



Universidad de Concepción
Dirección de Posgrado
Facultad de Ciencias Forestales
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Effects of forest fragmentation on biodiversity
in the Andes region

Efectos de fragmentación de los bosques sobre la
biodiversidad en la región de los andes

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JIN KYOUNG NOH

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Profesor Guía: Cristian Echeverría Leal, Ph.D.

Profesor Co-guía: Aníbal Pauchard, Ph.D.

Dpto. de Manejo de Bosques y Medioambiente

Facultad de Ciencias Forestales

Universidad de Concepción

Effects of forest fragmentation on biodiversity in the Andes region

Comisión Evaluadora:

Cristian Echeverría (Profesor guía)
Ingeniero Forestal, Ph.D.

Aníbal Pauchard (Profesor co-guía)
Ingeniero Forestal, Ph.D.

Francis Dube (Comisión Evaluador)
Ingeniero Forestal, Doctor

Horacio Samaniego (Comisión Evaluador)
Ingeniero Forestal, Ph.D.



Directora de Posgrado:

Darcy Ríos
Bióloga, Ph.D.

Decano Facultad de Ciencias Forestales:

Jorge Cancino
Ingeniero Forestal, Ph.D.

DEDICATORIA

활짝 웃으며 내 손잡고, 길고 힘들었던 여정을 동행해 준 나의 사랑하는 남편 **파블로**,
바쁜 엄마를 이해하고 위로하고 사랑해주는 나의 소중한 두 꼬맹이 **테오와 벤자민**,
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TABLE OF CONTENTS

<i>DEDICATORIA</i>	<i>iii</i>
<i>ACKNOWLEDGMENTS</i>	<i>iv</i>
<i>TABLE INDEX</i>	<i>vii</i>
<i>FIGURE INDEX</i>	<i>ix</i>
<i>ANNEX INDEX</i>	<i>xi</i>
<i>ABSTRACT</i>	<i>xii</i>
<i>CHAPTER 1</i>	<i>1</i>
General introduction	1
Aichi goals and international initiative	1
Biodiversity conservation and landscape ecology.....	2
<i>Spatial patterns and habitat fragmentation</i>	3
<i>Island biogeography & metapopulation theory and fragmentation impacts</i>	6
<i>Extinction debt</i>	11
<i>Conservation status of territorial ecosystems</i>	13
Literature	19
<i>CHAPTER 2</i>	<i>25</i>
Extinction debt in a biodiversity hotspot: The case of the Chilean winter rainfall-valdivian forest	25
Introduction	25
Materials and methods	29
<i>Study site</i>	29
<i>Forest cover data</i>	31
<i>Plant species richness</i>	35
<i>Analysis</i>	36
Results	38
<i>Habitat fragmentation and actual plant richness</i>	38
<i>Influence of past habitat on plant species richness</i>	40
<i>Changes of the single long-lived species' DPS</i>	42
DISCUSSION	43
<i>Detection of extinction debt</i>	43
<i>Change of long-lived species' DPS during 1979 - 2011</i>	47
<i>Value of small size patches in rapidly changing landscape</i>	48
<i>Suggestions for preventing future biodiversity loss in the NMR</i>	50
Conclusion	51
Acknowledgements	52
Literature	52
Annex	61
<i>CHAPTER 3</i>	<i>65</i>

National assessment of forest ecosystem fragmentation in Ecuador: strong needs of landscape management in Tropical Andes.....	65
Introduction.....	65
Materials and methods	70
<i>GIS data.....</i>	70
<i>Deforestation rate, change rate of land cover types and forest fragmentation index</i>	76
<i>Analysis</i>	78
Results.....	78
<i>Land use change in forest ecosystems.....</i>	78
<i>Forest fragmentation.....</i>	82
<i>Relationship between forest fragmentation and human land use.....</i>	83
Discussion.....	85
Conclusion	89
Literature	89
CHAPTER 4	94
Warning about conservation status of forest ecosystems in Tropical Andes: national assessment in Ecuador, based on IUCN criterion	94
Introduction.....	94
Materials and methods	98
Study area	98
Framework of assessment based on IUCN criteria	100
Assessment of criterion B	100
Evidences of ongoing decline of an ecosystem.....	101
Decline of spatial extent (B1ai OR B2ai)	102
Decline of environmental quality to characteristic biota (B1aii OR B2aii).....	103
Number of locations (B1c OR B2c)	104
Results.....	105
Identification of spatially restricted forest ecosystems	105
Potential threats of forest ecosystem collapse	108
<i>Current land use and forest fragmentation.....</i>	108
<i>Conversion to cultivated land</i>	109
<i>Number of locations.....</i>	110
Discussion.....	112
Conclusion	115
Acknowledgements.....	116
Literature	116
Annex	129
CHAPTER 5	132
General conclusion	132

TABLE INDEX

Chap.2. Extinction debt in a biodiversity hotspot: The case of the Chilean winter rainfallvaldivian forest

Table 1. Description of land cover types defined in the study area.....	32
Table 2. Number of selected patches and sampling plots per patch size.....	36
Table 3. Changes in landscape pattern indices for the native forests in 1979 and 2011.....	40
Table 4. (A) Current richness of different assemblage of plant species, n: species number. (B) Linear regression testing the relationship between the current and past patch size and current richness of plant species.....	40
Table 5. Multiple regression of the current and past connectivity relationship on the current richness.....	43

Chap.3. National assessment of forest ecosystem fragmentation in Ecuador: strong needs of landscape management in Tropical Andes

Table 1. Description and source of land cover types defined in the study area....	74
Table 2. Spatial scale (region-ecoregion-ecosystem), altitudinal range and Forest Fragmentation Index (FFI: proportion of non-continuous forest in a given ecosystem) of 64 natural forest ecosystems in the Ecuadorian continent.....	75
Table 3. Summary of FAD fragmentation class thresholds, names and color assignment.....	78
Table 4. Standard coefficients of multiple regressions testing the relationship between forest fragmentation index (FFI) and human land use in 2014 in three regions of Ecuador.....	84
Table 5. Standard coefficients of multiple regressions testing the relationship between forest fragmentation index (FFI) and human land use for 2014 in forest ecosystems divided by FFI value (Low: $FFI \leq 10$, Moderate: $10 < FFI \leq 60$, High: $FFI > 60$).....	85

Chap.4. Warning about conservation status of forest ecosystems in Tropical Andes: national assessment in Ecuador, based on IUCN criterion

Table 1. Summary of IUCN Red list criteria B for ecosystems V. 2.0 and Subcriterion applied for the present study.....	101
Table 2. Land use and cover types that may be found within the potential distribution of forest ecosystem clases.....	103
Table 3. Summary of data sources.....	105
Table 4. List of 64 terrestrial forest ecosystems in Ecuador, assessed by IUCN RLE criterion B.....	106



FIGURE INDEX

Chap.1. General introduction

Figure 1. Different classifications of habitat fragmentation.....	5
Figure 2. Four approaches for evaluating extinction debt from Kuussaari et al. (2009).....	12
Figure 3. Structure of the IUCN Red List of Ecosystems Categories (IUCN, 2017).....	14

Chap.2. Extinction debt in a biodiversity hotspot: The case of the Chilean winter rainfallvaldivian forest

Figure 1. Map of study area including study ecosystem (Costal temperate deciduous forest of <i>N.nervosa</i> & <i>P.lingue</i>) and the major land cover types in 1979 and 2011.....	35
Figure 2. Generalized linear model for current richness of long-lived specialist plants and patch size in 1979 (solid line and symbols) and 2011(dotted line and open symbols).....	42
Figure 3. Changes in dwelling patch size (size value at maximum probability of presence) of single long-lived species (n = 27) for period 1979 and 2011.....	45

Chap.3. National assessment of forest ecosystem fragmentation in Ecuador: strong needs of landscape management in Tropical Andes

Figure 1. (A) Ecoregions of continental Ecuador. Elevation detail is shown. **(B)** The major land cover types inside 64 forest ecosystems in 1990, 2000, 2008 and 2014. **(C)** Distribution of each ecoregion's elevation. Cutting section of a geological map based on a red dotted line (A). **(D)** The major land cover types and changes of ecoregions (n=7) in 1990, 2000, 2008 and 2014, **(E)** The major land cover types that have replaced the original forest ecosystem of single ecosystems (n=64) in

2014. Ecosystems containing forest area <10 % (n=6) are marked with black outline.....	72
Figure 2. Scatter diagrams of forest ecosystems annual deforestation rate for the periods 1990-2000 and 2000-2014. (A) Changes in annual deforestation rate of single forest ecosystem (n=64) for the periods 1990-2000 and 2000-2014. Each point represents one forest ecosystem. Solid black outline is zoomed out (B) Changes in annual deforestation rate of single forest ecosystem (n=59), excluding extreme data (n=5) (Inset) The distribution of the ecosystem's differences in deforested area between 1990 and 2014. The vertical dotted line marks zero shifts, and the vertical solid line marks the median shift. The arrow describes the direction of the shift.....	80
Figure 3. Net change (i.e. gains plus losses), gains and losses for each land cover class as a percentage of three regions for the periods 1990-2000, 2000-2008 and 2008-2014.....	82
Figure 4. Temporal variation of number of different FAD (log) in three regions of Ecuador.....	83
Chap.4. Warning about conservation status of forest ecosystems in Tropical Andes: national assessment in Ecuador, based on IUCN criterion	
Figure 1. (A) Ecoregions of continental Ecuador. Elevation detail is shown. (B) The major land use and cover types inside the potential limits of 64 forest ecosystems in 1990, 2000, 2008 and 2014.....	100
Figure 2. The major land cover types of single ecosystems (n=64) in 2014. Continuous and separated native forests were distinguished based on the Forest Area Density (FAD) values calculated from GUIDOS. Human land use and cover includes agricultural land, pasture, forest plantation and urban area. Ecosystems containing either continuous native forests <30 % or human land use >40% (n=7) are E 10, 17, 32, 33, 34, 35 and 44.....	110
Figure 3. Map of 13 threatened forest ecosystems in mainland Ecuador, assessed by IUCN RLE criteria B.....	112

ANNEX INDEX

Chap.2. Extinction debt in a biodiversity hotspot: The case of the Chilean winter rainfallvaldivian forest

Annex 1. Confusion matrices for the two images.....	62
Annex 2. List of long-lived species and their habitat specialization degree in Nahuelbuta Mountain Range.....	62
Annex 3. List of long-lived species that were best described by unimodal bell-shaped model (n=27) displaying a highly significant Gaussian logit model (at the 0.001 level) for both periods of 1979 and 2011. DPS: dwelling patch size, VU: Vulnerable, NT: Near threatened.....	64

Chap.4. Warning about conservation status of forest ecosystems in Tropical Andes: national assessment in Ecuador, based on IUCN criterion

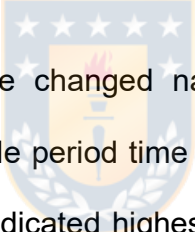
Annex 1. Spatial scale (nation-region-ecoregion-ecosystem) of the system under study and 64forest ecosystems of continental Ecuador.....	130
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ABSTRACT

Since rapid economic development, natural system decline and fragmentation is one of the core drivers of global change and has huge implications for ecosystem functioning and conservation. The impacts of habitat fragmentation can arise in the face of primarily biotic change, primarily abiotic change and a combination of both, including extinction, disruption of trophic interactions and increased susceptibility to disturbances (e.g. logging, fires and invasive species) (Holl and Aide 2011; Laurance et al. 2002; Letcher and Chazdon 2009; Turner 2010a). Some changes result in species extinction and system degradation retaining some original characteristics as well as novel elements, whereas larger changes will result in system replacement or collapse. Against this background, the present study aimed to analyze the effects of habitat fragmentation on different levels of biodiversity including species, community and ecosystems.

Previously the majority of efforts to conserve biodiversity have been focused on species, communities or their habitat under forest fragmentation, as well as on negative influences on species declines and extinctions. However, local extinction of different types of biodiversity can occur with a temporal delay following habitat fragmentation and such delay is called extinction debt. We assumed that the distribution of many vascular plant species in the Coastal Range of south-central Chile is not in equilibrium with the present habitat distribution. One of the aims of this research was to quantify patterns of habitat loss and to detect extinction debt from

relationships between current richness of different assemblage of vascular plants (considering longevity and habitat specialization) and both of past and current habitat variables. Results showed that native forests have been fragmented and reduced by 53%, with annual deforestation rate of 1.99%, in the study area between 1979 and 2011. Current richness of plant species was mostly explained by past habitat area and connectivity. Past habitat variables explained best for richness of long-lived specialist plants, which are characterized by restricted habitat specialization and slower population turnover. We also showed that habitat fragmentation has resulted in a significant reduction in long-lived plant species' Dwelling Patch Size (DPS) between 1979 and 2011.



At ecosystem level, human have changed natural systems more rapidly and extensively than in any comparable period time in human history over the past 50 years. Despite previous studies indicated highest rates of deforestation and forest fragmentation in Ecuador, there was no clear relationship between the degree of forest ecosystem fragmentation and human land use to better design conservation strategies. We quantified and graphed forest fragmentation on different spatial scales, according to the results using GUIDOS, which measures forest fragmentation and classify forests into five main categories—intact, core, perforated, edge, and patch—based on Forest Area Density (FAD) in a given forest pixels. Our results showed that forest fragmentation in 64 forest ecosystems was mostly explained by pasture between 2008 and 2014. Although forest fragmentation became the dominant process in the Coast and Andes, rapid increase of number of patchy and rare FAD was observed in the Amazon during 1990-2014.

As ecosystem changes do not occur at equal rates and patterns, the IUCN has developed criteria analogous to the Red List of Threatened Species to perform similar risk assessment on ecosystems, creating the Red List of Ecosystems (RLE) methodology. One of the most significant challenges for the construction of these lists is the gathering available information to apply criteria. Applying IUCN RLE criteria B (the extent of restricted geographic distribution of an ecosystem), we evaluated the threat level and its relationship between forest fragmentation and human land use to the 64 forest ecosystems of Ecuador mainland. The study showed that a 20% of forest ecosystems are classified as threatened, while the distribution of these threatened ecosystems is concentrated in the south Andes.

The present study provides the first evidence of potential future loss of plant species in two South American biodiversity hotspot: Chilean winter rainfall-valdivian forest and Ecuadorian Tropical Andes. Consequently, an unknown proportion of the species and ecosystems in the study areas would be extinct or collapsed, if there are no targeted restoration and conservation actions in the near future.

CHAPTER 1

General introduction

Aichi goals and international initiative

The adaptation by the world's governments, at the tenth conference of the Parties of the Convention on Biological Diversity (CBD) in Nagoya in 2010, of the 2020 Strategic Plan for Biodiversity and its associated 20 Aichi Targets, marked a watershed moment in the history of biodiversity conservation (Brooks et al., 2015). Because the primary driver of biodiversity loss is habitat loss, one of the main strategic goals of the Aichi Targets includes increasing the amount of protected terrestrial habitat (excluding Antarctica) from the current 13% to 17% across the globe by 2020 (Aichi Target 11). With nearly 200 nations agreeing to the principles of the Aichi Targets, this could lead to the most rapid rate of land preservation in history, even if the targets are not fully achieved. Another key goal is to prevent the extinction of species already known to be threatened with future extinction and to achieve improvement towards sustainability in their populations by 2020 (Aichi Target 12). This ten-year framework for effective and urgent action by all countries and stakeholders to save biodiversity and enhance its benefit for people is about to be elevated to even greater prominence.

Fortunately, existing mechanisms provide a strong basis from which Aichi challenges can be addressed. With the combination of different international initiatives for biodiversity conservation (e.g. IUCN Red list of species and ecosystems, UN list of

protected areas, UN Sustainable Development Goals, Key Biodiversity Areas by BirdLife International), key indicator towards the Aichi Targets are likely to product comprises standards, governance and quality control, data sets, tools, capacity building and ongoing processes for derivation of biodiversity conservation strategies. Yet identifying tools that can be used to assess progress towards these ecosystem-based conservation targets remains a fundamental challenge (Collen and Nicholson, 2014; Tittensor et al., 2014). The emergence of ecosystem risk assessment protocols such as the IUCN Red List of Ecosystems (IUCN, 2018), which provide decision rules for classifying ecosystems according to their risk of collapse, can help address this challenge.

Biodiversity conservation and landscape ecology

Biodiversity has been defined as “the variety of living organisms considered at all levels of organization, including the genetic, species, and higher taxonomic levels, and the variety of habitats and ecosystems, as well as the processes occurring therein” (Meffe and Carroll, 1997). Although the concept of genetic variation can be specific to the level of genetic diversity within an individual, in terms of biodiversity and landscapes, it is best viewed at a population level (Gutzwiller, 2002). On the other hand, biodiversity at community and ecosystem level is often characterized by a variety of species-diversity indices that quantify the number of species (richness) and the relative abundance of those species (evenness) (Whittaker, R. H., & Likens, 1975). The objective of biodiversity conservation is the long-term maintenance of populations or species or, more broadly, of ecosystems. As many of the threats are

related to human land use, virtually all conservation issues are ultimately land-use issues (Gutzwiller, 2002).

Landscape ecology is an interdisciplinary field that studies landscape structure, function, and change (Forman and Godron, 1986). Although landscape ecology provides a spatial systems perspectives, its application in biodiversity conservation and management has been lagging (Forman and Godron, 1986). Likewise, biodiversity conservation actions have not been fully utilized for the advancement of landscape ecology (Liu and Taylor, 2004). Given these needs and potential benefits, key future studies may be to identify links and ways of bridging the gaps between landscape ecology and biodiversity conservation.

Spatial patterns and habitat fragmentation

Basic knowledge of species richness patterns and species distributions within a region is a necessary starting point to predict species extinction under habitat loss, as well as to prioritize conservation efforts and designing conservation areas (Margules and Pressey, 2000). Because organisms are distributed neither uniformly nor at random in nature, ecologists have begun to realize the importance of not only biotic response to species occurrences, but also the influence of spatial patterns and relationship (Liebhold and Gurevitch, 2002). Therefore, spatial pattern is essential to understanding the consequences of fragmentation and habitat loss for wildlife understanding the response of a species to a spatial structure (Collinge, 2001).

Landscape spatial pattern is defined as the composition and configuration of spatial elements in the landscape (Turner et al. 2003). In particular, habitat fragmentation

can be measured by quantifying changes in the spatial structure of the landscape, which refers to the spatial relationship between patches or fragments (Turner et al. 2001). These measurements are made through spatial metrics or indices of landscape, and its use is very useful, as they can provide information about the occurrence of deforestation and fragmentation (Li and Wu 2004). These rates can be applied to landscape thematic maps, which can be generated from satellite images (Kerr and Ostrovsky 2003).

The changes produced by the fragmentation are reflected in the spatial structure of the landscape as the size, shape or position of the fragments in the landscape (Turner, Gardner and O'Neill, 2001). Some studies have applied levels of landscape as the size of fragments suggest that high levels of fragmentation are associated with predominance of smaller sized fragments (Fitzsimmons, 2003). Other indices such as insulation and as fragments have also been applied to assess the degree of fragmentation of ecosystems, reporting higher levels of fragmentation dominated by fragments with greater isolation and regular shapes (Bustamante and Castor, 1998; Echeverria *et al.*, 2006).

Not all species depend on habitat area, isolation and landscape context equally (Tschamtkke *et al.*, 2002). (1) Habitat specialists are more affected by habitat loss than generalists, (Warren *et al.*, 2001). (2) The surrounding landscape is inhabitable for habitat specialists, but at least partly habitable for generalists, supporting the prediction that habitat isolation affects habitat specialists more than generalists (Jonsen and Fahrig, 1997). (3) High landscape diversity in the surrounding matrix provides more different habitat types for generalists or species with other habitat

preferences, supporting the prediction that landscape diversity enhances the number of generalists, especially at edges, but hardly specialists (Jonsen and Fahrig 1997).

Fragmentation and loss of natural habitats are of global concerns due to negative implications on biodiversity conservation (Wiens and Moss, 2005; Fraterrigo, Pearson and Turner, 2009). Anthropogenic activities have modified the natural environment to the point that the most common landscape is a mosaic of human settlements, farmlands and fragmented natural ecosystems surrounding protected areas (Cox, Dickman and Hunter, 2004).

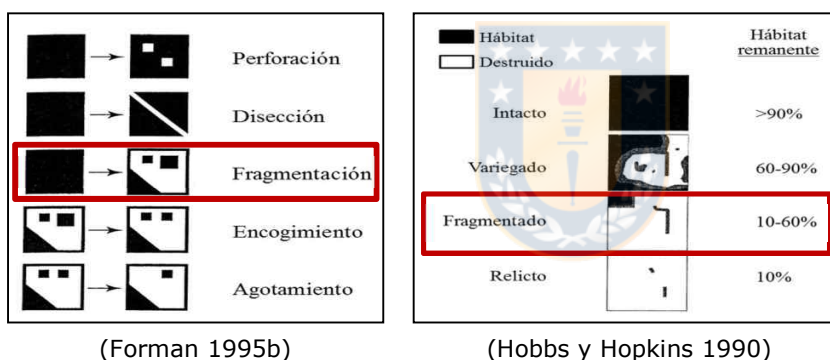


Figure 1. Different classifications of habitat fragmentation

Habitat fragmentation is an active and dynamic process resulting in the reduction in size and isolation of natural systems over time (Cox et al. 2004). According to Bennett and Saunders (2010), “fragmentation” is defined as the changes that occur when contiguous natural habitats are broken into small and scattered remnants.

Different classifications of landscape change have been identified in terms of structural thresholds (Forman and Godron, 1986; McIntyre and Hobbs, 1999) or the prevalent land use (Hobbs and Hopkins, 1990). In addition to these classifications,

a model that synthesizes four landscape states (intact, variegated, fragmented and relictual) was proposed by merging the previous classifications of landscape change (McIntyre and Hobbs 1999) (Figure 2). According to Forman's (1995) models, the current classifications of landscape change are typically represented by a decrease in connectivity and remaining cover, and an increase in edge effects. On the other hand, Bennett et al. (2003) characterized fragmentation by: a) loss of natural habitat in the landscape, b) natural habitat size reduction, c) isolation of habitat fragments and, d) human use of the matrix surrounding isolated fragments increase and intensified.

Island biogeography & metapopulation theory and fragmentation impacts

Island biogeography theory emphasizes the roles of area and geographical isolation as the main determinants of species diversity. Based on the assumption that colonization rates are determined by the degree of geographical isolation and extinction rates are determined by the size (area) of the island, the theory predicts that species richness should be positively correlated with island size and negatively correlated with the degree of isolation (MacArthur and Wilson, 1967). This presents a "nonequilibrium" view of ecological communities in the sense that species composition is constantly changing over time (Chaves *et al.*, 2002). According to this view, species diversity in a local community reflects a dynamic balance between colonization (arrival of new species) and extinction of species already present in the community. Island biogeography theory ignores functional differences among species and, in recent formulations (He *et al.*, 2005), explicitly considers all species to be ecologically equivalent.

Metapopulation theory is a popular basis for conserving species in patchy or fragmented environments (McCullough, 1996). Most studies of metapopulations consider the dynamics of populations divided into a number of subpopulations that exchange migrants and that may be subject to local extinction and recolonization (Hanski, 1997). Tilman *et al.*, (1994) considered the order of extinctions in relation to competitive dominance. This concept is specifying the number or proportion of extant species predicted to become extinct as the species community reaches a new equilibrium after habitat fragmentation. It can also be applied to single-species metapopulations by estimating the number or proportion of local populations that are predicted to become extinct (Bulman *et al.* 2007; Hanski *et al.* 1996).

Fragmentation is a dynamic process in which the habitat is progressively reduced into smaller patches that become more isolated and increasingly affected by edge effects (Forman and Godron, 1986; Turner, Gardner and O'Neill, 2003). And, it has effects not only on almost all ecological patterns and processes, but also on species extinction. The major impact of fragmentation is species loss due to habitat loss and size reduction (Cox, Dickman and Hunter, 2004; Moser *et al.*, 2007; Mapelli and Kittlein, 2009; Fitz-Gibbon *et al.*, 2013).

In general, larger patches of habitat contain more species and often a greater number of individuals than smaller patches of the same habitat (Turner *et al.* 2003), because many species cannot maintain viable populations in small habitat patches, which lead to local extinction and loss of biodiversity (Forman and Godron, 1986). Small habitat fragments contain small populations, which are more vulnerable to extinction due to environmental and demographic stochasticity (Shaffer, 1981;

Lande, 1988). In addition, small populations may be more prone to extinction due to the loss of genetic variation (Frankham, 1996). A decreasing population size may result in erosion of genetic variation through the loss of alleles by random genetic drift. In addition, increased selfing (in plants) and mating among closely related individuals in small populations may result in inbreeding and a reduction of the number of heterozygotes (Young, Boyle and Brown, 1996). Over the short term decreasing heterozygosity and the expression of deleterious alleles may result in reduced fitness (Keller LF and DM, 2002; Reed *et al.*, 2002). In the long term lower levels of genetic variation may limit a species' ability to respond to changing environmental conditions through adaptation and selection (Booy *et al.*, 2000). Also, patch size has effects on within-patch processes, such as nitrogen cycling and recruitment, and processes that connect patches, such as dispersion and movement (McIntyre and Hobbs, 1999).

Moreover, the degree of connectivity between patches of equally suitable habitat can constrain the spatial distribution of a species by making some areas accessible and others inaccessible. Once suitable habitat for a species of interest is characterized, determining whether the habitat is or is not spatially connected is often of interest (Turner, Gardner and O'Neill, 2003). Finally, edges provide both positive and negative effects in movement, mortality, feeding or reproductive subsidies and species interaction (Liu and Taylor, 2002). Fragmentation leads to the formation of marked edges creating a distinctive contrast in the structural and floristic composition between different patches (Kupfer, Malanson and Franklin, 2006) and they impact negatively species movement patterns through the landscape affecting species

ability to colonize adequate habitats and by limiting their access to food (Alderman *et al.*, 2005).

When the amount of native vegetation in a region drops below about 20-30%, fragmentation of the remaining vegetation may lead to disproportionate reductions in populations (Radford, Bennett and Cheers, 2005). Individual remnants lose species due to chance extinctions, the negative effects of habitat edges, the inability or unwillingness to disperse among isolated remnants and loss of key resources. These local species losses may accumulate until a species goes extinct locally and even regionally (Saunders, 1989). And, if species become isolated in a fragment, their survival depends on fragment size, quality and spatial configuration of remnants (Brouwers and Newton, 2009), species' dispersal ability and population dynamics (Lauga and Joachim, 1992; Castelletta, Thiollay and Sodhi, 2005).

In order to link landscape matters and species ecology, one of the central themes of landscape ecology is concerned with four features of spatial structure, such as (i) patch quality, (ii) boundaries, (iii) patch context and (iv) connectivity (Liu and Taylor, 2002).

The difference in landscape elements are generally structural and organisms translate into differences in threats and opportunities (Liu and Taylor, 2002). The elements of landscape are bounded and these boundaries play a critical role in determining the movement or flows of individuals, nutrients, materials or disturbances across a landscape (Wiens, Crawford and Gosz, 1985; Holland and Risser, 1991). A permeable boundary to flows contributes to the linkages among the

elements in a landscape, while an impermeable boundary relatively, on the other hand, reflects movements back into the patch and internalizes dynamics within landscape elements (Liu and Taylor, 2002). The surroundings of a patch in a landscape influence both patch quality and boundary, creating differences in within- and between-patch dynamics among neighboring landscape elements (Liu and Taylor, 2002). Connectivity, the ability of organisms to move through a landscape, is a function of a boundary permeability and patch contexts that characterize a given mosaic (Taylor *et al.*, 1993; Tischendorf and Fahrig, 2000).

Some studies have emphasized that connectivity is a priority attribute of the landscape spatial configuration that has to be recovered in order to improve biodiversity (Luque, Saura and Fortin, 2012; Tambosi and Metzger, 2013). This is mainly due to the fact that a reduction in connectivity can lead to a decline in species dispersal, gene flow and even local extinction (Bennett and Saunders, 2010). The sharpness of habitat edges and contrast across habitat boundaries can directly affect the connectivity, as they can determine the degree of movement of organisms across the landscape (Stevens *et al.*, 2006; Peyras *et al.*, 2013). A marked contrast in the community attributes at the interface (high-contrast forest edge) between natural habitats and human-related land can inhibit many organisms from readily moving across the edge (Wiens, Crawford and Gosz, 1985). Applying resistance estimates of high-contrast edges to improve connectivity have been highlighted for the implementation of wildlife corridors and biodiversity conservation (Zeller, McGarigal and Whiteley, 2012; Cushman *et al.*, 2013).

In many tropical countries, forest ecosystem fragmentation is occurring at an alarming rate by changes in human land use activities (Laurance 1999; Rudel and Roper 1997; Sanchez-Azofeifa, Harriss, and Skole 2001). The fragmentation of tropical forests is considered highly relevant to changes of ecological function and services and effect negatively on natural recovery after disturbances as catalysts of rapid ecological change (Holl and Aide 2011; Letcher and Chazdon 2009; Turner 2010). To date, the relationship between land use change by human activities and forest ecosystem fragmentation has been widely studied, described and interpreted by using landscape metrics, (e.g. mean patch size, edge density, mean shape index: O'Neil et al. 1999, Echeverria et al. 2006) or quantitative measurement (e.g. Morphological spatial pattern analysis: Soille and Vogt 2009, Landscape mosaic index: Ritters et al. 2009, and Forest connectivity index: Saura and Torné 2009). The specific studies of forest ecosystem fragmentation carried out in Tropical Andes are initiated in late 1980's (D. Armenteras, Gast, and Villareal 2003; Dolores Armenteras et al. 2006; Gómez, Anaya, and Alvarez 2005; Rodríguez Eraso, Armenteras-Pascual, and Alumbrosos 2013). In the eastern Andes of Colombia, Armenteras et al. (2003) have incorporated the degree of fragmentation for ecosystem conservation planning, using five landscape metrics; patch number, largest patch index, mean patch size, mean nearest neighbor distance, and landscape shape index.

Extinction debt

Species can initially survive habitat fragmentation but later become extinct without any further habitat change, which has been known as delayed extinction, also called

extinction debt (Tilman *et al.*, 1994; Malanson, 2008). The concept of extinction debt emerged from the Theory of Island Biogeography (MacArthur and Wilson, 1967). Because species richness on an island depended on a balance between colonization (a function of isolation) and extinction rates (a function of island area), islands that become smaller or more isolated should lose species.

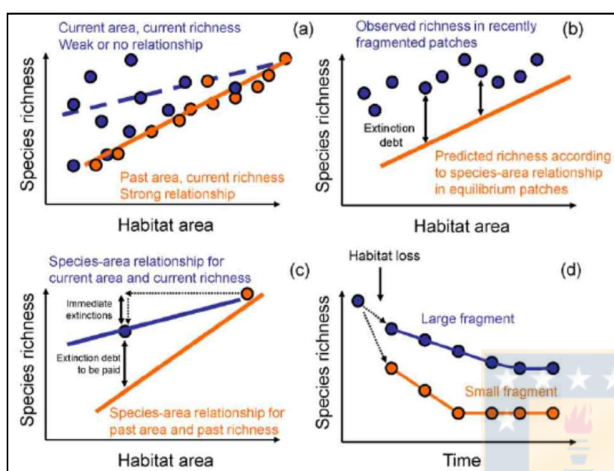


Figure 2. Four approaches for evaluating extinction debt from Kuussaari *et al.* (2009)

Based mainly on the type of data available, extinction debt may be detected, estimated and tracked. Most studies on extinction debt rely on assumption of community equilibrium from relationships between species richness and habitat variables, for example species–area relationships (SAR). In order to evaluate extinction debt, five groups of conceptual and empirical approach were classified by Kuussaari *et al.* (2009): (a) past and present habitat information; (b) comparison of stable versus unstable landscapes; (c) past and present information on species and habitats; (d) time series data on species and habitats; and (e) empirically based spatially explicit modeling for single species (Fig. 3). Many studies on extinction debt have examined species occupancy or richness at the level of past and current habitat

patch, because these data are available generally. If current species richness is better described by past than by present landscape variables, the presence of extinction debt can be assumed, although the magnitude of the extinction debt can, however, not be estimated using this approach (Kuussaari *et al.*, 2009).

However, all empirical approaches have clear limitations. It is important to target the habitat specialist species analyzing with appropriate habitat parameters and the scale, because extinction debt depends on specialization and scale (Batáry *et al.*, 2007; Kuussaari *et al.*, 2009; Cousins and Vanhoenacker, 2011). Moreover, high-quality historical data and long-term monitoring of community equilibrium is a key limiting factor for studying extinction debt (Lewis, 2006; Cousins, 2009).

Recent studies have revealed the importance of spatial configuration to detect extinction debt on rapidly fragmented landscape. In comparison with a large number of studies undertaken in fragmented grassland in Europe (Lindborg and Eriksson, 2004; Adriaens, Honnay and Hermy, 2006; Ranius, Eliasson and Johansson, 2008), few researchers have explored the species' responses to fragmentation in temperate forest (Vellend *et al.*, 2006; Noh *et al.*, 2018) and very little work has been done in Southern Hemisphere forests.

Conservation status of territorial ecosystems

Despite systematic methods for assessing the threat of extinction of individual species were notably advanced in recent years, there is few widely accepted scientific framework for tracking the status of Earth's ecosystem and identifying those with a high probability of loss or degradation (Nicholson, Keith and Wilcove,

2009; Keith *et al.*, 2013). Recognizing this gap, ecosystem-level extinction risk assessment began to develop comparable global standards in the last 10 years.

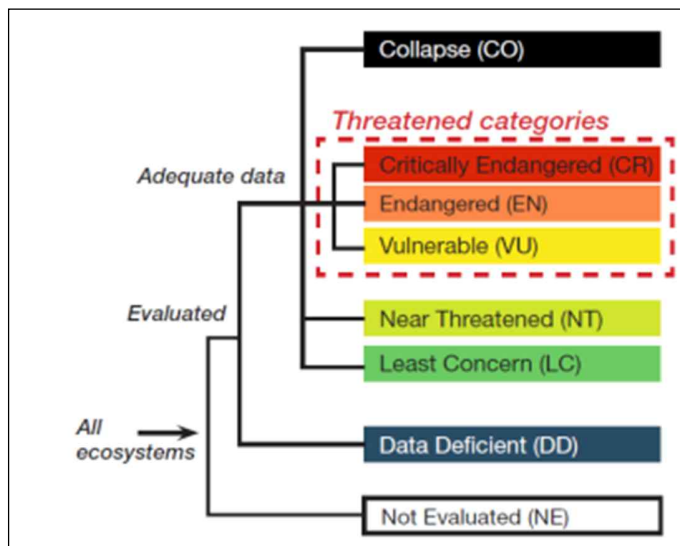


Figure 3. Structure of the IUCN Red List of Ecosystems Categories (IUCN, 2017)

The IUCN Red List of Ecosystems is a newly developed system for assessing the risk of ecosystem collapse, which is designed to evaluate four symptoms of ecosystem degradation: declining distribution, restricted distribution, degradation of abiotic environment and altered biotic processes. Among the application of five rule-based IUCN criteria of ecosystem, a criteria B, which assess the restricted distribution, must compile all the evidence required by subcriteria within estimating extent of occurrence (EEO) and area of occurrence (AOO). In addition, this conservation status assessments were then modified by consideration of the possible future impact of threats leading ecosystem degradation and conversion (Miles *et al.*, 2006; Alaniz, Galleguillos and Perez-Quezada, 2016; Tan *et al.*, 2017). Spatially explicit threats, e.g. forest fire, extreme weather events, forest

fragmentation, land conversion, invasion, are commonly eligible as threats of ecosystem distribution. In spite of quantification of actual EOO and AOO is applicable to diverse ecosystem classification, direct standardized measurement of the level of threat to ecosystem or species is relatively difficult because it depends on biological, social and economic factors specifically tailored for each region (Mace *et al.*, 2008). Moreover, as many systems show multiple threatening process acting together (Brook, Sodhi and Bradshaw, 2008), the combined negative effects and their interaction must be assessed for future conservation action.

A series of global assessment has been employed to provide an overview of the conservation status and distribution of territorial tropical ecosystems based on important determinates of ecosystem loss; land use, climate, atmospheric carbon dioxide, vegetation, human population, oil /gas and other known sensitivity of ecosystem to these change (Doumenge *et al.*, 1995; Tilman *et al.*, 2001; Miles *et al.*, 2006; Tarrasón *et al.*, 2010). Regional studies demonstrate that for tropical forests in Latin America, land-use change probably will have the largest effect, followed by climate change (Sala *et al.*, 2000; Salazar, Nobre and Oyama, 2007; Jarvis *et al.*, 2010). However, statements regarding the relative underlying drivers to area with high-diverse ecosystem are difficult to make with precision (Rodríguez Eraso, Armenteras-Pascual and Alumbremos, 2013). In many biodiversity hotspot regions and nations associated with rapid global change, it is still unknown how much of these endemic ecosystems are left, and how likely are they to disappear by predicting combination of local-scale forcing drivers and threatening process. Improved deforestation forecasting is necessary for implementing land management

strategies that target the development of local communities as well as future policy decision making.

The tropical Andes range is classified as a center of biodiversity and endemism in the world (Myers et al., 2000). The specific studies of ecosystem threats and risk assessment carried out in Tropical Andes are initiated in late 1980's (Armenteras, Gast and Villareal, 2003; Armenteras et al., 2006; Rodríguez Eraso, Armenteras-Pascual and Alumbrosos, 2013; Cuenca, Arriagada and Echeverría, 2016). These previous studies may suggest that two main threats of concern are human land use and system fragmentation in the region. Despite ecological importance, highest deforestation rate is occurred by human activities (logging, agriculture, grazing, etc.) during last 30 years in this region (Sierra et al., 1999; Mena, 2008; Tapia-Armijos et al., 2015; Cuenca and Echeverria, 2017). Recent studies are increasingly worrying negative effects on biodiversity by forest fragmentation in the tropical Andes (Cuenca and Echeverria, 2017; Cuesta et al., 2017). Notwithstanding the growing literature on threats which drives ecosystem collapse under land use change by anthropogenic disturbances, few studies have assessed simultaneously conservation status at ecosystem level, based on IUCN criterion.

Research questions

1. How does a temporal delay of response to habitat fragmentation exhibit in a rapidly changing landscape at the plant species and community level?

2. How did forest fragmentation change at the ecosystem level in Tropical Andes during last decades? In particular, which human land uses drive the forest ecosystem fragmentation in Tropical Andes?
3. How do forest fragmentation incorporate in the assessment of the potential collapse of forest ecosystems?

Hypotheses

1. Current richness of vascular plant species is more related to patch size and connectivity of past habitat than current habitat.
2. The richness of short-lived plants, as well as long-lived plants, exhibits a temporal delay of response to habitat fragmentation in a rapidly changing landscape.
3. Long-lived species' observations are more probable in smaller patch size in 2011 compared to in 1979 in a rapidly changing landscape.
4. It exists differences on human land use type associated to forest fragmentation at ecosystem level among three regions of Ecuador mainland.

General objectives

1. To detect extinction debt from relationship between current richness of vascular plants and habitat variables of 1979 and 2011 in fragmented temperate forests of Chile.
2. To quantify forest fragmentation and analyze its relationship with human land use in Ecuador mainland.
3. To assess the conservation status of forest ecosystems in Ecuador mainland.

Specific objectives

1. To evaluate relationships between current richness of vascular plants (short-lived plants, as well as long-lived plants) and spatial patterns (patch size and connectivity) of both the past and the current habitat in fragmented temperate forests of Chile.
2. To compare dwelling patch size of long-lived plants between 1979 and 2011 in fragmented temperate forests of Chile.
3. To quantify and graph forest change (deforestation, forest fragmentation) in Ecuador mainland during 1990-2000-2008-2014.
4. To relate the degree of forest fragmentation for 2014 to human land use at ecosystem level in Ecuador mainland.
5. To assess the conservation status of 64 forest ecosystems, using IUCN RLE criteria, in Ecuador mainland.

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CHAPTER 2

Extinction debt in a biodiversity hotspot: The case of the Chilean winter rainfall-valdivian forest¹

Introduction

Habitat fragmentation has become a major research theme in conservation biology (Fazey et al. 2005; Haila 2002) as one of the main threats to biodiversity (CBD Secretariat, 2001). Habitat fragmentation is associated with reduction of habitat area and increased isolation of remaining habitats (Laurance et al. 2002; Loreau et al. 2001), and leads to species declines and extinctions (Lienert 2004; Ouborg et al. 2006; Young et al. 1996; Young and Clarke 2000). Species extinction associated with habitat fragmentation begins as a result of deterministic and stochastic threatening processes which are exogenous (Bennett et al. 2003; Fischer and Lindenmayer 2007). Although a large proportion of exogenous extinctions typically occur almost immediately, endogenous threatening processes can cause local extinction for many years due to demographic, genetic or environmental variability in an isolated small-size

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population (Lindenmayer and Fischer 2006). This means local extinction of individual species is often characterized by considerable time-lags (= relaxation time) following habitat fragmentation because species do not always respond instantly to habitat changes (Dullinger et al. 2013; 2012; Gilbert and Levine 2013; Kuussaari et al. 2009). This is known as extinction debt (= time-delayed extinction), future extinction of species due to events in the past (Tilman et al. 1994) Such extinction debt implies that, although the species are still present, the conditions for species persistence are no longer met (Hanski and Ovaskainen 2002; Tilman et al. 1994).

Over the last two decades, many studies have attempted to understand such extinction debt and predict the extinction proneness of species and length of relaxation times. The following four factors about extinction debt have been reliable to date (Kuussaari et al. 2009; Lindenmayer and Fischer 2006). First, Lindborg (2007) showed that species vary in their sensitivity to habitat fragmentation depending on life history traits. It has been suggested that species with short generation and habitat specialization might be the most sensitive to habitat changes, and thus have shortest relaxation time, whereas these expectations remain largely unconfirmed by empirical data. (Allendorf and Hard 2009; Koh et al. 2004; Kuussaari et al. 2009). Secondly, the species response to habitat fragmentation, in many cases, depends on the patch attributes (e.g., spatio-temporal configuration of habitat patches) (Lindborg and Eriksson

2004). In many studies on extinction debt, habitat patch size and connectivity are considered as crucial spatial configuration (Cousins and Vanhoenacker 2011; Helm et al. 2006; Kolk and Naaf 2015; Piqueray et al. 2011). Thirdly, historical contingency can affect the results. For example, the time since the habitat was altered is crucial because of the possibility that extinction debt has already been paid via realized extinctions (Hanski 2000). Finally, the nature of the alteration, which refers to the spatial and temporal dynamics of landscape perturbation (e.g., perturbation frequency, size, intensity and return interval), affects the time of extinction after the metapopulation falls below an extinction threshold (Ovaskainen and Hanski 2002, 2004; Turner 2010b).

As knowledge of species richness in the past is rarely available, past and present habitat information can be mostly used to detect ongoing extinction debt from the relationships between current species richness and habitat variables (Lindborg and Eriksson 2004; Piessens and Hermy 2006; Ranius et al. 2008). Aside from the large number of studies undertaken in European fragmented grasslands and temperate forests (Adriaens et al. 2006; Cousins et al. 2007; Gustavsson et al. 2007; Lindborg and Eriksson 2004; Öster et al. 2007), few researchers have explored identifying the presence of extinction debt in the rest of the world (Vellend et al. 2006) and very little work has been done in the Southern Hemisphere's temperate forests. While the presence of an extinction debt has been largely tested in well-delimited areas, where natural cover

(forests or grassland) has been relatively stable over the last couple of centuries (Lindborg 2007; Piqueray et al. 2011; Vellend et al. 2006), extinction debt in rapidly changing landscapes has been little studied (Piqueray et al. 2011). Thus, empirical studies that specifically examine potential extinction debt have been focused on species occupancy or richness at the community level (Cousins et al. 2007; Lindborg and Eriksson 2004), whereas identifying individual species at increased risk of extinction in the near future is rare (Piqueray et al. 2011). Because response to habitat fragmentation is species-dependent (Lindborg 2007; Mildén et al. 2007), identification of particular species at a high risk of extinction among grouping species that share a common set of life history traits is vital for developing appropriate conservation action.

The Chilean coastal range (CCR) is identified as a center of biodiversity and endemism in the South American Temperate Rainforests (Armesto et al. 1998). Because of their geographic isolation, these rainforests are characterized by a highly endemic flora and fauna (Armesto et al. 1996), and are considered to be globally threatened ecosystems (Armesto et al. 1998; Myers et al. 2000b). During the last few decades, native forests in the CCR were rapidly destroyed, fragmented and associated with small size patches (<100 ha) of native forest surrounded by exotic species plantations (Aguayo et al. 2009; Echeverria et al. 2006a). Despite an ongoing trend of forest fragmentation and decline, this area still contains high species diversity and endemism among plants (Cavieres et al. 2005).

Therefore, we assumed that the distribution of many vascular plant species in the CCR is in disequilibrium with the present habitat distribution (Grez et al. 2005; Wolodarsky-Franke and Herrera 2011). The recent deforestation and forest fragmentation of the CCR, with its dramatic decline in patch area and connectivity could provide an excellent model system to test for the presence of an extinction debt in a wide range of ecological traits.

Our objective was to evaluate relationships between current richness of vascular plant species and spatial patterns of both the past and the current habitat in a rapidly changing biodiversity hotspot located in Chilean temperate forests. We tested the following hypotheses: 1) current richness of vascular plant species is more related to patch size and connectivity of past habitat than current habitat; 2) the richness of short-lived plants, as well as long-lived plants, exhibits a temporal delay of response to habitat fragmentation in a rapidly changing landscape and 3) long-lived species' observations are more probable in smaller patch size in 2011 compared to in 1979.

Materials and methods

Study site

The study was carried out in coastal temperate deciduous forest of *Nothofagus nervosa* and *Persea lingue*, with elevations ranging between 600 and 1000 m.a.s.l. (Luebert and Pliscoff 2006) (Figure 1). It is one of

six vegetation formations (ecosystems) located in the Nahuelbuta mountain range (NMR) of the CCR (37°11'-38°45'S, 73°13'O). The range is located in a transition zone of two ecosystems: Mediterranean vegetation and temperate rainforest. This feature of the study area allows an increase in plant species richness over the rest of the Chilean temperate forest (Hinojosa and Villagrán 1997). Native vascular plant species dwelling in the range are 690, of which 265 are endemic (Wolodarsky-Franke and Herrera 2011). However, recent data suggests a pessimistic future for this globally important area. Many specialist plants including nine representative trees (e.g. *Myrceugenia pinifolia*, *Araucaria araucana*, *Pitavia punctata*, *Gomortega keule* and *Prumnopytis andina*) have been evaluated as threatened species by IUCN (2017). The NMR's landscape structure over the past 40 years has been highly dynamic, with reductions in native forest cover of 33.2 % (Otavo and Echeverría 2017). Moreover, the high rate of native forest loss and turnover has been continuing (31.5% of native forest loss in unprotected areas between 1999 and 2008) (Altamirano et al. 2013) in a landscape where only 1.8% of the land is under protection (Wolodarsky-Franke and Herrera 2011). At present, the landscape is dominated by massive commercial plantations of exotic species of *Pinus radiata* and *Eucalyptus* spp. and large plantation industrial companies own most of the remaining native forests (Wolodarsky-Franke and Herrera 2011). Recognizing the continuing threats in this area of biologically important value, the NMR has been currently reported as a global conservation priority by The World Wildlife

Fund (WWF), The International Union for Conservation of Nature (IUCN), The World Resources Institute and Birdlife International (Owen 2007).

Table. 1. Description of land cover types defined in the study area

Land cover type	Description
Old-growth/secondary forest	Vegetation with native tree species >2m height, >25% canopy cover, including old growth forests with species as <i>Nothofagus nervosa</i> , <i>Araucaria araucana</i> , <i>Cryptocarya alba</i> , <i>Persea lingue</i> , <i>Gevuina avellana</i> and secondary forest with mainly <i>Nothofagus oblique</i> as dominant species.
Shrubland	Vegetation with native species <2m height, tree cover <25%, and shrubland cover of 10-75%.
Industrial plantation	Vegetation with planted exotic species like <i>Pinus radiata</i> and <i>Eucalyptus sp.</i> Including young and harvested plantations.
Crop field	Crops of wheat, maize and vegetables. Also including annual and semi-annual pastures.
Urban areas	Land occupied by cities, industry and other anthropogenic surfaces.
Open water	Land occupied by water bodies such as small lakes and ponds.
Bare ground	Cleared land, rocks and river beds.

Forest cover data

We obtained forest cover data from spring and summer Landsat satellite scenes (<10% cloudcover) acquired from different sensors: 1979 (Multi Spectral Scanner, MSS) and 2011 (Thematic Mapper, TM), which had been pre-processed and classified by the Laboratory of Landscape Ecology, University of Concepción through FONDECYT (Chilean National

Fond for Scientific and Technological Development) Research Project 1140531. Each image had been corrected geometrically, atmospherically, and topographically (Chander et al. 2009), with shadow reduced hillshade correction (Reese and Olsson 2011). Three resources were available to aid the image classification: 1) "Catastro", a GIS-based data set of thematic maps derived from aerial photographs and satellite imagery (CONAF 1999) which provide detailed information on land use and forest types; 2) forest cover maps generated from aerial photograph between 1978 and 1987 (Lara et al. 1989) for the 1979 image classification and 3) a set of 300 training sites used in the 2011 image classification. Owing to the availability of ground-based data sets, we used a supervised classification method (Echeverría et al. 2006a; Otavo and Echeverría 2017) and generated 30 x 30 m raster land cover maps using Arc-GIS (ESRI). The statistical decision criterion of Maximum Likelihood was used in the supervised classification to assist in the classification of overlapping signatures, in which pixels were assigned to the class of highest probability. A minimum mapping unit of greater than 5 pixels was used in this study. This enabled differences in data quality produced by the resampling of the MSS images to be minimized (Echeverría et al. 2006a). To increase the accuracy of the land cover classifications, we added calculated raster for the Normalized Difference Vegetation Index (NDVI), Simple Ratio (SR), Soil-Adjusted Vegetation Index (SAVI) and Land Surface Water Index (LSWI) (Huete 1988; Rouse Jr et al. 1974). In the

classification models, ridge regression was used to reduce collinearity among selected land use variables (Lesaffre and Marx 1993).

Apart from the land cover classification, a wholly independent verification data set was generated for an accuracy assessment of the classification results of each image. Importantly, three different sample points were used in the present study: 1) 300 training sites for 2011 image classification; 2) 452 verification points for the classification results of the 1979 image and 3) 653 verification points for the classification results of the 2011 image. The data used for accuracy assessments of land cover classification based on MSS in 1979 were conducted using aerial photograph-based land cover maps developed by Lara et al. (1989). The points were overlaid on the reference land cover maps and assigned to their respective classes. The accuracy of the land cover classification based on TM in 2011 was assessed between 2012 and 2013. Confusion matrices were constructed to compare the class identified for each sample point with the land covers derived from the satellite images. Overall agreement of the classification was 80.3% for the 1979 MSS, and 82.4 % for the 2011 TM (see Appendix 1).

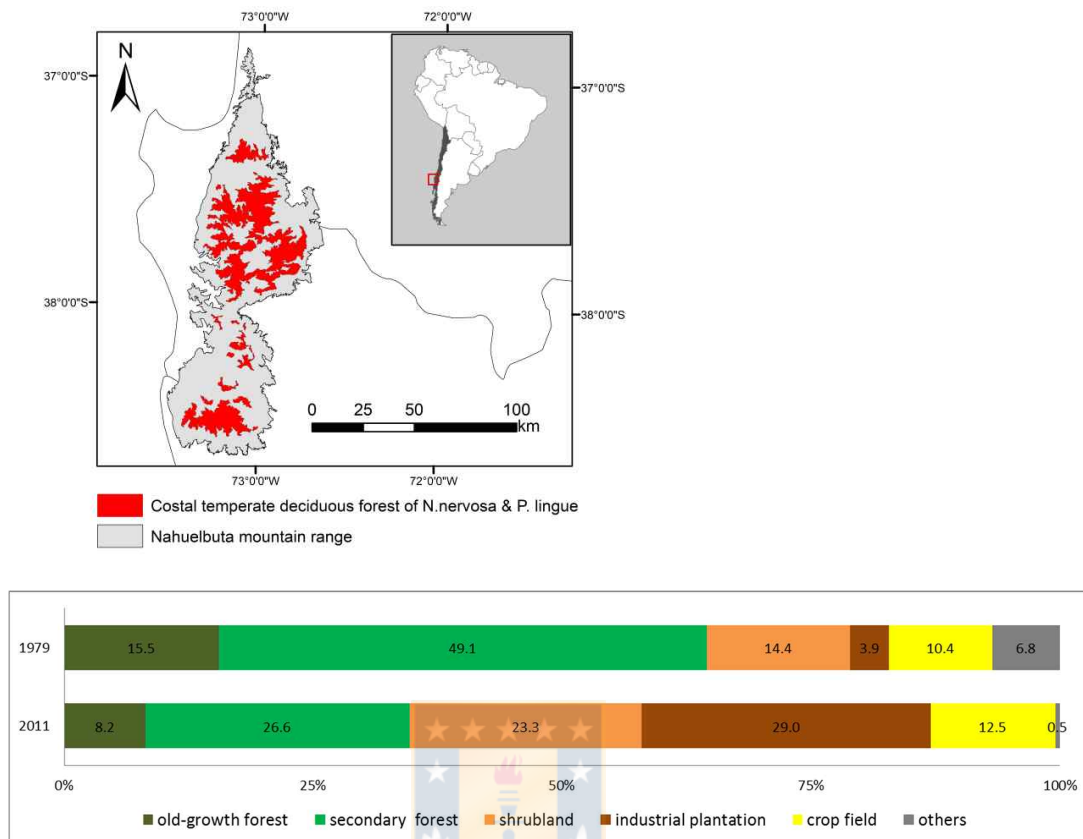


Figure 1. Map of study area including study ecosystem (Costal temperate deciduous forest of *N.nervosa* & *P.lingue*) and the major land cover types in 1979 and 2011.

In the present study, the following land cover types were distinguished: old-growth forest, secondary forest, shrubland, industrial plantation with exotic species, crop field, urban areas, open water, bare ground and others (Table 1). These categories were based on the land cover types defined by Catastro (CONAF et al., 1999). Furthermore, habitat maps were derived using two land cover types: secondary forest and old-growth forest. Both of these forests are dominated by tree species of height

greater than 2 m and covered by at least 50% of forest (CONAF et al., 1999) (Table 1).

Plant species richness

A total list of vascular plant species was completed by surveys from 46 sampling plots within 31 patches based on the land cover map in 2011 (Table 2). To ensure sampling independence, a minimum distance (1600 m, z-score: 1.20, p-value: 0.22) among fragments was calculated using Moran's *I* coefficient (Moran 1950), based on sample size. We randomly set up different numbers of sampling plots of 20 x 10 m (200 m²) according to patch size and accessibility. Each plot was divided into eight contiguous subplots of 5x5 m, and the current occurrence of all vascular plant species (Tree, shrub, herb, fern, climbing plant and epiphyte) were identified and recorded in each of these subplots during 2014-2015.

Table 2. Number of selected patches and sampling plots per patch size

Patch size (ha)	Number of selected patch	Number of sampling per patch
< 1	13	1
1-10	8	1
10-100	5	2
100-1000	5	3
Total	31	46

By considering that many native trees in South American temperate forests have lifespans of more than 200 years (Donoso et al. 2006), longevity of plant species were divided into two groups (Comes and

Kadereit 1998): 1) long-lived species referred to as trees and 2) short-lived species to herbs, ferns and climbings. Habitat specialization for long-lived species was classified by considering the following factors: 1) the type of species considered (endemic plant as specialist; Harrison 1999) ; 2) the number of habitat classes (specialists as species occurring in few habitat classes, while generalists in many habitat classes (Owens and Bennett 2000) and 3) local expert knowledge (an ability to determine which habitat is appropriate for which species; Gregory et al. 2005). The degree of habitat specialization was quantified as high, medium and low (see Appendix 2).

Analysis

The spatial patterns of habitat fragmentation were assessed using the following indices of FRAGSTATS (Echeverría et al. 2012; McGarigal et al. 2002; Nagendra et al. 2009): 1) patch density (number of habitat patches per 100 ha); 2) largest patch index (% of the landscape comprised by the largest habitat patch) and 3) total edge length (km). These indices provide information about the patterns of subdivision of forest patches, in which forest cover becomes disaggregated and isolated across the landscape (Forman and Godron 1986). The annual deforestation rate was calculated with the formula proposed by Puyravaud (2003) :

$$P = \frac{100}{t_2 - t_1} \ln \frac{A_2}{A_1}$$

Where A_1 and A_2 are the forest cover at times t_1 and t_2 .

For 31 forest patches, the habitat patch size (ha) was measured in GIS. In order to measure patch connectivity, we analyzed a simple proportional index – the proportion of old-growth forest and secondary forest, within different buffer distance around each patch. This index has been implemented and recommended when habitat patches are oddly shaped and relatively close together (Winfrey et al. 2005). Buffer distances of 100, 500 and 1,500 m were chosen to reflect the potential dispersal rates of different vascular plant species in temperate forests of South America (Donoso et al. 2006; García et al. 2009).

The relationship between plant species richness and patch variables was tested through regression analysis with Poisson error distribution and log link function. The dependent variables were species richness of (i) all vascular plants, (ii) long-lived plants (trees), (iii) long-lived specialist plants (specialist trees) and (iv) short-lived plants (herbs, ferns and climbings). The independent variables were: 1) current patch size; 2) past patch size; 3) current connectivity and 4) past connectivity.

In order to compare the maximum probability of a single long-lived species' presence between 1979 and 2011, we also investigated changes in patch size over the study area using Gaussian logit model (Lenoir et al. 2008; ter Braak and Looman 1986). Logistic regression is a generalized linear modeling technique using a logit link function computed with the

log-likelihood expression of Bernoulli distribution (presence/absence). We rewrote the model defined as a second-degree polynomial with logarithmic link function (Jamil et al. 2014):

$$\text{Logit}(p) = b_0 + b_1x + b_2x^2$$

where p is probability of presence, and x is patch size.

To track changes in species' dwelling patch sizes, we compared the dwelling information criterion between two periods. This parameter for dwelling patch size (DPS) can be easily found by the following formula (Ter Braak and Barendregt 1986; ter Braak and Looman 1986):

$$\text{DPS} = - \frac{b_1}{2b_2}$$

where b_1 and b_2 are the two coefficients of the Gaussian logit model using maximum likelihood. The DPS represents the habitat patch size at which the probability of presence reaches its maximum. All statistical analyses were made with open source software R (version 3.2.2).

Results

Habitat fragmentation and actual plant richness

Between 1979 and 2011, native forests were reduced by 53% in the study area (Figure 1). In 1979, there were 4,672 habitat patches covering an area of 115,132 ha with a mean patch size of 24.64 ha. By 2011, the mean patch size had declined to 1.44 ha, ranging from 0.09 to 5,731 ha.

During this period, habitat loss (old-growth forest plus secondary forest) occurred at a rate of $1.99\% \text{yr}^{-1}$ in the study area. The process of habitat fragmentation was accompanied by the loss of the largest forest patch, ranging from 43 % in 1979 to 9.42 % of the total area in 2011, while patch density and total edge increased between 1979 and 2011 (Table 3).

Table 3. Changes in landscape pattern indices for the native forests in 1979 and 2011

	1979	2011
Total area (ha)	115,132	60,846
Number of patches	4,672	42,094
Mean patch area (ha)	24.64	1.44
(a) Patch density	4.05	69.18
(b) Largest patch index (%)	43.72	9.42
(c) Total edge (km)	9,606	17,985

A total of 84 vascular plant species (36 trees, 17 shrubs, 19 herbs, 5 ferns, 6 climbing plants and 1 epiphyte) were identified in 31 habitat patches, with a mean richness of 14.77 per patch (SD = 4.16; range 4-23) (Table 4. A). There were 36 long-lived species (7.97 per patch; SD = 3.38), of which 18 species were specialists (3.161 per patch; SD = 2.29). Mean richness of short-lived plants was 3.19 per patch (SD = 1.76) (Table 4. A).

Table 4. (A) Current richness of different assemblage of plant species, n: species number. (B) Linear regression testing the relationship between

the current and past patch size and current richness of plant species, F :
 F -test value.

Plant assamblage	(A) Richness		(B) Patch size	
	n	mean \pm SD	current F	past F
All vascular plants	84	14.77 \pm 4.16	0.051	2.371
Long-lived plants	36	7.97 \pm 3.38	2.426	7.406 *
Long-lived specialists	18	3.16 \pm 2.29	3.160	11.650 **
Short-lived plants	31	3.19 \pm 1.75	1.505	1.786

* $P < 0.05$

** $P < 0.01$

Influence of past habitat on plant species richness

The study patch size ranged between 0.09 ha and 628.65 ha in 2011 and between 1.8 ha and 15,077 ha in 1979. The linear regression models revealed significant relationship between the past patch size and the current richness of long-lived plants and long-lived specialist plants (Table 4. B). Among them, richness for long-lived specialist plants was best explained by past patch size (Figure 2). The current richness of plant assemblages could not be explained by the current patch size of the native forest.

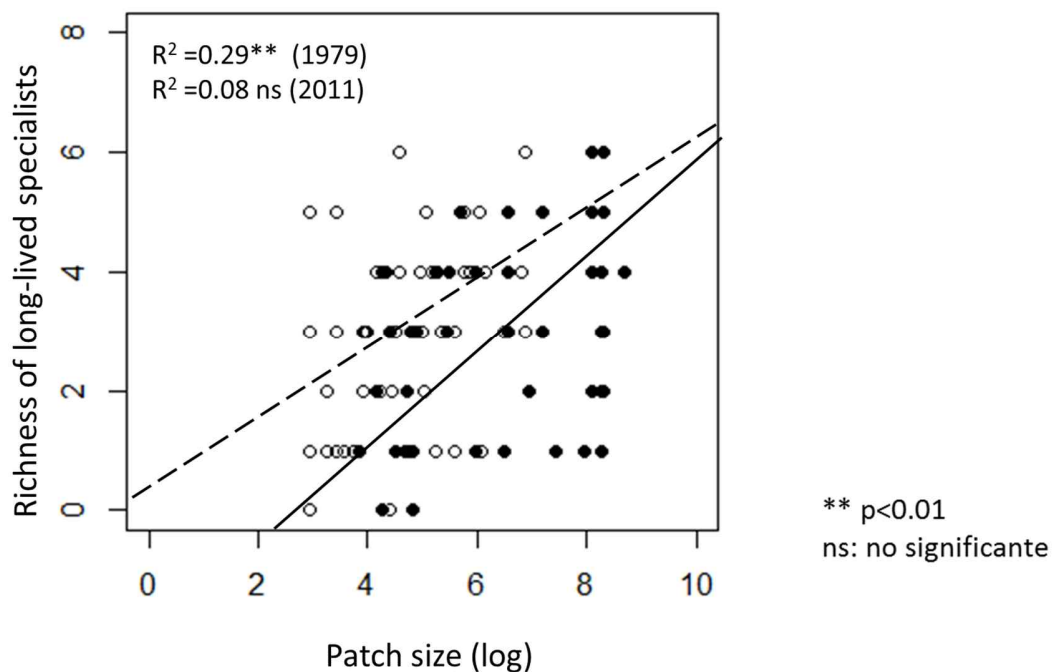


Figure 2. Generalized linear model for current richness of long-lived specialist plants and patch size in 1979 (solid line and symbols) and 2011 (dotted line and open symbols)

The connectivity index of study patches varied between 0.015 (isolated) and 0.972 (connected) in 1979, and between 0.02 and 0.941 in 2011. A positive significant relationship was found between past connectivity and the richness of different plant assemblages, except in short-lived plants. This strengthened as the buffer distance increased. Likewise, the model for long-lived specialist plants with a 1,500 m buffer was best explained by past connectivity (Table 5). Current connectivity had a mostly negative relationship with short-lived plant richness.

Table 5. Multiple regression of the current and past connectivity relationship on the current richness (β : regression coefficients, F : F -test value)

Buffer distance (the focal patch included)		All plant spp.		Long-lived plants		Long-lived specialists		Short-lived plants	
		β	F	β	F	β	F	β	F
100	current	-1.63	0.18	1.10	0.53	0.20	0.10	-2.10	-2.10
	past	5.18	4.28 *	4.78	6.25 *	2.88	4.60 *	0.38	0.38
	R ²	0.14		0.19		0.14		0.11	
500	current	-5.75	1.29	-1.30	0.01	-1.32	0.09	-1.82	1.15
	past	6.06	5.01 *	5.90	7.96 **	3.38	5.25 *	-0.53	0.19
	R ²	0.18		0.22		0.16		0.05	
1500	current	-12.7	4.85 *	-0.08	1.390	-4.22	0.84	-0.94	0.52
	past	8.82	4.83 *	9.74	9.77 **	6.69	9.87 **	-1.98	1.12
	R ²	0.26		0.29		0.28		0.06	

* $P < 0.05$

** $P < 0.01$

Changes of the single long-lived species' DPS

We computed the patch size of maximum probability of presence, also called dwelling patch size (DPS), within each period for 27 long-lived species that were best described by a unimodal bell-shaped model. The DPS of these species was reduced from 8,063 to 145 ha during the study period (Appendix 3.). Species patch size reduction between 1979 and 2011 was statistically highly significant [mean difference in DPS was 7918 ha, 95% CI for mean = 4700.2, 11136.1; student's paired sample t test, $t = 5.06$; $df = 26$; $P < 0.001$], amounting to an average of -267.5 ha per year. Current DPS was found at almost zero in seven long-lived specialists: *Araucaria araucana*, *Dasyphyllum diacanthoides*, *Drimys*

winteri, *Nothofagus nervosa*, *Prumnopitys andina*, *Saxegothaea conspicua* and *Weinmannia trichosperma* (Figure 3).

DISCUSSION

Detection of extinction debt

In this study, current species richness is generally better explained by past patch size and connectivity than by current patch size and connectivity, except in short-lived plants. If past landscape patterns explain current species richness better than the current landscape pattern (Kuussaari et al. 2009), this can be interpreted as evidence of an extinction debt. Consequently, an unknown proportion of the current vascular plants in the study area would be extinct.

Although the response to habitat fragmentation display different patterns of distribution of a particular organism, species that share the same ecological properties may show similar consistent patterns of changes (Dambrine et al. 1995). Studying richness within species groups that differ in their degree of habitat specialization may provide a more complete picture of the community-level consequences of habitat fragmentation than analyses focusing on total species richness (Brückmann et al. 2010; Reitalu et al. 2012). Species that have restricted ecological preferences (habitat specialists) are likely to be more strongly affected by habitat loss and fragmentation than species that have broader ecological tolerances and are able to occupy a wider range of habitats (generalists) (Devictor

et al. 2008; Polus et al. 2007). Additionally, the response to habitat fragmentation in long-lived specialists is slower than in other species groups in the same landscape (Krauss et al. 2010; Sang et al. 2010). Our results showed that long-lived specialist plants are best explained by past habitat area and connectivity (Table 4, Table 5) and confirmed that the detection of extinction debt clearly depends on the longevity and habitat specialization of study species (Cousins and Vanhoenacker 2011; Reitalu et al. 2012).

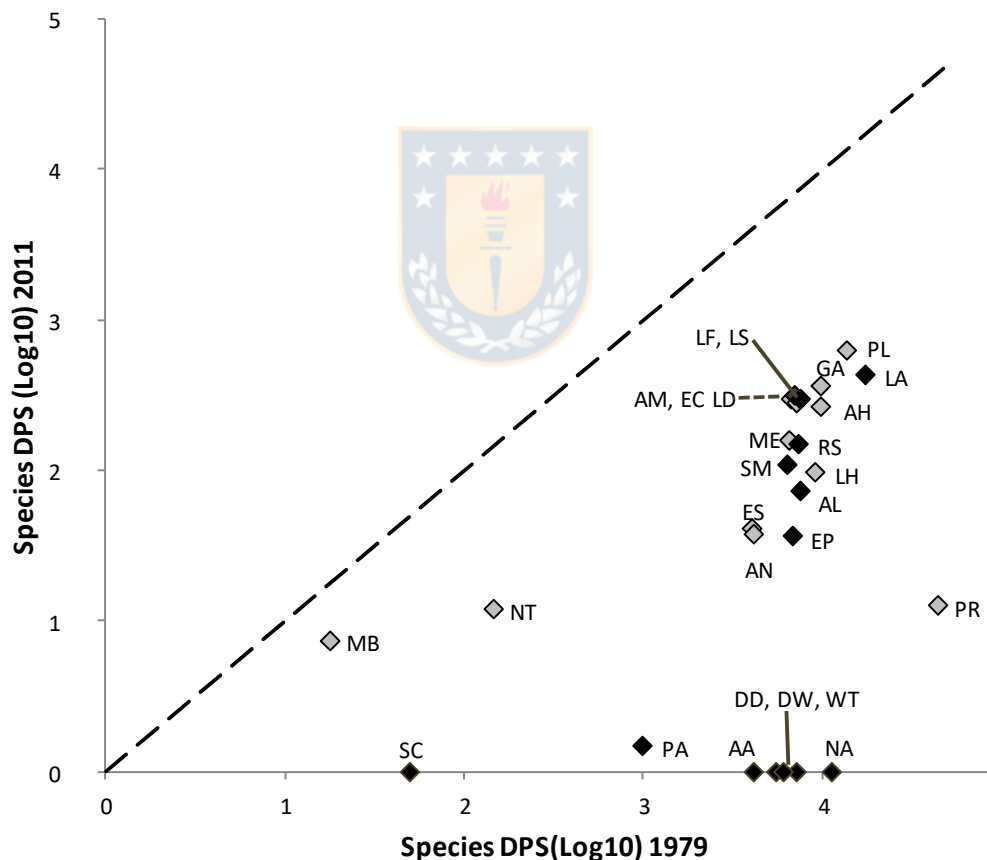


Figure 3. Changes in dwelling patch size (size value at maximum probability of presence) of single long-lived species ($n = 27$) for period

1979 and 2011. Each point represents one species: specialists are displayed as dark gray (◆) and solid line (n = 14), whereas remnant species are displayed as light gray (◇) and dotted line (n = 13). AA *Araucaria araucana*, AH *Aristotelia chilensis*, AL *Amomyrtus luma*, AM *Acacia melanoxydon*, AN *Azara dentata*, DD *Dasyphyllum diacanthoides*, DW *Drimys winteri*, EC *Eucryphia cordifolia*, EP *Escallonia pulverulenta*, ES *Acacia caven*, GA *Gevuina avellana*, LA *Luma apiculata*, LD *Lomatia dentata*, LF *Lomatia ferruginea*, LH *Lomatia hirsuta*, LS *Laurelia sempervirens*, NT *Nothofagus antarctica*, MB *Maytenus boaria*, ME *Myrceugenia exsucca*, NA *Nothofagus nervosa*, PA *Prumnopitys andina*, PL *Persea lingue*, PR *Pinus radiata*, RS *Rhaphithamnus spinosus*, SC *Sophora cassioides*, SM *Sophora cassioides*, WT *Weinmannia trichosperma*



In terms of relaxation time, a number of theoretical studies supported that species richness in patches was negatively correlated with time since fragmentation (Helm et al. 2006; Kuussaari et al. 2009; Saunders et al. 1991). Extinction debts are more likely in those landscapes where large-scale habitat destruction has occurred recently (Cousins 2009). However, field observations indicate the limited applicability of the relaxation time for describing the effect of habitat fragmentation on risks of species extinctions, varying in both space and time. In the temperate deciduous forests of Europe, for example, the extinction debt of forest plant species

was found to persist for more than a couple of centuries (Kolb and Diekmann 2005; Vellend et al. 2006), while other studies did not find any extinction debts over a similar period of time (Adriaens et al. 2006; Cousins et al. 2007). Likewise, studies from landscape with a large amount of remaining natural area supported the concept of an extinction debt, while highly fragmented landscapes did not provide any evidence of an extinction debt (Adriaens et al. 2006; Cousins 2009). We assumed that an extinction debt across a wider range of ecological traits may be identified in a rapidly changing landscape with recent fragmentation history and relatively large amounts of remnant forest area. Unlike our expectations, we could not detect any statistically robust effect of habitat configuration on the richness of short-lived plant species. This unpredictability of extinction debt of short-lived plants in the NMR may be explained as a combination of the following factors: 1) in southern Chile, alien herbaceous species are widely introduced by anthropogenic disturbances (logging and grazing) in understory layer (personal observation, Bustamante and Castor, 1998 Pauchard and Alaback, 2004, Braun and Vogt, 2014); 2) in the study area, secondary forest occupied 77% of native forest area. These secondary forests with relatively open canopy may have changed microclimates (light, wind, soil moisture, etc.) that have often been linked to the performance of native herb species (Bierzychudek 1982; Matlack 1994; Tilman 1990) and 3) changes in plant reproduction and recruitment (flowering, seed production, etc.) of understory native species due to current abiotic and biotic alteration

(personal observation, McKinney and Goodell, 2010, Schemske et al., 1978, Smith-Ramirez and Armesto, 1994).

Change of long-lived species' DPS during 1979 - 2011

To identify species which their current occurrences are highly connected to past habitat and have not yet paid an extinction debt, we investigated changes in long-lived species' dwelling patch size (DPS) over the study periods. Our results provided strong evidence that 27 long-lived species have already distributed in severely size-reduced patches in 2011 compared to 1979 (Figure 3, appendix 3).

We showed that many long-lived specialist plants have experienced notable decline in DPS over about 30 years (Figure 3), and are more affected and threatened by habitat fragmentation. Among them, *A. araucana* and to the *P. andina* are vulnerable (VU), and *S. conspicua* is near threatened (NT) according to the UICN red list of threatened species (2015) (Appendix 2). Although these specialist trees associated with small-size habitat patches seem to persist at present, their additional biological attributes that are directly linked with key threatening processes could act synergistically to elevate extinction risk and change this pattern quickly (Davies et al. 2004; Gaston et al. 1997; Lindenmayer and Fischer 2013; Valiente-Banuet et al. 2015). Two additional attributes of concern are population size and dispersal ability. Piqueray et al. (2011) showed that it is likely that grassland specialist species which cannot maintain relatively large populations in small habitat patches require larger habitat

patches. In the fragmented landscape of the CCR, several specialist trees were shown to have reduced population density in small size habitat. For example, *W. trichosperma* shows a reduced germination rate as well as a lower seedling survival rate in small patches (Lusk and Pozo 2002). Echeverría et al. (2007) observed that the seedling abundance of *P. andina* was significantly related to only large-sized forest patches. Poor dispersal ability might have another effect that increases the extinction risk which disrupts metapopulation functioning (Honnay et al. 1999; Jamoneau et al. 2011). Many previous studies suggested that specialist trees in our study area have traits associated with short-distance dispersal. For *N. nerviosa*, fruit dispersal only reaches between 50 and 100 m per year (Donoso Zegers 1993) and the average distance of pollen dispersal is also very short (<35m) (Marchelli et al. 2012). *A. araucana* is known as a gravity-dispersed species with poor dispersal distance due to the seed size (2-4 cm long, 1-2 cm wide) and heavy weight (3.5-5.0 g) (González and Veblen 2006). Conversely, the population density and seed dispersal of shade-intolerant generalist trees (e.g., *P. lingue*, *G. avellana*, *El. Cordifolia*, *L. dentate*) are likely to benefit from forest edges in a fragmented habitat surrounded by plantations of exotic species (Bustamante and Simonetti 2005; Echeverría et al. 2007).

Value of small size patches in rapidly changing landscape

Despite strong evidence of the importance of large areas of native vegetation (Gaston and Spicer 2013; Rosenzweig 1995) under

mechanisms underlying the species-area relationship (Arrhenius 1921), extinction debt is proportionally higher in recently fragmented small size patches than in historically fragmented large patches (Kuussaari et al. 2009). Patch-level extinction may occur faster in small patches than in large patches due to differences in susceptibility to disturbance between small and large patches (Sheil and Burslem 2003). Habitat fragmentation of Chilean temperate forests is associated with a rapid decrease in patch size (Echeverria et al. 2006a). A high number of plant species were observed in small-sized patches in the present study, which typically had shorter relaxation time. Although expanding the habitat area may be a straightforward solution to prevent future extinction of specialist species in the NMR, preserving or restoring large reserve areas is usually difficult because of the high costs involved.

In the CCR, a positive relationship between patch quality/connectivity and plant abundance/richness was reported in fragmented landscapes dominated by small size patches (Robledo-Arnuncio et al. 2014; Vergara et al. 2010). Similarly, Wulf and Kolk (2014) demonstrated that increasing the quality of small patches reaps more benefits than increasing patch area in the fragmented landscapes of Australia. Diamond (1975) found that if small size patches of remnant habitats are widespread in the landscape, they might be a contributing factor to a relatively lower extinction debt or longer relaxation time by enhancing habitat connectivity. Likewise, configuring the spatial arrangement to minimize isolation may

help to ensure that many of the species with extinction debts do not reach their extinction threshold in the long term (Paltto et al. 2006).

With these considerations, specific recommendations for the management of small-size habitat patches in the NMR should include 1) maintaining current quality and quantity of old-growth forests, which are at risk of rapid decline and degradation of their structure without active management (15.5% of old-growth forest rate in 1979, declining to 8.2% in 2011); 2) restoring habitat quality of secondary forests targeted for the re-development of old-growth attributes (Bauhus et al. 2009); 3) managing soften boundaries or creating buffers around ecologically sensitive areas, in order to reduce edge effect and enhance landscape connectivity (Lindenmayer and Fischer 2006; López-Barrera 2004) and 4) identifying and designing adequate landscape configuration based on the remnant small-size patches to enhance specialist species' persistence and resilience, because it is likely the current landscape configuration no longer supports the species habitat requirements (Suding et al. 2004; Tambosi and Metzger 2013).

Suggestions for preventing future biodiversity loss in the NMR

Early detection of an extinction debt of long-lived specialist plants can be considered a benefit to begin habitat restoration and conservation actions in an adequate time in the study area. However, as responses to habitat fragmentation are species-dependent, conservation actions which target species groups are inadequate. Future monitoring plans of extinction

dynamics must focus on single species of long-lived specialist plants rather than focusing on species richness or a set of species. In the fragmented landscapes of biodiversity hotspot, it may be crucial to identify and prioritize the conservation of species with extinction proneness over those that have no significant risk.

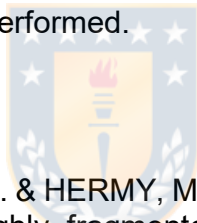
Finally, because a large portion of the study area is privately owned (Carruthers and Rodriguez 2009), participation and cooperation of the private sector is a key element to address biodiversity conservation goals in the NMR. It will be necessary to create appropriate conditions for the participation of all relevant stakeholders in the planning and implementation of conservation initiatives.

Conclusion

Our analyses provide the first evidence of potential future loss of many vascular plant species in South American temperate hotspot. However, as long as a species that is predicted to become extinct still persists, we believe that extinction debt provides new challenges and opportunities to current biodiversity conservation. However, it depends on valid timing because extinction debt payment is in progress and imposes an undefined deadline. Instead of waiting to launch large-scale conservation projects, we suggest immediate implementation of local or small-scale restoration projects in order to mitigate the existing extinction debt.

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Annex

A. 1. Confusion matrices for the two images

Classified data	Reference data							User's accuracy (%)
	Old-growth/secondary forest	Shrub -land	Industrial plantation	Crop field	Urban areas	Open water	Bare ground	
A. 1979 image								
Old-growth/secondary forest	69	5	12	0	0	0	0	80
Shrubland	5	55	1	1	0	0	0	89
Industrial plantation	14	7	53	0	0	0	0	72
Crop field	0	8	1	49	3	0	10	69
Urban areas	0	0	0	4	47	0	4	85
Open water	0	0	0	0	0	40	0	100
Bare ground	0	2	0	6	6	0	50	78
Total	88	77	67	60	56	40	64	
Omission error (%)	22	29	21	18	16	0	22	
Producer's accuracy (%)	78	71	79	82	84	100	78	
Overall classification accuracy: 80.3								
B. 2011 image								
Old-growth/secondary forest	126	12	18	0	0	0	0	81
Shrubland	14	121	5	4	0	0	0	84
Industrial plantation	11	14	86	0	0	0	0	77
Crop field	0	8	1	60	5	0	5	76
Urban areas	0	0	0	4	50	0	0	93
Open water	0	0	0	0	0	40	0	100
Bare ground	0	2	0	8	4	0	55	80
Total	151	157	110	76	59	40	60	
Omission error (%)	17	23	22	21	15	0	8	
Producer's accuracy (%)	83	77	78	79	85	100	92	
Overall classification accuracy: 82.4								

A. 2. List of long-lived species and their habitat specialization degree in

Nahuelbuta Mountain Range

Family	Scientific name	Habitat specialization*
Aextoxicaceae	<i>Aextoxicon punctatum</i> Ruiz & Pav.	M

Anacardiaceae	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	G
Araliaceae	<i>Pseudopanax laetevirens</i> (Gay) Franchet	M
Araucariaceae	<i>Araucaria araucana</i> (Molina) K. Koch	S
Asteraceae	<i>Dasyphyllum diacanthoides</i> (Less.) Cabrera	S
Celastraceae	<i>Maytenus boaria</i> Molina	G
Cunoniaceae	<i>Weinmannia trichosperma</i> Ruiz & Pav.	S
Elaeocarpaceae	<i>Aristotelia chilensis</i> (Molina) Stuntz	G
Escalloniaceae	<i>Escallonia pulverulenta</i> (Ruiz & Pav.) Pers.	S
Eucryphiaceae	<i>Eucryphia cordifolia</i> Cav.	M
Fabaceae	<i>Acacia melanoxylon</i> R. Br.	G
	<i>Sophora cassioides</i> (Phil.) Sparre	S
Gomortegaceae	<i>Gomortega keule</i> (Molina) Baill.	S
Icacinaceae	<i>Citronella mucronata</i> (Ruiz & Pav.)D. Don	M
Lauraceae	<i>Cryptocarya alba</i> (Molina) Looser	G
	<i>Persea lingue</i> (Miers ex Bertero) Nees	G
Mimosaceae	<i>Acacia caven</i> (Molina) Molina	S
	<i>Laureliopsis philippiana</i> (Looser) Schodde	S
	<i>Laurelia sempervirens</i> (Ruiz & Pav.) Tul.	S
	<i>Peumus boldus</i> Molina	G
Myrtaceae	<i>Amomyrtus luma</i> (Molina) Legrand & Kausel	S
	<i>Luma apiculata</i> (DC.) Burret	S
	<i>Myrceugenia exsucca</i> (DC.) Berg.	M
Nothofagaceae	<i>Nothofagus nervosa</i> (Poepp. & Endl.) Oerst.	S
	<i>Nothofagus dombeyi</i> (Mirb.) Oerst.	G
	<i>Nothofagus obliqua</i> (Mirb.) Oerst.	G
	<i>Nothofagus pumilio</i> (Poepp. & Endl.) Krasser	M
	<i>Nothofagus antarctica</i> (Forster) Oerst.	M
Pinaceae	<i>Pinus radiata</i> D. Don	G
	<i>Prumnopitys andina</i> (Poepp. ex Endl.) de	
Podocarpaceae	Laub.	S
	<i>Podocarpus saligna</i> D. Don	S
	<i>Saxegothaea conspicua</i> Lindl.	S
Proteaceae	<i>Embothrium coccineum</i> J.R. & G. Forster	G
	<i>Gevuina avellana</i> Molina	G
	<i>Lomatia dentata</i> (Ruiz & Pav.) R. Br.	S
	<i>Lomatia ferruginea</i> (Cav.) R. Br.	S
	<i>Lomatia hirsuta</i> (Lam.) Diels ex J.F.Macbr.	G

Rutaceae	<i>Pitavia punctata</i> (Ruiz & Pav.)Molina	S
Salicaceae	<i>Azara dentata</i> Ruiz & Pav.	S
Verbenaceae	<i>Rhaphithamnus spinosus</i> (Juss.) Moldenke	S
Winteraceae	<i>Drimys winteri</i> J.R. & G. Forster	S

*S: highly habitat specialized species (specialist), G: lowly habitat specialized species (generalist), M: middle-level habitat specialized species

A. 3. List of long-lived species that were best described by unimodal bell-shaped model (n=27) displaying a highly significant Gaussian logit model (at the 0.001 level) for both periods of 1979 and 2011. DPS: dwelling patch size, VU: Vulnerable, NT: Near threatened

Species	Red list (UICN 2015)	Precedence * *	DPS (Ha)	
			1979	2011
<i>Araucaria araucana</i>	VU	Native	4156	0
<i>Aristotelia chilensis</i>	-	Native	9850	268.92
<i>Amomyrtus luma</i>	-	Native	7569	73.60
<i>Azara dentata</i>	-	Endemic	4080	41.01
<i>Dasyphyllum</i>				
<i>diacanthoides</i>	-	Native	7103	0
<i>Drimys winteri</i>	-	Native	5505	0
<i>Eucryphia cordifolia</i>	NT	Native	6931	312.24
<i>Embothrium coccineum</i>	-	Native	4126	37.82
<i>Escallonia pulverulenta</i>	-	Endemic	6872	36.50
<i>Acacia caven</i>	-	Native	7569	301.63
<i>Gevuina avellana</i>	-	Native	9880	368.99
<i>Luma apiculata</i>	-	Native	17243	429.39
<i>Lomatia dentata</i>	-	Native	6668	295.74
<i>Lomatia ferruginea</i>	-	Native	7125	284.05
<i>Lomatia hirsuta</i>	-	Native	9042	96.64
<i>Laurelia sempervirens</i>	NT	Endemic	7569	301.63
<i>Maytenus boaria</i>	-	Native	18.02	7.48

<i>Myrceugenia exsucca</i>	-	Native	6518	157.12
<i>Nothofagus nervosa</i>	-	Native	11189	0
<i>Nothofagus antarctica</i>	-	Native	144.9	12.12
<i>Prumnopitys andina</i>	VU	Native	991.3	1.50
<i>Persea lingue</i>	NT	Native	13836	621.24
<i>Pinus radiata</i>	-	Introduced	43934	12.74
<i>Rhaphithamnus spinosus</i>	-	Native	7281	147.90
<i>Saxegothaea conspicua</i>	NT	Native	49.57	0
<i>Sophora cassioides</i>	-	Endemic	6441	109.21
<i>Weinmannia trichosperma</i>	-	Native	6019	0

*Donoso et al. (2006)



CHAPTER 3

National assessment of forest ecosystem fragmentation in Ecuador: strong needs of landscape management in Tropical Andes²

Introduction

Since rapid economic development, natural system decline and fragmentation is one of the core drivers of global change and has huge implications for ecosystem functioning and conservation (Fahrig 2003). The impacts of habitat fragmentation can arise in the face of primarily biotic change, primarily abiotic change and a combination of both, including extinction, disruption of trophic interactions and increased susceptibility to disturbances (e.g. logging, fires and invasive species) (Holl and Aide 2011; Laurance et al. 2002; Letcher and Chazdon 2009; Turner 2010a). Some changes result in system degradation retaining some original characteristics as well as novel elements, whereas larger changes will result in system replacement or collapse (Hobbs et al. 2009). Previously the majority of efforts to conserve biodiversity have been focused on species, communities or their habitat under forest fragmentation (Wiens and Moss 2005; Wu 2013a), although there is clearly a need to more effective conservation policy focusing on ecosystems which include fundamental biotic and abiotic components and ensure the protection of a

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sufficient portion of all ecosystems in these regions (Bennett and Saunders 2010; Hughes et al. 2000; Schmidt 1996; Sierra et al. 2002)

In many tropical countries, forest ecosystem fragmentation is occurring at an alarming rate by changes in human land use activities (Laurance 1999; Rudel and Roper 1997; Sanchez-Azofeifa, Harriss, and Skole 2001). The fragmentation of tropical forests is considered highly relevant to changes of ecological function and services and negative effects on natural recovery after disturbances as catalysts of rapid ecological change (Holl and Aide 2011; Letcher and Chazdon 2009; Turner 2010). To date, the relationship between land use change by human activities and forest ecosystem fragmentation has been widely studied, described and interpreted by using landscape metrics: e.g. mean patch size, edge density, mean shape index:(Echeverria et al. 2006b), O'Neil et al. 1999 or quantitative measurement (e.g. Morphological spatial pattern analysis: (Soille and Vogt 2009), Landscape mosaic index: (Riitters et al. 2009), and Forest connectivity index: (Saura and Torn 2009). The specific studies of forest ecosystem fragmentation carried out in Tropical Andes are initiated in late 1980's (Armenteras et al. 2003; Armenteras et al. 2006; Gmez et al. 2005; Gómez Mora et al. 2005; Rodríguez Eraso et al. 2013). In the eastern Andes of Colombia, Armenteras et al. (2003) have incorporated the degree of fragmentation for ecosystem conservation planning, using five landscape metrics; patch number, largest patch index, mean patch size, mean nearest neighbor distance, and landscape shape index.

Despite such studies are abundant and has received much attention in tropics, very few studies showed the relationship between the degree of forest fragmentation and

human land use at the ecosystem level. Over the past 50 years, human have changed ecosystems more rapidly and extensively than in any comparable period time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fiber and fuel (Duraiappah and Naeem 2005). Thus, this ecosystem degradation (e.g. fragmentation) by human activities is associated with a substantial and largely irreversible loss in the diversity of life on Earth, and leads to the degradation of many ecosystem services, increased risks of nonlinear changes and the exacerbation of poverty for some groups of people (Duraiappah and Naeem 2005). The challenge of reversing the degradation of ecosystems while meeting increasing demands may initiate to understand what changes happened in ecosystems under interaction with human land use.

Nevertheless, one of the major reasons, why the relationship between forest fragmentation and human land use at ecosystem level has been little studied, is that there is no universally accepted global taxonomy of ecosystems (Keith et al. 2013) to date. This means the classification and delimitation of ecosystems are rarely studied and available in most countries. In addition, human-fragmentation study is the lack of a commonly accepted method for quantifying fragmentation (Butler et al. 2004). As not all landscape metrics can capture the entire extent of forest fragmentation in a particular landscape (Cain et al. 1997), most studies about forest fragmentation have been described the relationship with human land use based on landscape metrics. In many studies on ecosystem fragmentation, increase in number of patches, decrease in patch size and increased patch isolation together address the quantitative measures of fragmentation (Echeverria et al. 2006a; kyoung Noh et

al. 2018). Although these studies have often magnified the controversy because of correlation among multiple landscape metrics (e.g. edge, isolation and area), together with these correlative observation, Ibanez et al (2014) reveal that fragmentation has multiple simultaneous effects that are interwoven in complex ways and that operate over potentially long time scales. With these considerations, to date few researchers have shown the relationship between human land use and forest ecosystem fragmentation using an explicit single forest fragmentation index at ecosystem level. For example, Butler et al. (2004) have produced a forest fragmentation index for western Oregon and western Washington that combined measures of forested area, percentage edge and interspersion. Likewise, Abdullah and Nakagoshi (2007) developed a single forest fragmentation index based on a combination of three landscape metrics: (i) non-forest area; (ii) forest edge, and (iii) patch size coefficient of variation, in the state of Selangor, Malaysia. A central benefit of quantifying forest fragmentation through a single index is feasible to be statistically correlated to human land use. The impact of human land use on specific forest ecosystem fragmentation can support political justification of sustainable landscape planning and management based on contribution to human well-being (Wu 2013).

Ecuador is located in tropical Andes range and known as one of the most mega-diverse worldwide per surface unit, with 1,250 species of plants belonging to 136 different families registered in 1 km² (León et al. 2011; Valencia et al. 1994) and also home of high-diverse terrestrial ecosystems that exhibits very high levels of endemism (Olson and Dinerstein 2002). Despite its ecological importance, highest rates of forest decline and fragmentation were reported last 30 years (Cuenca et al.

2016; Mena 2008a; Sierra and Stallings 1998; Tapia-Armijos et al. 2015). This recognition is resulting in a collective shift in empirical studies on biodiversity and biological conservation in the country (Cadilhac et al. 2017; Cuenca and Echeverria 2017b; Cuesta et al. 2017; Lessmann et al. 2014). In the conservation point of view, one of the most remarkable achievements in Ecuador might be the establishment of official identification, classification and delimitation of the national-wide ecosystems (MAE, 2013), after initiative framework of the ecosystem classification by Sierra et al. (1999) and Josse et al. (2003). Unfortunately, literature review reveals that this baseline information has not fully exploited to generate a monitoring system of national ecosystem changes. For example, Cuesta et al. (2017) used this ecosystem maps and species distribution models to identify priority areas for biodiversity conservation in mainland Ecuador. Likewise, MAE (2015) attempted to assess ecosystem fragmentation and risk based on the ecosystem map (considered all land cover type inside ecosystem), using patch numbers, mean patch size, and patch size coefficient of variation. Their studies complement current conservation efforts, but cannot provide relationship between the degree of forest ecosystem fragmentation and human land use at ecosystem level to better design conservation strategies integrated into land use planning and management in Ecuador.

Against this background, we aimed to (i) quantify and graph forest change (deforestation, forest fragmentation) in Ecuador mainland during 1990-2000-2008-2014 on different spatial scales, and (ii) relate the degree of forest fragmentation to human land use at ecosystem level in 2014. The present study considered 'ecosystem' as standard reporting unit for national level assessment and have

utilized landscape metrics to analyze forest fragmentation. The present study is allowing us to answer the following research question: 1) How did forest fragmentation change in Tropical Andes during last decades? ; 2) Which human land use drive the current forest ecosystem fragmentation in Tropical Andes?

This paper provides a broad review of how recent forest fragmentation at ecosystem level has affected by practices in human land use. By illuminating the critical gaps between forest conservation strategies and actual practices employed in human land use, we suggest ecosystem-level conservation implementation based on a land-use-related planning and sustainable development in Ecuador, which involve significant changes in policies, institutions, and practices that are not currently under way.

Materials and methods

GIS data

The baseline information used consisted of satellite images (Landsat – 5 TM) obtained in 1990, 2000, 2008 and 2014, which were classified by the Ecuadorian Ministry of Agriculture (MAGAP) and Ministry of the Environment (MAE), using LANDSAT 4 and 5 TM for 1990, LANDSAT ETM+ for 2000, LANDSAT ETM+ and ASTER for 2008 (MAE 2012), and LANDSAT 8 OLI, LANDSAT ETM+ and Rapid Eye satellite images for 2014 (MAE, 2015). Except the thematic map of the 2014, which was classified by supervised classification using data from field surveys (at least 30 sites were monitored for each land use type), the other three maps of previous dates were generated by using unsupervised classification (MAE, 2015).

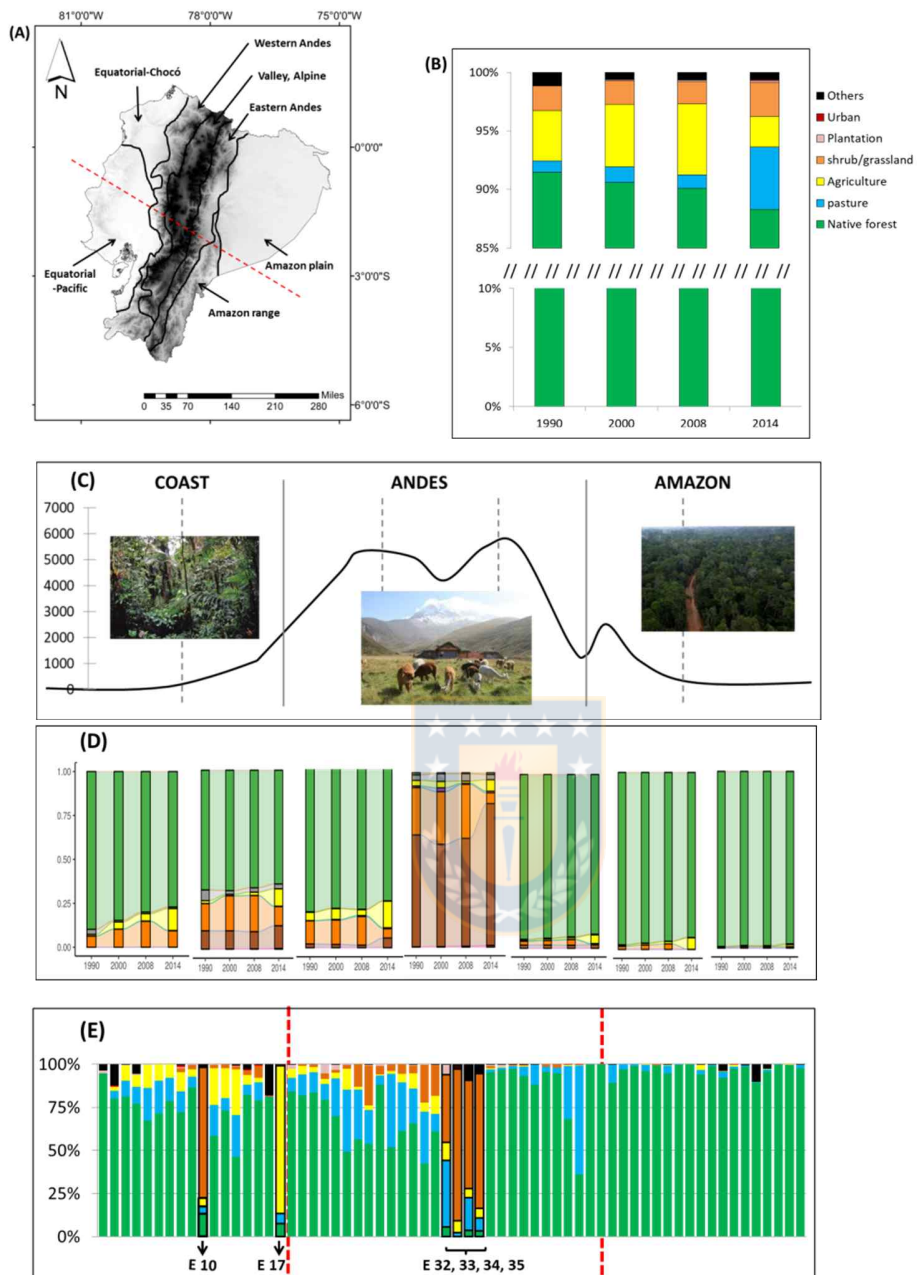


Figure 1. (A) Ecoregions of continental Ecuador. Elevation detail is shown. **(B)** The major land cover types inside 64 forest ecosystems in 1990, 2000, 2008 and 2014. **(C)** Distribution of each ecoregion's elevation. Cutting section of a geological map based on a red dotted line (A). **(D)** The major land cover types and changes of

ecoregions (n=7) in 1990, 2000, 2008 and 2014, **(E)** The major land cover types that have replaced the original forest ecosystem of single ecosystems (n=64) in 2014. Ecosystems containing forest area <10 % (n=6) are marked with black outline.

In the present study, seven land cover types were mainly considered for the land use change analysis (Table 1). Furthermore, human land use was distinguished using seven land cover types: industrial plantation (PLT), pasture (PST), annual farming (AFM), permanent farming (PFM), semipermanent farming (SFR), inhabited area (HBT) and infrastructure (IFR) (Table 1). To perform the analysis of ecosystem-level deforestation and forest fragmentation, this study considered category of native forest, which cover about 14 million hectares, as the following four forest types:

- 1) *Higher mountain forest*: trees reach 10-15 m of height with thick and sometimes gnarled trunks, with adventitious roots occupying up to 70 m² (Buytaert, Iñiguez, and Bièvre 2007; Sierra et al. 1999).
- 2) *Cloud mountain forest*: Trees reach a height of 15-25 m. The underwood is very rich and epiphytes and mosses are very abundant. Persistent presence of fog at the vegetation level, which significantly reduces incident solar radiation and evapotranspiration (Céleri and Feyen 2009).
- 3) *Lower mountain forest*: The canopy height can reach 20-35 m tall with sporadic trees of 40 m. Composed by different layers such as canopy, sub-canopy, shrub and herbaceous species (Valencia, Balslev, and Paz Y Miño C 1994).
- 4) *Foothill forest*: Forest transition between the foothills of Eastern and Western ranges and Amazonian forest. Substrate mainly composed by volcanic rocks

and sediments of recent origins. The canopy height reaches 30 m and sub-canopy and understory are very dense (Bendix et al. 2009).

Table 1. Description and source of land cover types defined in the study area

Main land use	No.	Land cover type	Description	Source
Forest	1	Native forest	Vegetation with native tree species, including higher mountain forest, cloud mountain forest, lower mountain forest and foothill forest.	MAE (2016)
Shrub/Grassland	2	Shrubland	Area with a substantial component of non-arboreal native woody species. It includes degraded areas in transition to dense canopy.	MAE (2011)
	3	Grassland	Native grassland with a spontaneous growth, which do not receive special care, and use for sporadic grazing or protection	MAGAP (2012)
	4	Paramo	Typical ecosystem of tropical Andes, located above 3400 m.a.s.l. Vegetation can reach 50 cm height.	MAGAP (2012)
Industrial plantation	5	Industrial plantation (PLT)	Vegetation with planted exotic species, including young and harvested plantations.	MAE (2011)
Pasture	6	Pasture (PST)	Cultivated grassland, dominated by introduced species of gramineas and leguminosas, for feeding livestock	MAGAP (2012)
Agriculture	7	Annual farming (AFM)	Cultivated land for annual crops	MAGAP (2012)
	8	Permanent farming (PFM)	Mainly orchards and lands for permanent crops and vegetables.	MAGAP (2012)
	9	Semipermanent farming (SFM)	Cultivated land for 2 or 3-year-cycle crops	MAGAP (2012)
Urban	10	Inhabited area (HBT)	Land mainly occupied by housing and buildings for communities and public services	MAGAP (2012)
	11	Infrastructure (IFR)	Land occupied by roads, industries and other anthropogenic surfaces (e.g. shrimp fishery)	MAGAP (2012)
Others	12	Natural water	Land occupied by natural water bodies such as small lakes and ponds.	MAGAP (2012)
	13	Artificial water	Land or flowing water associated with anthropic activities and water resource management	MAGAP (2012)
	14	Bare ground	Cleared land, rocks and river beds.	MAGAP-IEE (2012)
	15	Glacier	Snow and ice	MAGAP-

In Ecuador, the definition, classification and delimitation of total 91 national territorial ecosystems (87 natural ecosystems with four other systems such as: area of human intervention, water, other areas and no information) are established and completed on the basis of the following factors: 1) physiognomy; 2) bioclimate; 3) biogeography; 4) geoform; 5) general flooding; 6) Phenology; 7) bioclimatic floor, and 8) substratum. (MAE 2013). According to the vegetation physiognomic classification (forest, shrubland and grassland), we selected 64 forest ecosystems including two mangroves (Table 2), among 87 natural territorial ecosystems in whole Ecuador.

Table 2. Spatial scale (region-ecoregion-ecosystem), altitudinal range and Forest Fragmentation Index (FFI: proportion of non-continuous forest in a given ecosystem) of 64 natural forest ecosystems in the Ecuadorian continent

Region	Ecoregion	Cod e	Forest Ecosystems (forest vegetation type)	Altitudinal range (m)	FFI 2014
COAST	Equatorial -Chocó	E1	Flood alluvial plain forest of the Equatorial Chocó	50-200	10.68
		E2	Equatorial Chocó mangrove	0-20	32.20
		E3	Evergreen forest of the Equatorial Chocó lowland	0-300	22.18
		E4	Flood intertidal plain forest of the Equatorial Chocó	0-50	23.14
		E5	Seasonal evergreen forest of Equatorial Chocó lowlands	0-300	41.70
		E6	Piedmont seasonal evergreen forest of the Chocó coastal range	200-400	36.16
		E7	Low montane evergreen forest of Chocó coastal range	>400	25.81
	Equatorial -Pacific	E8	Semideciduous forest of the Jama-Zapotillo lowland	0-300	33.50
		E9	Semideciduous forest of the Equatorial Pacific coastal range	>200	19.29
			Low forest and deciduous shrubland of the Jama-Zapotillo lowland	0-400	87.37
		E11	Piedmont seasonal evergreen forest of the Equatorial Pacific coastal range	200-400	54.04
		E12	Low montane seasonal evergreen forest of the Equatorial Pacific coastal range	400-860	31.64
		E13	Seasonal evergreen forest of the Jama-Zapotillo lowland	0-400	65.46

		E14	Deciduous forest of the Jama-Zapotillo lowland	0-400	21.09
		E15	Deciduous forest of the Equatorial Pacific coastal range	>200	23.95
		E16	Jama-Zapotillo mangrove	0-10	30.11
		E17	Seasonal flood alluvial plain evergreen forest of the Jama-Zapotillo	0-300	98.62
ANDES	Western-range	E18	Piedmont evergreen forest of the western Andean range	300-1400	18.51
		E19	Low montane evergreen forest of the western Andean range	1400-2000	23.58
		E20	Montane evergreen forest of the western Andean range	2000-3100	23.16
		E21	High montane evergreen forest of the western Andean range	3100-3600	39.45
		E22	Piedmont seasonal evergreen forest of the western Andean range	300-1400	35.28
		E23	Piedmont seasonal evergreen forest of the Catamayo-Alamor	400-1600	63.45
		E24	Low montane seasonal evergreen forest of the Catamayo-Alamor	1600-2000	56.93
		E25	Montane evergreen forest of the Catamayo-Alamor	2200-2900	58.11
		E26	High montane evergreen forest of the Catamayo-Alamor	2900-3400	38.30
		E27	Low montane evergreen forest of the Catamayo-Alamor	1600-2200	60.31
		E28	Piedmont evergreen forest of the Catamayo-Alamor	400-1600	55.02
		E29	Piedmont semideciduous forest of the Catamayo-Alamor	400-1600	38.20
		E30	Low montane semideciduous forest of the Catamayo-Alamor	1600-2200	63.05
		E31	Piedmont deciduous forest of the Catamayo-Alamor	400-1600	42.67
		E32	Low montane deciduous forest of the Catamayo-Alamor	1600-2200	96.81
	Valley,	E33	Semideciduous forest and shrubland of the North Valleys	1200-2600	99.99
	Alpine	E34	Semideciduous forest and shrubland of the South Valleys	1200-2000	99.40
		E35	Páramo evergreen forest	3200-4100	99.76
	Eastern-range	E36	High montane evergreen forest of the north-eastern Andean range	3000-3700	18.51
		E37	Montane evergreen forest of the north-eastern Andean range	2000-3000	2.55
		E38	Low montane evergreen forest of the north-eastern Andean range	1200-2000	2.95
		E39	Piedmont evergreen forest of the north-eastern Andean range	400-1200	8.73
		E40	Low montane evergreen forest of the south-eastern Andean range	1660-2200	13.97
		E41	Montane evergreen forest of the south-eastern Andean range	2200-3000	7.59
		E42	High montane evergreen forest of the south-eastern Andean range	3000-3400	25.06
		E43	Piedmont evergreen forest of the south-eastern Andean range	400-1650	42.54
		E44	Piedmont semideciduous forest of the south-eastern Andean range	500-1300	78.61

AMAZO N	Range	E45	Low montane evergreen forest of Galeras	1300-1700	0.00	
		E46	Piedmont evergreen forest of Galeras	600-1300	0.00	
		E47	Piedmont evergreen forest of the C3ndor-Kutuk3 range	350-1400	13.81	
		E48	Low montane evergreen forest of the C3ndor-Kutuk3 range	1400-1900	3.12	
		E49	Montane evergreen forest of the C3ndor-Kutuk3 range	1900-2400	1.42	
		E50	Piedmont evergreen forest on sandstone plateaus of the C3ndor-Kutuk3 range	350-1400	4.89	
		E51	Montane evergreen forest on sandstone plateaus of the C3ndor range	1900-2700	1.10	
		E52	Piedmont evergreen forest on limestone outcrops of the Amazonian range	600-1400	6.08	
		E53	Low montane evergreen forest on sandstone plateaus of the C3ndor-Kutuk3 range	1400-1900	0.62	
		E54	Evergreen forest on sandstone plateaus of the C3ndor range in the lower Ecuadorian Amazon	243-550	0.02	
		Plain	E55	Evergreen forest of the Aguarico-Putumayo-Caquet3 lowland	168-350	8.24
			E56	Flood alluvial plain palm forest of the Amazon	171-350	1.19
			E57	Flood river (originated in the Andean and Amazonian ranges) alluvial-plain forest	164-350	8.87
			E58	Lowland evergreen forest of the Napo-Curaray	170-350	3.30
	E59		Flood alluvial plain forest of the Amazon	158-350	1.41	
	E60		Flood forest and lacustrine-riparian vegetation of the Amazonian black water	170-350	10.59	
	E61		Flood river (originated in the Amazon) alluvial plain forest	158-350	4.29	
	E62		Evergreen bamboo forest of the Amazonian lowland	196-500	0.00	
	E63		Evergreen forest of the <i>Tigre-Pastaza</i> lowland	166-350	0.48	
	E64		Evergreen forest of the <i>Pastaza</i> fan-shaped lowland	197-350	2.69	

Deforestation rate, change rate of land cover types and forest fragmentation index






The annual deforestation rate was calculated with the formula proposed by Puyravaud (2003):

$$P = \frac{100}{t_2 - t_1} \ln \frac{A_2}{A_1}$$

Where A_1 and A_2 are the forest cover at time t_1 and t_2 .

In order to calculate change rate of land cover types, a cross-tabulation procedure between the classifications was processed with ArcGIS 10.5; gains and losses were calculated as proposed by Pontius et al. (2004). Fragmentation analyses were performed using the approach by Forest Area Density (FAD), which is a simple metric of fragmentation as a contextual variable associated with a given forest pixel (Riitters and Wickham 2012). The result is a set of a map showing FAD values in [0, 100]% for neighborhood area over each forest pixel (Table 3). If forest is not fragmented in the vicinity of a given forest pixel, then by definition FAD equals 1.0 for a neighborhood with contains that forest pixel. On the other hand, if forest is fragmented in the vicinity, then the value of FAD is less than 1.0 in proportion to the degree of fragmentation (i.g. number of non-forest pixels) within the neighborhood. At the present study, we evaluated FAD with square neighborhood areas of length 27 pixels and the FAD values were classified into the following forest fragmentation classes:

Table 3. Summary of FAD fragmentation class thresholds, names and color assignment

FAD class	Color	FAD range
1 Rare		FAD < 10 %
2 Patchy		10% ≤ FAD < 40%
3 Transitional		40% ≤ FAD < 60%
4 Dominant		60% ≤ FAD < 90%
5 Interior		90% ≤ FAD ≤ 100%

To characterize forest fragmentation in each forest ecosystem using a forest fragmentation index (FFI), we first summed continuous forest using ratio between the number of FAD $\geq 40\%$ classified as “Interior”, “Dominant” and “Transitional”, divided by the total number of pixels in that forest ecosystem (Vogt 2018). Then, FFI was defined as a proportion of non-continuous forest in a given ecosystem.

Analysis

The relationship between FFI and current human land use was tested through regression analysis with Poisson error distribution and log link function. The independent variables were the percentage of human land uses in potential forest ecosystems in 2014 (Table 1). The dependent variables were FFI of grouping ecosystems that share a common set of the following biogeographic characters and forest fragmentation rate; (1) region; and (2) FFI degree in 2014. All statistical analyses made with open source software R (version 3.2.2).

Results

Land use change in forest ecosystems

Between 1990 and 2014, native forests have been cleared approx. 454,000 ha in 64 forest ecosystems of Ecuador mainland, averaging 7100 ha per each ecosystem (Figure 1.B, Figure 2.B). Deforestation rate of 64 forest ecosystems significantly increased between 1990-2000 and 2000-2014 [mean difference in deforestation rate was 0.6%, 95% CI for mean = -0.15, 0.45; student's paired sample t test, $t = 2.18$, $df = 63$, $p < 0.01$].

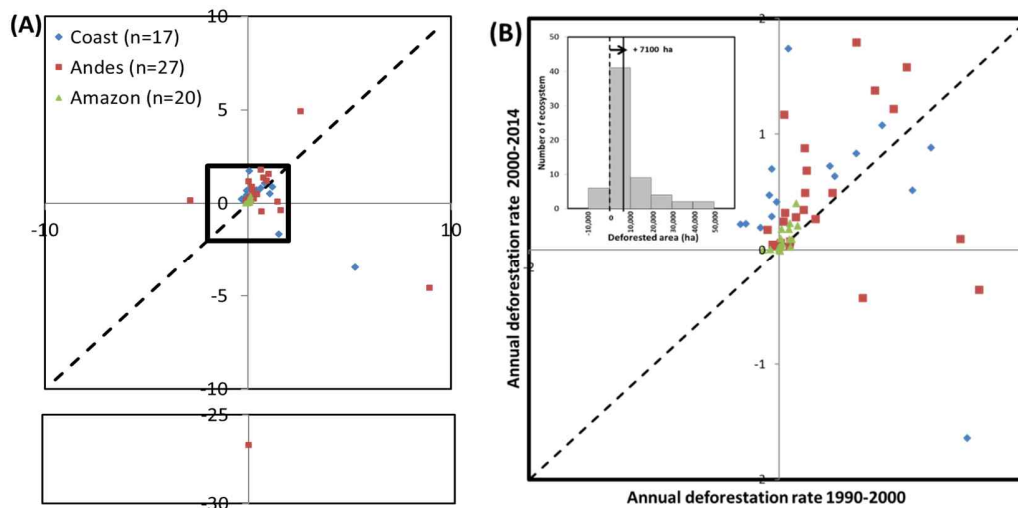


Figure 2. Scatter diagrams of forest ecosystems annual deforestation rate for the periods 1990-2000 and 2000-2014. **(A)** Changes in annual deforestation rate of single forest ecosystem ($n=64$) for the periods 1990-2000 and 2000-2014. Each point represents one forest ecosystem. Solid black outline is zoomed out **(B)**. **(B)** Changes in annual deforestation rate of single forest ecosystem ($n=59$), excluding extreme data ($n=5$) **(Inset)** The distribution of the ecosystem's differences in deforested area between 1990 and 2014. The vertical dotted line marks zero shifts, and the vertical solid line marks the median shift. The arrow describes the direction of the shift.

In 64 forest ecosystems, E44 showed the highest deforestation rate of $3.95\% \text{ yr}^{-1}$, followed by $1.34\% \text{ yr}^{-1}$ in E23 and $1.30\% \text{ yr}^{-1}$ in E32. In 2014, percentage of forest cover was under 10 % of spatial extent in six forest ecosystems: E33 (0.11 % of forested area), E35 (1.7 %), E34 (3.44 %), E32 (5.65 %) and E17 (7.4 %) (Figure 1.E). During the whole study period, five forest ecosystems showed an increase in

area: E4 (8.3% of gain in forest area), E33 (1700%), E35 (29.69%), E56 (0.70%) and E64 (0.03%).

In forest ecosystems, human land use (agriculture, industrial plantation, urban and pasture) showed a rapid increase of 54% over 24 years (Figure 1.B). At national level, agriculture was the major anthropogenic land use in 1990 (4.3 %), 2000 (5.4 %) and 2008 (6.1 %), but declining to 2.6 % by 2014. In 2014, pasture, rising from 1.1 % in 2008 to 5.4 % in 2014, became the largest single human land cover class. The other notable features of the data are the relatively stable proportion of the natural shrubland/grassland (≈ 2 %) during 1990 to 2008, and an increase (≈ 3 %) in 2014. Industrial plantation and urban areas showed a slight increase in area across the study period.



Land cover changes did not occur at equal rates during all time intervals in the three regions (Figure 3). The most intensive change was located in the Coast, where frequent exchanges between pasture and agriculture land as well as pasture, shrubland and agriculture land (particularly rotations between pastures, herbaceous crops and fallow cycles), were found. The most consistent trend of changes among land uses between 2008-2014 was a progressive increase in pasture at the expense of agriculture and native forest. Thus, a slight increase in urban area was observed in all regions over the whole study period.

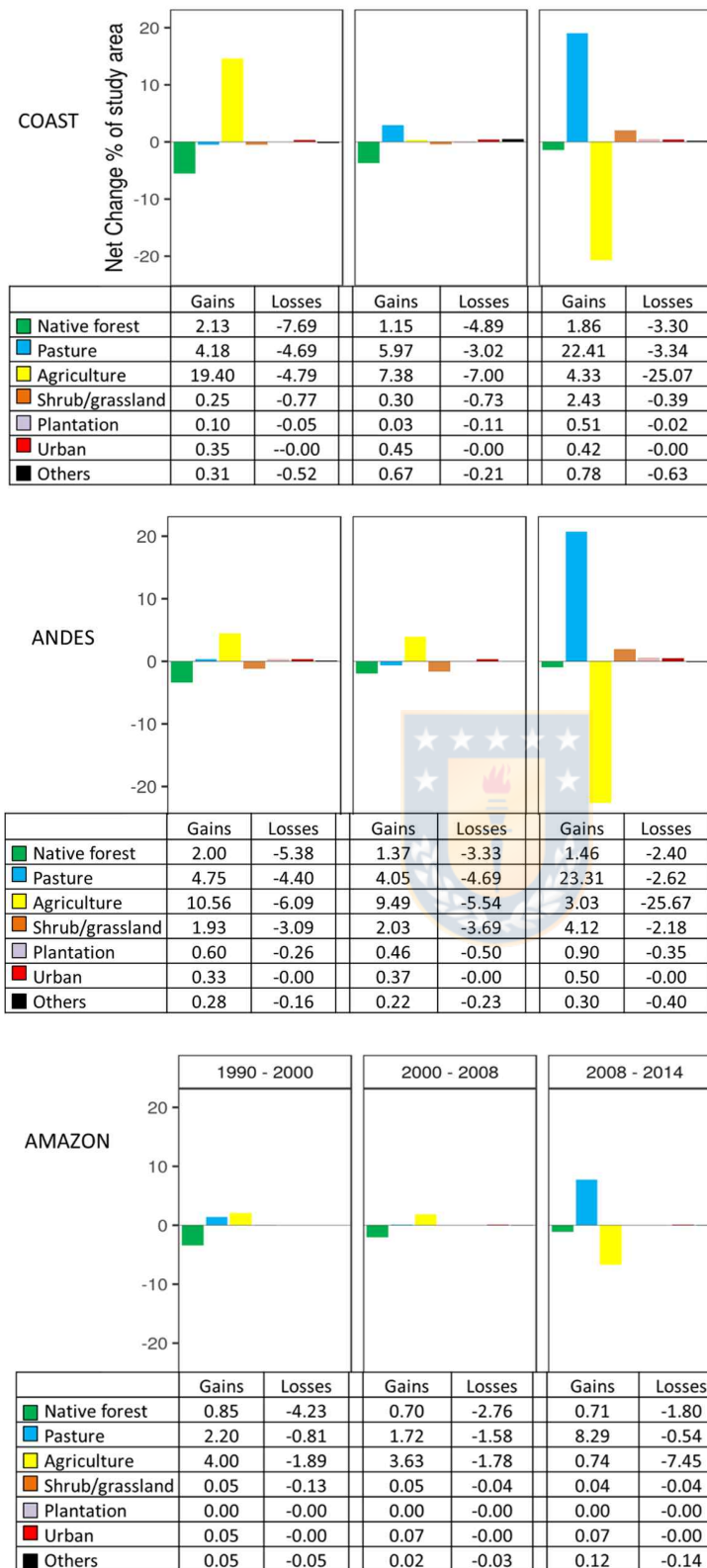


Figure 3. Net change (i.e. gains plus losses), gains and losses for each land cover

class as a percentage of three regions for the periods 1990-2000, 2000-2008 and 2008-2014

Forest fragmentation

By 2014, continuous fragmentation became the dominant process, owing to a decline in number of interior and dominant FAD classes and a slight increase in patchy and rare FAD in the Coast and Andes (Figure 4). In the Amazon, forest fragmentation was accompanied by the rapid increase in the number of patchy and rare FAD. The amount of interior FAD decreased following the introduction of these disturbed fragments into the matrix.

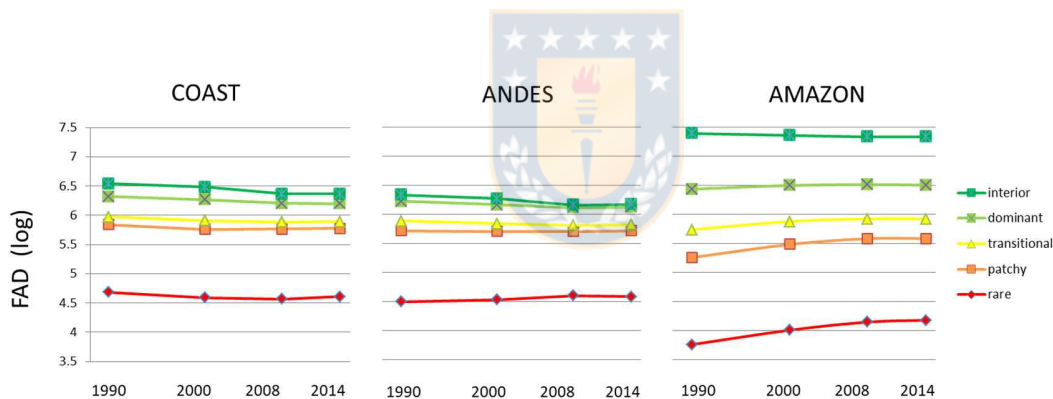


Figure 4. Temporal variation of number of different FAD (log) in three regions of Ecuador

The FFI varied between 0 (no fragmented) and 99.99 (highly fragmented) in 2014 (Table 2). The highest FFI was recorded for the semideciduos forest and shrubland of the North Valleys (E33), while the lowest FFI (value=0) was observed in E45, E46 and E62.

Relationship between forest fragmentation and human land use

The increase in human land uses had a significantly positive relationship on forest fragmentation in all forest ecosystems of Ecuador (Table 4). At national level, positive significant relationship was constantly found between forest fragmentation and two human land uses: pasture (PST) and habited area (HBT). Additional results using regions were presented in more detail (Table 4). In the Andes, we detected statistically robust relationships of pasture (PST) and habited area (HBT) on forest fragmentation. Thus, regional regression model indicated that forest fragmentation was mostly explained by permanent (PFM) and semi-permanent farming (SFM), and habitat area (HBT) in the Andes, and pasture (PST) in the Amazon, respectively.



Table 4. Standard coefficients of multiple regressions testing the relationship between forest fragmentation index (FFI) and human land use in 2014 in three regions of Ecuador

Adj.R ²	F	Human Land Use						
		PLT	PST	AFM	PFM	SFM	HBT	IFR
All (n=64)								
0.646	17.41 ***	2.52	1.30 ***	1.45	0.18	1.23	59.78 ***	6.57
Coast (n=17)								
0.572	4.06 *	0.126	-0.47	-5.64	2.58 .	4.61 .	59.74 .	54.47
Andes (n=27)								
0.854	4.89 **	0.70	1.31 ***	0.44	-4.10	3.67	106.48 **	-358.21
Amazon(n=20)								
0.003	5.31 **	-	1.08 **	-26.97	-9.53	16.00	-87.06	-98.74

PLT: industrial plantation; PST: pasture; AFM: annual farming; PFM: permanent farming; SFM: semi-permanent farming; HBT: inhabited area; IFR: infrastructure

. p < 0.1

* p < 0.05

** p < 0.01

*** $p < 0.001$

The regression models indicated that the forest fragmentation had mostly positive relationship with pasture (PST) in ecosystems of low, moderate and high fragmentation in 2014 (Table 5). In addition, forest fragmentation in ecosystems associated to high FFI value was positively explained by semi-permanent farming (SFM) and infrastructure (IFR), and negatively by permanent farming (PFM). Lowly fragmented forest ecosystems also showed negative significant relationship between forest fragmentation and industrial plantation (PLT).

Table 5. Standard coefficients of multiple regressions testing the relationship between forest fragmentation index (FFI) and human land use for 2014 in forest ecosystems divided by FFI value (Low: $FFI \leq 10$, Moderate: $10 < FFI \leq 60$, High: $FFI > 60$)

Adj.R ²	F	Human Land Use						
		PLT	PST	AFM	PFM	SFM	HBT	IFR
Low (n=22)								
0.936	45.39 ***	-2.08 *	1.20 ***	46.67 ***	-3.51	3.33	-63.78	0.88
Moderate (n=31)								
0.302	2.61 *	1.90	0.63 *	1.55 .	0.43	0.34	4.92	1.2358.21
High (n=11)								
0.995	232 **	9.23	0.37 *	0.43	-0.61 *	1.28 .	10.30	93.33 *

PLT: industrial plantation; PST: pasture; AFM: annual farming; PFM: permanent farming; SFM: semi-permanent farming; HBT: inhabited area; IFR: infrastructure

. $p < 0.1$

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Discussion

To understand how changes in forest structure interact with human land use, we need information on what kind and magnitude of changes happen as a first step (Lambin et al. 2003). This study aimed at providing some of this relevant information based on comparative studies across different spatial scales of the forest ecosystems in Ecuador.

Considering the three regions of continental Ecuador, the Coastal forest ecosystems showed significant forest conversion by human land use (Figure 1). This region has supported much of the country's agriculture and has suffered from significant urban development (Lessmann et al. 2016; Senz and Onofa 2005; Sierra 1999b). Specifically, the equatorial pacific is under higher transformation trends from native forest to human land use than equatorial Chocó (Figure 1.D). The Andes showed the largest gap between human land use and conservation efforts. Even though many studies set priorities for forest conservation efforts in the tropical Andes (Mittermeier et al. 1998; Olson and Dinerstein 2002), we observed that forest ecosystems in Andean valley have a very low proportion of original native forests and are aware of the loss of defining features and replacement by a novel ecosystem by transforming diagnostic component. On the other hand, as the western Andes harbor less protected areas than the eastern Andes, human land use is more proportioned and represented in western Andes than east Andes (MAE 2015). Expansion of agropastoral land-use trends in Andes was recognized as the main reason of deforestation and forest conversion (Brandt and Townsend 2006; Wunder 2000). As reporting recently higher rate of deforestation in Amazonian region (MAE,

2015) than in the Coast and Andes, we expected significant influence of human land use on native forest ecosystems in this region. Unlike our expectation, human land use is poorly observed in the Amazon region comparing the rests. This unpredictability of human land use in forest ecosystems in Amazon may be explained by their larger extension comparing with the rest. In contrast to the Coast and Andes, forest ecosystems in Amazon are much more extensive. As the rate of human land use in Amazon is relatively smaller than the rest of regions, it seems that there is no urgent need to be assigned to initiatives within the priority areas of biodiversity conservation at landscape level. Similarly, Sierra et al. (2002) mainly prioritize conservation of natural ecosystems in the Coast and Andes based on ecosystem-risk-representativeness approach, as the highest risk areas. However, results using species as conservation targets may differ from the results using ecosystem level approach. For example, from a species-based perspective, Lessmann et al. (2014) suggest that more conservation efforts are needed in the northern Amazon where the highest species richness can be found. It is noteworthy that, ecosystem level conservation should be considered apart from species-only approach (e.g. based on richness or endemism).

Our most remarkable finding was to identify the different degrees of forest changes at the ecosystem level across Ecuador. Although overall forest loss and fragmentation is slightly observed between 1990 and 2014 in 64 natural forest ecosystems, we identified several seriously modified ecosystems. For example, the 2014 native forest proportion reached only 0.11% for Semideciduos forest and shrubland of the North Valleys. Declining total forest area of spatial extent in an

ecosystem type, it seems that the forest ecosystem has undergone transformation of identity. Importantly, Suding and Hobbs (2009) address such severe changes in natural ecosystems could be mostly observed when human activities change frequently (e.g. cultivation land rotation). As Ecuador is dominated by patterns of small-holder land use that reflect fragmented and heterogeneous livelihood strategies, our results seem to be explained by frequent land use change by human activities. These severe changes in ecosystems can be characterized by pressure on resource use and short fallow shifting cultivation as a type of rotational land use (e.g. forest-pasture-shrubland or forest-shrubland-pasture-crop) (Brown and Schreckenberg 1998). Forest conversion to pasture for cattle grazing has been one of the main reasons for deforestation in tropical forests (Amelung and Diehl 1992; Holl et al. 2000). In southern Ecuador, high deforestation rate is reported by conversion to pastures, in spite of its high diversity of forest ecosystems (Potthast et al. 2010). Although these cultivated or fallow lands are abandoned after several years, the natural regeneration is detected by increasing forest fragmentation (e.g. decline of mean patch area, increase of patch number in the study site) (Cubina and Aide 2001; Myster 2004). Zahawi and Augspurger (1999) found that herbaceous species are dominated in early plant succession of abandoned pastures in Ecuadorian Andes, whereas a successional trajectory toward a forested condition (secondary forests) was estimated between 20 and 30 years after land abandonment. Therefore, in most Ecuadorian forest ecosystems, losses and gains of native forests are treated as equal when calculating net change, but the loss of primary native forest is qualitatively different from the gain of early-successional secondary forests (Rudel et al. 2005).

Ecuadorian policies have been developed in response to the issue of forest loss and change from the 2000s. Despite being a small country (284,000 km²), Ecuador has 44 state-protected areas that cover approximately 19% of its whole territory (Cuenca et al. 2016) and is known as a leader in the debate to have avoided deforestation, credits 'recognized by international climate-change conventions (Cuenca et al. 2018). In addition, the Ecuadorian government has invested around 56 million dollars in direct payment program (Socio Bosque) to achieve native forest conservation. Regarding the Government's goal of avoiding deforestation, there are two important lessons that can be learned from this study. First, it is important to optimize the protection efficiency in forest ecosystems. We observed lack of protection in small-sized and/or highly-fragmented forest ecosystems, which may result in conservation gaps for species and ecosystems in the country (Lessmanneta 2014). Although establishing new areas under protection is a long and difficult process due to conflicts with relevant stakeholders (Redpath et al. 2013), it will be necessary to create appropriate conditions for the active participation and cooperation of private sector in planning and implementation of conservation initiatives in these forest ecosystems. Secondly, the main conservation challenge in the highly-fragmented forest ecosystems which has experienced extensive transformation of the original ecosystems by human activities. However, small patches of native forest still remain in these ecosystems. Therefore, forest structure in highly fragmented ecosystems could improve by following landscape approaches: 1) creating buffers around native forests to mitigate the trend toward a forest fragmentation; 2) connecting fragments of native forests in order to enhance landscape connectivity and 3) identifying and

designing an adequate landscape configuration based on the remnant small-size patches, to enhance ecosystem persistence and resilience (Suding et al. 2004).

Conclusion

Conservation of forest areas is contingent upon understanding of the anthropogenic pressures on them. This study represents a baseline for understanding potential ecological effects of fragmentation and deforestation on biodiversity and ecosystems in Ecuador. Even though the present work has used analysis at the landscape scale, more comprehensive local analyses will be necessary to recognize the underlying factors that have resulted in the distinct trends observed in Ecuador's forest ecosystems.



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CHAPTER 4

Warning about conservation status of forest ecosystems in Tropical Andes: national assessment in Ecuador, based on IUCN criterion³

Introduction

Since development of agriculture, habitat fragmentation is one of the core drivers of biodiversity loss at local, regional and global scales (Fahrig 2002). There is a clear need to manage fragmented systems in order to maintain and conserve the diversity of species or ecosystems (Dale et al. 2000; Saunders et al. 1991). Previously the majority of efforts to conserve biodiversity have been focused on species, communities or their habitat, but currently there has been an increasing awareness of the importance of considering larger-scales such as entire ecosystems and landscapes with the aim of benefiting both biodiversity and human well-being (McIntyre and Wiens 1999; Wiens and Moss 2005; Wu 2013b). Likewise, the general tendency in conservation planning is focused on ecosystem-level assessment, which ensures not only the protection of a sufficient portion of all ecosystems in a country, but also the persistence of lower-level of biodiversity (e.t. genetic diversity, species, etc.) (Liebhold and Gurevitch 2002; Loreau et al. 2001; Sierra et al. 2002).

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Despite systematic methods for assessing the threat of extinction of individual species were notably advanced in recent years, there is few widely accepted scientific framework for tracking the status of Earth's ecosystem and identifying those with a high probability of loss or degradation (Keith et al. 2015). Recognizing this gap, ecosystem-level extinction risk assessment began to develop and implement comparable global standards from IV World Conservation congress in 2008. The IUCN Red List of Ecosystems is a newly developed system for assessing the risk of ecosystem collapse, which is designed to evaluate four symptoms of ecosystem degradation: declining distribution, restricted distribution, degradation of abiotic environment and altered biotic processes (2013).

An ecosystem is considered under collapse “when it is virtually certain that it defining biotic or abiotic features are lost, and the characteristic native biota is no longer sustained’ (Rodrguez et al. 2012). A key task is to identify transition between states either as part of natural variability within an ecosystem type, or as a process of collapse and replacement by different or novel ecosystem type (Rodrguez et al. 2012). As land use change is identified as the major driver for changes in terrestrial ecosystems (Sala et al. 2000), this human process could cause some ecosystems to be closer to collapse. The loss of plant cover has been considered one of the main triggers of degradation, since the structure of the ecosystem is directly involved (Crespin and Simonetti 2015). For example, Tozer et al. (2015) use a state-and-transition framework to identify processes that drive transitions between different state of a woodland ecosystem, and identify the states that represent ecosystem collapse.

IUCN provide an effective assessment protocol for establishing a systematic Red List of world's ecosystems (Balmford et al. 1998). There are five criteria in the risk assessment protocol (Keith et al. 2015): Criterion A refers to the reduction in the distribution of the ecosystem over a certain period of time (50 years in the past, 50 years in the future, 50 years in any range and historical loss); B refers to ecosystems with a limited geographic distribution; C refers to the degradation of the ecosystem's abiotic or environmental components over a certain period of time (same as Criterion A); D refers to the disruption of biotic processes or interactions fundamental to the ecosystem in certain period of time (same as Criterion A); and E refers to a quantitative analysis that estimates the likelihood of an ecosystem's collapse. Among these five rule-based IUCN RLE criteria, criterion B must compile all the evidence required by subcriteria to estimate extent of occurrence (EEO) and area of occurrence (AOO). Spatially explicit threats, e.g. forest fire, extreme weather events, forest fragmentation, land conversion, invasion, are commonly eligible as threats of ecosystem distribution or process decline. In terrestrial ecosystems, literature review reveals that temporal trends in the distribution of land uses have been proposed and applied as threat for assessing the status of some types of ecosystems (Reyers et al. 2007; Rodriguez et al. 2007). For example, Rodriguez et al. (2008) used land cover loss and the rate of changes in land cover across multiple spatial scales for ecosystem risk assessment. On the other hands, because threats may be assessed in at least three dimensions: immediacy, scope and severity, forest loss represents current forest ecosystems' composition, structure and function. As many systems show multiple threatening process acting together (Brook et al. 2008), the combined

negative effects and their interaction leading to ecosystem extinction must be tested for future conservation action.

The tropical Andes range is classified as a center of biodiversity and endemism in the world (Myers et al. 2000a). The specific studies of ecosystem threats and risk assessment carried out in Tropical Andes are initiated in late 1980's (Armenteras et al. 2003; Armenteras et al. 2006; Cuenca et al. 2016; Rodríguez Eraso et al. 2013). These previous studies may suggest that two main threats of concern are human land use and forest fragmentation in the region. Despite ecological importance, the highest deforestation rate has been related to human activities (logging, agriculture, grazing, etc.) during last 30 years in this region (Cuenca and Echeverria 2017b; Mena 2008a; Sierra 1999a; Tapia-Armijos et al. 2015). Recent studies are increasingly worrying negative effects on biodiversity by forest fragmentation in the tropical Andes (Cuenca and Echeverria 2017a; Cuesta et al. 2017). Notwithstanding the growing literature reporting forest decline and land use change driving ecosystem collapse, few studies have assessed conservation status at ecosystem level based on IUCN criteria (Fajardo et al. 2005).

Ecuador is home to high-biodiversity terrestrial ecosystems that exhibit very high levels of endemism in the tropics (Olson and Dinerstein 2002). The tropical Andes of Ecuador is characterized by landscapes with peculiar climatic and topographic conditions where human settlements both affect and depend on natural forest ecosystems (Gaglio et al. 2017). During the last few decades, Ecuador's native forests have been destroyed, fragmented and associated with anthropogenic disturbances such as agriculture, logging and grazing (Cuenca and Echeverria

2017b; Tapia-Armijos et al. 2015). Despite an ongoing trend of forest change (loss and fragmentation), this area still contains high diversity of forest ecosystems (Jimnez et al. 2017).

Against this background, we aimed to assess the conservation status of 64 forest ecosystems in entire Ecuadorian mainland. Our analyses provide the first evidence of potential risk of collapse of forest ecosystem in Ecuador. Considering that many forest ecosystems of the present study are unique, their loss poses significant impacts for biodiversity conservation across global level. From the conservation point of view, urgent and effective conservation actions may allow the recovery of threatened forest ecosystems located in this biodiversity hotspot.

Materials and methods

Study area

The study was carried out in 64 forest ecosystems equivalent to 54% of national territory ($\approx 135,936 \text{ km}^2$) of whole Ecuadorian mainland with elevations ranging between 0 and 6000 m a.s.l. (Figure 1, A1). Ecuador is located in a transition zone of two biodiversity hotspots: 1) Choco/Darlen western Ecuador and 2) Tropical Andes (Myers et al. 2000b). Likewise, Ecuadorian Amazon is known as one of the most biodiverse places on Earth with apparent world species richness record, including a considerable number of threatened species and regional endemics (Bass et al. 2010; IUCN 2018). This feature of the study area allows an increase in endemic species richness and conservation priority.



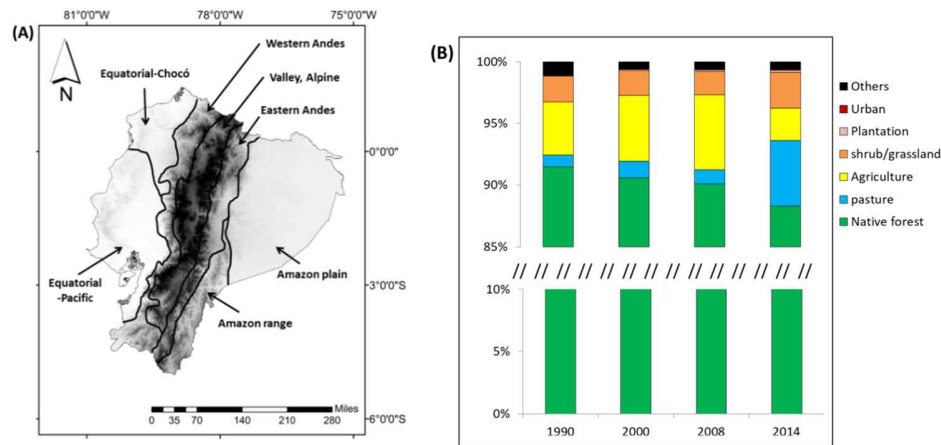


Figure 1. (A) Ecoregions of continental Ecuador. Elevation detail is shown. (B) The major land use and cover types inside the potential limits of 64 forest ecosystems in 1990, 2000, 2008 and 2014.

Despite of its biological importance, recent data suggests a pessimistic future of this globally important country. According to the Food and Agriculture Organization of the United Nations (FAO 2014), Ecuador has maintained the highest deforestation rates of South America at the country level during the last 20 years (annual rates of 1.5% and 1.8% for the 1990-2000 and 2000-2010 periods, respectively). To date, agriculture expansion, wood extraction commercial logging, cacao and banana plantations, mining and road construction are reported as main drivers of ongoing land cover change in Ecuador (Cuenca and Echeverria 2017b; Mena 2008b).

Baseline information of ecosystem types at national scale for Ecuador was used in this study. Definition, classification and delimitation of 91 terrestrial ecosystems were

established on the basis of the following factors: 1) physiognomy; 2) bioclimate; 3) biogeography; 4) geoform; 5) general flooding; 6) phenology; 7) bioclimatic soil, and 8) substratum (MAE 2013). Among 91 terrestrial ecosystems in whole Ecuador, 89 correspond to natural ecosystems: 64 forests, 13 grasslands and 12 shrublands. In the present study, we selected and analyzed the potential distribution of 64 forest ecosystems including two mangroves (Table 2, A1). The potential distributions of these forest ecosystems may include other types of land use and cover as a result of human-induced changes (Ecuador 2013). To apply Criterion B, the map of native forest in 2014 was used, identifying those ecosystems with a limited distribution.

Framework of assessment based on IUCN criteria

Due to the lack of available geospatial data across time for the application of criteria A, C and D, we only applied criterion B in this study.

Assessment of criterion B

Current distribution of 64 forest ecosystems are quantified applying IUCN criterion B: the extent of geographic distribution of an ecosystem influences its risk of collapse when exposed to spatial threats (Keith et al. 2013). For each ecosystem we calculated EOO and AOO using ArcGIS 10.2.2. (Table 1).

Table 1. Summary of IUCN Red list criteria B for ecosystems V. 2.0 and Subcriterion applied for the present study

Criterion B: restricted geographic distribution indicated by ANY of B1, B2 or B3	Critically Endangered (CR)	Endangered (EN)	Vulnerable (VU)
1 Extent of Occurrence (EOO)	≤2,000 km ²	≤20,000 km ²	≤50,000 km ²

and observed or inferred continuing decline at least one of the following:

- (a) i) a measure of spatial extent appropriate to the ecosystem; OR ii) a measure of environmental quality appropriate to characteristic biota of the ecosystem; OR iii) a measure of disruption to biotic interactions appropriate to the characteristic biota of the ecosystem.
- (b) Observed or inferred threatening processes that are likely to cause continuing declines in geographic distribution, environmental quality or biotic interactions within the next 20 years.
- (c) Ecosystem exits at

1 location ≤ 5 locations ≤ 10 locations

2	Number of 10x10 km grid cell (AOO)	≤2	≤20	≤50
	and observed or inferred continuing decline at least one of the following: (same as for B1)			
3	Number of locations	Very small (generally fewer than 5) AND prone to the effects of human activities or stochastic events within a very short time period in an uncertain future, and thus capable of Collapse or becoming critically Endangered within a very short time period (B3 can only lead to a listing as VU)		

Evidences of ongoing decline of an ecosystem

Spatial data describing current threats to forest loss were obtained from a number of sources (Table 3). To capture threats, we decided to use a 30-m grid scale in the map of ecosystem as well as forest. Analysis was carried out separately for each ecosystem. Subcriteria B1a and B2a address continuing declines in ecosystem distribution, abiotic environment or biotic processes.

Decline of spatial extent (B1ai OR B2ai)

As land use and cover have profoundly changed the natural habitats (Vanacker et al. 2018), we analyzed the current land use inside potential distribution of each forest ecosystem class, using five main land use types (Table 3) in 2014. Human-related land use types were considered as agricultural land and urban areas. As a threat, severe human land use was defined as a human land use > 40% of total ecosystem area in 2014.

Also, the native forest conversion rate to agriculture, pasture and forest plantation within each ecosystem class was assessed using land use maps of 1990 and 2014. The agricultural land included: permanent, semi-permanent, annual and mixed agriculture, industrial plantation and pasture (Table 3). 'Severe forest conversion to cultivated land' was defined as at least 30% during 24 years.

Table 2. Land use and cover types that may be found within the potential distribution of forest ecosystem classes

No.	Main land cover	No.	Sub category
1	Native forest	1	Native forest
2	Grassland/shrubland	2	Grassland
		3	Shrubland
		4	Paramo
3	Agricultural land	5	Permanent
		6	Semi-permanent
		7	Annual

		8	Mixed
		9	Pasture
		10	Industrial plantation
4	urban	11	Inhabited area
		12	Infrastructure
5	Others	13	Natural water
		14	Artificial water
		15	Bare soil
		16	Glacier

Decline of environmental quality to characteristic biota (B1aii OR B2aii)

As a measure of environmental quality to characteristic biota of an ecosystem, we analyzed forest fragmentation in each ecosystem. As fragmentation is a summary descriptor addressing a variety of spatial attribute of a forest, the analysis of forest fragmentation assessment was conducted using GUIDOS (Vogt 2018) which accounts for key aspects of fragmentation, such as the area and shape of continuous forest, forest integrity (amount, shape and area of perforations inside intact forests), and the spatial inter-patch distance distribution of forest patches separated by non-forest lands (Soille and Vogt 2009). Vogt (2018) reports the methodology to describe and quantify forest fragmentation and temporal change by measuring forest area density (FAD). The FAD values at 27 pixels-length scale, are classified as two classes: separated ($FAD < 40\%$) and continuous ($40\% \leq FAD \leq 100$). Ecosystems with low values of continuous FAD are subject to high levels of fragmentation.

'Severe fragmentation' was defined as continuous native forests of $\leq 30\%$ within an ecosystem.

Number of locations (B1c OR B2c)

A location is defined as a geographically or ecologically distinct area in which a single threatening event can rapidly affect all occurrences of an ecosystem types (IUCN 2017). As the most severe threat to the ecosystem in tropical landscape is land transformation associated with agricultural expansion, the number of location therefore determined using three jurisdictional zones with different regulatory control on land use: i) county boundary, ii) public protected area, and iii) private protected area (Keith et al. 2013). Data were derived from the National Parks and Reserves Network (NPRN) and Socio Bosque Program (SBP), which are managed by the Ministry of the Environment of Ecuador, and county map from the National Mapping Agency (IGM) (Table 3). It was superimposed over the distribution map of forest ecosystems to generate ecosystem extent incorporated within different land use control.

Table 3. Summary of data sources

Name	Resolution	Source
Territorial Ecosystem map	30m	MAE 2013
Land use thematic map	30m	MAGAP 2018
County map	30m	IGM 2018
NPRN	30m	MAE 2015
Socio Bosque Program	30m	MAE 2014

Results

Identification of spatially restricted forest ecosystems

We identified 60 ecosystems with restricted EOO (11 ecosystems of EOO $\leq 2,000$ km², 30 of $> 2,000$ and $\leq 20,000$ km² and 19 of $> 20,000$ and $\leq 50,000$ km²) and 28 ecosystems with restricted AOO (4 ecosystems of AOO ≤ 2 , 15 of > 2 and ≤ 20 , and 9 of > 20 and ≤ 50). A total of 28 ecosystems are classified as restricted geographic distribution indicated by either EOO or AOO (Table 4).

Table 4. List of 64 terrestrial forest ecosystems in Ecuador, assessed by IUCN RLE criterion B

Ecosystem code	Criteria B		Sub-criteria assessed (+: detected evidence)				Criteria determining overall status	IUCN status
	EOO(km ²)	AOO (# 10 km x 10 km)	Current human LU	Conversion to Agriculture	Forest fragmentation	No. location		
E01	3.32	1				2	B3	VU
E02	6,338.54	26				67	B1, B2	NT
E03	22,444.80	100				429	B2, B3	LC
E04	679.66	14				36	B1, B2	NT
E05	20,512.71	75				107	B2, B3	LC
E06	4,476.46	53				69	B1, B2	LC
E07	2,877.61	34				49	B1, B2	NT
E08	54,091.38	216				341	B1, B2	LC
E09	27,147.75	107				150	B1, B2	LC
E10	32,207.88	91				158	B1, B2	LC
E11	23,261.57	148				225	B1, B2	LC

E12	23,185.29	84				168	B1, B2	LC
E13	47,546.70	122	+	+	+	157	B1(a),ii	VU
E14	45,460.15	153				306	B1, B2	LC
E15	10,183.20	40				93	B1, B2	NT
E16	22,742.13	79				45	B1, B2	LC
E17	193.53	4	+	+	+	8	B1(a),ii	CR
E18	27,846.44	173				724	B1, B2	LC
E19	31,046.19	171				519	B1, B2	LC
E20	36,784.07	193				695	B1, B2	LC
E21	33,510.24	146				457	B1, B2	LC
E22	8,130.38	43				49	B1, B2	NT
E23	4,333.59	48	+	+		192	B1(a),ii	EN
E24	3,763.32	20				60	B1, B2	NT
E25	8,325.38	57				153	B1, B2, B3	LC
E26	4,087.80	20				121	B1, B2	NT
E27	547.67	10	+			54	B1(a),ii	CR
E28	125.85	3				11	B1, B2, B3	NT
E29	6,123.16	65				155	B1	LC
E30	3,657.26	44				72	B1, B2	LC
E31	2,660.12	20				62	B1, B2	NT
E32	184.98	2	+	+	+	6	B1, B2(a),ii	CR
E33	1,012.12	11	+		+	81	B1(a),ii	CR
E34	2,069.48	9	+	+	+	17	B1, B2(a),ii	EN
E35	8,870.84	13	+		+	164	B1, B2(a),ii	EN
E36	20,023.85	139				382	B1, B2	LC
E37	21,641.19	152				391	B1, B2	LC
E38	15,052.86	130				527	B1, B2	LC

E39	18,298.44	158				657	B1, B2	LC
E40	15,732.84	127				286	B1, B2	LC
E41	18,133.01	165				305	B1, B2	LC
E42	14,426.60	125				136	B1, B2	LC
E43	12,877.16	89				221	B1, B2	LC
E44	193.80	4	+	+	+	5	B1(a),ii	CR
E45	39.34	2				9	B3	VU
E46	135.55	3				16	B1,B2	NT
E47	17,786.25	152				280	B1, B2	LC
E48	13,552.64	121				195	B1, B2	LC
E49	10,581.21	73				144	B1, B2	LC
E50	8,094.90	26				22	B1, B2	LC
E51	4,297.49	20				47	B1, B2	NT
E52	6,523.91	23				37	B1, B2	NT
E53	5,837.63	35				99	B1, B2	LC
E54	18.79	1				2	B3	VU
E55	23,716.19	227				660	B1, B2	LC
E56	64,968.60	424				720	B1, B2	LC
E57	70,216.35	194				186	B1, B2	LC
E58	25,123.32	237				411	B1, B2	LC
E59	55,127.77	316				241	B1, B2	LC
E60	5,256.45	14				25	B1, B2	NT
E61	43,108.96	153				59	B1, B2	LC
E62	4,372.73	12				6	B3	VU
E63	26,774.64	289				1,320	B1, B2	LC
E64	8,822.89	98				40	B1, B2	LC

Potential threats of forest ecosystem collapse

Current land use and forest fragmentation

In 2014, many forest ecosystems located in Coast, western Andes and Valley were affected from direct human activities (Figure 2). For example, native forest remained only 7.6% in 'Seasonal flood alluvial plain evergreen forest of the Jama-Zapotillo (E17)' in the landscape dominated by human land use. Across the entire country, the primary form of land use change in forest system was the creation to pastures (45.67% of converted area), followed by natural shrub/grassland (24.77%), agricultural land (22.31%), others (5.48%), industrial plantation (1.18%) and urban (0.60%) (Figure 1. B). Based on the definition of 'severe human land use', it was found that six forest ecosystems have shown strong effects on human activities in 2014 (Figure 2).

As evidence of decline of environmental quality to characteristic biota, the analysis of forest fragmentation showed the distribution of continuous forests across potential limit of 64 forest ecosystem class (Figure 2). We mainly distinguished seven ecosystems in severe forest fragmentation: E10, E17, E32, E33, E34, E35 and E44.

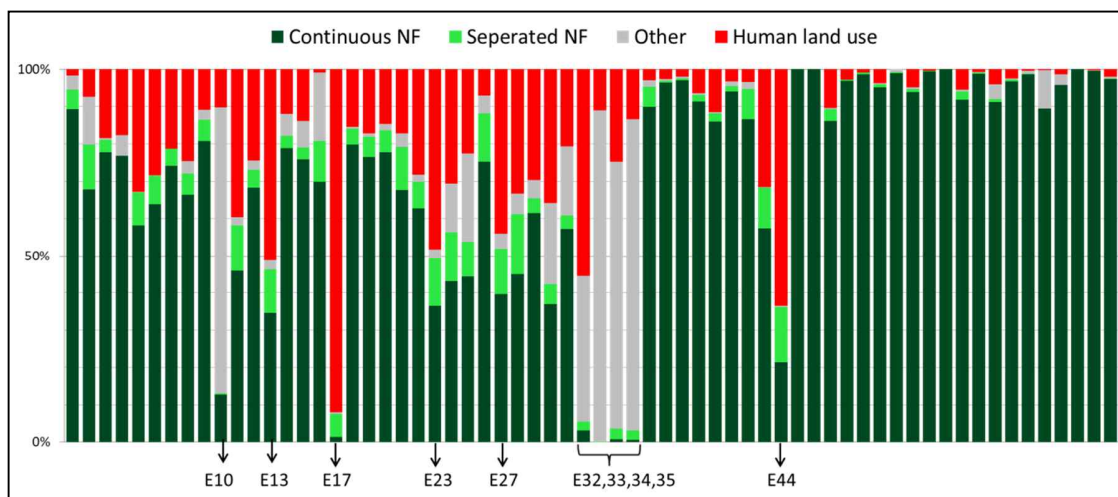


Figure 2. The major land cover types of single ecosystems (n=64) in 2014. Continuous and separated native forests were distinguished based on the Forest Area Density (FAD) values calculated from GUIDOS. Human land use and cover includes agricultural land, pasture, forest plantation and urban area. Ecosystems containing either continuous native forests <30 % or human land use >40% (n=7) are E 10, 17, 32, 33, 34, 35 and 44.

Conversion to cultivated land

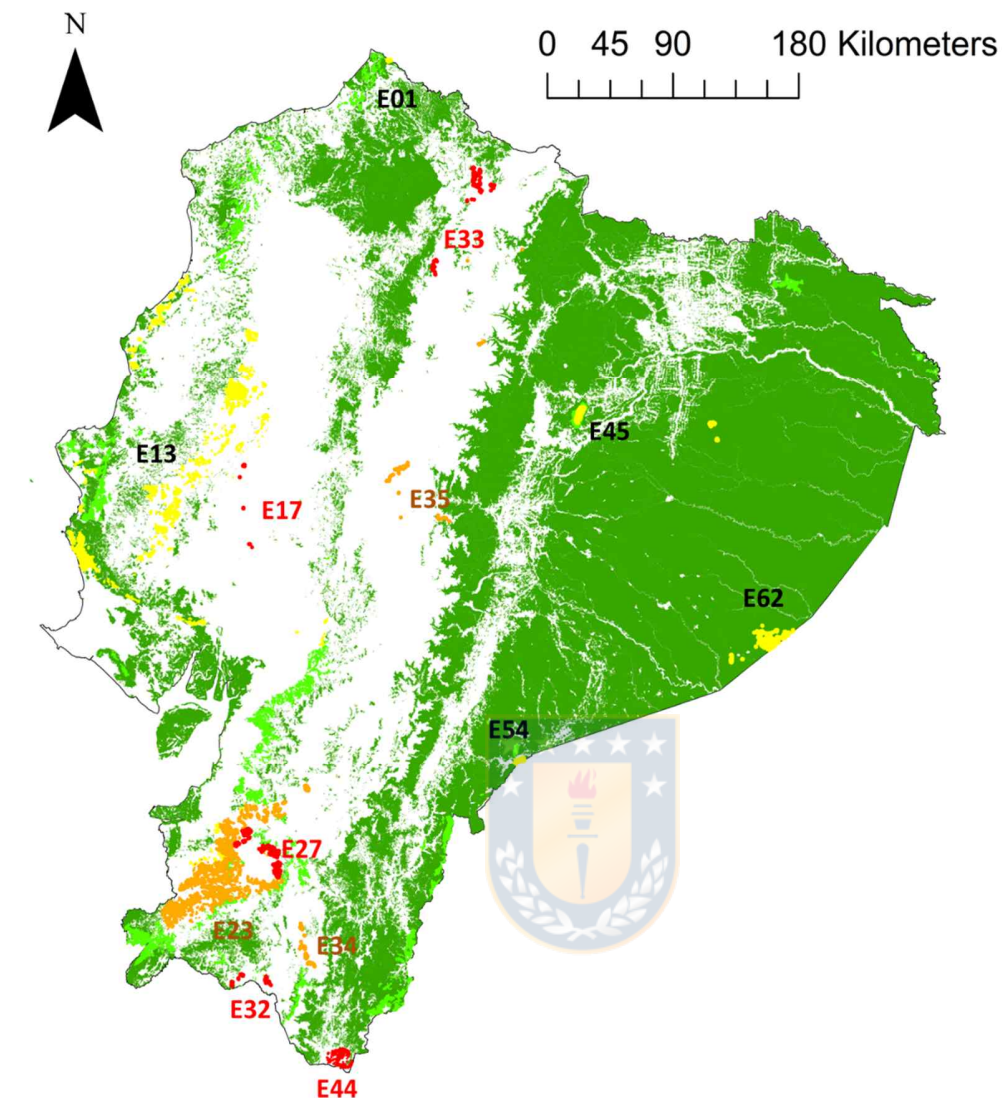
Forest conversion rate to cultivated land between 1990 and 2014 ranged from 0.5 % to 98.9 % in ecosystems located in the Coast; between 0.7 % and 60 % in Andes, and between 0 % to 4 % in Amazon. Forests were not converted to any type of cultivated land in three forest ecosystems in Amazon: E52, E 55 and E64. Conversely, six forest ecosystems classified as severe conversion to cultivated land: E17 (98.8%), E44 (60.0%), E23 (36.8%), E34 (34.4%), E32 (33.4%) and E13(31.6%).

Number of locations

According to estimated number of locations that are occupied relative to the extent of serious plausible threat of land use change, we identified seven ecosystems under 10 locations: E4 (2 locations), E17 (8), E32 (6), E44 (5), E45 (9), E54 (2) and E 62 (6).

In 2014, the percentage of protected land in each ecosystem varied (SD = 28.3, Range 0-100). Only in the case of E24, entire land extent is under protection. A total of 34 forest ecosystems (5 ecosystems in Coast, 16 in Andes and 13 in Amazon) were identified fewer than 17 % of protected land. Among them, 15 ecosystems where 0% of its land is under protection were: E18, E25, E28, E33, E34, E37, E39, E41, E44, E46, E47, E50, E51, E52 and E54. Also, calculating the difference between proportion of native forest and protected land in a given ecosystem, deforestation within protected areas was observed in 4 forest systems: E11, E17, E24 and E32 (A. 2). An example is the E17, which showed the only 7.4 % of native forest in a landscape under 59.75% of land protection in 2014 (A. 3).

Our results revealed that 13 ecosystems are threatened: five were categorized as CR (E17, E27, E32, E33, E44), three as EN (E23, E34, E35) and five as VU (E1, E13, E45, E54, E62) (Table 4, Figure 3), which represent 20% of total forest ecosystems and 2.2 % ($\approx 2,996.28 \text{ km}^2$) of total area of forest ecosystems.



- CR**
- E17 Seasonal flood alluvial plain evergreen forest of the Jama-Zapotillo
 - E27 Low montane evergreen forest of the Catamayo- Alamor
 - E32 Low montane deciduous forest of the Catamayo- Alamor
 - E33 Semideciduo forest and shrubland of the North Valleys
 - E44 Piedmont semideciduous forest of the south-eastern Andean range
- EN**
- E23 Piemontano seasonal evergreen forest of the Catamayo-Alamor
 - E34 Semideciduo forest and shrubland of the South Valleys
 - E35 Páramo evergreen forest
- VU**
- E1 Flood intertidal plain forest of the Equatorial Chocó
 - E13 Seasonal evergreen forest of the Jama-Zapotillo lowland
 - E45 Low montane evergreen forest of Galeras
 - E54 Evergreen forest on sandstone plateaus of the Cóndor range in the lower Ecuadorian Amazon
 - E62 Evergreen bamboo forest of the Amazonian lowland

Figure 3. Map of 13 threatened forest ecosystems in mainland Ecuador, assessed by IUCN RLE criteria B

Discussion

Many forest systems in Ecuador suffered from human activities and pressure, particularly in the sub-montane area. However, it is difficult to assess precisely the local extent of such pressures in terms of their effects on structure and composition or disappearance of the systems. Our most important, but perhaps least surprising result is that many tropical Andean forest systems are indeed faced extinction risk at national and local scales in Ecuador. In the present study, we estimated that several Tropical Andean forest systems are rapidly changing and probably disappearing faster than other forest ecosystems. The results suggest that the success of ecosystem conservation will increase when the merits of a conservation prioritization system based on the ecological and biogeographic knowledge known as ecosystem (Harris et al. 2008; Laumonier et al. 2010).

As knowledge of biogeographic zoning at national level is rarely available, previous studies about RLE focusing on single territorial ecosystems, small areas or regions reported and assessed a probability of loss or degradation. In northern Venezuela, Rodriguez et al. (2008) assessed extinction risk categories of tropical dry forests using historical and current dry forest cover. Likewise, conservation status of temperate grasslands in southern Africa was estimated by combination of two landscape-scaled factors: level of protection and degree of land transformation (Carbutt et al. 2011). However, these results provide limited information to facilitate identification of critical zones for shaping the national conservation policy. On the other hands, methods for assessing the threat of extinction of individual ecosystems

were not systematized in many of the previous studies. For example, although Sierra et al. (2002) identified the prioritization among 46 natural ecosystems for the conservation of Ecuador's biodiversity using a multi-criteria model, their criteria (representativeness in the current reserve network, human pressure, habitat loss and species-level value based on bird species data) associated with developed model are not directly linked with key symptoms of ecosystem degradation. Therefore, unlike the results of Sierra et al. (2002) which were found 26 critical ecosystems, we identified 13 threatened ecosystems; three in the Coast, seven in the Andes and three in the Amazon.

A central benefit of assessing conservation status of nationwide ecosystems from systematic method is that policy-makers may become explicitly aware of the spatial scale at which their policies are implemented or affected between conservation and development of a given ecosystem. Forest system change is particularly severe in tropical regions of developing countries under the pressure of strong socio-economic changes (Geist and Lambin 2002; Lambin et al. 2003; Sanchez-Azofeifa et al. 2001). To mitigate the dramatic deforestation rate of the country, Ecuadorian government promoted incentive-based policies for the conservation of native forests, such as the Socio Bosque program (Cuenca et al. 2018) as well as the establishment of several protected areas (Cuenca et al. 2016). In the conservation point of view, there are two concerns on existing forest protection policy. The first one is the NPRN in Ecuador is not optimized the protection of natural forest ecosystems. For example, because of higher poverty and a shortage of adult labor, the farms are characterized by large pasture areas around dwellings, small areas used for subsistence

agriculture and forest patches (< 20km²) in South Ecuador. Although threatened or near threatened forest ecosystems are concentrated in this area, we demonstrated that the current NPRN coverage does not provide appropriate protection for these critical ecosystems. Secondly, despite the protected areas seem to be effective for avoiding or reducing deforestation in Ecuadorian Tropical Andean forests (Cuenca et al. 2016), it was found that the passive landscape conservation focused on biodiversity may not be sufficient to maintain forest ecosystems, as land protection seems to be failed avoiding deforestation in several forest ecosystems (SI 2). Thus, meanwhile private and community land owners can benefit from a financial incentive in exchange for conservation of forests through the Socio Bosque Program, stakeholders and funding agencies now raise the question to what are effective and efficient for nationwide ecosystem conservation (Andam et al. 2010; Vanacker et al. 2018).

The main challenge to future forest ecosystem conservation is a paucity of explicit policies for management and use. The role of specific forest ecosystems on scientific-based ecosystem services can support political justification based on contribution to human well-being (Wu 2013a). Recognizing provisional ecosystem services' supply and demand of a locally-threatened ecosystem may promote informed decisions regarding investments in protection or restoration (Rodríguez et al. 2008). Aiming to strengthen conservation, valorization and sustainable use of natural resources, ecosystem services and biodiversity, ecosystem conservation strategies may be designed to further achieve environmental sustainability and territorial development. Thus, such targets, efforts and goals assigned to ecosystem

conservation should be updated considering the knowledge and experience gained by stakeholders and associated institutions participating in management plans.

Our analyses provide the first potential evidence of future loss of tropical Andean ecosystems in the tropical Andean biodiversity hotspot according to IUCN RLE criteria. Specific recommendations and more detailed future field studies for the management of these threatened or near-threatened ecosystems should include; (1) restoring forest quality and mitigating the trend toward a loss and degradation of ecosystem, (2) managing soft boundaries or creating buffers around remaining surface of forests, in order to reduce edge effect and landscape connectivity, (3) one of the limitations of this study is that mapping of intrinsic threats were restricted at the scale used (30 m-resolution). With these consideration, we suggest future research on adaptive capacity of the threatened ecosystems with regard to anthropogenic (e.g. logging, agriculture, fragmentation) and intrinsic (e.g. forest fire, flooding, climate change) threats and their synergy, (4) researches to determine the threshold of resilience and vulnerability of the remaining forest patches in each ecosystems, (5) promoting off-reserve conservation on privately or communally owned lands, and (6) identifying and designing adequate landscape configuration based on the remnant forests to enhance ecosystem persistence and resilience (Suding et al. 2004; Tambosi and Metzger 2013).

Conclusion

The present analysis of conservation status of forest ecosystems in Ecuador drew several conclusions: i) only small extent of forest patches remain in several forest

system; ii) these forest systems are in danger of complete elimination due to pressure from human land use, and iii) the official management institutions are limited with respect to protection of forest ecosystems. This study stands as baseline for understanding and measuring forest ecosystem change, threats and potential extinction risk at landscape scale. It complements current conservation efforts and could contribute to guide land-use planning at local and national scales in mainland Ecuador.

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Annex

A1. Spatial scale (nation-region-ecoregion-ecosystem) of the system under study and 64 forest ecosystems of continental Ecuador

Region	Ecoregion	Code	Forest Ecosystems (forest vegetation type)	Altitudinal range (m)
COAST	Equatorial-Chocó	E1	Flood alluvial plain forest of the Equatorial Chocó	50-200
		E2	Equatorial Chocó mangrove	0-20
		E3	Evergreen forest of the Equatorial Chocó lowland	0-300
		E4	Flood intertidal plain forest of the Equatorial Chocó	0-50
		E5	Seasonal evergreen forest of Equatorial Chocó lowlands	0-300
		E6	Piedmont seasonal evergreen forest of the Chocó coastal range	200-400
		E7	Low montane evergreen forest of Chocó coastal range	>400
	Equatorial-Pacific	E8	Semideciduous forest of the Jama-Zapotillo lowland	0-300
		E9	Semideciduous forest of the Equatorial Pacific coastal range	>200
		E10	Low forest and deciduous shrubland of the Jama-Zapotillo lowland	0-400
		E11	Piedmont seasonal evergreen forest of the Equatorial Pacific coastal range	200-400
		E12	Low montane seasonal evergreen forest of the Equatorial Pacific coastal range	400-860
		E13	Seasonal evergreen forest of the Jama-Zapotillo lowland	0-400
		E14	Deciduous forest of the Jama-Zapotillo lowland	0-400
		E15	Deciduous forest of the Equatorial Pacific coastal range	>200
		E16	Jama-Zapotillo mangrove	0-10

		E17	Seasonal flood alluvial plain evergreen forest of the Jama-Zapotillo	0-300
ANDES	Western-range	E18	Piedmont evergreen forest of the western Andean range	300-1400
		E19	Low montane evergreen forest of the western Andean range	1400-2000
		E20	Montane evergreen forest of the western Andean range	2000-3100
		E21	High montane evergreen forest of the western Andean range	3100-3600
		E22	Piedmont seasonal evergreen forest of the western Andean range	300-1400
		E23	Piemontano seasonal evergreen forest of the Catamayo-Alamor	400-1600
		E24	Low montane seasonal evergreen forest of the Catamayo-Alamor	1600-2000
		E25	Montane evergreen forest of the Catamayo-Alamor	2200-2900
		E26	High montane evergreen forest of the Catamayo-Alamor	2900-3400
		E27	Low montane evergreen forest of the Catamayo- Alamor	1600-2200
		E28	Piedmont evergreen forest of the Catamayo-Alamor	400-1600
		E29	Piedmont semideciduous forest of the Catamayo-Alamor	400-1600
		E30	Low montane semideciduous forest of the Catamayo-Alamor	1600-2200
		E31	Piedmont deciduous forest of the Catamayo-Alamor	400-1600
		E32	Low montane deciduous forest of the Catamayo- Alamor	1600-2200
	Valley, Alpine	E33	Semideciduo forest and shrubland of the North Valleys	1200-2600
		E34	Semideciduo forest and shrubland of the South Valleys	1200-2000
		E35	Páramo evergreen forest	3200-4100
	Eastern-range	E36	High montane evergreen forest of the north-eastern Andean range	3000-3700
		E37	Montane evergreen forest of the north-eastern Andean range	2000-3000
		E38	Low montane evergreen forest of the north-eastern Andean range	1200-2000
		E39	Piedmont evergreen forest of the north-eastern Andean range	400-1200
		E40	Low montane evergreen forest of the south-eastern Andean range	1660-2200
		E41	Montane evergreen forest of the south-eastern Andean range	2200-3000
		E42	High montane evergreen forest of the south-eastern Andean range	3000-3400
		E43	Piedmont evergreen forest of the south-eastern Andean range	400-1650
		E44	Piedmont semideciduous forest of the south-eastern Andean range	500-1300

AMAZON	Range	E45	Low montane evergreen forest of Galeras	1300-1700	
		E46	Piedmont evergreen forest of Galeras	600-1300	
		E47	Piedmont evergreen forest of the C3ndor-Kutuk3 range	350-1400	
		E48	Low montane evergreen forest of the C3ndor-Kutuk3 range	1400-1900	
		E49	Montane evergreen forest of the C3ndor-Kutuk3 range	1900-2400	
		E50	Piedmont evergreen forest on sandstone plateaus of the C3ndor-Kutuk3 range	350-1400	
		E51	Montane evergreen forest on sandstone plateaus of the C3ndor range	1900-2700	
		E52	Piedmont evergreen forest on limestone outcrops of the Amazonian range	600-1400	
		E53	Low montane evergreen forest on sandstone plateaus of the C3ndor-Kutuk3 range	1400-1900	
		E54	Evergreen forest on sandstone plateaus of the C3ndor range in the lower Ecuadorian Amazon	243-550	
		Plain	E55	Evergreen forest of the Aguarico-Putumayo-Caquet3 lowland	168-350
			E56	Flood alluvial plain palm forest of the Amazon	171-350
			E57	Flood river (originated in the Andean and Amazonian ranges) alluvial-plain forest	164-350
			E58	Lowland evergreen forest of the Napo-Curaray	170-350
E59	Flood alluvial plain forest of the Amazon		158-350		
E60	Flood forest and lacustrine-riparian vegetation of the Amazonian black water		170-350		
E61	Flood river (originated in the Amazon) alluvial plain forest		158-350		
E62	Evergreen bamboo forest of the Amazonian lowland		196-500		
E63	Evergreen forest of the <i>Tigre-Pastaza</i> lowland		166-350		
E64	Evergreen forest of the <i>Pastaza</i> fan-shaped lowland		197-350		

CHAPTER 5

GENERAL CONCLUSION

Although highly fragmented landscapes may conserve high diversity of species and ecosystems, a close look at their composition reveals a deterministic consequence that the landscape has surpassed its essential threshold for the forest conservation. However, as long as a different type of biodiversity (e.g. species, community and ecosystem) that is predicted to become extinct still persists, we believe that they provide new challenges and opportunities to current biodiversity conservation. It will depend on valid timing because species extinction and ecosystem collapse are ongoing processes and imposes an undefined deadline. Instead of waiting to develop large-scale conservation projects, we suggest the immediate implementation of local or small-scale restoration projects in order to reduce the biodiversity loss.

This study provide evidence on the potential ecological effects of fragmentation on biodiversity and measuring the vulnerability of forests due to forest fragmentation in biodiversity hotspots. Even though the present investigation has analyzed forest species and ecosystems at the landscape scale, more comprehensive local level analyses will be necessary to recognize the underlying factors that have resulted in the distinct changes observed in forests of the Andean region

We suggest the following recommendations for preventing future biodiversity loss

- i) Early detection of an extinction debt of long-lived specialist plants can be considered a benefit to begin habitat restoration and conservation actions in an adequate time in the study area. However, as responses to habitat fragmentation are species-dependent, conservation actions which target species groups are inadequate. Future monitoring plans of extinction dynamics must focus on single species of long-lived specialist plants rather than focusing on species richness or a set of species. In the fragmented landscapes of biodiversity hotspot, it may be crucial to identify and prioritize the conservation of species with extinction proneness over those that have no significant risk.
- ii) Specific recommendations and more detailed future field studies for the management of these threatened or near-threatened ecosystems should include; (1) restoring forest quality and mitigating the trend toward a loss and degradation of ecosystem, (2) managing soften boundaries or creating buffers around remaining surface of forests, in order to reduce edge effect and landscape connectivity, (3) further researches to determine the threshold of resilience and vulnerability of the remaining forest patches in each ecosystems, (4) promoting off-reserve conservation like agroforestry management on privately or communally owned lands, and (5) identifying and designing adequate landscape configuration based on the remnant forests to enhance ecosystem persistence and resilience.

iii) Because a large portion of the study area is privately owned in Chile and Ecuador, participation and cooperation of the private sector is a key element to address biodiversity conservation goals in the study area. It will be necessary to create appropriate conditions for the participation of all relevant stakeholders in the planning and implementation of conservation initiatives.

