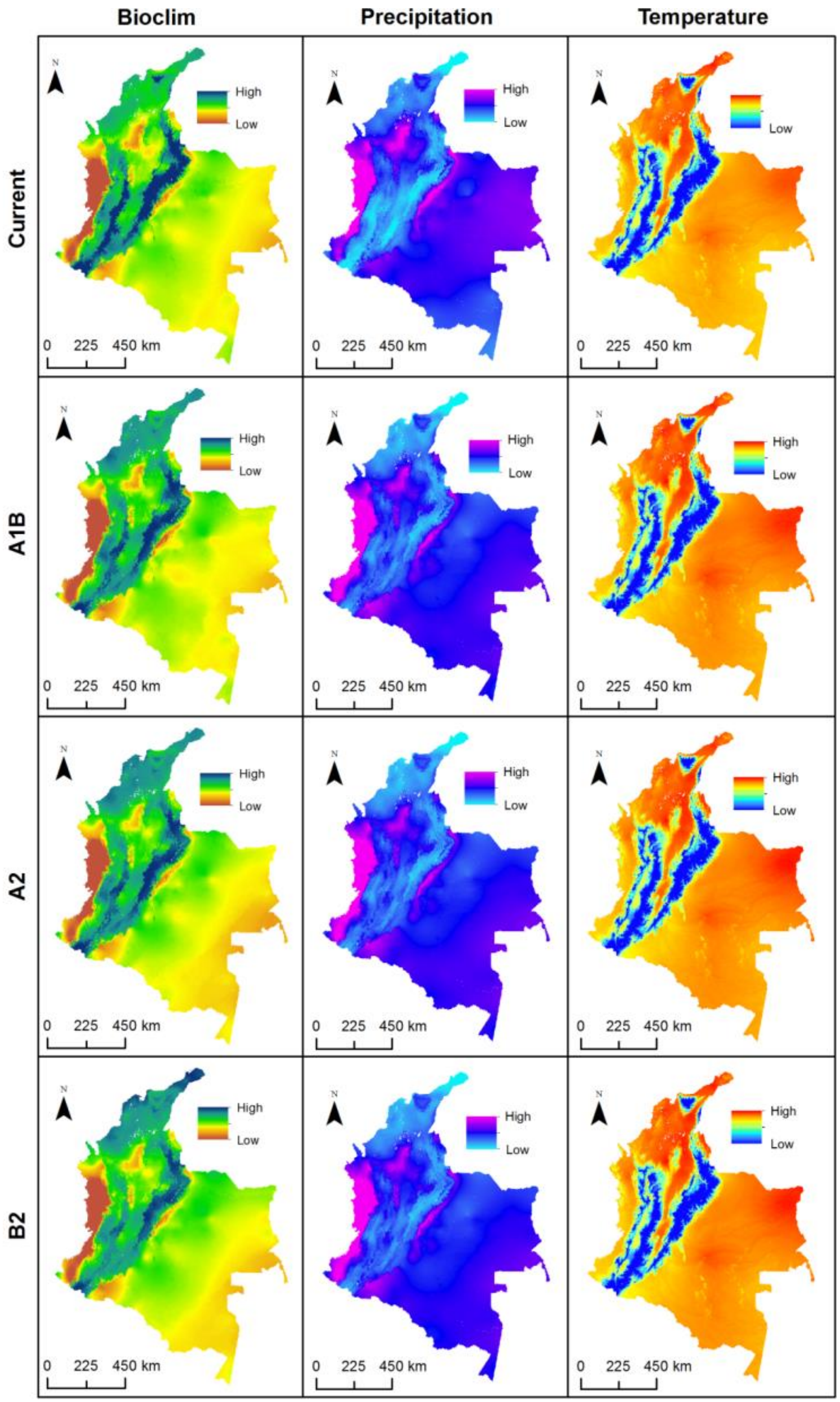

Bioclim
Precipitation
Temperature
Current
A1B
A2
B2
N
High
Low
0 225 450 km

Figure 22. Climatic envelopes for current and futures scenarios. Bioclim (dimensionless variable), precipitation and temperature are normalized between 0 and 100.

3.2 Current and Future Potential Distributions for Ateline Species

Each species' distribution limit corresponds to a combination of known spatial and altitudinal limits, the boundary points of species occurrences, and a logistic threshold applied to the MaxEnt model output. The later was applied where limits of species distribution were not clear (see the chapter: Species' Distributions Ranges). Resultant distributions of species are shown in Figure 23 and can be compared to only expert knowledge of distributions proposed by Defler (2010) (Figure 1) or IUCN (Figure 12).

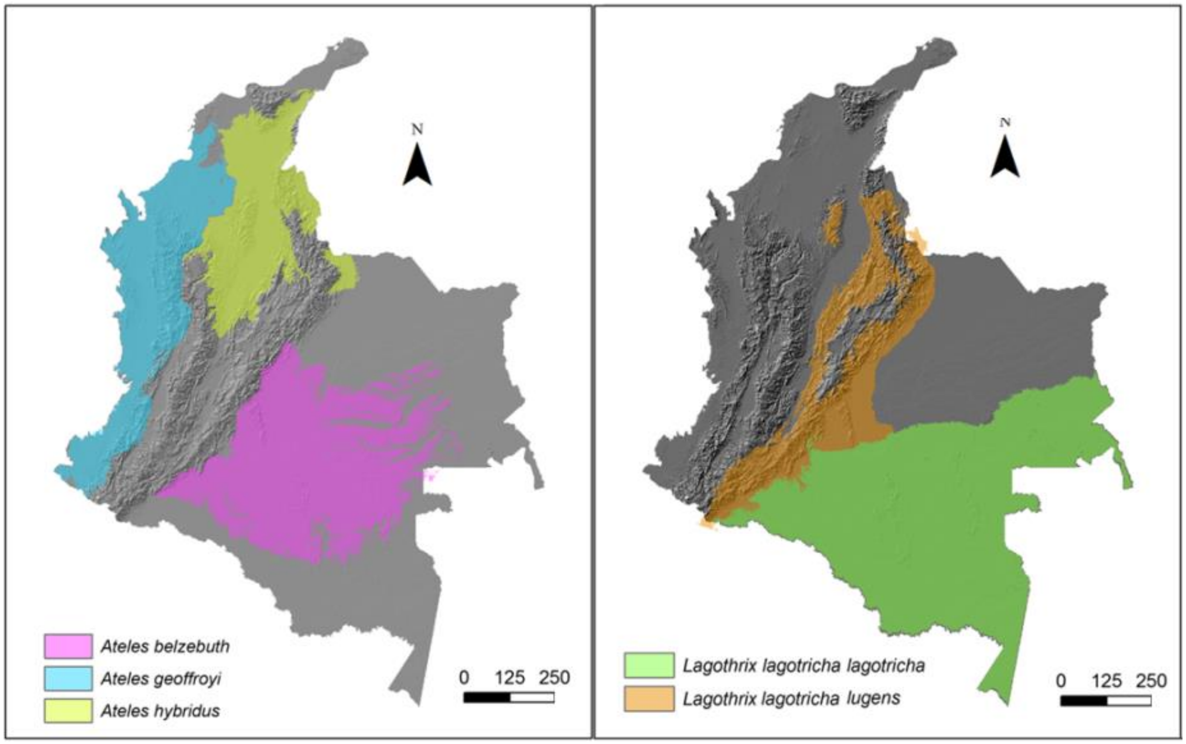


Figure 23. Adjusted species' distributions using expert knowledge and the MaxEnt models.

Boundaries obtained for *Ateles belzebuth* distribution are the río Upía to the north; sixty percentile training presence of MaxEnt on the east, northeast and southeast; the río Caquetá on the south, and 1300 m of altitude on the west. For *Ateles geoffroyi* the distribution is Canal del Dique on the north; the Pacific Ocean on the west; the río Cauca on the east; and the minimum training presence of MaxEnt on the northeast, southeast and south (in combination with the national frontier). For *Ateles hybridus* the boundaries are the minimum training presence of MaxEnt on the north, south and southeast; the National frontier on the northeast; the río Cauca on the southwest; and the río Magdalena on the northwest. For *L. l. lagothricha* the boundaries are the national frontier on the south, east and west; the río Uva on the northwest; and a combination of thirty percentile training presence of MaxEnt for both *Lagothrix lagothricha* subspecies on the northeast. For *L. l. lugens* the boundaries are 3000 m of altitude on the north in combination with minimum training presence of MaxEnt; the thirty percentile training presence of MaxEnt on the southeast; the limit of the western slopes of Cordillera Central on the southwest; and the minimum training presence of MaxEnt on the east and the west.

Resultant ranges for species (Figure 23) are concordant in area (Table 17) and spatial distribution (Figure 25 and Figure 26) to the ones proposed by IUCN. Differences are very close, just a 15% as maximum error was calculated for distributions of *A. belzebuth* and *L. l. lugens* (Table 17). Remaining habitat for species and their distributions follows the same pattern of deforestation and regeneration described for natural regions in Colombia (Figure 21). For species in Andean and Caribbean regions (*A. hybridus* and *L. l. lugens*) the deforestation pattern is predominant, while for species of the Pacific, Amazon, and Orinoquia regions (*A. geoffroyi, A. belzebuth,* and *L. l. lagothricha*) there are constant proportions of their remaining habitat (Table 17 and Figure 24).

Ateles hybridus and *L. l. lugens* original habitat has decreased more than 50%. Almost all forest in lowlands and a large proportion of Andean forest have been deforested for both species. Also, major remaining habitats across the three years are distributed in regions like Catatumbo, Serranía de San Lucas, Tama, El Cocuy and Serranía de los

Yariguies for both species, and in addition the eastern slopes of Cordillera Central in department of Antioquia have decreased for *A. hybridus*, and the foothills of the eastern slopes of Cordillera Oriental in Orinoquia and Amazon for *L. l. lugens* (Figure 25 and Figure 26). Major deforestation fronts are found at high altitudes and on foothills, especially the piedmont of Caquetá and Putumayo, and Serranía de San Lucas, where a strong deforestation process is also projected into 2020 (Figure 21).

Table 17. Remaining habitat for ateline species.

	Orig. Distribution (km^2)	**2000 (km^2)**	**2010 (km^2)**	**2020 (km^2)**
A. belzebuth	242,524 (15.1%)	184,014 (75.9%)	176,645 (72.8%)	178,182 (73.5%)
A. geoffroyi	150,009 (-10.9%)	93,403 (62.3%)	90,054 (60%)	89,145 (59.4%)
A. hybridus	125,635 (4.9%)	35,085 (27.9%)	31,621 (25.2%)	29,524 (23.5%)
L. l. lagothricha	384,404 (-4.8%)	359,880 (93.6%)	354,502 (92.2%)	356,400 (92.7%)
L. l. lugens	146,178 (-14.7%)	70,581 (48.3%)	63,499 (43.4%)	62,479 (42.7%)

* Percentages for original distributions correspond to the proportion of change between this and the distributions proposed by the IUCN. Negative values indicate smaller distributions with respect to the IUCN and vice versa. Percentages for years correspond to proportions of remaining habitat with respect to the original proposed distribution.

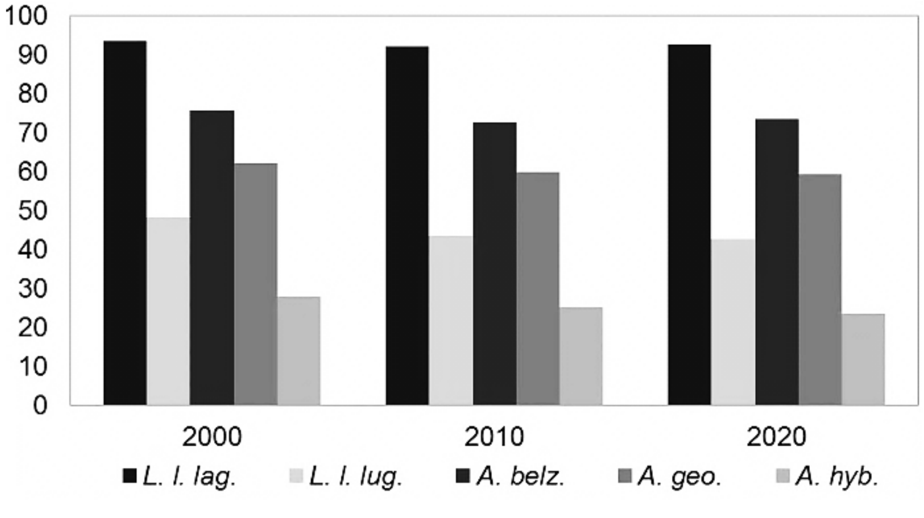


Figure 24. Remaining forest area for ateline species within their distributions

For *A. geoffroyi* major regions with habitat loss are the lowlands of Antioquia and Córdoba, while for *A. belzebuth* and *L. l. lagothricha* forest loss has occurred in the foothills and lowlands of Caquetá and Putumayo (Figure 25 and Figure 26). Remnant habitat for Amazonian species is still significant even for projections into 2020; however, for *A. geoffroyi* a declining trend in habitat area corresponds to a forest proportion near 60%, in addition to a fragmentation process projected into its core distribution for 2020, suggesting that significant reductions will occur in the remaining habitat for this species, particularly near to foothills of the western slope of Cordillera Occidental (Figure 21, Figure 25 and Figure 26).

Climatic habitat suitability varies for each species and for current and future climate change scenarios (Figure 27 and Figure 28); however, this variation is determined in some proportion by different sources used in the data for interpolating climatic surfaces (Figure 22). For *A. belzebuth*, patterns of suitability are predominantly given by precipitation following humid areas that correspond to foothills in a greater proportion respect to lowland regions in future scenarios, in addition to a highly suitable area in A2 and B2 scenarios respect to A1B scenario. For *A. geoffroyi* there is not a single climatic factor explaining habitat suitability; nevertheless, a combination of humid and warm areas seems to be more suitable for the species. Between climatic scenarios there are no notorious differences, although A2 scenario projects more suitable areas for the species*. Ateles hybridus* suitability is higher over humid, hot and low regions. For this species it is evidently possible a migration process to higher areas (e.g., see projections over Serranía de San Lucas) due to projected climatic warming, since climatic scenarios show a general extension of habitat suitability over higher altitudes (Figure 27).

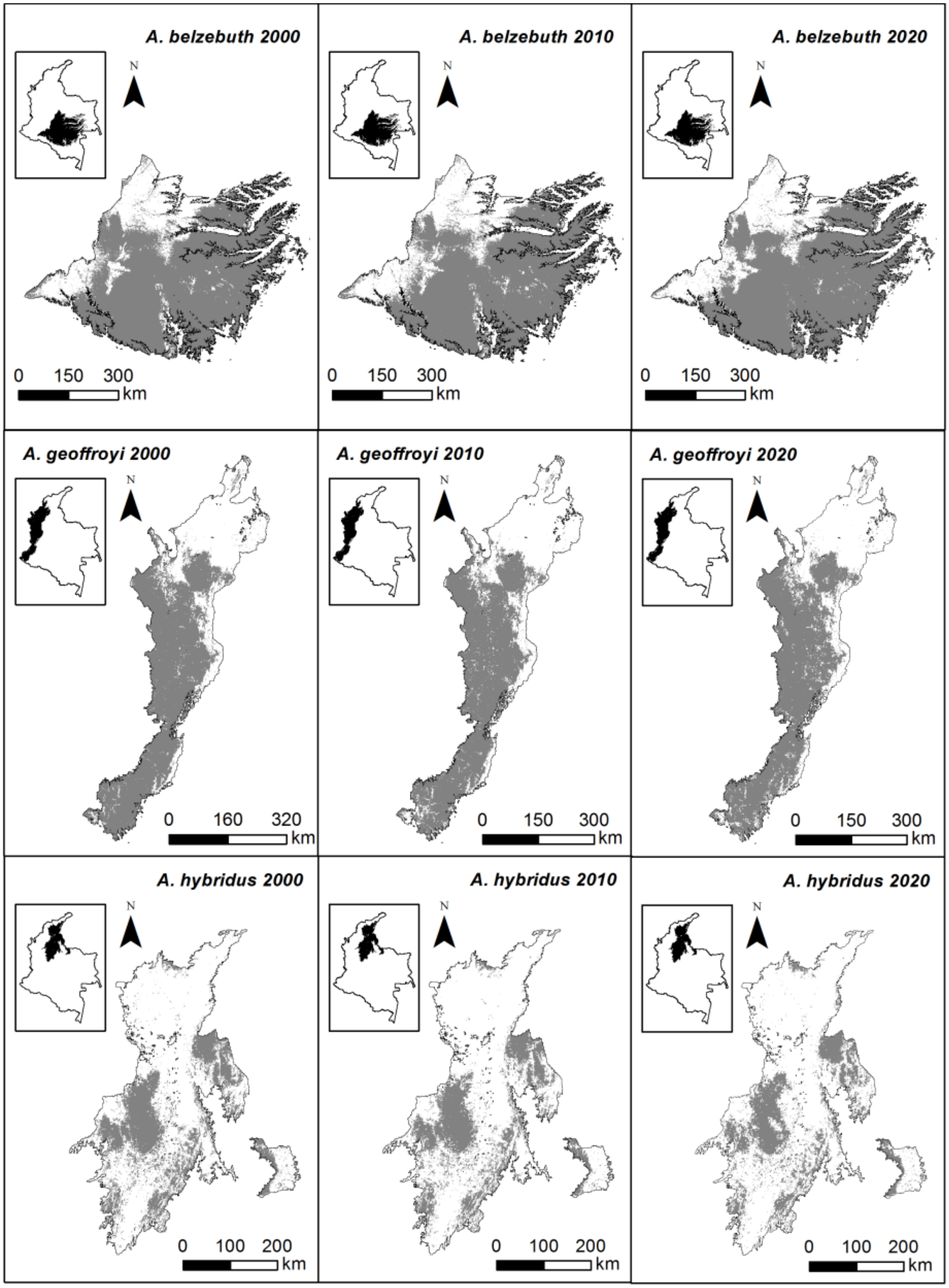


Figure 25. Remaining habitat for *Ateles spp*. in the period 2000-2020.

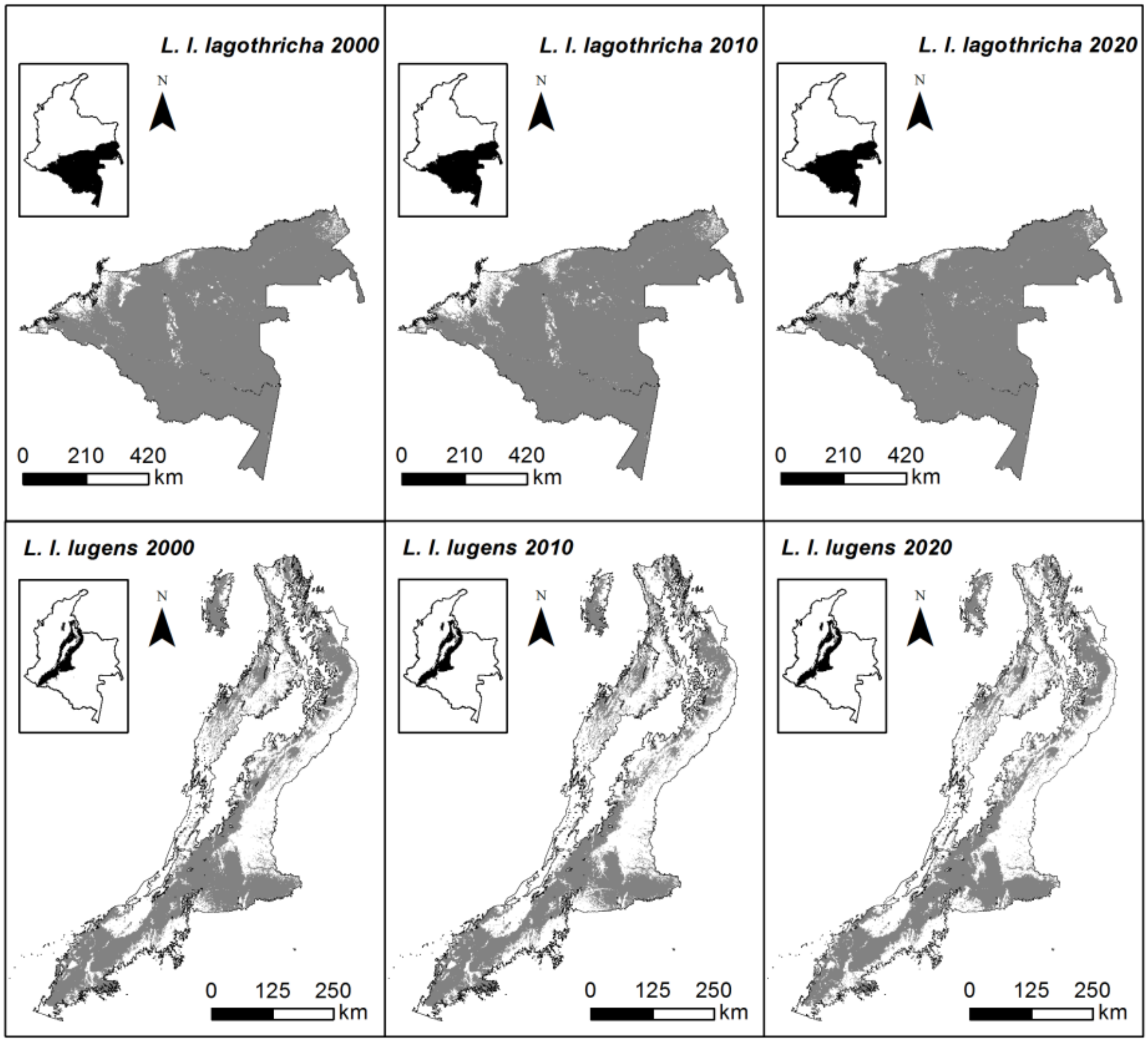


Figure 26. Remaining habitat for *Lagothrix lagothricha* in the period 2000-2020.

For *L. l. lagothricha*, suitability is defined by humid and warm zones, similar to *A. belzebuth*. Several differences do exist between current and future projections, however most climatic favorable scenario (B2) projects a more suitable area near the current scenario. It is strange for this species that in the foothills of the Cordillera Oriental where is supposed to begins the distribution of *L. l. lugens*, the climatic habitat suitability is the lowest. For the latter, average precipitation values and warm lowland zones are more suitable. Like *A. hybridus*, future projections of *L. l. lugens* show an improvement of climatic habitat suitability in the Serranía de San Lucas, however in higher altitudes migration would not be probable (Figure 28).

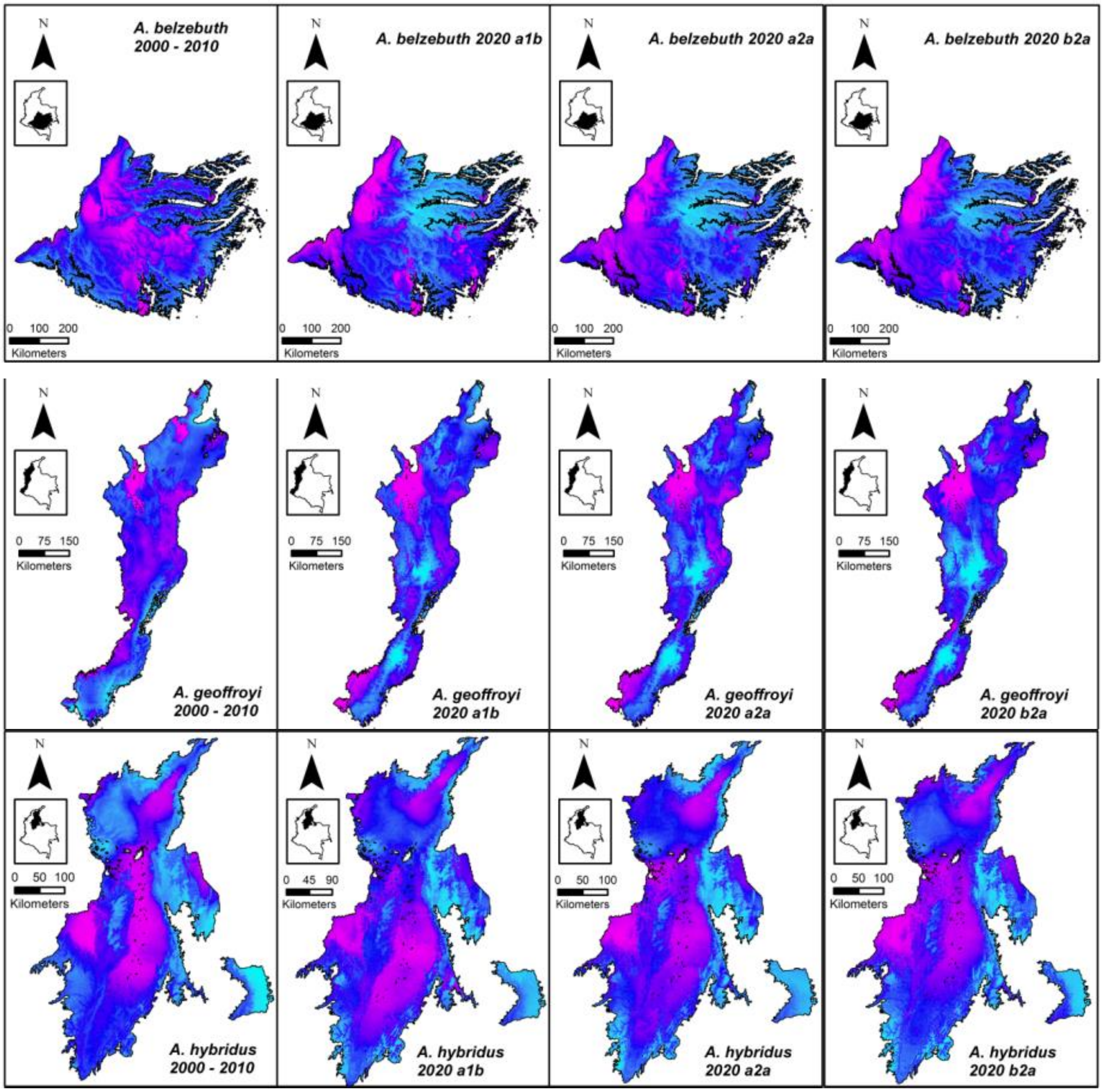


Figure 27. Climatic habitat suitability for *Ateles spp.* in the period 2000-2020. Magenta, blue and cyan colors indicate high, medium and low climatic habitat suitability respectively.

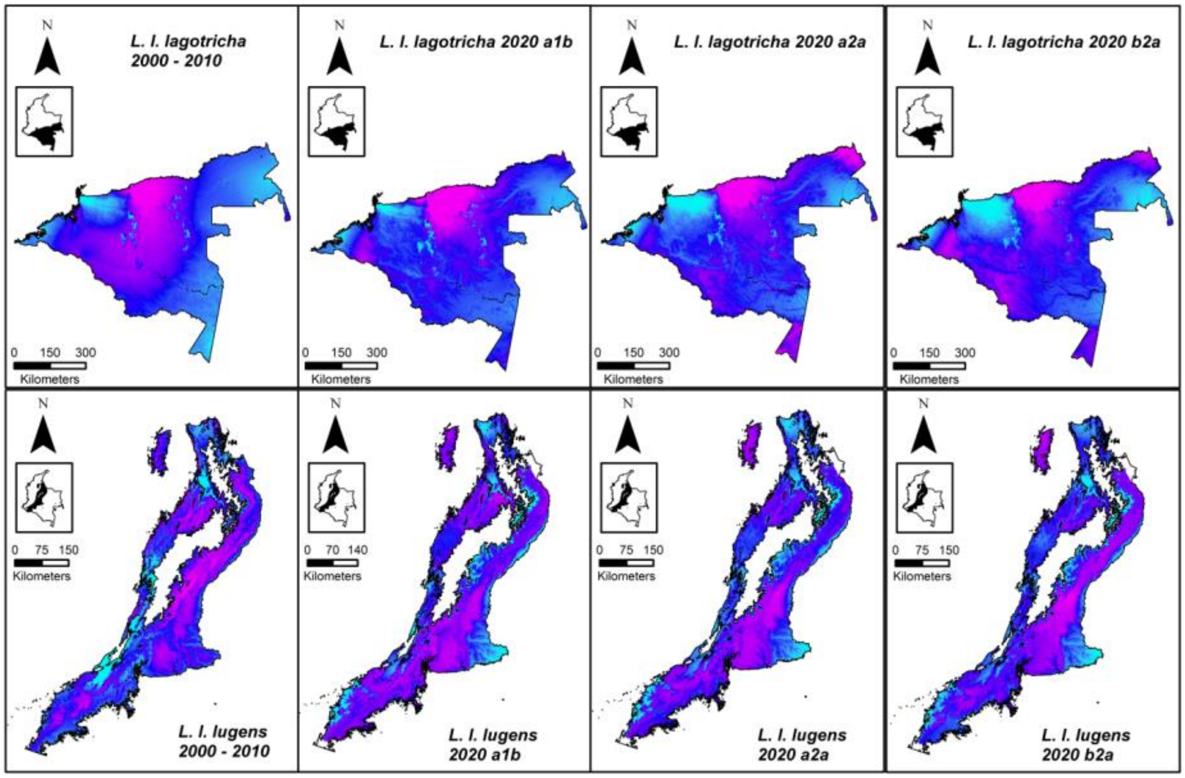


Figure 28. Climatic habitat suitability for *Lagothrix lagothricha* in the period 2000-2020. Magenta, blue and cyan colors indicate high, medium and low climatic suitability respectively.

3.3 Habitat Quality and Cost Flow

High values of habitat quality for all species correspond to regions where forest exists (Figure 25, Figure 26, Figure 29 and Figure 30), which also are related to low human population density and high NPP zones (Figure 14 and Figure 15). Climatic habitat suitability is not clearly related to the same pattern (Figure 27 and Figure 28); however, some climatically suitable regions are in correspondence to high quality values, therefore cost flow for the movement of species over these areas could be low.

In the Amazon region almost all areas have high quality habitat values for *A. belzebuth* and *L. l. lagothricha*, corresponding to the desirable values of the variables included in the calculations. Low quality habitats for this area correspond to the eastern foothills of the Cordillera Oriental y departments of Putumayo and Caquetá (for both species), and the southern areas in the department of Meta (for *A. belzebuth*). Both are essentially related to the absence of forest cover, although average and high values of population density are also found (Figure 14, Figure 25 and Figure 26). A very slight decline in habitat quality is reflected in projected scenarios affecting both species in the central area of the Amazon, due to values in NPP and climatic suitability decreases (Figure 15, Figure 27, Figure 28, Figure 29 and Figure 30). For both species it is expected that movement has a low cost flow, promoting species dispersal according to scenarios used across space and time.

For *A. geoffroyi*, the habitat quality is high in almost all the core distribution of species in the Pacific region (Figure 29), varying in some areas due to fluctuations presented by the NPP and climatic suitability (Figure 15 and Figure 27). Nevertheless, in the Caribbean portion of the species' distribution the absence of forest results in a high cost flow for the species' movement (Figure 25). It is important to notice that in future projections the western slopes of the Cordillera Occidental decline habitat quality for the species because of predicted habitat fragmentation; however, in this area, climatic suitability for the species improves according to the scenarios used (Figure 27).

For *A. hybridus* high quality zones are (Figure 29) i) Catatumbo, ii) Seranía de San Lucas, iii) Serranía de los Yariguies, iv) Serranía de las Quinchas, v) Tamá and vi) the east foothills in Cocuy. These areas contain the only remaining forest habitat, high values of NPP and also high climatic suitable areas, although surrounding population density is a limiting factor for habitat quality and a pressure for the species (Figure 14). The right bank of río Magdalena in Department of Magdalena is the area with the least habitat quality, in addition to the southern distribution in Arauca, and western slopes of the Cordillera Oriental in the municipalities of San Gil, Barichara and surroundings. For the first area, all included variables have the worse values for species flow, and for the other areas a combination of low values in NPP and a minimum proportion of forest is the main cause for low habitat quality. Although, in future scenarios the intensity of cost flow values is lower due to climatic suitability, the dispersion of species over these areas are almost improbable since there is no current or projected remaining habitat (Figure 27).

In *L. l lugens'* distribution, the same patterns described before determine the habitat quality for the species (Figure 30), mainly associated with the presence of forest cover (Figure 26), although similarly to *A. hybridus* the high human population levels for the Andean region is a major concern (Figure 14). Principal areas with low cost flow for species movement are the foothills of the eastern slopes of Cordillera Oriental in Orinoquia and the Amazon, the Andean forests over the Cordillera Oriental where the species is potentially found (Chingaza[2], Sumapaz, Pisba, El Cocuy and Tamá), as well as the Serranía de San Lucas and the remaining forest over high elevations in the limits between the departments of Huila, Cauca, Nariño, Putumayo and Caquetá. Low habitat quality areas correspond to low lands in the foothills of the Central and Oriental Cordilleras where high climatic suitability is projected (Figure 28).

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[2] According to Defler (pers. com.), Chingaza has a population of *L. l. lugens* in the western parts.

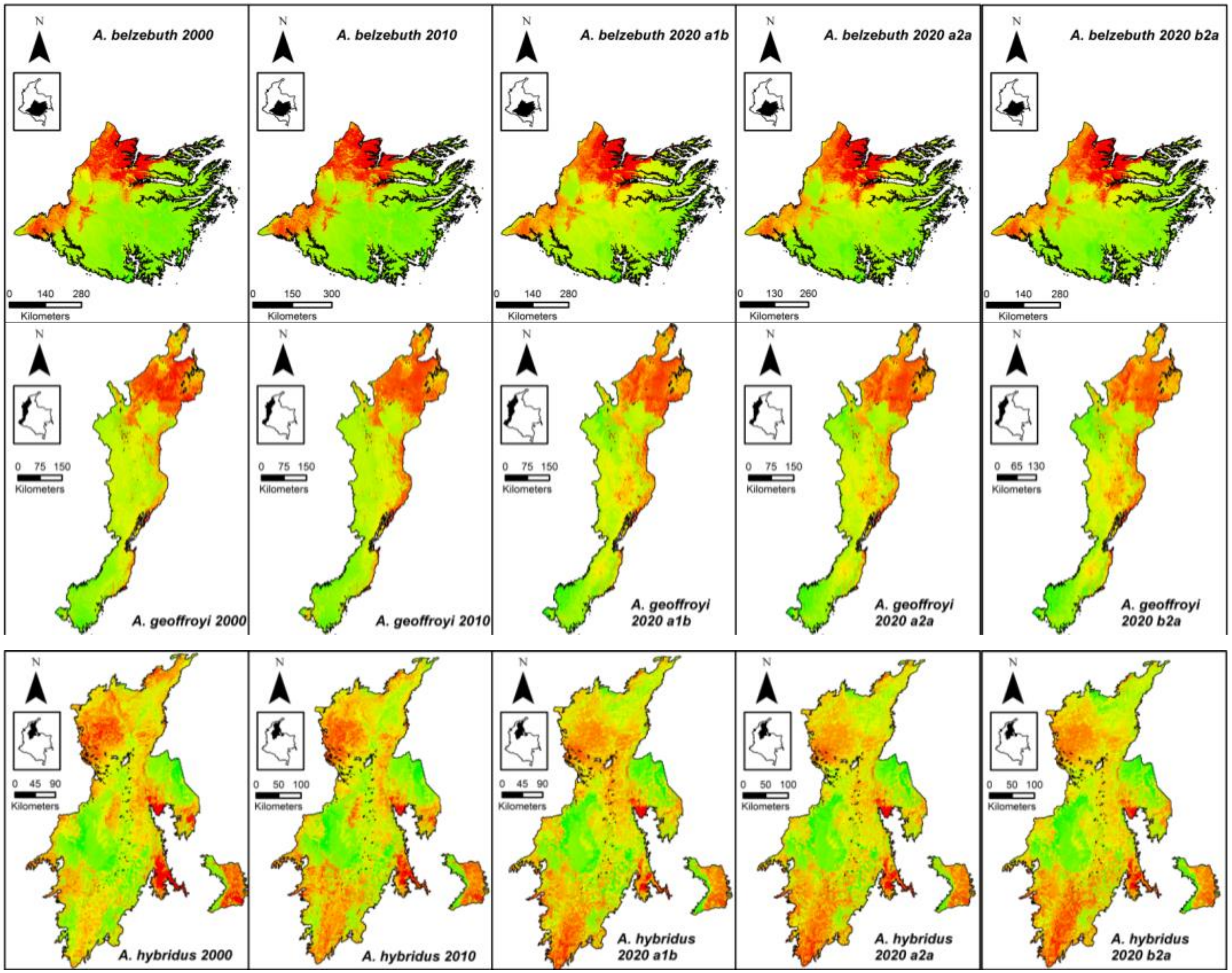

N
A. belzebuth 2000
0 140 280 Kilometers
A. belzebuth 2010
0 150 300 Kilometers
A. belzebuth 2020 a1b
0 140 280 Kilometers
A. belzebuth 2020 a2a
0 130 260 Kilometers
A. belzebuth 2020 b2a
0 140 280 Kilometers
0 75 150 Kilometers
A. geoffroyi 2000
A. geoffroyi 2010
A. geoffroyi 2020 a1b
A. geoffroyi 2020 a2a
0 65 130 Kilometers
A. geoffroyi 2020 b2a
0 45 90 Kilometers
A. hybridus 2000
0 50 100 Kilometers
A. hybridus 2010
A. hybridus 2020 a1b
A. hybridus 2020 a2a
A. hybridus 2020 b2a

Figure 29. Habitat quality in the period 2000-2020 for *Ateles spp*. Green, yellow and red colors indicate high, medium and low habitat quality respectively.

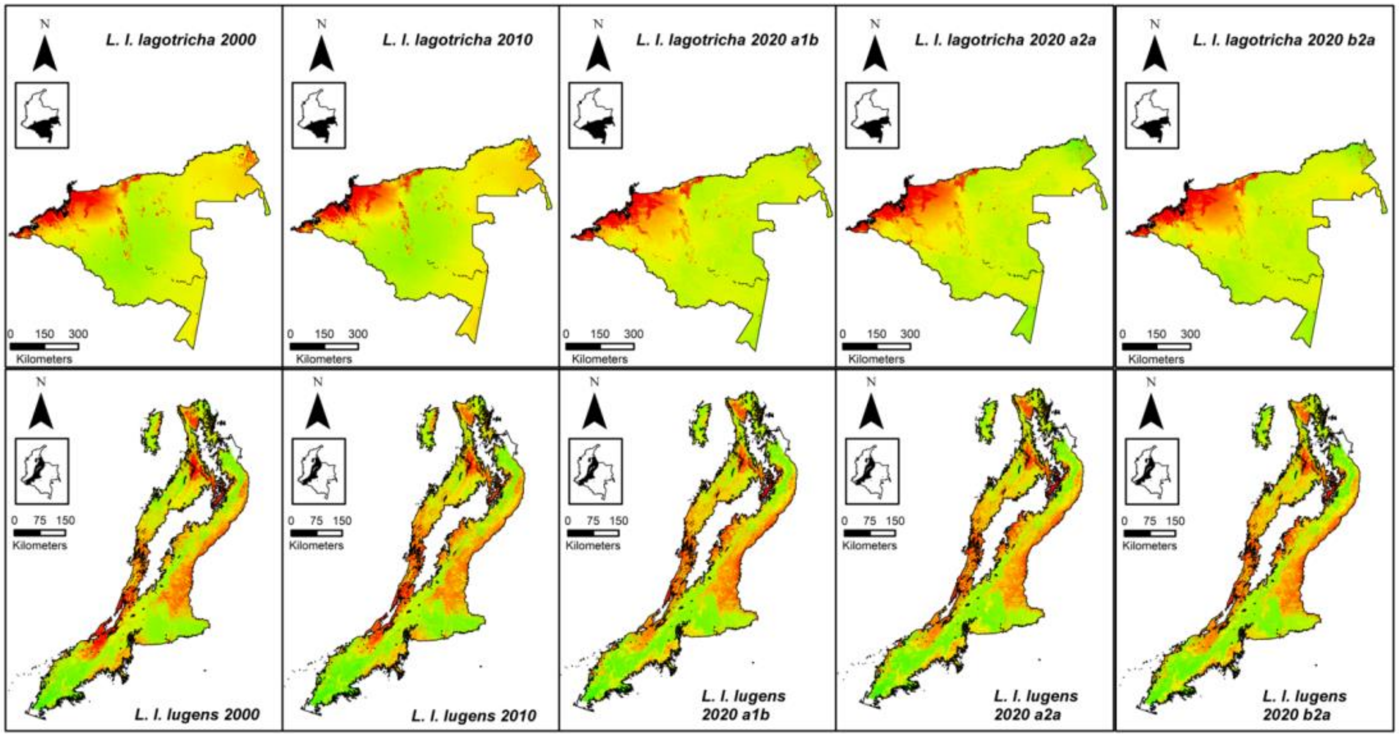


Figure 30. Habitat quality in the period 2000-2020 for *Lagothrix lagothricha*. Green, yellow and red colors indicate high, medium and low habitat quality respectively.

3.4 Connectivity and Dispersal Corridor Analysis

According to values in graph, node and edge metrics, no differences are found between climatic scenarios A1B, A2 and B2 (Table 18 and Figure 31). Metrics taken into account for this analysis correspond to probabilistic metrics, since binary metrics do not incorporate the habitat quality of patches, the probability of dispersal, or the dispersal flux calculations, that are the variables created to measure the effects of climate variability on the species (Table 11). In Table 18 the graph metrics of PC and Diameter show minimal variations for the different scenarios and for each species in concordance with Figure 31, where superposition of points indicates no differences between scenarios using either node metrics or patch metrics. In this order of ideas, we decided to use only the A1B scenario for 2020 representing future projections of climate change and land cover.

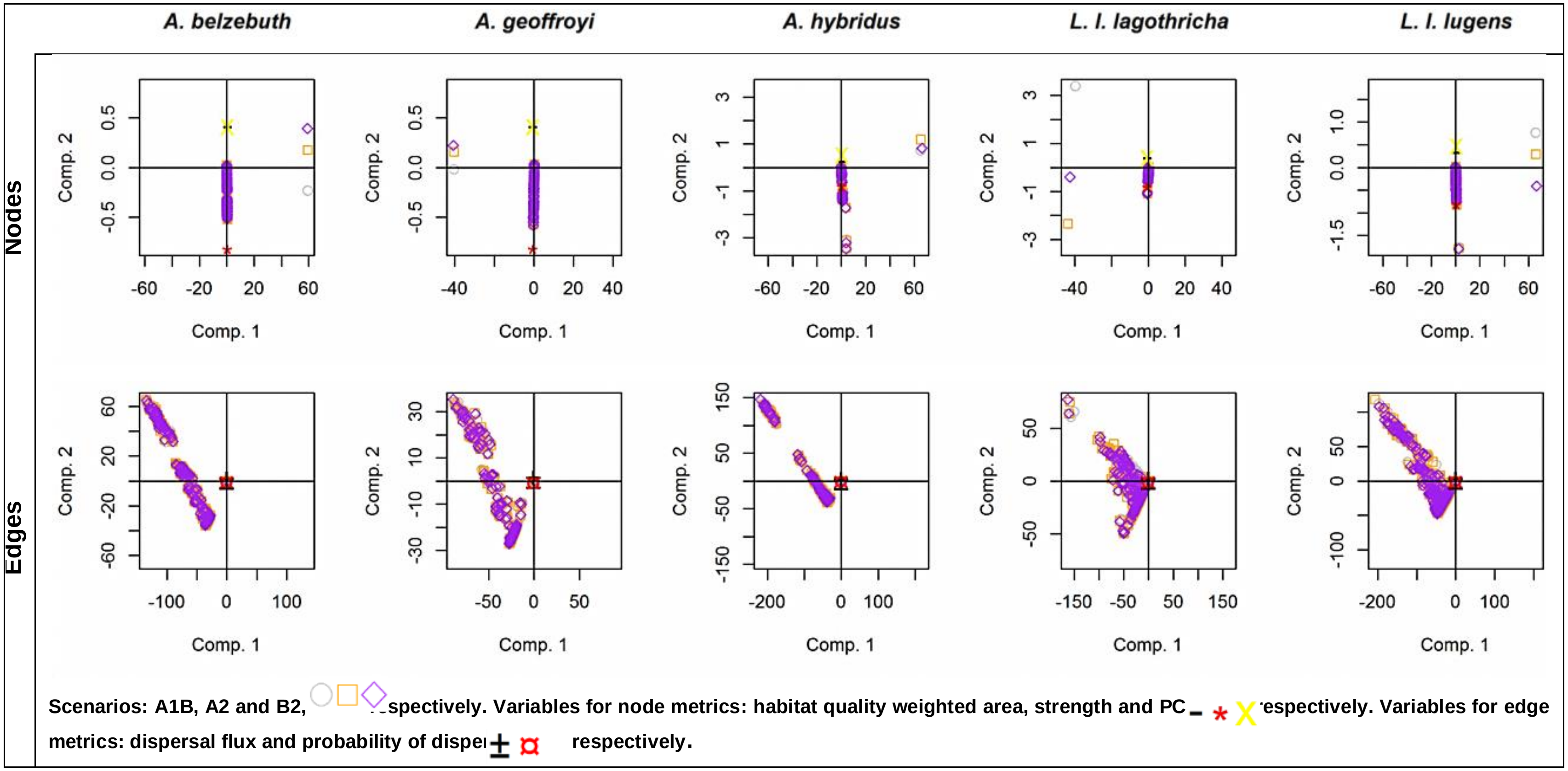
Comparing all graph metrics among the three years, no substantial differences were found for each species, and the same pattern contextualized by deforestation in natural regions was associated with results obtained using the metrics (Table 18). Andean and Caribbean species are similar in metrics values, and Amazonian species do not differ from A. *geoffroyi* due to the large proportions of forest. Transitivity values are higher in *A. hybridus* and *L. l. lugens,* since there are more patches and there is a higher probability of connectivity due to the existence of more neighbors. It is also positively correlated with the number of nodes, edges and the CPL metric (Table 11), since with a greater number of patches and connections the number of groups increases, which is also evident through time with increases or decreases of deforestation and the corresponding increases or decreases in the number of patches and connections (Table 19).

Diameter and connectivity metrics (LCP, IIC and PC) are inversely correlated with the ones described before (Table 19). These measures are based on HQ-WA, dispersal probability and dispersal flux, which are higher in the Amazon, hence explaining higher metric values for *A. belzebuth* and *L. l. lagothricha* due to a more connected and with better habitat quality patches respect to the other regions.

Table 18. Graph metrics of the ateline species for each year and scenario.

Species	Year/Scenario	LCP	IIC	PC	Diameter	CPL	Edges	Nodes	Transitivity
A. belz.	2000	0.3700	0.3700	0.3700	205869.35	2.5555	708	995	0.0035

	2010	0.3720	0.3720	0.3720	197301.29	2.8047	778	1124	0.0049
	2020-A1B	0.3160	0.3160	0.3160	213563.96	2.8262	654	1172	0.0026
	2020-A2	0.3200	0.3200	0.3200	213542.57	2.8262	654	1172	0.0026
	2020-B2	0.3230	0.3230	0.3230	211662.59	2.8262	654	1172	0.0026
A. geo.	2000	0.2280	0.2280	0.2280	91262.57	2.4160	292	532	0.0056
	2010	0.2450	0.2450	0.2450	90276.33	2.2967	272	452	0.0046
	2020-A1B	0.2270	0.2270	0.2270	87713.22	2.2973	284	556	0.0044
	2020-A2	0.2330	0.2330	0.2330	88391.70	2.2973	284	556	0.0044
	2020-B2	0.2390	0.2390	0.2390	90146.28	2.2973	284	556	0.0044
A. hyb.	2000	0.0066	0.0066	0.0066	12911.09	2.7367	930	1405	0.0156
	2010	0.0058	0.0058	0.0058	12309.63	2.8727	916	1303	0.0312
	2020-A1B	0.0056	0.0056	0.0056	11768.55	3.1576	852	1478	0.0164
	2020-A2	0.0057	0.0057	0.0057	11410.03	3.1576	852	1478	0.0164
	2020-B2	0.0061	0.0061	0.0061	12032.75	3.1576	852	1478	0.0164
L. l. lag.	2000	0.4320	0.4320	0.4320	284230.27	2.2956	398	448	0.0037
	2010	0.4350	0.4350	0.4090	300176.28	2.5804	410	532	0.0034
	2020-A1B	0.4090	0.4090	0.4090	402423.98	2.7850	392	602	0.0024
	2020-A2	0.4090	0.4090	0.4090	433238.25	2.7850	392	602	0.0024
	2020-B2	0.4150	0.4150	0.4150	444487.95	2.7850	392	602	0.0024
L. l. lug.	2000	0.0471	0.0471	0.0471	49877.34	3.1442	914	1268	0.0109
	2010	0.0494	0.0494	0.0494	38424.11	3.5520	924	1305	0.0103
	2020-A1B	0.0528	0.0527	0.0527	43565.24	2.8303	922	1472	0.0062
	2020-A2	0.0525	0.0525	0.0525	45846.96	2.8303	922	1472	0.0062
	2020-B2	0.0531	0.0531	0.0531	42835.37	2.8303	922	1472	0.0062



Scenarios: A1B, A2 and B2, ○□◇ spectively. Variables for node metrics: habitat quality weighted area, strength and PC – * X espectively. Variables for edge metrics: dispersal flux and probability of dispe ± ¤ respectively.

Figure 31. Biplots for each species, comparing climatic scenarios for 2020: A1B, A2 and B2.

Table 19. Correlation between all graph metrics. Observations included in the correlation analysis correspond to all species in all years (Table 18).

	LCP	IIC	PC	Diameter	CPL	Edges	Nodes	Transitivity
LCP	-	1.000	1.000	0.892	-0.522	-0.707	-0.749	-0.746
IIC		-	1.000	0.892	-0.522	-0.707	-0.749	-0.746
PC			-	0.893	-0.523	-0.707	-0.748	-0.748
Diameter				-	-0.240	-0.538	-0.593	-0.618
CPL					-	0.770	0.758	0.455
Edges						-	0.963	0.580
Nodes							-	0.550
Transitivity								-

For node and edge metrics the first, and first and second components product of the PCA respectively summarize almost all the variability found in patches and connections (Table 20). Less explained variation is presented for *A. hybridus* and *L. l. lugens*, since in Andean and Caribbean regions the dynamics of habitat fragmentation are more complex than in other regions, and is also expressed in the network constructed for the species' distributions.

Table 20. Variance explained for node and edge metrics as products of PCA. Node values correspond to the variance explained by the first component, while edge values correspond to the variance explained by two first components.

	Nodes			Edges		
	2000	**2010**	**2020**	**2000**	**2010**	**2020**
A. belzebuth	99.400	98.775	98.406	89.222	62.624	76.594
A. geoffroyi	98.513	98.796	99.081	88.931	90.339	89.597
A. hybridus	86.377	93.965	91.393	85.256	83.786	83.886
L. l. lagothricha	99.658	99.146	98.546	90.767	68.968	84.870
L. l. lugens	93.829	95.278	96.365	86.246	65.117	83.761

In Figure 32 and Figure 33 the biplots for node and edge metrics are shown respectively. Relationships between the variables are not clear due to scale problems in plotting that respond to extreme values in the generated components. For this reason at least two groups of nodes and edges are characteristic in all species across years.

The first group is characterized by the patches with the highest values in all metrics, proportionally very far from the others. Almost all edges associated to these nodes have the highest values in the corresponding metrics; however, this relationship also depends on the surrounding matrix of patches measured in the dispersal probability, a reason why more than one edge has closer values to the highest. These nodes and edges can be characterized as source patches and connections (HQ_WA, strength, degree, dispersal flux, and probability of dispersal) with the highest degree of connectivity (LCP, IIC, PC), and a large amount of movement of species across them (betweenness). The second group is composed of the remaining nodes and edges that can be assumed as being not significant in a landscape for species dispersal.

Node metrics for all species are represented in Figure 34 and Figure 35 by the first component of PCA analysis, which explains almost all their variability (Table 20), and is also highly correlated with them (Table 21). For edges metrics, connectivity (IIC and LPC) of species is represented in the first component of the PCA, while the possibility of dispersion (dispersal probability and dispersal flux) is expressed by the second component, responding to correlation between the first and second components of the PCA and the metrics (Table 22). Nevertheless, the concordance in the space of the two groups of edge metrics (Figure 33), shows that although these are better represented in each one of the two components, the edges characterized by these metrics take a proportional value for the respective component, i.e., an edge characterized by high connectivity is also an edge with high possibility for dispersal; hence, only the first component summarizing edge metrics is presented, assuming that characterization of the second component is also spatially depicted in the first one (Figure 36 and Figure 37).

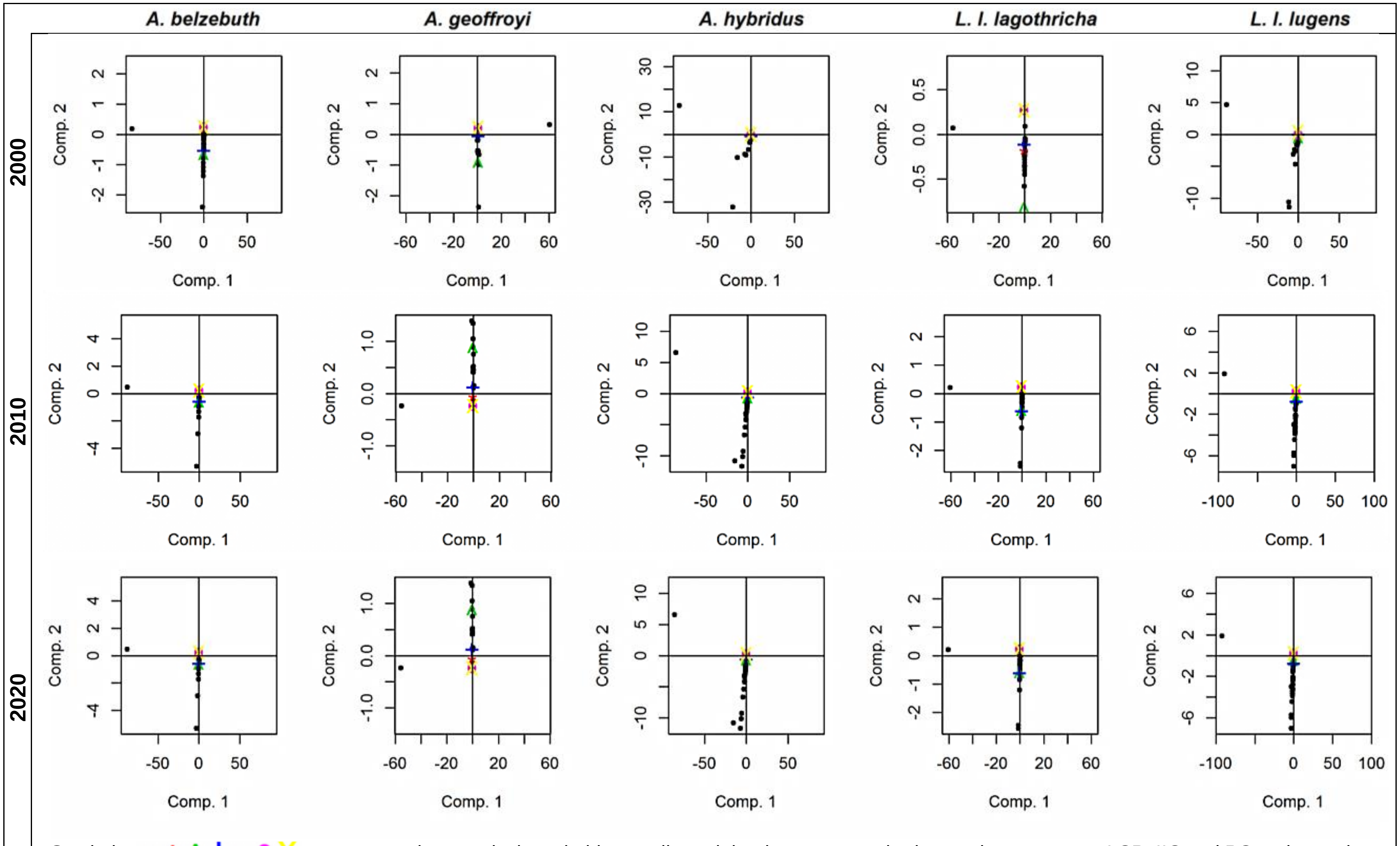
Table 21. Correlation between node metrics and components 1 and 2 of PCA.

Species	Year	Component	HQ_WA	Strength	Degree	Betweenness	LCP	IIC	PC
A. belzebuth	**2000**	**1**	**0.999**	**0.996**	**0.993**	**0.994**	**0.999**	**0.999**	**0.999**
		2	0.037	0.031	0.102	0.080	0.037	0.037	0.037
	2010	**1**	**0.998**	**0.995**	**0.984**	**0.985**	**0.998**	**0.998**	**0.998**
		2	0.058	0.054	0.151	0.137	0.058	0.058	0.058
	2020	**1**	**0.998**	**0.994**	**0.980**	**0.979**	**0.998**	**0.998**	**0.998**
		2	0.066	0.058	0.163	0.166	0.066	0.066	0.066
A. geoffroyi	**2000**	**1**	**0.998**	**0.992**	**0.974**	**0.989**	**0.998**	**0.998**	**0.998**
		2	0.054	0.014	0.226	0.011	0.054	0.054	0.054
	2010	**1**	**0.998**	**0.992**	**0.981**	**0.991**	**0.998**	**0.998**	**0.998**
		2	0.050	0.014	0.191	0.028	0.050	0.050	0.050
	2020	**1**	**0.999**	**0.994**	**0.983**	**0.996**	**0.999**	**0.999**	**0.999**
		2	0.046	0.010	0.183	0.006	0.046	0.046	0.046
A. hybridus	**2000**	**1**	**0.982**	**0.957**	**0.758**	**0.620**	**0.952**	**0.951**	**0.952**
		2	0.178	0.132	0.589	0.730	0.298	0.298	0.298
	2010	**1**	**0.988**	**0.969**	**0.795**	**0.832**	**0.974**	**0.974**	**0.974**
		2	0.131	0.027	0.539	0.427	0.215	0.215	0.215
	2020	**1**	**0.985**	**0.979**	**0.787**	**0.713**	**0.975**	**0.974**	**0.975**
		2	0.167	0.083	0.532	0.640	0.214	0.216	0.215
L. l. lagothricha	**2000**	**1**	**0.999**	**0.997**	**0.995**	**0.998**	**0.999**	**0.999**	**0.999**
		2	0.031	0.020	0.091	0.012	0.031	0.031	0.031
	2010	**1**	**0.999**	**0.995**	**0.991**	**0.990**	**0.999**	**0.999**	**0.999**
		2	0.048	0.046	0.118	0.120	0.048	0.048	0.048
	2020	**1**	**0.998**	**0.992**	**0.986**	**0.980**	**0.998**	**0.998**	**0.998**
		2	0.060	0.061	0.124	0.179	0.060	0.060	0.060
L. l. lugens	**2000**	**1**	**0.974**	**0.979**	**0.946**	**0.975**	**0.949**	**0.987**	**0.969**
		2	0.211	0.166	0.315	0.005	0.305	0.010	0.232
	2010	**1**	**0.994**	**0.990**	**0.947**	**0.919**	**0.993**	**0.993**	**0.993**
		2	0.105	0.101	0.213	0.359	0.110	0.110	0.110
	2020	**1**	**0.996**	**0.992**	**0.932**	**0.968**	**0.994**	**0.994**	**0.994**
		2	0.088	0.055	0.347	0.141	0.107	0.107	0.107

Table 22. Correlation between edge metrics and components 1 and 2 of PCA.

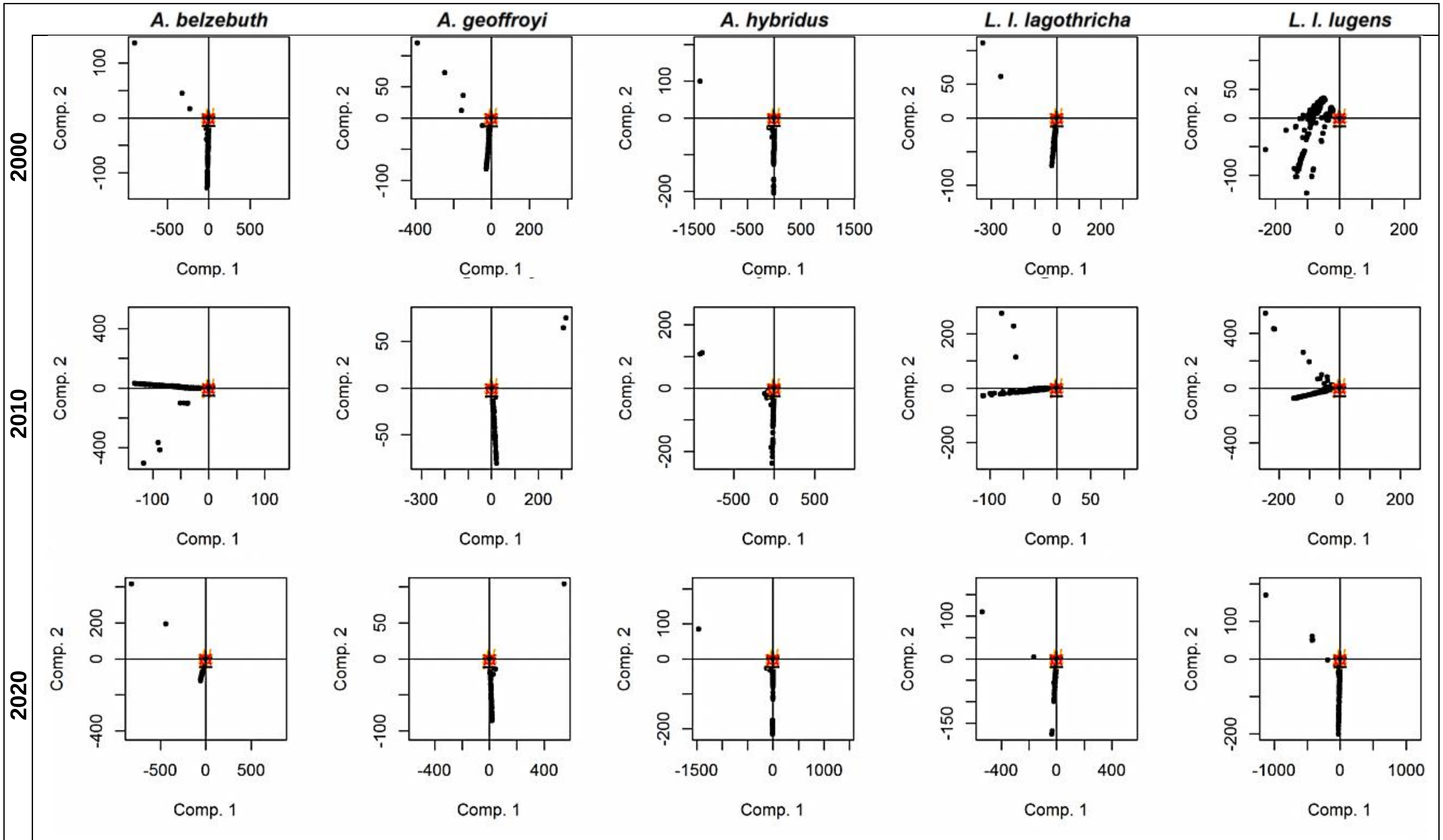
Species	Year	Component	LCP	IIC	Dispersal Flux	Probability of Dispersal
A. belzebuth	2000	1	**0.983**	**0.985**	0.134	0.226
		2	0.163	0.154	**0.880**	**0.859**
	2010	1	0.150	0.134	**0.840**	**0.862**
		2	**0.689**	**0.702**	0.223	0.012
	2020	1	**0.781**	**0.792**	0.383	0.480
		2	0.417	0.399	**0.776**	**0.717**
A. geoffroyi	2000	1	**0.948**	**0.948**	0.278	0.451
		2	0.304	0.306	**0.847**	**0.759**
	2010	1	**0.968**	**0.969**	0.210	0.358
		2	0.247	0.247	**0.876**	**0.822**
	2020	1	**0.976**	**0.979**	0.175	0.295
		2	0.210	0.200	**0.875**	**0.840**
A. hybridus	2000	1	**0.997**	**0.997**	0.057	0.133
		2	0.079	0.080	**0.839**	**0.828**
	2010	1	**0.990**	**0.990**	0.092	0.230
		2	0.130	0.129	**0.823**	**0.786**
	2020	1	**0.998**	**0.997**	0.043	0.120
		2	0.066	0.067	**0.824**	**0.814**
L. l. lagothricha	2000	1	**0.940**	**0.938**	0.277	0.403
		2	0.303	0.308	**0.875**	**0.822**
	2010	1	0.169	0.189	**0.886**	**0.917**
		2	**0.709**	**0.707**	0.257	0.028
	2020	1	**0.935**	**0.943**	0.166	0.256
		2	0.208	0.176	**0.867**	**0.844**
L. l. lugens	2000	1	**0.908**	**0.789**	0.651	0.912
		2	0.351	0.199	**0.695**	**0.319**
	2010	1	0.321	0.299	**0.761**	**0.828**
		2	**0.690**	**0.701**	0.393	0.161
	2020	1	**0.966**	**0.965**	0.120	0.236
		2	0.150	0.153	**0.842**	**0.813**

∗ For the species: *A. belzebuth* (2000), *A. geoffroyi* (2010), *L. l. lagothricha* (2010) and *L. l. lugens* (2010), characterization of metrics according to components are inverted, responding to coordinates of eigen vectors in PCA (Figure 33).



Symbols: − * Λ +, · o X correspond respectively to: habitat quality weighted area, strength, degree, betweenness, LCP, IIC and PC node metrics.

Figure 32. Biplots of node metrics for each species and each year.



Symbols:#÷±¤ correspond respectively to: LCP, IIC dispersal flux, and probability of dispersal.

Figure 33. Biplots of edge metrics for each species and each year.

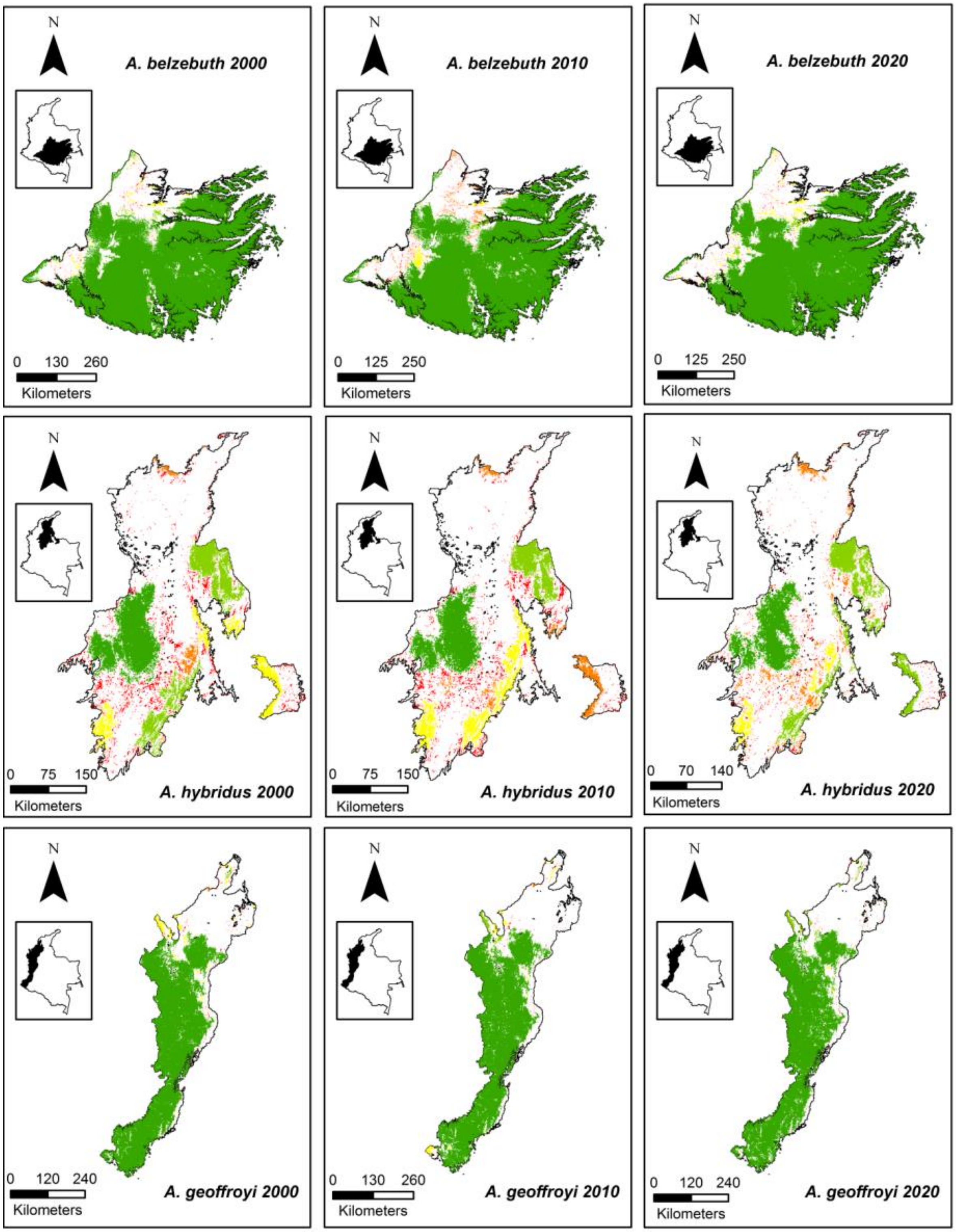

N
A. belzebuth 2000
0 130 260
Kilometers
N
A. belzebuth 2010
0 125 250
Kilometers
N
A. belzebuth 2020
0 125 250
Kilometers
N
0 75 150
Kilometers
A. hybridus 2000
N
0 75 150
Kilometers
A. hybridus 2010
N
0 70 140
Kilometers
A. hybridus 2020
N
0 120 240
Kilometers
A. geoffroyi 2000
N
0 130 260
Kilometers
A. geoffroyi 2010
N
0 120 240
Kilometers
A. geoffroyi 2020

Figure 34. First component from PCA for node metrics of *Ateles spp.* Green to yellow and red colors represents respectively: high, medium and low values of metrics in corresponding patches.

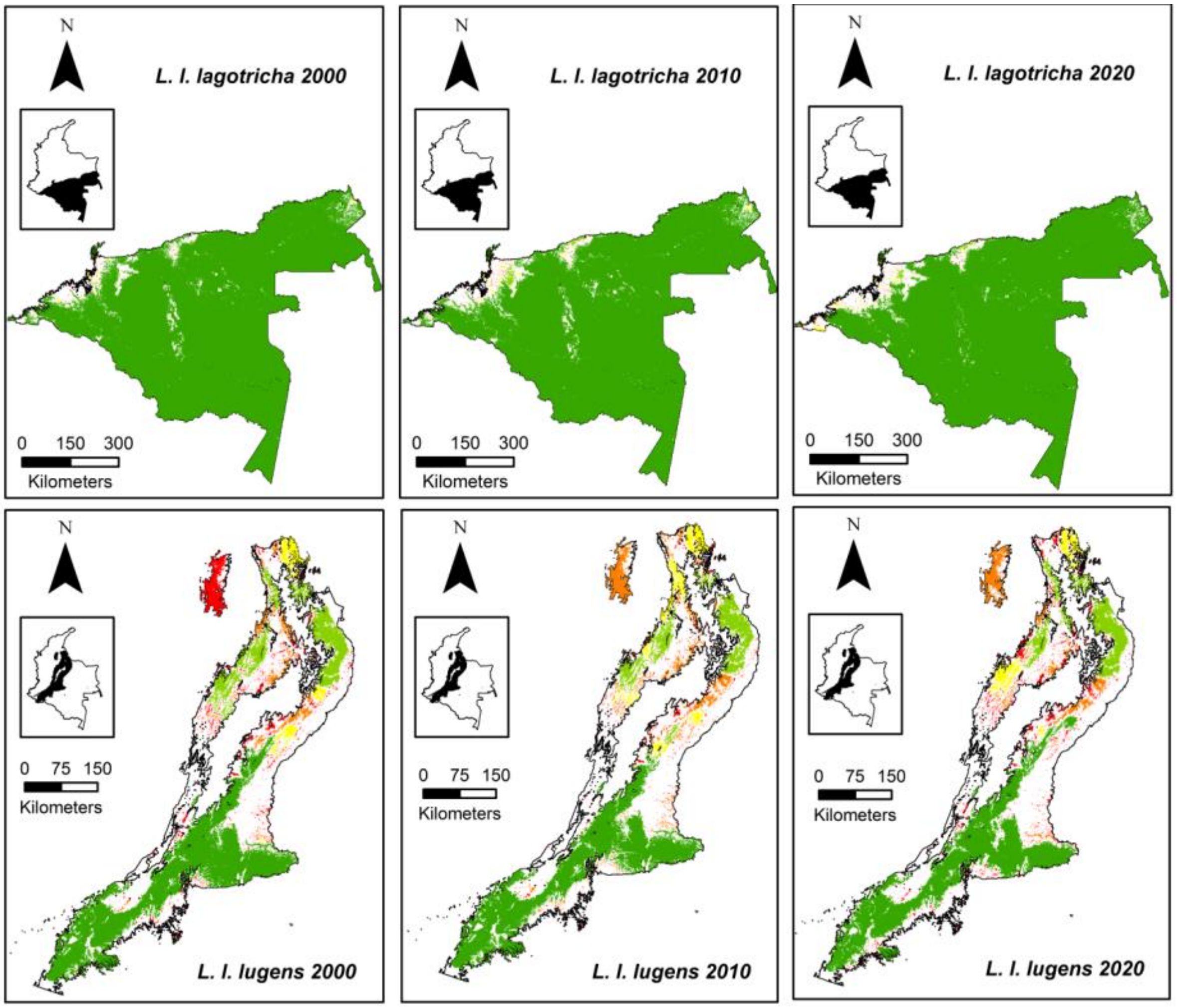


Figure 35. First component from PCA for node metrics of *Lagothrix Lagothricha.* Green to yellow and red colors represents respectively: high, medium and low values of metrics in corresponding patches.

In general, two groups of metrics are identified here: i) a measure of connectivity and dispersal, and ii) a measure of quality and capacity. In concordance, two groups of elements (nodes and edges) are characterized by these metrics: the ones with high extreme positive values, and the ones with medium and low values. From this, we can interpret that patches and connections with high values in metrics, correspond to elements with high connectivity, quality and capacity for species dispersal. These are the source patches for the species.

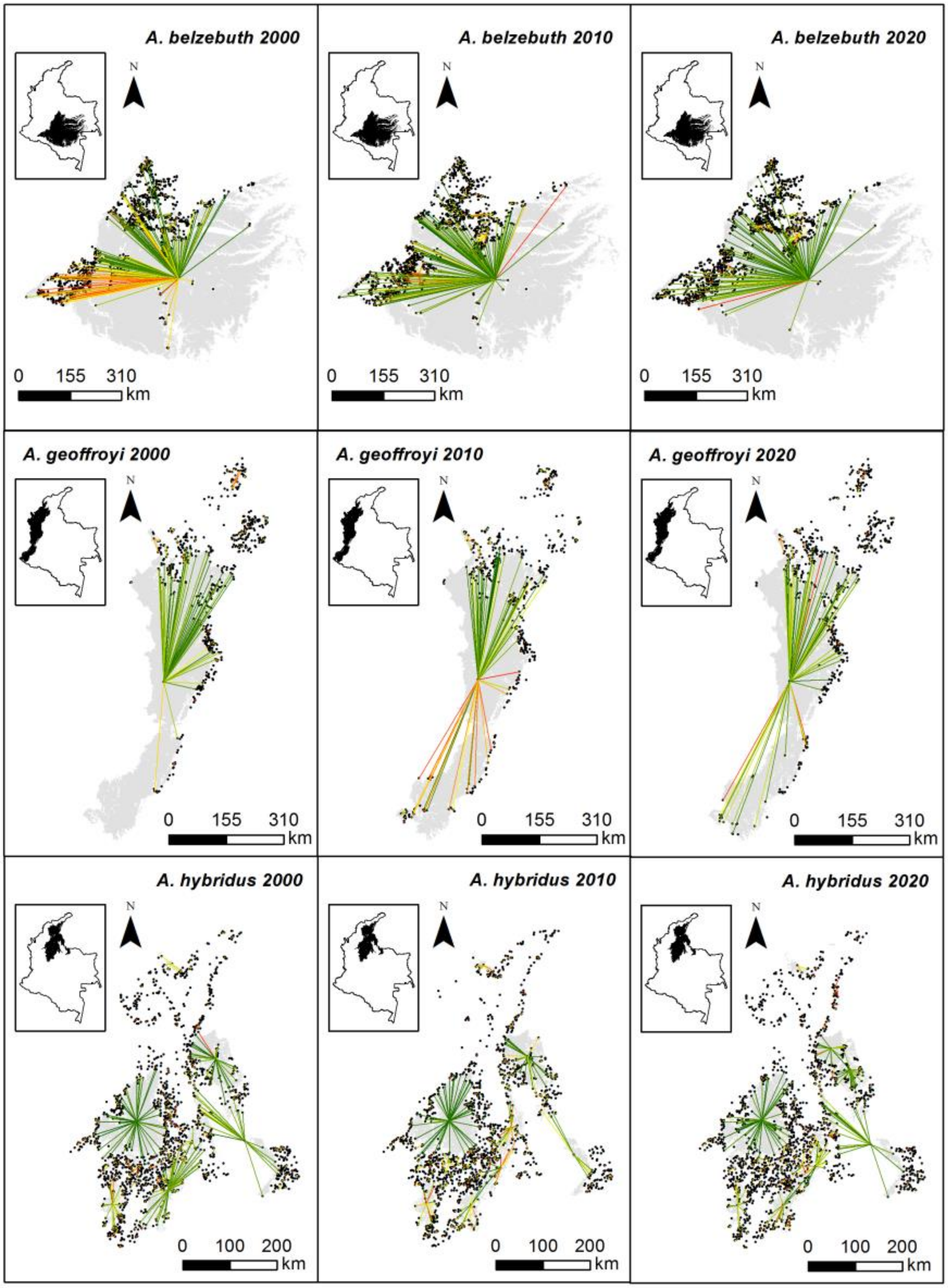


Figure 36. First component from PCA for edge metrics of *Ateles spp*. Green to yellow and red colors represents respectively: high, medium and low values of metrics in corresponding edges.

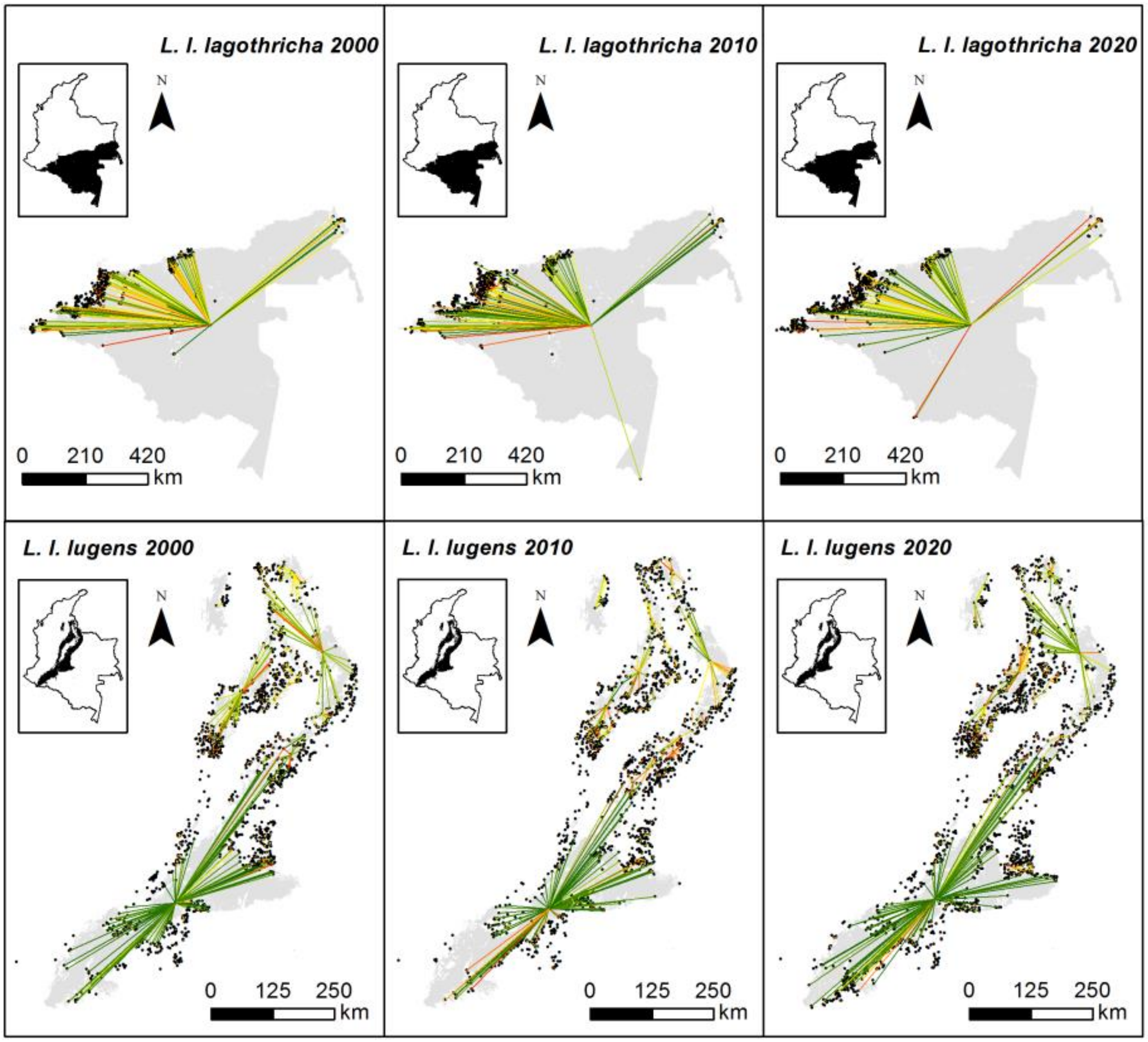


Figure 37. First component from PCA for edge metrics of *Lagothrix Lagothricha*. Green to yellow and red colors represents respectively: high, medium and low values of metrics in corresponding edges.

With respect to changes in nodes and edges through space and time, the same configuration described for graph metrics was found. Places and years where habitat loss occurs (e.g., Andean region over high altitudes in 2010), increment the number of nodes and connections, transforming the landscape connectivity and the capacity of dispersal, as is evident for *A. hybridus* and *L. l. lugens* (Figure 37). In addition the capacity and quality of patches and connections change over space and time. Larger and conserved patches that are highly connected tend to remain through time, while patches and connections in a fragmented landscape tend to disappear. Also this pattern applies to quality and capacity, but these changes are more noticeably over time, being variable in all regions and particularly greater in the Amazon.

3.5 Prioritization of Conservation Areas for Ateline Persistence

Patches with high quality are concordant with high values of HQ (Figure 29 and Figure 30) and node metrics summarized in the PCA (Figure 34 and Figure 35), both described before in previous results. In turn, these patches coincide with large areas and greater connectivity, and can be conceived as source patches for atelines populations (Figure 36 and Figure 37) including all the elements considered in the identification of priority areas: the size, capacity, and connectivity of patches.

Persistence areas in habitat patches during the three years are shown in Figure 38. Persistence is an essential characteristic, since we assume that persistence areas maintain populations through time because they have a tendency of no-change. These, follow the pattern described for habitat loss and the fragmentation process. For Andean species, persistence areas are drastically reduced in comparison to original and remnant areas in every year (Table 17 and Figure 38). In *A. hybridus'* distribution, only 19% of the original area persists over time, while for *L. l. lugens* just 37% persists. This area is concentrated in larger patches, supporting the idea that the spatial autocorrelation of deforestation is very strong and a principal explaining factor for persistence of forests.

The presence of forest due to the autocorrelation process is also evident for the remaining species (*A. belzebuth*, *A. geoffroyi* and *L. l. lagothricha*), for which the persistence area is very close to remnant habitat area in each year. However, in the case of *Ateles spp*. the process of change is much more noticeable, because of the proximity to eastern foothills in Cordillera Oriental in the case of *A. belzebuth*, and the high rates of deforestation in the Caribbean region for the case of *A. geoffroyi* (Table 17 and Figure 38).

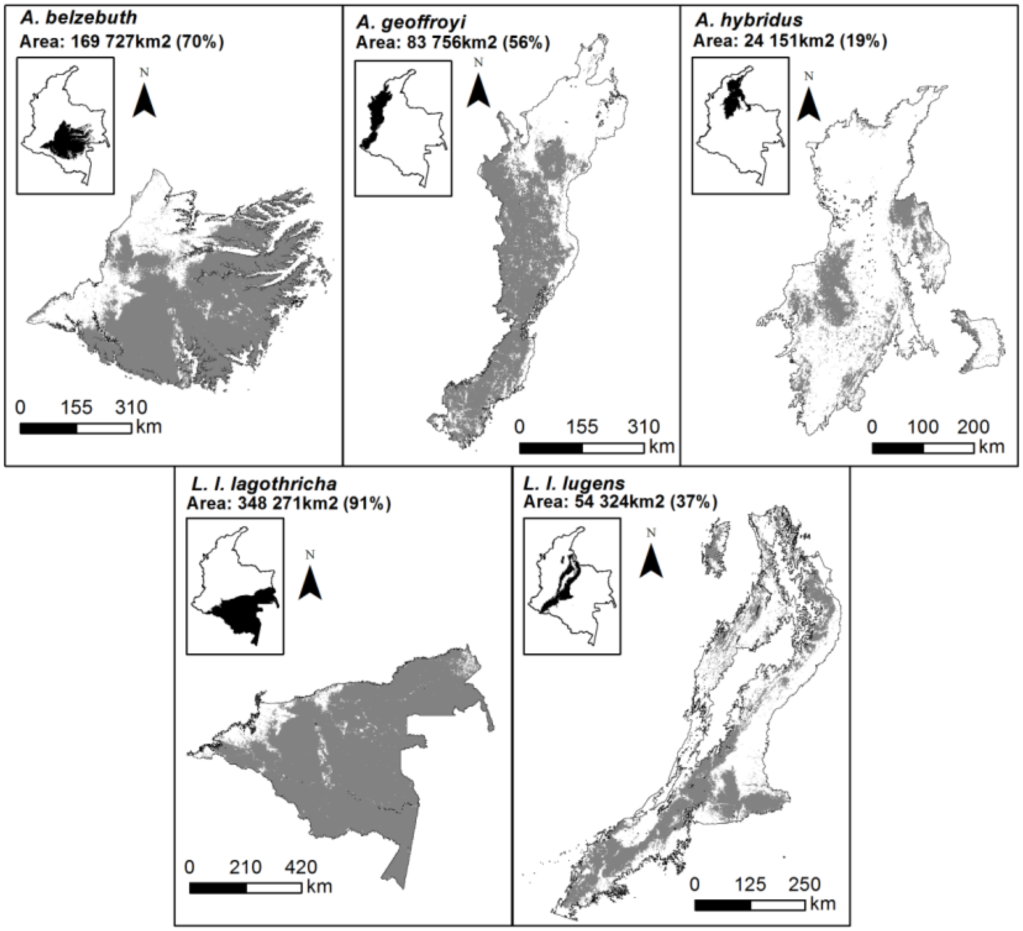


Figure 38. Persistence area for atelines during period 2000-2020. Percentages correspond to the proportion between persistence areas and the entire distributional area for each species.

Areas of habitat loss and regeneration correspond to the ones shown and analyzed before (Figure 21). The highest rates of deforestation are found in the Caribbean and Andean regions, but also in the lowlands near the western foothills of Cordillera Occidental in the Pacific region, and in the eastern foothills of the Cordillera Oriental in Orinoquia and the Amazon regions, with particular attention on the departments of Caquetá and Putumayo, where major deforestation has occurred in past, present and future scenarios. Regeneration processes have effects in the core of Amazon and Pacific regions and in isolated areas of the Andean region, mainly at the northern limit of the Serranía de San Lucas, the region of Catatumbo, and the surrounding area of Sierra Neveda de Santa Marta.

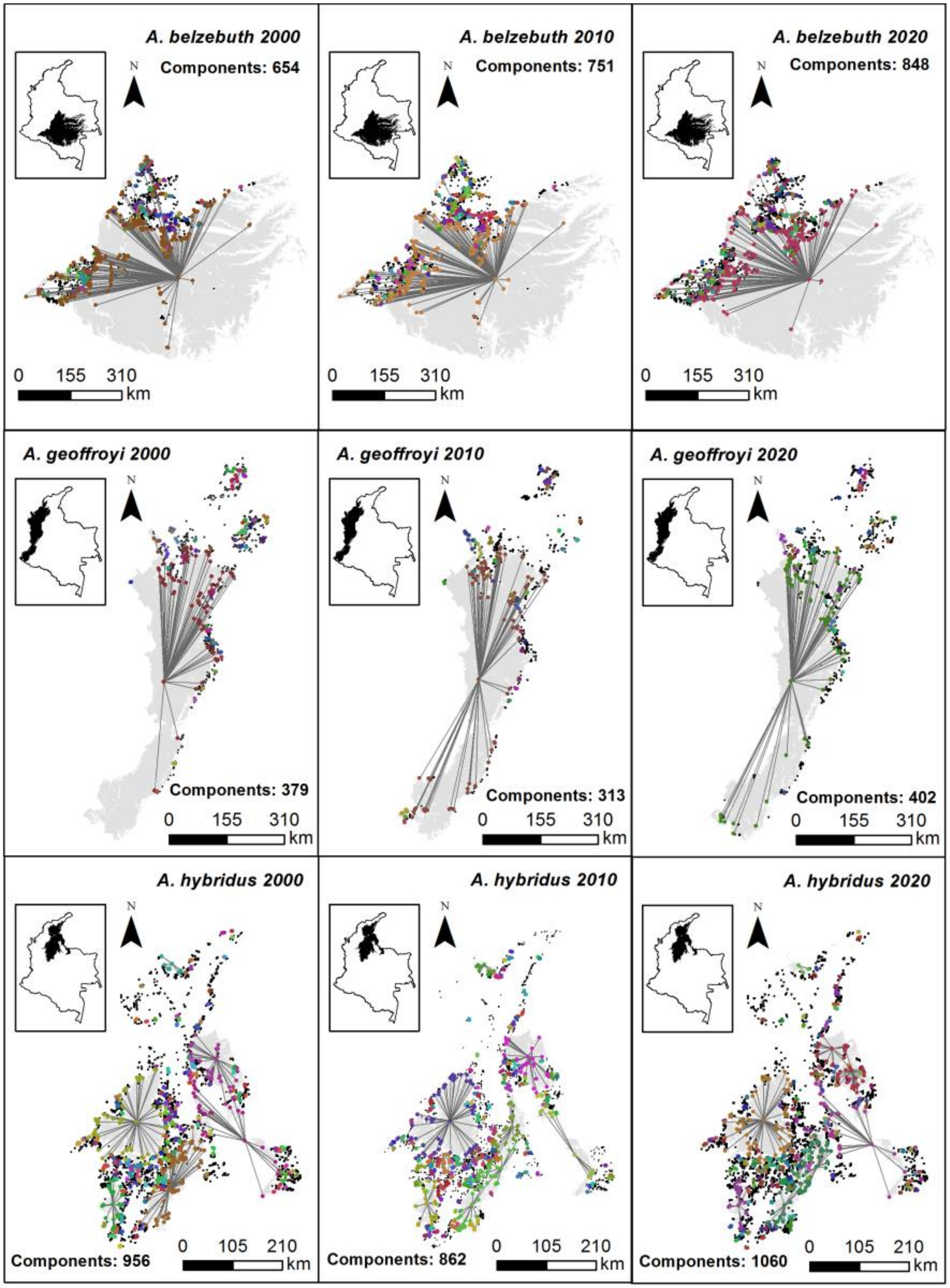


Figure 39. Patches and edges included in the MSTs for *Ateles spp*. Black patches are not part of the MSTs. Each group of circles (component) with the same color (random in each year) corresponds to nodes from different MSTs.

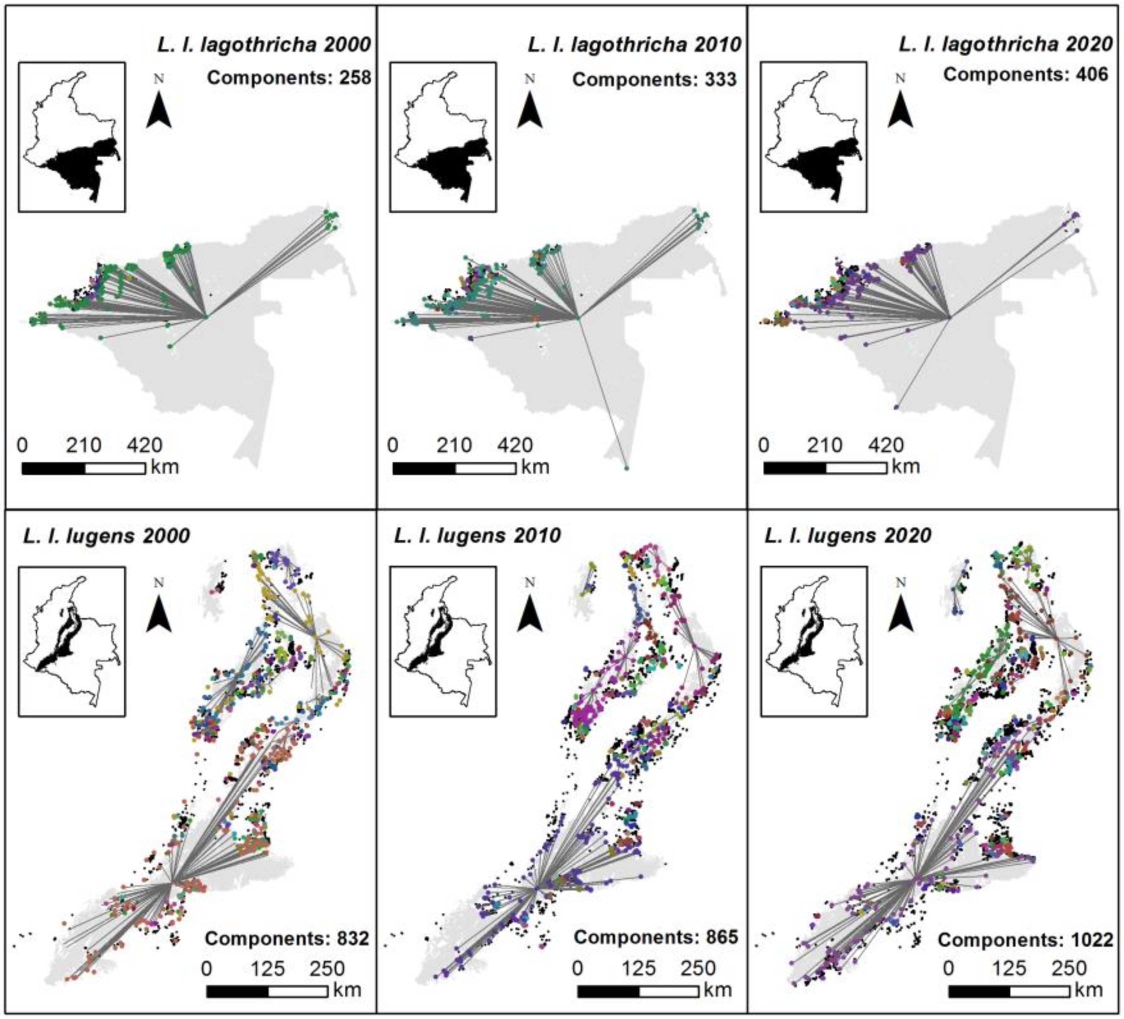


Figure 40. Patches and edges included in the MST for *Lagothrix lagothricha*. Black patches are not part of the MSTs. Each group of circles (component) with the same color (random in each year) corresponds to nodes from different MSTs.

The MST (Figure 39 and Figure 40), represents the connected backbone of each component (sub-graph) in the network (graph), i.e., it is the parsimonious sequence of nodes and edges where species dispersal occurs, hence its importance in terms of conservation. However, because of the number of components it is difficult to identify all the MSTs present in the entire species distribution; two connected nodes can form a single MST, and isolated patches form a single component (black patches in Figure 39 and Figure 40), therefore only visible MSTs are taken into account for the analysis. For species of the Andean and Caribbean regions, 4 or 5 MSTs are clearly recognized through time and have been identified in previous sections, while for the Amazon and Pacific regions species 1 (almost the entire Amazonian region in Colombia) or a maximum 3 MSTs can be assessed.

Cut-nodes or stepping stones are single links connecting the landscape; therefore, their removal would break the network into smaller sections (components) (Figure 41 and Figure 42). In the calculation, their subtraction necessarily has to increase the number of connected components in the graph, hence, a node whose removal does not form new connected sub-graphs is not considered a cut-node, i.e., some patches whose exclusion is evident for breaking the connection of network are not necessarily considered as stepping stones (e.g. source patches), because their removal is not creating new components, since their neighbors are only connected to this patch.

On species' distributions, there is no pattern to identify the occurrence of stepping stones trough time, since cut nodes are not constant from one year to the other for almost all species. It is relevant, that new patches different from the ones with high quality, capacity and connectivity were determined in order to improve the dispersal that specially occurs in isolated patches (Figure 41 and Figure 42).

Areas where dispersal most likely occurs correspond to the region between patches separated by 1 km from border to border with the minimum cost flow for species according to habitat quality (Figure 29 and Figure 30). These areas are shown in Figure 43 and Figure 44. As expected, dispersal occurs from border of source patches to neighbor patches and their flux and the probability of dispersal follow the same pattern of habitat quality layers (Figure 29 and Figure 30). These areas are susceptible to a consideration for restoration or reforestation since is probable that species dispersal can occur on there.

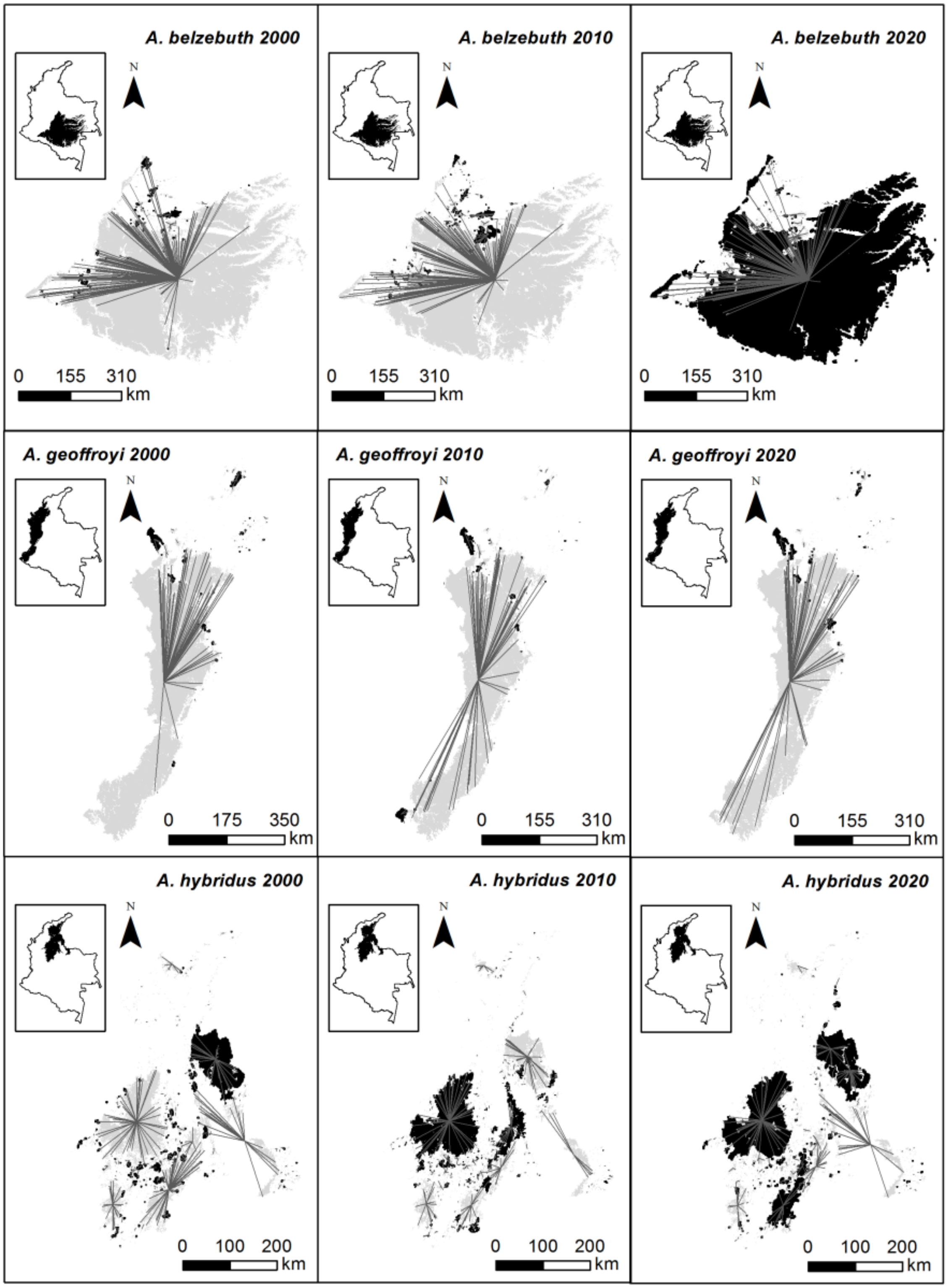


Figure 41. Cut-nodes or stepping stones (in black) for *Ateles spp*.

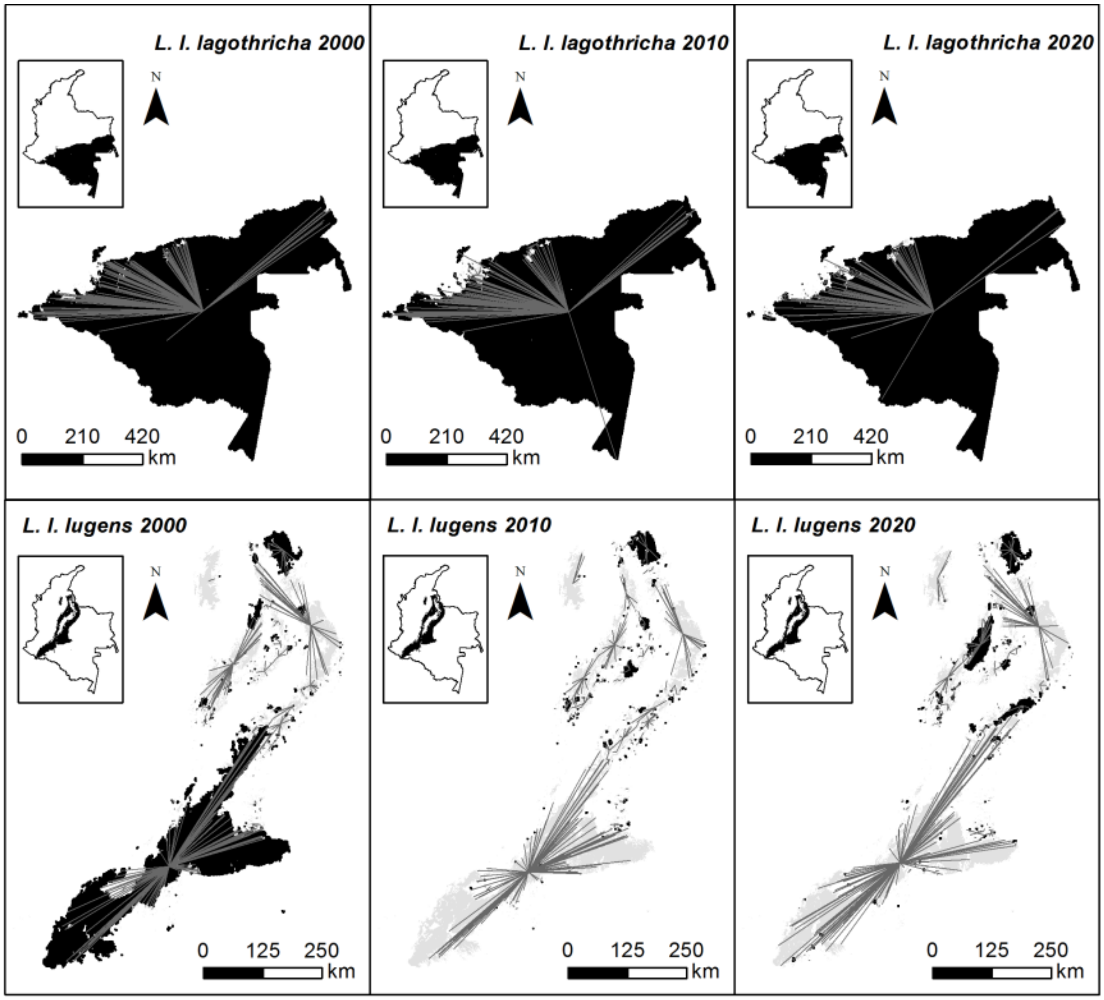


Figure 42. Cut-nodes or stepping stones (in black) for *Lagothrix lagothricha*.

The sum of the above conservation targets (Table 12) conform the priority areas proposed for the conservation of the Atelinae (Figure 45 and Figure 46). Areas with the highest values (red colors) correspond to cells within the largest patches where land change (deforestation or regeneration) is taking place, or physical dispersal of species probably is occurring. These are the highest priority areas, since in them the possibility of species dispersal can be directly affected. The largest source patches are the next priority areas (orange colors), however all source patches (Figure 36 and Figure 37) have to be considered in this group (including green patches) due to their importance in supporting denser populations and their persistence through time (Figure 38). Middle values (yellow colors) correspond to stepping stones and deforestation areas.

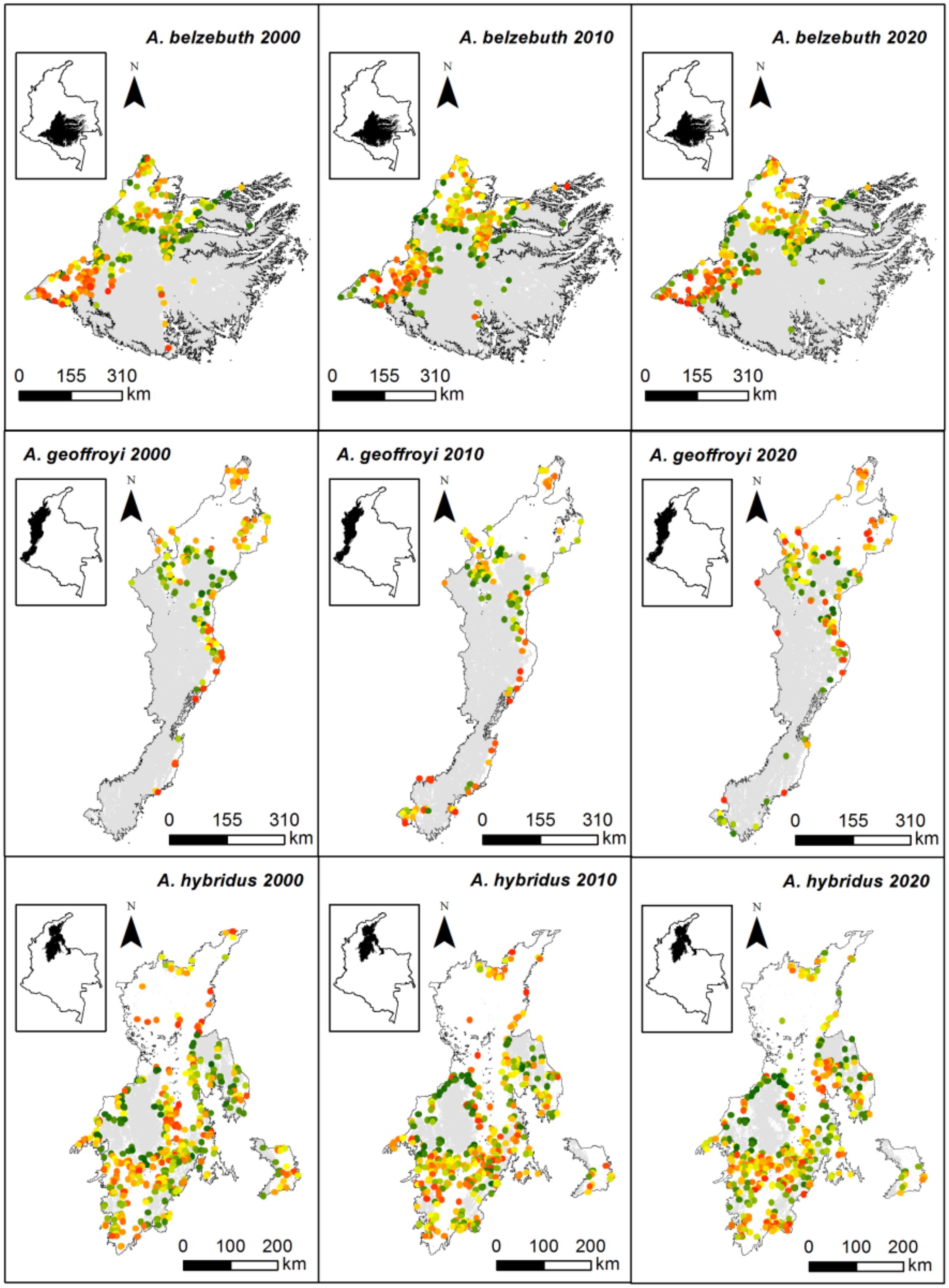


Figure 43. Potential areas for *Ateles spp.* dispersal. Green to yellow and red colors represent respectively: high, medium and low values of edge metrics.

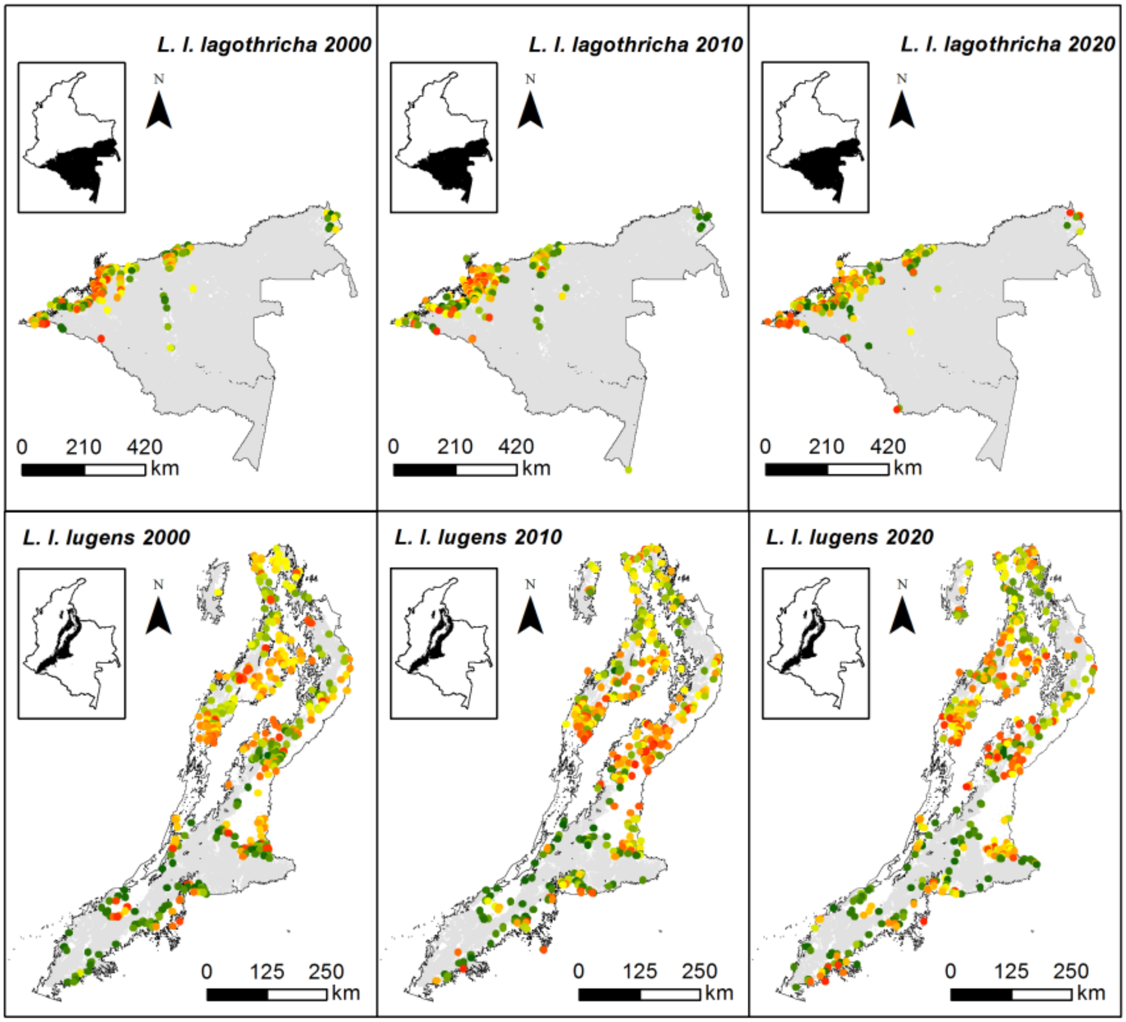


Figure 44. Potential areas for *Lagothrix lagothricha* dispersal. Green to yellow and red colors represent respectively: high, medium and low values of edge metrics.

For *A. hybridus* and *L. l. lugens* the main priority areas are i) the Catatumbo and the foothills in ii) Arauca, iii) Tama, iv) El Cocuy, v) Serranía de San Lucas, vi) Serranía de los Yariguies and vii) Serranía de las Quinchas, in addition to viii) the eastern slopes of the Cordillera Central and ix) Cordillera Oriental in north of the department of Antioquia, and the x) southern and western portions of the Sierra Nevada de Santa Marta for *A. hybridus*; and the xi) foothills of the eastern slopes of Cordillera Oriental in

Orinoquia and Amazon for *L. l. lugens* (Figure 25 and Figure 26). In the above regions connected and persistence source patches exist for both species.

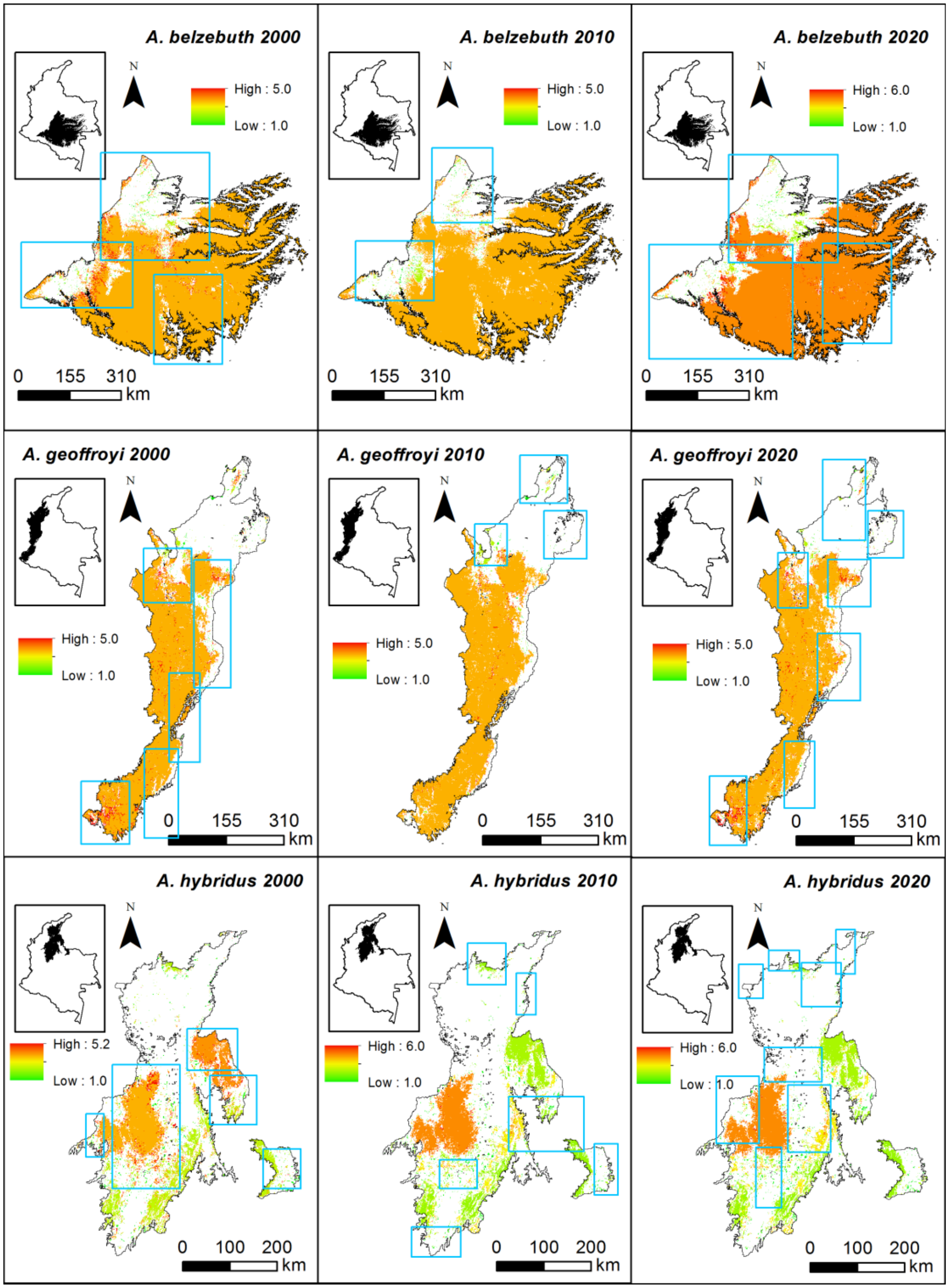


Figure 45. Priority areas for *Ateles spp*. Within the blue box: on the left are areas where processes of land use change have occurred, are occurring, or will occur; in the middle, areas where the presence of the species should be reviewed (in addition

to unknown limits, see also Figure 1); and on the right, areas where climate suitability in future scenarios is the highest (see also Figure 27).

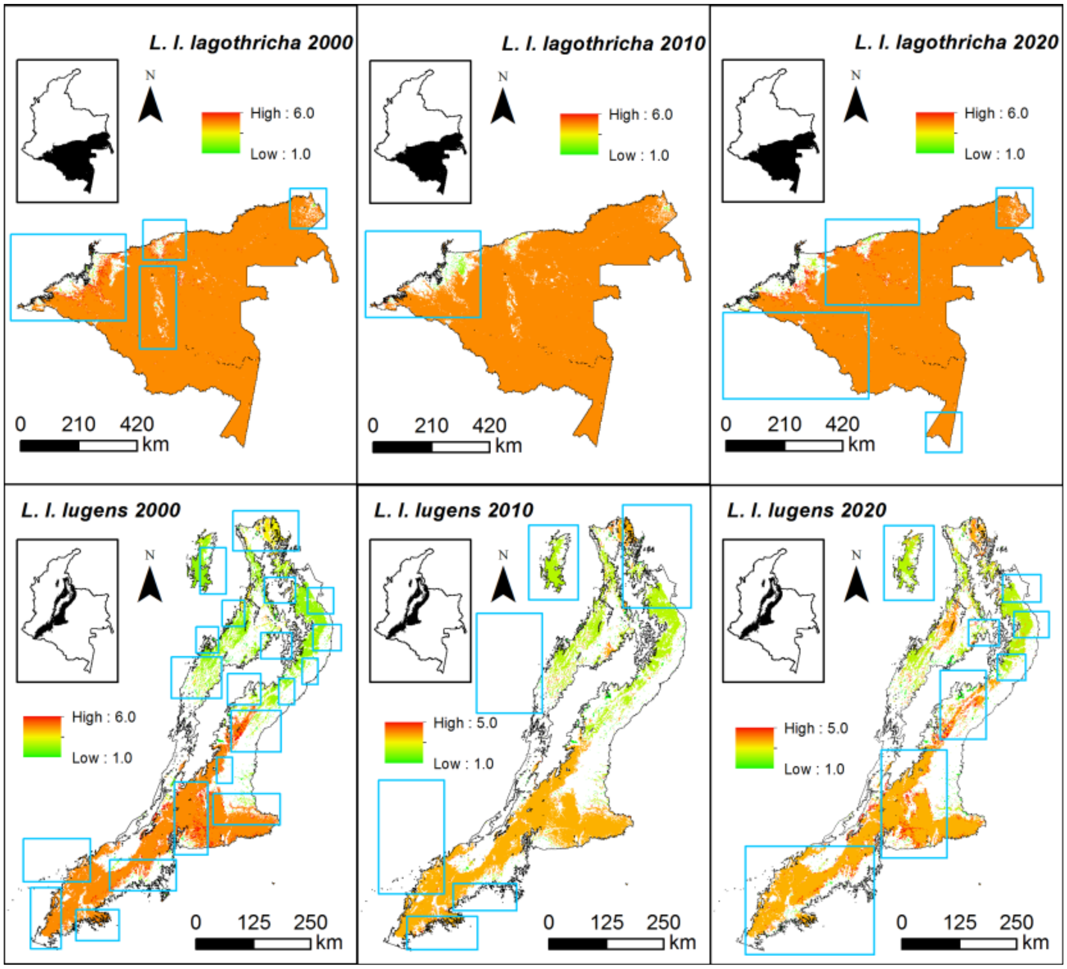


Figure 46. Priority areas for *Lagothrix lagothricha*. Within the blue box: on the left, areas where processes of land use change have occurred, are occurring, or will occur; in the middle, areas where the presence of the species should be reviewed (in addition to unknown limits, see also Figure 1); and on the right, areas where climate suitability in future scenarios is the highest (see also Figure 28).

Major deforestation fronts are found in high altitudes and foothills for both Andean species. For *A. hybridus*, special attention should be paid to the foothills surrounding Serranía de San Lucas, in addition to the remaining patches in the western foothills of the Cordillera Central in the Serranía de los Yariguies and Serrania de las Quinchas of the Cordillera Oriental. The latter are susceptible to deforestation but can be also acting as stepping stones, connecting the three places. This region also shows high climatic suitability in addition to dry regions in the departments of Bolivar, Magdalena and la Guajira. Forest in the Cordillera Oriental in Catatumbo and Tama, including the lowest altitudes in Cocuy and foothills in Arauca would be a single source patch for species since connection exists (Figure 39); therefore the existence of species between the discontinuous regions in Norte de Santander and Arauca is proposed to be revisited.

For *L. l. lugens*, forests at high altitudes of both slopes of the Cordillera Oriental are source patches for the species, almost in the same regions as *A. hybridus*. However, the presence of the species is poorly documented in this region, where it potentially could be found in zones like Chingaza[3], Cocuy and Perijá between others, where main areas of climatic suitability exist. All ateline species´ distributions are susceptible to deforestation, especially the foothills of Caquetá and Putumayo. The major region that species inhabit according to a widely studied prioritization of areas is the PNN Tinigua in Serranía de la Macarena but also the PNN Los Picachos.

For *A. geoffroyi* the major regions with lost habitat are the lowlands of Antioquia and Córdoba, while for *A. belzebuth* and *L. l. lagothricha* major lost habitat has occurred in the foothills of Caquetá and Putumayo. Therefore, these areas are a main priority for these species. Remnant and persistent habitats that are also the main source patches for species is the core of the Pacific and Amazon regions respectively. Climatic suitability for species is consistent with regions where species have suffered, are suffering or are projected to suffer major fragmentation processes.

Representativeness of larger PAs in species’ distributions is inversed related to their status of conservation; more threatened species (Andean species) have less proportion of national PAs than the other species (Figure 47 and Table 23). PA proportions for each species with respect to their original distributions are less than 30%. The most critical species is *A. hybridus* with only 5% of its original distribution

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[3] According to Defler (pers. com.), Chingaza has a population of *L. l. lugens* in the western parts.

protected, and on average, just 11% of its remaining habitat is protected in this study. Even worse, the main source patch for species (Serranía de San Lucas) does not have any kind of protection either inside or in surrounding areas, therefore dispersal and maintenance of its populations is priority in terms of legal protection.

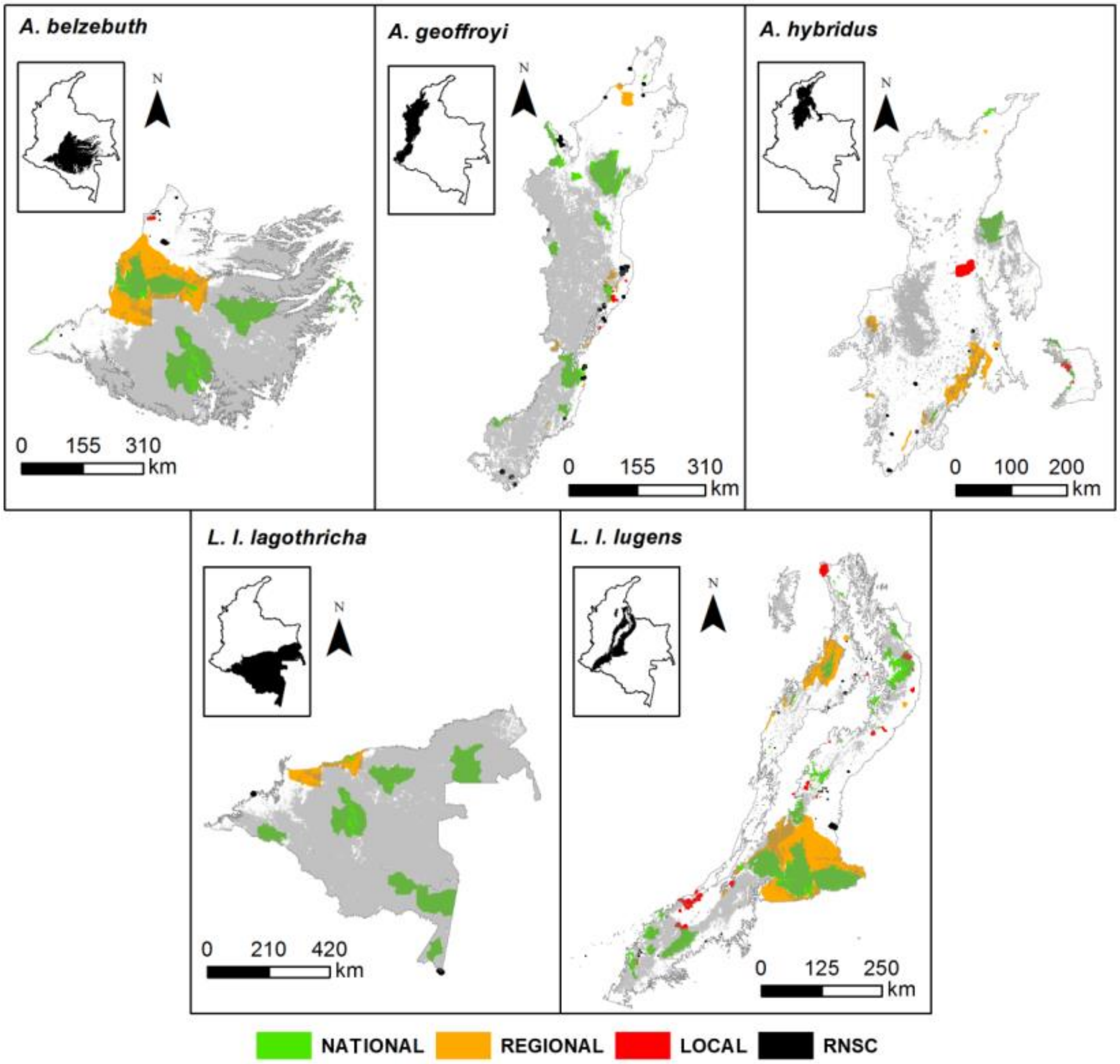

Figure 47. Spatial arrangement of PAs in the distribution of each species. Gray areas are the persistent areas for species.

The other critical species *L. l lugens*, has apparently higher protection than other species (Table 23), however it is overestimated by three regional PAs corresponding to i) Distrito de Manejo Integrado Serranía de los Yariguies in north, and ii) Distritos de Manejo Integrado la Macarena Norte and iii) Ariari - Guayabero in south, which can be considered as management areas instead of physical PAs. It is evident that this kind of PA does not conserve the persistent habitat for this and almost for any of the species (Figure 47).

National PAs contribute in a higher proportion than other figures for the conservation of species. In *A. hybridus* the low proportion of national areas and the presence of Distrito de Manejo Integrado Serranía de los Yariguies balance the proportions between national and regional PAs, but for the other species the national PAs are more and larger (Table 23). It is also evident that a process of persistence and regeneration occur with a higher proportion in national PAs, although deforestation is also taking place. This is clear evidence of protection exerted by the largest and national PAs represented by the PNN Cordillera de los Picachos, Serranía de la Macarena and Tinigua, which maintain persistent forested areas in the distributions of *A. belzebuth* and *L. l lugens*, avoiding the accumulating deforestation from the Amazonian foothills in the departments of Caquetá and Putumayo. The Figure 47 shows the marked correlation between the shape of the patch in the area and the PA formed by the three PNN.

Table 23. Representativeness of PAs in the distribution of each species. Intersection areas between PAs are summed in the type of PA with the highest scale, with National PAs possessing the highest scale when the conflict was present.

Sp.	PA	Area - Original Distribution (km2)	Persistence (Area km2)	Deforestation (Area km2)	Regeneration (Area km2)	Yr.	Area - Remaining Habitat (km2)	Conservation Targets (Sum)
Ateles belzebuth	**Nat.**	31799 (13%)	28992 (17%)	789 (5%)	2043 (21%)	**00**	29735 (16%)	89781 (16%)
						10	29230 (17%)	87634 (17%)
						20	30989 (17%)	124476 (18%)
	Reg.	23032 (9%)	5620 (3%)	6072 (39%)	2513 (26%)	**00**	11321 (6%)	35209 (6%)
						10	8497 (5%)	24545 (5%)
						20	7762 (4%)	28594 (4%)
	Loc.	0 (0%)	0 (0%)	0 (0%)	0 (0%)	**00**	0 (0%)	0 (0%)
						10	0 (0%)	0 (0%)
						20	0 (0%)	0 (0%)
	RNSC	136 (0%)	6 (0%)	34 (0%)	11 (0%)	**00**	30 (0%)	80 (0%)
						10	36 (0%)	86 (0%)
						20	7 (0%)	19 (0%)
	Tot.	54967 (23%)	34618 (20%)	6895 (44%)	4567 (47%)	**00**	41086 (22%)	125070 (23%)
						10	37763 (21%)	112265 (21%)
						20	38758 (22%)	153089 (22%)
Ateles geoffroyi	**Nat.**	12344 (8%)	10124 (12%)	1037 (9%)	687 (10%)	**00**	15 (0%)	36 (0%)
						10	15 (0%)	42 (0%)
						20	12 (0%)	33 (0%)
	Reg.	1984 (1%)	886 (1%)	130 (1%)	49 (1%)	**00**	1008 (1%)	2873 (1%)
						10	966 (1%)	2734 (1%)
						20	927 (1%)	2743 (1%)
	Loc.	91 (0%)	9 (0%)	10 (0%)	7 (0%)	**00**	15 (0%)	36 (0%)
						10	15 (0%)	42 (0%)
						20	12 (0%)	33 (0%)
	RNSC	75 (0%)	44 (0%)	11 (0%)	3 (0%)	**00**	55 (0%)	166 (0%)
						10	50 (0%)	150 (0%)
						20	47 (0%)	143 (0%)
	Tot.	14494 (10%)	11063 (13%)	1188 (10%)	746 (10%)	**00**	1093 (1%)	3111 (1%)
						10	1046 (1%)	2968 (1%)
						20	998 (1%)	2952 (1%)
A - hybridus	**Nat.**	2199 (2%)	1930 (8%)	93 (1%)	109 (1%)	**00**	2019 (6%)	5948 (6%)
						10	1955 (6%)	4194 (4%)
						20	2035 (7%)	5894 (6%)

Sp.	PA	Area - Original Distribution (km2)	Persistence (Area km2)	Deforestation (Area km2)	Regeneration (Area km2)	Yr.	Area - Remaining Habitat (km2)	Conservation Targets (Sum)
Ateles hybridus	**Reg.**	3991 (3%)	1467 (6%)	796 (6%)	393 (5%)	**00**	2019 (6%)	5948 (6%)
						10	1955 (6%)	4194 (4%)
						20	2035 (7%)	5894 (6%)
	Loc.	607 (0%)	53 (0%)	21 (0%)	20 (0%)	**00**	67 (0%)	162 (0%)
						10	63 (0%)	132 (0%)
						20	66 (0%)	140 (0%)
	RNSC	23 (0%)	6 (0%)	2 (0%)	0 (0%)	**00**	8 (0%)	16 (0%)
						10	8 (0%)	23 (0%)
						20	6 (0%)	14 (0%)
	Tot.	6820 (5%)	3456 (14%)	912 (7%)	522 (7%)	**00**	4113 (12%)	12074 (13%)
						10	3981 (13%)	8542 (9%)
						20	4142 (14%)	11942 (13%)
Lagothrix lagothricha lagothricha	**Nat.**	55506 (14%)	53468 (15%)	268 (2%)	1539 (17%)	**00**	53699 (15%)	214852 (15%)
						10	53651 (15%)	214443 (15%)
						20	54970 (15%)	219951 (15%)
	Reg.	10329 (3%)	3281 (1%)	2777 (22%)	1372 (15%)	**00**	5872 (2%)	24005 (2%)
						10	4505 (1%)	16133 (1%)
						20	4467 (1%)	16689 (1%)
	Loc.	0 (0%)	0 (0%)	0 (0%)	0 (0%)	**00**	0 (0%)	0 (0%)
						10	0 (0%)	0 (0%)
						20	0 (0%)	0 (0%)
	RNSC	2 (0%)	1 (0%)	1 (0%)	1 (0%)	**00**	5872 (2%)	24005 (2%)
						10	4505 (1%)	16133 (1%)
						20	4467 (1%)	16689 (1%)
	Tot.	65837 (17%)	56750 (16%)	3046 (24%)	2912 (32%)	**00**	65443 (18%)	262862 (18%)
						10	62661 (18%)	246709 (17%)
						20	63904 (18%)	253329 (18%)
Lagothrix lagothricha lugens	**Nat.**	20173 (14%)	16589 (31%)	1692 (9%)	1435 (14%)	**00**	18253 (26%)	68463 (29%)
						10	17165 (27%)	48753 (29%)
						20	17996 (29%)	52725 (30%)
	Reg.	18472 (13%)	5997 (11%)	4140 (23%)	1641 (16%)	**00**	18253 (26%)	68463 (29%)
						10	17165 (27%)	48753 (29%)
						20	17996 (29%)	52725 (30%)
	Loc.	937 (1%)	413 (1%)	99 (1%)	59 (1%)	**00**	0 (0%)	0 (0%)
						10	0 (0%)	0 (0%)
						20	0 (0%)	0 (0%)

Sp.	PA	Area - Original Distribution (km2)	Persistence (Area km2)	Deforestation (Area km2)	Regeneration (Area km2)	Yr.	Area - Remaining Habitat (km2)	Conservation Targets (Sum)
L. l. lugens	**RNSC**	149 (0%)	20 (0%)	33 (0%)	11 (0%)	**00**	43 (0%)	92 (0%)
						10	49 (0%)	131 (0%)
						20	21 (0%)	46 (0%)
	Tot.	39731 (27%)	23019 (42%)	5964 (32%)	3146 (31%)	**00**	36549 (52%)	137019 (57%)
						10	34379 (54%)	97637 (57%)
						20	36013 (58%)	105497 (60%)

4. Discussion

4.1 Current and Future Scenarios

For current and future scenarios, a main discussion topic is the uncertainty implicit from the sources used and the products generated for the analysis, since this is inherent in remote-sensing and their derivate constructions (Van Leeuwen et al. 2006; Soudani et al. 2008). Therefore, in this discussion strong reference to uncertainty is implicit and analyzed for the models and sources included in this study.

For example, VCF layers have inter-annual fluctuations in the percentage of tree cover from year to year, thus inter-annual comparisons have to be carefully done. The VCF products are validated just to stage-1, i.e., precision was estimated through an assessment of the training data's accuracy, and from the limited in situ field validation datasets (Townshend et al. 2011). Thus, uncertainty is not only present in source products (VCF and forest layers), it is also inherent in the classification, resampling, hold-fixing and merging processes.

Even when expert knowledge of land cover results for the period 2000-2020 have been well tested, the proportions of cover types and processes of deforestation, regeneration and habitat persistence into the species' distribution are relative values and not absolute ones. However, we think that they are too close to the recent (2000), current (2010), and future (2020) proportions of remaining habitat for atelines, due to the fact that they reflect the major issues in terms of conservation for each one of them (Table 2), and because of the spatial match of the trends in forest losses and gains found respect to the most recent study of land cover change in Colombia developed by Sánchez-Cuervo et al. (2012).

Major deforestation in the Caribbean and Andean regions occur primarily due to demographic impacts and cattle practices of the present and also since pre-Hispanic and Hispanic times, (Etter & Van Wyngaarden 2000; Etter et al. 2008). Therefore, the deforestation trend projected particularly in the Andes is concordant with this historic tendency.

Remaining forest zones in the three Cordilleras are defined by altitude and topography, due complicated accessibility for other uses (Armenteras et al. 2011). Some forest regeneration that was found and projected into the future for the region Serranía de San Lucas and Sierra Nevada de Santa Marta are particular from areas where larger patches of forest are found (Figure 21). These forest gains are concordant with the results described by Sánchez-Cuervo et al. (2012), showing a surprising woody vegetation recovery in the Andean region and other zones in Colombia.

Sánchez-Cuervo et al. (2012) attribute regeneration patterns to 3 factors: i) oil palm plantations, ii) inter-annual variation in precipitation and iii) coca crop eradication programs. The first two are influencing cover classifications, and the third one, induced by a national program. According to our results a fourth explaining factor can be added corresponding to the strong autocorrelation process of forest cover, since major regeneration and forest stability processes are in areas with large forest patches, like the Pacific and the Amazon. This conclusion is also in concordance with Sánchez-Cuervo et al. (2012).

Specific areas where deforestation occurred during the period 2000-2010 and a quick regeneration was also projected for the year 2020 (like Caquetá and Putumayo, or the southern limit of Pacific region in Tumaco and surroundings municipalities) have to be analyzed carefully (Figure 21). In the piedmont of the Amazonian region the colonization front has been the main cause of forest losses, (described by Etter et al. 2006a) for the period 1989-2002), and was also found in our results and the results of Sánchez-Cuervo et al. (2012) for the transition between 2000 and 2010.

The projected cover change for 2020 showing a high forest recovery in the departments of Putumayo and Caquetá and other projected regeneration areas, place a high degree of uncertainty in land cover projections. It is difficult to assume the growth of large areas of forest over predominantly deforested regions in just 10 years. However, other areas of regeneration that are projected like Darien, the north portion of Serranía de San Lucas or the Sierra Nevada de Santa Marta are likely to have forest gains, since a regeneration process was found for the period 2000-2010 in our results and in the results of Sánchez-Cuervo et al. (2012).

For current and climate scenarios a high degree of uncertainty is associated with the products used as well. In the choice of the climate model, some constraints are described by Beaumont et al. (2008): i) not all climate models are equally reliable, ii) some regions could be represented poorly by climate models, iii) one or a limited number of climate models are just a sample of un unknown fraction of the uncertainty in future conditions, and iv) the internal climate model variability, uncertainty and bias.

Another source of uncertainty is the interpolation of original data (Hijmans et al. 2005; Ramirez & Jarvis 2010b), due to current and future layers corresponding to different interpolation sources: climate stations for current scenarios and the GCM output for future scenarios. For example, the absence of meteorological stations in particular areas like the Orinoquean and Amazonian regions can be the cause of different patterns in current and future scenarios, even when the interpolation method is the same.

Nevertheless, differences found between current and future climate scenarios are in agreement with estimations of IPCC (2007), where increases of temperature and precipitation values for the tropical zone are projected. These are explanatory factors for why we found larger and drier regions for Orinoquia and larger and moister regions for Amazonia in the scenarios projected. However, the increase or decrease in the magnitude of these values projected for the three climatic envelopes is not widely evident because of the normalization of values. In the same sense, future climatic projections for NPP can be underestimated, since these were based on climatic envelopes.

Normalization of values can be also affecting the dispersal probabilities and dispersal flux in future scenarios, since these are based on HQ and CF that in turn depend on NPP. Constant or lower than expected values in climatic envelopes could produce constant or lower than expected values in NPP; since in the model constructed, and in the physics of the real process, the NPP is positively correlated with the precipitation and temperature (Figure 15) (Field et al. 1995; Moldenhauer & Lüdeke 2002; Matsushita et al. 2004).

NPP as proxy for availability resources in forest measure should be highly weighted in the HQ and CF functions forest productivity is a determinant factor for the ateline primates in terms of habitat quality and movement patterns (Stevenson et al. 2000; Defler 2010). Factors influencing production in ecosystems like precipitation, temperature and soils nutrient supply (Running et al. 1999), are also the same in their effect on resource availability in forests inhabited by these primates. There is a positive correlation between abundant sunlight, warmth and rainfall, and high productivity presented by forests (Defler 1996; Defler & Defler 1996; Di Fiore 2004; Link & Di Fiore 2006).

Relating the scenarios proposed to the climatic suitability of species, some key aspects to consider when using SDMs under climate change scenarios have been proposed: i) Consider and try to incorporate dispersion abilities of species and therefore their future dispersion ranges based on connectivity; ii) Selectivity in the choice of predictive variables in terms of scale, their relevance to the biology of the species and the interpolation methods used, iii) The amount and the bias implicit in the observations of occurrences. iv) The model used because of its ability to limit the overestimation of results, their biological significance and the use of thresholds to define species distributions (Elith & Leathwick 2009; Graham et al. 2011). All of these were taken into account for future projections of species.

Besides uncertainties in land cover and climate scenarios, some limitations are present in SDMs too, related to ENMs, and environmental variables and records of species presences used for modelling. According to Phillips et al. (2006), the SDM based on the ecological niche model follows certain assumptions as follow: i) The localities of occurrence are from a source habitat and not a sink habitat, which may not have the necessary conditions to maintain the species´ population. ii) The environmental conditions at the localities of occurrence are realized niche samples. iii) A niche model is a version of the realized niche of the species only in the study area and with the particular environmental dimensions considered.

Phillips et al. (2006) include some assumptions implicit in the set of environmental variables used to model, the most important are these: i) Temporarily, there must be correspondence between the localities of occurrence and the environmental variables. ii) Spatially, the variables should be sufficient to describe all the parameters of the fundamental niche of the species that are relevant for distribution to the scale of analysis. iii) There may be errors in the data manipulation, due to inaccuracies in the climate models used to generate the climate variables, or due to interpolation.

Finally, certain conditions in the species records can affect the accuracy of the models and these include: i) The geographical bias, since the records are commonly spatially correlated to paths (rivers or roads) (Reddy & Dávalos 2003). ii) The spatial correlation between records. iii) The variability between efforts and sampling methods (Anderson et al. 2003). iv) Errors in the localities of occurrence, due to transcription errors or lack of geographically detailed information requiring default geographic coordinates. v) Misidentification of species. vi) Low number of localities of occurrence to reliably estimate model parameters (Stockwell & Peterson 2002; Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008).

In this context of limitations and uncertainties, models based on bioclimatic variables tend to over-predict species occurrences in areas where they are not present because of historical or geographical barriers and/or biotic factors (Graham et al. 2010a). Particularly in Colombia, the three main cordilleras have very similar climates, hence models generated for a species that exists on one or two cordilleras often predict suitable habitat on the other cordilleras (Velásquez-Tibatá et al. 2012). Therefore, the necessity of evaluating the proposed distribution in conjunction with an expert, underlines the concordance between these and the ones existing.

For generated distributions and the dynamics of climatic suitability, we recognize that many other factors like biotic interactions, evolutionary change and dispersal ability play an important role. However, taking into account the complexity that natural systems present for predictive modeling, we are in concordance with Pearson & Dawson (2003) in the use of a bioclimatic envelope approach, since it has been widely and successfully used as a good approximation for current and future species' distributions.

However, climatic suitability generated for species cannot be compared to other studies, since the spatial effect of climate change on the atelines is unknown in Colombia. One exception in population ecology is a study conducted by Wiederholt & Post (2010), who found relationships between El Niño Southern Oscillation (ENSO) and the dynamics of atelines populations across Central and South America. Wiederholt & Post (2010) found that all ateline genera experienced a direct or a lagged negative El Niño effect as measured from their population structure or through their resource levels (arboreal phenology). Furthermore, they showed a high degree of interspecific population synchrony (respect to yearly primate abundances) over large scales across Central and South America, explicable through the recent trends in large-scale climate. Then, these results emphasize that climate change could pose additional threats to the persistence of multiple species of endangered primates and their habitats by directly affecting the individual abundances or through the plants phenology, affecting fruit production.

Thus, there is a strong possibility for distributional shifts in future climates caused by species movements, due to the fact that primate species are suffering or will likely suffer changes in their distributions as a response to phenological shifts of plant species (Bradley et al. 1999; McCarty 2001; Walther et al. 2002; Badeck et al. 2004; Visser & Both 2005; Cleland et al. 2007; Wiederholt & Post 2010). Therefore, a study comparing the distribution of the most consumed plants by atelines under the same climatic conditions and the generated distributions could be a starting point for predicting which would be more suitable areas at higher elevations for Andean species and at lower, warmth and moister areas for the other species (Figure 27 and Figure 28).

The climatic suitability for species is concordant with altitudinal movements that are projected for different species around the world (IPCC 2002; Walther et al. 2002; Bennett 2003; Visser & Both 2005; del Barrio et al. 2006; Parmesan 2006), and it is also related to projections for the NPP (Nemani et al. 2003; Matsushita et al. 2004); hence, the habitat quality of the species may not be apparently affected in the future. However in some species like *L. l. lugens*, our scenarios proposed show low habitat quality areas in the foothills of the Central and Oriental Cordilleras where major processes of deforestation occur are also related to zones of higher climatic suitability (Figure 28 and Figure 30). A similar situation is presented for *A. hybridus'* distribution, where high climatic suitability over the Magdalena valley is projected, to result in dry forest virtually inexistent (Figure 27 and Figure 29).

No single measure for establishing the current or potential effects on the distribution or pattern of movements for the species is needed. A framework of connectivity and dispersal of species, measuring all influencing factors is a more robust approach in addressing the changes that the species may suffer and that may aid in identifying some priorities for their persistence.

4.2 Connectivity and Dispersal

In principle, connectivity analysis has two limitations for evaluating species dispersal through proposed scenarios: i) A no dispersal scenario with respect to the boundaries of their distributional ranges in future scenarios. ii) A potential measure of species dispersal which not necessary represents their actual dispersal.

In the context of the first limitation, this analysis measures the exposure of species' distributions to climate changes and habitat fragmentation, but it does not take into account the possible migrations that species would suffer to other suitable areas because of future transformations of their habitat (Araújo et al. 2011). As a response to future scenarios, the boundaries of species' distributional ranges were not changed; thus, the potential species distributions would be extended or reduced in other types of analysis, where dispersion of species outside the known limits of their distribution could be modeled.

With respect to the second limitation, the graph-theoretical approach used measures a potential dispersion of species based on a probable connection in the landscape, according to the dispersal distance threshold established (Calabrese & Fagan 2004). This analysis cannot measure the actual dispersal of species, since we are not sure if individuals are actually moving via the landscape links proposed.

Moilanen (2011) gives some limitations of graph-theoretic connectivity approaches in spatial ecology and conservation that are included in four themes: i) A multitude of measures with uncertain ecological relevance and novelty value. ii) Losses of information by using thresholds. iii) Computational limitations in application to high-resolution GIS grids. iv) An overemphasis on the relevance of landscape connectivity. This latter is discussed in the analysis for prioritization of conservation areas.

The first limitation proposed by Moilanen (2011) is evident in the reviewed metrics of Table 11, which is also reflected in our results, since all metrics could be synthetized in the first component of the PCA, where there is a high correlation between metrics (Table 21 and Table 22). This also supports the idea of Rothley & Rae (2005), indicating the patch area as the most simplistic approach to quality, capacity and connectivity of patches, which we have summarized in source patches.

The second and third limitations proposed by Moilanen (2011) are related to the scale of analysis. Our experience suggests that computational requirements to calculate metrics for finer resolutions in widely distributed species should be a major issue, although different approaches like parallelization or slicing (in python context) programming are solutions to this problem. On existing software these are just available for programming platforms like R or Python under igraph (http://igraph.wikidot.com), but these are currently unavailable in Conefor (Saura & Torné 2009) and probably in others software (Kupfer 2012).

The landscape model for graph-theoretical approaches is binary, since nodes and connections are limited to habitat and no-habitat connected areas, discarding transitional zones like ecotones, that can link (like stepping stones) or act as sink patches for species dispersal (Chetkiewicz et al. 2006). In our approach, we establish thresholds to both nodes and edges, in part for the necessity of the graph method but also due to the grain of spatial information. We assume that all forest pixels were habitat patches for the atelines due to the problems generating a more complex land cover surface that can include transitional habitats for the species. Secondly we assign a higher threshold for species dispersal than the probable maximum dispersal distance for them, due to the minimum resolution available (1 km).

Both thresholds contribute to losses of information, since we are inferring a simplification of the landscape and the use that species put it to. However, changes in the described and analyzed scenarios are consistent with the changes introduced into the connection networks that describe the landscape for each species, i.e., the changes in fragmentation and climate change described above explain the changes in networks for each species and each scenario. These results validate the analysis of connectivity proposed, since we found that dispersal of species responds to the landscape characteristics, which in turn, according to expert knowledge, represent the main landscape elements in the scale of analysis. In general, and for a variety of ecological systems, network analysis is a remarkably robust framework for habitat connectivity (Urban et al. 2009), with inferences for populations (Minor & Urban 2007) and species dispersal (Lookingbill et al. 2010).

Thus, if we project a reduction in the remnant habitat of a species as a product of deforestation, this will result in a fragmentation process promoting the node increases, but also the increase or disappearance of some of the potential connections. This is characteristic for the species of the Andean and Caribbean regions (*A. hybridus* and *L. l. lugens*), but it happens at a lower proportion for all other species.

As the same time, HQ and hence CF also changes spatially and temporally. The cover and climate pattern of change is repeated on networks. In the Amazon and Pacific species (*A. belzebuth, A. geoffroyi* and *L. l. lagothricha*), source patches and their associated connections promote higher dispersal compared to sink patches and the other regions, since climatic and cover changes are more suitable over source patches in forest zones.

However, overall actual or future dispersion of the atelines in the Andean region is very compromised, not only by changes in coverage and climate, but also by its dispersal ability. The natural habitat of atelines monkeys is primary forest in the different ecosystems where they are found, preferring the highest canopy levels and moving primarily between middle and upper segments (Ford & Davis 1992; Defler 2010). They descend to the ground rarely and usually under specific conditions (Campbell et al. 2005), then the existence of a not-frosted matrix might make their movement almost impossible.

A main element to take into account in this discussion is resource availability. When the habitat provides a large amount of resources, the individuals will not have to travel long distances because resources can be easily found, but inhabiting poor habitats that do not provide enough resources will force the displacement of individuals to be longer in order to find resources in other habitats (Stevenson 2000; Stevenson et al. 2002, 2005; Link & Di Fiore 2006). Even though atelines change the proportions in their diet in order to compensate for the scarcity of resources (Charnov 1976; Strier 1992; Stevenson et al. 2000; Di Fiore & Rodman 2001), a faster adaptive foraging or dispersal is needed to avoid human changes.

Adaptive foraging requires that species recognize some characteristics related to both quality (Loeuille 2010), and the spatial distribution of existing patches (Pyke et al. 1977; Andersson 1978; Pyke 1984), which in turn, are associated with negative and positive fitness in response to landscape configuration. After some time and depending of species adaptability, this process would result in a probable change of the species movements (Tischendorf & Fahrig 2000).

Terrestrial behavior of Atelines can be adaptive to the environment (Campbell et al. 2005; Estrada et al. 2012). According to Kokko & López-Sepulcre (2006), adaptation can be both fast and significant for the ability of a species to colonize new areas in a short time, since some recent examples suggest several ways in which changes in species dispersal can either constrain, or accelerate, their responses to environmental changes. Even more, processes of contemporary evolution (times less than 100 years) have been documented in response to different changes induced to the environment (Stockwell et al. 2003). Based on the use of agroecosystems as feeding habitats or steeping stone patches by some primates species (Estrada et al. 2012), we propose that the process of adaptive dispersal in atelines species can exists in the same way that opportunistic foraging responds to resource scarcity, since contemporary behavioral process of adaptation in atelines have taken place in response to the human presence (Papworth et al. 2013).

Campbell et al. (2005) reported individuals descending to the ground looking for water in less desirable locations during dry seasons when sources of drinking are scarce, a probable condition if we are expecting that climate changes increase the temperature in humid forest where these species live. Estrada et al. (2012) reviewed the dispersal of atelines (*A. geoffroyi grisescens* in Central America and *L. l. lagothricha* in Colombia) through agroecosystems like cacao, coffee or fruit plantations, using this kind of patches for foraging activities. Then, if the environment conditions like habitat fragmentation or climate change force the species to move, they will probably do it if there is additional habitat available (Figure 48). Nevertheless, the goal is to improve the landscape connectivity for species dispersal to different habitat patches with the lowest degree of susceptibility for them.

Therefore, for conservation planning purposes we need to link landscape structure to underlying ecological processes, since connectivity for species is functional (Kent 2009). According to Urban & Keitt (2001a), this determines how a given species might perceive and disperse through the landscape, which in practical terms reflects how a species might act as a metapopulation.

The necessities for improvement of landscape connectivity are not the same for all atelines, due to different underlying ecological processes. These are derived from particularly different habitat fragmentation effects that can be exacerbated by climate change according to these results, and which in turn correspond to different LUCC over Colombia, and result historically from the different human settlement patterns over natural regions (Etter et al. 2008).

Figure 48. *Ateles hybridus* dispersal over a non-forest matrix.

In synthesis, the landscape connectivity for *A. geoffroyi*, *A. hybridus* and *L. l. lugens*, and for *A. belzebuth* and *L. l. lagothricha*, are different and correspond to the different patterns of habitat fragmentation described in the regions that they inhabit. In this vein, the definition of conservation areas is priority to guarantee enough time for adaptive foraging and includes also the conditions in the landscape that affect the dispersal process, particularly in the Andean region, since the results obtained in this study suggest the potential dispersal of species even in fragmented landscapes, although seriously compromised.

4.3 Prioritization of Conservation Areas for Persistence

The main objective of connected ecological networks is to permit the movement of species through unsuitable areas. Nevertheless, these are proposed as a simplification of complex ecological concepts, and therefore their use in biodiversity conservation is limited. Ecological networks are particular to the species and therefore they are scale dependent; however, the information of species requirements for its implementation is always incomplete. Additionally, information about how to build them (e.g., width, shape, structure, and content) or processes to validate in the practice how do they ensure connectivity and enhance biodiversity conservation are unknown (Boitani et al. 2007).

Despite this picture, it is clear that connectivity of habitat patches is important for movement of genes, individuals, populations, and species over multiple temporal and spatial scales (Wiens et al. 1993). Through a network framework, it is possible to provide inferences about rates and paths of species movements and their vulnerability to disturbance (Minor & Urban 2008), in addition to identifying patches that are very important to habitat connectivity and thus long-term population persistence across the landscape (Minor & Urban 2007).

In this sense, the fourth issue of Moilanen (2011) proposes that there exists an overemphasis on the relevance of landscape connectivity in graph-theoretical approaches, since any measure of connectivity can give a fully reliable estimate of the persistence, extinction risk, or resilience of a species at a regional scale. According to Moilanen (2011), connectivity only informs us about the immigration and emigration components of populations, although we are supposing that the presence or abundance of species can be related to size, quality, and connectivity of the patch as proxies to the persistence of populations, according to Minor & Urban (2007). Based on the multi-temporal analysis, we argue our position respect to the relationship between population persistence and the quality of the patches.

Over the networks constructed during the period 2000-2020, source patches (the ones with higher size, quality, and connectivity) are also persistence patches; therefore it can be associated to persistence of populations as well. Source patches can support more individuals and are associated with populations with higher sizes, that are expected to grow over time (Pulliam 1988; Pulliam & Danielson 1991), since the size and quality of the largest patches support the populations and the connectivity process, promoting migration and immigration fluxes (Pulliam et al. 1992; Dunning et al. 1995; Wiens 1997; Johst et al. 2002; Treml et al. 2007).

Although graph theory networks do not require knowledge of behavior, fecundity, or mortality parameters, these data can be incorporated and used to create a more ecologically complex graph model (Minor & Urban 2008). Towards a conservation planning application, results obtained require further empirical validation, refinement and calibration for the species in order to evaluate their correlation with descriptors of population dynamics such as colonization, extinction events or population sizes, between others (Saura & Rubio 2010).

Therefore, to understand how landscape structure affects movement and, hence, the population dynamics of atelines, a clear empirical knowledge about movement patterns, and especially about the dispersal of the species is needed to implement actions for their conservation (Selonen & Hanski 2003). In practical terms, to complement this study and the correct selection of conservation corridors to connect defined priority areas (Figure 45 and Figure 46), a field study based on the potential areas where dispersal of species can occur (Figure 43 and Figure 44) would be ideal.

Conserving priority areas for the atelines is not a conservation strategy for the persistence of species *per se*. Their principal ecological role as seed dispersers is extremely important in order to maintain forest diversity (Stevenson et al. 2002; Defler 2010), to the point that their absence may have negative effects on plant populations, especially large-seeded plants, that are rarely swallowed by other seed dispersers (Wunderle 1997; Peres & van Roosmalen 2002).

In this sense, Chetkiewicz et al. (2006) argue that connections between PAs through corridors and networks that facilitate the dispersal of species would be the most important and required action for ensuring the persistence of species and their ecosystems. PAs must be close, or connected enough, to allow for the preservation of species and large-scale ecological and evolutionary processes (such as gene flow, migration, and range shifts in response to climate change) (Minor & Lookingbill 2010).

Nevertheless, the actual SINAP in Colombia has a highly fragmented PA system, especially in the Andes where higher connectivity levels are required (Figure 47). Landscape connectivity can be improved in two main ways, i) according to the spatial pattern of landscape elements by managing the entire mosaic to favor movement, or by ii) managing specific habitats for specific responses (habitat corridors and stepping stones) (Bennett 2003).

For *A. belzebuth, A. geoffroyi* and *L. l. lagothricha* the first option presented by Bennett (2003) might be better, since there is a specific habitat patch (the core of the Amazon and the Pacific regions) and a specific corridor (through the specific patch) as the most important landscape elements to maintain connectivity (Jordán et al. 2003). For *A. hybridus and L. l. lugens* the second option is the only solution, since the landscape is highly fragmented. Establishing strategic habitat corridors that connect remaining habitats or increasing the number of stepping stones even with agroecosystems should be a conservation priority, in the same sense of Minor & Lookingbill's (2010) proposal for small mammals in USA.

In order to rank defined priority areas, the structure of connected conservation areas is the first option (corresponding to MST in each component). Thus, the main source patch in the Pacific and Amazon regions has a higher priority, while in the Andean and Caribbean regions, both source patches and sink patches acting like stepping stones are needed to conserve (Minor & Urban 2007). On the next level, according to Rothley & Rae (2005), the best surrogate for conservation value is the patch size, which in our results also reflects the sources patches containing higher quality, capacity and connectivity (Figure 36 and Figure 37). Other conservation targets proposed (Table 12) are included in previous; therefore, prioritize the improvement of the MSTs established over source patches for the ateline primates, is a main concern for improving species persistence over time.

In addition, some particular areas which have to be undelaying to the ones established are identified below. For *L. lagothricha sspp.* and *A. belzebuth*, the piedmont in the departments of Caquetá and Putumayo and the network formed by natural parks Picachos, Tinigua and Serranía de la Macarena are main conservation regions. For the first area, a major process of deforestation (Figure 21) affects the distribution of both species and also may be a key area in evolutionary and biogeographic terms for the genera *Lagothrix*, since it is proposed as a region where processes of diversification (Defler 2010) or even speciation have occurred (Botero et al. 2010; Mantilla-Meluk 2013). For the second one, a major process to avoid deforestation from the eastern foothills of the Cordillera Oriental has occurred (Figure 47). In general terms both areas including the eastern slopes of the Cordillera Oriental are high climatic suitability areas for the species (Figure 27 and Figure 28).

For *A. geoffroyi* the regions of Darien and the entire low-lands in the western slope of the Cordillera Occidental are exposed to fragmentation and a high climatic suitability according to scenarios proposed (Figure 21 and Figure 27). Although it may not be worrisome in the near future (10 years), the presence of the species should be constantly evaluated in these zones. For *A. hybridus*, the most threatened of the Atelinae species, the Serranía de San Lucas is the major area that needs to be conserved, since it is not legally protected. It is the main source patch for the species, and it is projected to be fragmented at the same time as an increase in its climatic habitat suitability in the scenarios projected for the species (Figure 21 and Figure 27).

5. Conclusions

The species connectivity and dispersal are closely related to patterns in habitat deforestation and regeneration in the species' distributions. The Andean and Caribbean species (*A. hybridus and L. l. lugens*) are susceptible to fragmentation processes in almost their entire distribution in past present and future scenarios of land cover. Therefore, improvement of habitat connectivity for this species is needed immediately. *A. belzebuth*, *A. geoffroyi* and *L. l. lagothricha* are species less affected by habitat fragmentation; nevertheless, some specific areas like piedmont in Caquetá and Putumayo and the lowlands in western foothills of Cordillera Occidental are priority areas to conserve.

Climate change effects for each species movement vary. For *A. hybridus and L. l. lugens*, higher habitat climatic suitability values are found in moderate elevations for both species, and in the Magdalena valley and foothills of the Cordillera Oriental for each species respectively. This agrees with the global hypothesis of altitudinal migration of species due to temperature increases. For both species, major potential migrations because climate changes are projected over less suitable areas in terms of habitat quality due to fragmentations processes affecting dry and Andean forests. For the species *A. belzebuth*, *A. geoffroyi* and *L. l. lagothricha,* a better and more suitable habitat is projected in suitable climates corresponding to moister and lower areas of the Pacific and Amazonian regions, coinciding with higher precipitation and temperature rates projected for the tropics, where the NPP is also supposed to increase.

Representativeness of PAs in ateline species' distributions is low. Larger PAs like national natural parks are more representative, since they are larger, more numerous and protect higher proportion of remaining habitat for the species. These may constitute an effective measure for conserving populations, since patches of remaining habitat under these zones are mostly conserved, and respond to the spatial configuration and size of most PAs. Both characteristics are fundamental for species foraging ecology, where larger extensions of habitat for their movements are needed. In addition larger protected areas can form source patches, since they are a good proxy for habitat quality, capacity and connectivity in the context of species dispersal and persistence.

In order to rank the defined priority areas the structure of connected conservation areas is the first option (corresponding to MST in each component), followed by source patches, which contain the highest values for quality, capacity and connectivity. Other conservation targets have been included previously; therefore, to prioritize the improvement of MSTs established over source patches for atelines is a main concern for improving species persistence over time. In concordance two way of landscape management is proposed, by managing the entire mosaic to favor movement for *A. belzebuth, A. geoffroyi* and *L. l. lagothricha*, since there is a specific habitat patch (the core of the Amazon and the Pacific regions) and a specific corridor (through the specific patch); and by managing specific habitats for specific responses (habitat corridors and steeping stones) for *A. hybridus and L. l. lugens*, since landscape is highly fragmented.

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