

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador



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**Linkages between biodiversity and ecosystem services: an
assessment of land use change along altitudinal and
climatic gradients in the highlands of northern Ecuador**

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To my father and mother.

I hope I have made you proud.

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Résumé

Alors que l'impact de la transformation des terres pour répondre aux besoins en ressources naturelles de l'homme, appelé ici changement d'utilisation des terres (LULC en anglais), a été documenté dans le monde entier, il y a encore une lacune dans la connaissance des conséquences de ces transformations pour la biodiversité et pour la réalisation de services écosystémiques dans les écosystèmes de montagne tropicaux. Il est essentiel de comprendre comment l'utilisation des terres impacte la biodiversité et les fonctions des écosystèmes afin de déterminer les conséquences du changement global sur les écosystèmes de montagne pour la planification et la gestion des paysages afin de fournir des services écosystémiques vitaux à des millions d'habitants des hautes et basses terres.

Compte tenu de cet enjeu, notre recherche vise à approfondir la compréhension des impacts des changements d'occupation et d'utilisation des terres sur les systèmes montagneux de l'Équateur. Pour atteindre cet objectif, nous avons testé une version adaptée du cadre conceptuel « Driver-Pressure-State-Impact-Response (DPSIR) » pour les systèmes tropicaux de montagne. Dans ce cadre, nous avons réalisé une évaluation de l'écosystème dans un paysage montagneux représentatif du nord de l'Équateur avec les questions spécifiques suivantes : 1) caractériser les modèles spatio-temporels d'utilisation des terres dans le paysage étudié, 2) révéler les forces motrices des transitions du paysage, 3) exposer les effets du changement d'utilisation des terres sur la biodiversité locale, les fonctions écologiques et les services écosystémiques, et 4) évaluer si le changement d'utilisation des terres affecte la capacité d'approvisionnement des services écosystémiques au fil du temps dans le paysage étudié.

Tout d'abord, la caractérisation de la dynamique du changement d'utilisation des terres à l'aide des probabilités de la chaîne de Markov en fonction de l'altitude et du cadre géographique a révélé des modèles clairs. Nous avons constaté une expansion significative de la floriculture (13 fois) et des zones urbaines (25 fois), atteignant ensemble près de 10% du territoire entre 1990 et 2014 sur d'anciennes terres agricoles situées à des altitudes plus basses à l'est du territoire étudié. Nos résultats ont également révélé une tendance inattendue de stabilité du páramo (avec des probabilités de persistance comprises entre 0,75 et 0,9), mais aussi une réduction de 40 % des forêts montagnardes, avec la plus faible probabilité (<0,50) de persistance dans la bande d'altitude de 2800-3300 m ; les terres agricoles remplacent ces classes LULC à plus haute altitude. Ces tendances soulignent la menace croissante d'une perte définitive de la biodiversité indigène des montagnes, déjà vulnérable. Les tendances détectées en matière d'occupation des sols ont été intégrées dans un modèle additif généralisé (GAM en anglais) avec des données géospatiales et temporelles accessibles au public sur les facteurs socio-économiques, les variables démographiques et d'infrastructure et les paramètres environnementaux. Les GAM des facteurs socio-économiques, démographiques, des variables d'infrastructure et des paramètres environnementaux expliquent entre 21 et 42% de la variation des transitions LULC

observées dans la région d'étude, où les facteurs topographiques sont les principaux moteurs du changement (chapitre 2).

Deuxièmement, en utilisant le cadre de la santé des sols, nous avons évalué l'impact de la conversion des forêts indigènes en systèmes anthropiques (forêts plantées, pâturages et monocultures) sur la fertilité des sols et la conservation de la biodiversité dans les hautes terres du nord de l'Équateur. La dimension biologique de notre évaluation s'est concentrée sur la diversité, l'abondance et la biomasse des communautés de macro-invertébrés édaphiques comme indicateurs des fonctions du sol. Les communautés d'invertébrés du sol et les paramètres chimiques du sol ont été étudiés dans des échantillons de terre végétale à l'aide de monolithes de 25×25×10 cm, obtenus à partir de dix sites d'échantillonnage choisis au hasard dans chaque catégorie d'utilisation des terres. Nos résultats ont montré que les forêts indigènes présentaient des valeurs plus élevées pour la richesse, l'uniformité et la diversité des communautés de macro-invertébrés du sol que les autres catégories, démontrant une perte significative de la biodiversité taxonomique au niveau des ordres et des genres. Nous avons également constaté une réduction significative de la diversité trophique dans les forêts indigènes converties en environnements anthropiques. Les résultats des paramètres chimiques du sol ont également confirmé la distinction de la santé du sol entre les forêts indigènes et les environnements anthropiques. Nos résultats soulignent le risque associé aux tendances actuelles de perte de forêts natives et de conversion à des systèmes gérés dans les écosystèmes de haute montagne dans les tropiques, illustrant comment ces altérations pourraient causer une perte de biodiversité et une dégradation des attributs chimiques de la santé du sol (chapitre 3).

Troisièmement, en ce qui concerne l'effet du changement des classes LULC sur le microclimat, comme nous nous y attendions, les forêts indigènes se caractérisent par un microclimat plus stable, montrant des températures significativement plus basses et des valeurs d'humidité relative plus élevées que les autres classes LULC. Cet effet sur le microclimat s'explique de manière significative par les températures les plus élevées aux niveaux intermédiaires de la fraction d'espace, qui représente la quantité de rayonnement lumineux atteignant la strate inférieure d'une forêt, puis, un proxy pour les différences de couverture végétale entre les utilisations des terres. En outre, nous avons observé que les forêts indigènes ont eu un effet tampon sur les variations du mésoclimat, alors que les variations de température locales enregistrées sur les systèmes modifiés par l'homme (forêts plantées et pâturages) ont été expliquées de manière significative par la variation du mésoclimat, à l'exception des monocultures qui présentaient un décalage entre les deux échelles du climat. Ces résultats soulignent l'importance de la forêt native pour la régulation du microclimat, un service écosystémique qui peut agir en synergie avec d'autres objectifs de conservation de la biodiversité pour gérer durablement les paysages dans les systèmes montagneux andins (chapitre 4).

Quatrièmement, en ce qui concerne le changement temporel de la distribution des services écosystémiques sur le territoire étudié, des modèles clairs de distribution ont été détectés à la fois dans l'espace et dans le temps. Une diminution de la fourniture de nourriture a été observée précisément là où l'infrastructure urbaine a été étendue, à

l'est du territoire. Alors que dans la partie sud-ouest du territoire, en plus de l'altitude plus élevée de toutes les paroisses, une valeur plus élevée a été détectée pour les services écosystémiques de régulation et de culture (chapitre 5).

Enfin, nous considérons que le cadre DPSIR proposé et sa mise en œuvre pratique constituent une bonne alternative pour réaliser des évaluations d'écosystèmes qui pourraient être reproduites dans les paysages de montagne tropicaux. Ce cadre pourrait contribuer à l'élaboration de plans de gestion foncière judicieux susceptibles de prévenir une dégradation irréversible des écosystèmes à grande échelle. Cette phase a été initialement mise en œuvre en partageant nos principaux résultats avec les autorités locales et les parties prenantes. Cependant, des efforts supplémentaires sont nécessaires pour relier les résultats de la recherche obtenus dans le cadre de notre étude afin d'aller de l'avant et de guider la mise en œuvre locale du processus décisionnel.

Abstract

The study of land use land cover change (LULC) provides a measure of how landscapes are transformed to meet the natural resource needs of humans. Unraveling how land use constrains biodiversity and ecosystem functions, to determine the consequences of global change for mountain ecosystems, is critical for landscape planning and management to supply vital ecosystem services to millions of upland and lowland inhabitants. This understanding is particularly important for assessing impacts on tropical mountain ecosystems, where altitudinal and climatic gradients can produce sensitivities in ecosystem responses and affect the long-term provision of services and the well-being of associated human populations.

Given this issue, this research aimed to further the understanding of the impacts of land use changes on mountain systems of Northern Ecuador. To achieve this goal, we tested an adapted version of the Driver-Pressure-State-Impact-Response (DPSIR) framework for tropical mountain systems. Within this framework, I conducted an ecosystem assessment in a representative mountainous landscape of northern Ecuador with the following specific objectives: 1) characterize spatio-temporal patterns of land use, 2) reveal driving forces for the land use transitions, 3) analyze the effects of land use change on local biodiversity, ecological functions, and ecosystem services, and 4) evaluate if land use change affects the capacity to supply ecosystem services.

The study region comprises the territory of the canton of Pedro Moncayo, located in the Andean province of Pichincha, and encompasses 332 km² distributed among five parishes. It is a landscape with climatic conditions, and land use legacies characteristic of the highlands of northern Ecuador. The territory has a wide altitudinal gradient ranging from 1900 to 4000 m.a.s.l. and it encompasses a mosaic of different natural ecosystems and distinct land uses which can be described following the altitudinal gradient. The higher altitudinal zone (above 3300 m) is dominated by native ecosystems, represented by páramo and highland montane forests. The middle altitudinal area (2800-3300 m) has been extensively used for agriculture and livestock over time, causing severe soil degradation, and the lower lands are characterized by shrub-dominated dry ecosystems.

First, land use change dynamics characterized by Markov chain transition probabilities along elevation and geographic gradients revealed clear patterns. A significant expansion of floriculture (13 times) and urban areas (25 times) was found, reaching together almost 10% of the territory from 1990 to 2014 on previous agricultural land located at lower elevations in the east of the studied territory. Our findings also revealed an unexpected high probability of persistence (between 0.75 and 0.9) of páramo, but also a 40% reduction of montane forests, with the lowest probability (<0.50) of persistence in the elevation band of 2800-3300 m where agricultural land is replacing this land use and land cover (LULC) class at higher elevation. These trends highlight the threat of permanently losing the already vulnerable native mountain biodiversity. The LULC trends detected were integrated with publicly available geospatial and temporal data for socio-economic factors,

demographic, infrastructure variables, and environmental parameters into a generalized additive models (GAMs). GAMs of socio-economic factors, demographic, infrastructure variables, and environmental parameters explained between 21 to 42% of the variation of LULC transitions observed in the study region, where topographic factors were the main explanatory variable for most of the models.

Second, using the soil health framework, I assessed the impact of native forest conversion to anthropic systems (planted forests, pastures, and monocultures) on soil fertility and biodiversity conservation in the highlands of northern Ecuador. The biological dimension of our assessment focused on the diversity, abundance, and biomass of edaphic macroinvertebrate communities as proxies for soil functions. The soil invertebrate communities and soil chemical parameters were studied in topsoil samples using 25×25×10 cm monoliths, obtained from ten sampling sites randomly selected in the reference and the anthropic systems. Our results showed that native forests presented greater values for richness, evenness, and diversity of soil macroinvertebrate communities than the other land use categories, demonstrating a significant loss of taxonomic biodiversity at order and genus levels after forest conversion to anthropic environments. This piece of research also found a significant reduction of trophic diversity in native forests converted to anthropic environments. The results from the soil chemical parameters also confirmed the distinction in soil health between native forests and anthropic environments. Our results highlight the risk associated with current trends of native forest loss and conversion to managed systems in high mountain ecosystems in the tropics, illustrating how these alterations could cause biodiversity loss and degradation of the chemical parameters of soil fertility.

Third, in relation to the effect of LULC changes on microclimate, native forests provided more stable environmental conditions, where significantly lower temperatures and higher relative humidity values were documented than the other land use types. This effect on microclimate was significantly explained by the highest temperatures at intermediate levels of gap fraction, which represents the amount of light radiation reaching the lower stratum of a forest serving as a proxy for vegetation cover differences among land uses. In addition, native forests provided a buffer effect on the variations in mesoclimate, defined as climatic processes occurring at a scale of tens to hundreds of kilometres, whereas local temperature variations registered on human altered systems (planted forests and pastures) were significantly explained by the mesoclimate variation, except for monocultures that exhibited a mismatch between the two scales of climate. These results highlight the importance of native forest for microclimate regulation, an ecosystem service which can act synergistically with other biodiversity conservation goals to sustainably manage landscapes in tropical Andean Mountain systems (Chapter 4).

Fourth, in relation to the temporal change in the distribution of ecosystem services in the studied territory, clear patterns of distribution were detected both spatially and temporally. A decrease in the provision of food was observed precisely where urban infrastructure has been extended, in the east of the territory. Whereas in the southwestern part of the territory, in addition to the higher elevations of all the

parishes, a higher value was detected for regulatory and cultural ecosystem services (Chapter 5).

Finally, I consider that the proposed DPSIR framework and its practical implementation is a good alternative for conducting ecosystem assessments that could be replicated in other tropical mountain landscapes. This framework could help develop sound land management plans that could prevent broad scale, irreversible ecosystem degradation. This phase was initially implemented by sharing our major findings with local authorities and stakeholders. However, more effort is needed to link the research insights gained from our study with local implementation and to guide decision making processes.

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1

General Introduction

This chapter presents the general context for conducting this research, the thesis framework, development of the problem, thesis objectives, and the structure of the thesis.

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

Research position

A natural ecosystem is characterized by a diverse array of species, with each species occupying a unique ecological niche. Natural ecosystems typically have high levels of biodiversity, with many different plant and animal species interacting with one another in complex ways. These ecosystems are often able to support a range of ecosystem services, such as carbon sequestration, water filtration, and nutrient cycling. In contrast, anthropogenically modified ecosystems are typically characterized by a reduction in biodiversity and the simplification of ecological interactions. Anthropogenic systems may be altered to serve a specific human need, such as food production, material extraction or urban living, and are often managed in a way that prioritizes productivity and efficiency over natural ecological function (La Notte et al. 2017; Seddon et al. 2016)

The conceptualization of Ecosystem Services, defined as “the benefits people obtain from ecosystems” (Millennium Ecosystem Assessment (MEA) 2005), has had considerable impact on the development of environmental science and policy over the past two decades and underpins key global and national strategies, including the Convention on Biological Diversity (CBD) (2020), the Paris Agreement and the UN Framework Convention on Climate Change (UNFCCC) (United Nations Framework Convention on Climate Change (UNFCCC) 2015) and to Combat Desertification (UNCCD) (2017). The concept has evolved and currently includes a more integrative vision to understand complex socio-environmental interrelationships and diverse valuations of nature's contribution to people's wellbeing (Pascual et al. 2017)

The ecosystem services concept provides a valuable tool for highlighting the interdependences among people and ecosystems for supporting human well-being and promoting the sustainable management of natural resources (Schröter et al. 2016). However, the limitations of its application should be acknowledged (Barnaud and Antona 2014), such as the conceptual metaphor of economic production on which the definition is based on, because it emphasizes on the benefits of ecosystems to humans in terms of how the processes of nature deliver supplies and goods (Raymond et al. 2013). Despite these limitations, I consider that the ecosystem service approach is a practical tool to conduct ecosystem assessments to evaluate the consequences of human activities, such as land use change, by using a framework that links cause and effect relationships, as well as feedbacks between socio-ecological systems such as the Driver-Pressure-State-Impact-Response (DPSIR) model (Burkhard and Müller 2008).

In the Ecuadorian context, the ecosystem service approach is recognized and defined in the National Constitution, adopted in 2008, as the principle of “*buen vivir*” or “*sumak kawsay*”, which means living well in harmony with nature and society. Article 72 states that nature has the right to exist, persist, and regenerate its vital cycles, structures, functions, and processes in evolution. In addition, Article 74 recognizes the concept of ecosystem services and states that “*ecosystems provide essential services that contribute to the well-being of human beings and society, such as clean water, air, food, and cultural, spiritual, and recreational values*”. Similarly,

this Article states that *“Individuals, communities, peoples and nationalities shall have the right to benefit from the environment and natural resources that allow them to live well. Environmental services shall not be susceptible to appropriation; their production, provision, use and exploitation shall be regulated by the State”* (República del Ecuador 2008) Overall, the ecosystem service approach in the Ecuadorian Constitution is based on the recognition of the intrinsic value of nature and the interdependence between human well-being and the health of ecosystems. This approach promotes the sustainable use and conservation of natural resources, as well as the restoration and rehabilitation of degraded ecosystems to ensure their continued provision of essential services (República del Ecuador 2008) Therefore, this legal framework invites to test the ecosystem services approach to carry out analyses and assessments to understand the consequences of human impacts, such as land use change, on ecosystem health.

The idea of the interconnectedness of natural and socioeconomic systems is fundamental to thinking on sustainability and sustainable development. For this reason, the principle of interdisciplinarity, which calls for the integration of theories, concepts, techniques, and data from multiple disciplines such as ecology, geography, economics, sociology, and other fields (Porter et al. 2007), is equally crucial for conducting research that is both comprehensive and relevant to develop a holistic understanding of land use change and its impacts (Wu 2013)

Key integrated conceptual models that connect natural and socio-economic systems to governance include the cascade and the DPSIR framework (Haines-Young and Potschin 2010). The cascade conceptual framework identifies the capacity of ecosystems to provide services, emphasizing the connections of biodiversity, its ecological function, and the benefits to people. Likewise, the DPSIR framework illustrates the causal relationships between human activities that could exert pressure on the state of the ecosystems, affecting the delivery of ecosystem services (Burkhard and Müller 2008; Odermatt 2004). Therefore, proposing a DPSIR framework for tropical mountain systems could enhance our understanding of these unique and fragile environments, supports evidence-based decision-making, and facilitates the sustainable management and conservation of these valuable ecosystems.

Land use change is a complex process that involves the conversion of natural ecosystems and landscapes for human purposes, which can result from a variety of factors, including urbanization, agriculture, mining, forestry, and infrastructure development (Gergel and Turner 2017). Land use change is a critical issue in landscape sustainability science, as it has significant impacts on the natural environment, human societies, and their interactions (Wu 2012) Land use change could be explained by the Forest Transition Theory (FTT), since forest cover is subject to predictable positive or negative changes, which can be associated with reforestation and afforestation activities that occur due to the reduction or elimination of agricultural land, population changes, and the changing demand for products and transition in the valuation of forests, leading to a net increase and/or reduction of forest cover, resulting in secondary forests on forested lands and plantations on non-forested soils (Wilson et al. 2019).

Land use change can have significant consequences for the environment, including changes in the quality and quantity of water, soil erosion, loss of biodiversity, changes in the global carbon cycle and other essential benefits that humans obtain from nature (Cerretelli et al. 2018; Luyssaert et al. 2014). In this context, ecosystem services, defined as the direct or indirect components that are provided by the structure and function of the ecosystem, which are exploited for human benefits (Müller and Burkhard 2012); provides a useful framework for assessing the impact of land use change on the health of ecosystems (Angelstam et al. 2019). By assessing the changes in the provision of ecosystem services before and after land use change or comparing the differences between natural and anthropogenic ecosystems and considering the continuum from a "virgin" natural ecosystem to one highly modified by humans it is possible to gain a better understanding of the ecological and social consequences of land use change.

The Ecuadorian highlands are an ecologically and culturally diverse region that has experienced significant land use change over the past several decades (Gaglio et al. 2017; Guns and Vanacker 2013; Tapia-Armijos et al. 2015). Given the complexity of tropical mountain ecosystems and the diverse array and uncertainties of spatio-temporal dynamics and consequences on ecosystem health due to human induced modifications of natural ecosystems (Balthazar et al. 2015; Bonnesoeur et al. 2019; Peters et al. 2019; Vanacker et al. 2003), trends of change in a landscape in the northern highlands of Ecuador were examined through the Forest Transition Theory (Wilson et al. 2019). In addition, an ecosystem service approach, integrated within the DPSIR conceptual model was selected as a scientifically rigorous and holistic framework for assessing the impact of land use change on biodiversity and the provision of ecosystem services on the landscape studied. Based on the assessment of the impacts of land use change, it is possible to identify strategies to mitigate negative impacts and promote positive outcomes. I used a mixed methods research position, which involves combining qualitative and quantitative methods, to provide a more comprehensive understanding of the issue. Among the methods used in this project include: biophysical valuations, expert's perceptions and modelling research methods which provided a more nuanced understanding of complex issues.

Finally, epistemologically, the present research began with a positivism stance, where the researcher intended to analyze and synthesize relevant information for decision making in the territorial management of the landscape under study, highlighting the value and interdependence of natural ecosystems and their diversity for local well-being. However, during the development and completion of this formal academic phase that constitutes doctoral research, it was evident the need for this research to follow a dynamic process that interlinks the scientific information (including local knowledge) with the phase of policy and decision-making (Díaz et al. 2018) from a critical realism posture that could transcend to a post-normal scientific framework (Francis and Goodman 2010).

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

Theoretical framework

Connecting ecosystems to human well-being: Ecosystem Services

Concerns about a heavy human footprint on the environment and subsequent negative effects on human well-being have stimulated new concepts in policy, practice, and research (Mace 2014). In this context, the conceptualization of ecosystem services, defined as ‘the benefits people obtain from ecosystems’ (Millennium Ecosystem Assessment (MEA) 2005), was able to trigger a paradigm shift by placing ecological challenges at the core of human decision making because it recognizes that humans depend on and interact with the natural environment. It also highlights the importance of protecting and conserving ecosystems to ensure continued provision of ecosystem services in the face of environmental degradation (Millennium Ecosystem Assessment (MEA) 2005).

The definition of ecosystem services has undergone changes and has evolved since its postulation as the understanding of the relationship between humans and the natural environment has deepened. The concept of ‘environmental services’ was first proposed by Westman (1977), then, it was renamed ‘ecosystem services’ by Ehrlich and Mooney (1983) and, from then, it has evolved and gained importance. The Millennium Ecosystem Assessment (Millennium Ecosystem Assessment (MEA) 2005) popularized the definition of ‘the benefits that humans obtain from ecosystems’. Müller & Burkhard (2012) redefined it as the direct or indirect components that are provided by the structure and functionality of the ecosystem, which are exploited for human well-being. The main objective of this concept is to measure, assess, and value aspects of the societal dependence on natural ecosystems and to promote public interest in biodiversity conservation (Lele et al. 2013). The term ‘ecosystem services’ is very popular in the political and scientific sphere due to its significance for decision making on the sustainable use of natural resources and the ecosystem, and its application for land use and environmental planning (Burkhard et al. 2009).

The conceptualization of ecosystem services has resulted in numerous benefits for the development of science and policy, particularly in applications in developing countries and the Global South. These benefits include: improved understanding of natural systems and biodiversity conservation, sustainable agriculture, community-based conservation, water management, disaster risk reduction, climate change mitigation and adaptation, improved health and well-being, sustainable use of land resources, among others (UNEP 2018). While the ecosystem service approach has been valuable in highlighting the benefits that nature provides to human well-being, this concept has been subject of controversies. Some authors have argued that the concept has some limitations and constraints such as its anthropocentrism, the oversimplification of natural systems, the risk of marketization of nature as a solution to environmental degradation, among others (Barnaud and Antona 2014; Schröter et al. 2016).

More recently, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced the term ‘nature’s contributions to people’ (NCP), defined as ‘all the positive contributions, losses or detriments, that people obtain from nature’ to capture both the beneficial and harmful effects of nature on people’s quality of life (Pascual et al. 2017). The NCP approach has the potential to overcome the limitations of the ecosystem services definition, such as moving beyond market-based valuations and incorporating a wider set of viewpoints and stakeholders, especially local and indigenous people (Díaz et al. 2018) who are the guardians of biodiversity conservation around the world (Garnett et al. 2018). However, the implementation of the NCP approach, especially the harmful effects of nature, and its reporting categories is still in its infancy. Moreover, there is a risk that any implementation of the NCP approach will lack the analytical foundations that made the earlier framings both deliverable and measurable (Mace 2014).

From my point-of-view, the valuation of the benefits that humans derive from nature are context-dependent, which involves a diverse array of views, values and different knowledge systems, then, establishing a common ground for research will require the explication and discussion of underlying values (Hermelingmeier and Nicholas 2017). In this research we will use the definition of ecosystem services as proposed by Müller & Burkhard (2012) to conduct a primarily biophysical assessment, with a stock-based perspective, of the impact of land use change on biodiversity and ecosystem services in the territory under study. This initial exercise should, subsequently, be integrated into a holistic valuation, which in turn, leads to the implementation of decision-making processes to foster the sustainable land management with all the elements describe in the NCP approach (Pascual et al. 2017).

Likewise, ecosystem services have been categorized in different ways. Here we are following the Common International Classification of Ecosystem Services (CICES) (Haines-Young and Potschin 2018). This classification system includes three categories: regulating, provisioning, and cultural ecosystem services. Provisioning services are material goods or products obtained from nature that allow humans to survive and are tangible elements of biodiversity, which generally have a monetary value. These services are used by humans for nutrition, energy, and raw materials. Regulating services, on the other hand, are less visible because they are those that make ecosystems clean, sustainable, functional, and resilient to change. A regulating service is the benefit provided by ecosystem processes that moderate natural phenomena. Regulating services include pollination, decomposition, water purification, erosion and flood control, carbon storage, and climate regulation. Cultural services encompass the intangible benefits obtained from ecosystems, such as symbolic value, artistic value, spiritual, mental, and educational well-being, among others. Therefore, they are considered people’s non-consumptive uses of biodiversity such as recreation, tourism, education, science, and cultural identity (Haines-Young and Potschin 2018).

Ecosystem Services depend on the natural capital of an ecosystem, i.e., its biological structure (e.g., species composition) and ecosystem processes and/or functions (e.g., primary productivity, nutrient cycling, water cycling, soil formation and fertility, etc.)

to provide the benefits that people perceive (Potschin and Haines-Young 2016). Some authors have suggested the category of supporting services to account for these underlying structures and processes (Millennium Ecosystem Assessment (MEA) 2005). However, many experts have questioned the applicability of this latter category because, in certain cases, regulating and supporting services overlap (Burkhard et al. 2012). These ecosystem services are particularly important in a climate change adaptation and mitigation context, where the sequestration of carbon and climate modification of forests is a key component for environmental accounting and underpin core elements of the UN Framework Convention on Climate Change (United Nations Framework Convention on Climate Change (UNFCCC) 2021) and the Paris Agreement (United Nations Framework Convention on Climate Change (UNFCCC) 2015). Here we are using the three category of ecosystem services proposed by CICES (Haines-Young and Potschin 2018).

At the landscape level, the combination of ecosystem structures, properties, and functions results in a varied supply of ecosystem services, which present very complex interrelationships associated with time, topography, and multidimensionality (Wu 2013). Ecosystem function is generally defined in terms of the condition or performance of the system, its capacity to produce, regulate or maintain one or more services, especially in relation to human needs (Millennium Ecosystem Assessment (MEA) 2005). Because ecosystems and landscapes provide so many different types of services, they are considered to be multifunctional. Landscapes are managed for different and sometimes competing purposes, including natural resource and energy extraction, livestock grazing, recreation and the conservation of biological diversity (With 2019).

Interactions between multiple services depend on spatial scale, time, and ecological and social drivers, and can be positive (synergies) or negative (trade-offs) (Raudsepp-Hearne, Peterson, and Bennett 2010). In the real world, synergies are not as common, nor should it be assumed that a site has the capacity to provide all the ecosystem services that users require, i.e., a landscape may be well suited to provide certain services but not others, these negative interactions that ecosystems and landscapes exhibit are known as trade-offs, and these are more prevalent especially in landscape patches (Rieb and Bennett 2020). To sustain the provision of multiple ecosystem services in landscapes, solid empirical evidence about states and trends, and well-coordinated policies and plans across multiple scales and governance levels are required (Jones et al. 2013).

Conceptual models connecting biodiversity and ecosystem services: The cascade and DPSIR frameworks

The landscape approach allows us to conceptualize and evaluate the importance of humans in shaping the biophysical and cultural aspects of landscapes. This approach also expands the knowledge on how the structural, processing, and functional components of the landscape respond to human stressors that could also affect ecosystem services and human well-being at different scales (With 2019).

As demonstrated by the Millennium Ecosystem Assessment (2005), human well-being depends on the natural capital of ecosystems, which encompasses the different levels of biological diversity. The variability, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system (Díaz et al. 2006) are the basis for the provision of goods and services that contribute to human well-being..

Based on the conceptualization of ecosystem services as a key element for the connection between natural and human systems, several paradigms were identified that explain their interconnections (Wu 2013), one of these is the ‘cascade of services’. This conceptualization associates the configuration and composition of the landscape, its ecological functions, and the environmental services that provide benefits to people. This paradigm has an integral approach that highlights the connections of biodiversity to the delivery of ecosystem services in a spatial context. In addition, the cascade model emphasizes the interconnection of social appreciation and its intervention and action within the structure and natural dynamics of the ecosystems present within landscapes (Haines-Young and Potschin 2010). All this facilitates better decision-making regarding management and stewardship at a landscape scale (Potschin and Haines-Young 2016).

According to the cascade conceptual framework (Haines-Young and Potschin 2010), ecosystem services are central to a socio-ecological system. Ecosystem services depend on the capacity of the ecosystem and the number of specific contributions from the environment that humans use. Moreover, their condition can be affected by alterations and demands coming from the social and economic spheres in a social-ecological system. These two elements precisely constitute the extremes in a cascade from the supply to the demand of ecosystem services. It can be said that the ecosystems’ capacity to provide services constitutes the supply side of services. Then, the supply is regulated by the biophysical properties and ecological functions of a particular area in a given period, while the demand for ecosystem services is characterized by the level of consumption by the society of a specific ecosystem service, in a particular place, during a defined period. It is worth considering that demand changes over time and space, without depending on the capacity of the ecosystem to provide the service. On the other hand, the flow of ecosystem services is the path from supply to beneficiaries (Burkhard et al. 2012).

Drivers of change affect the ecological integrity of the ecosystem or landscape, and in turn may lead to increasing or decreasing supplies of selected or bundles of ecosystem services on which human societies depend. The balance in the supply and

demand of ecosystem services are important steps toward sustainability (Burkhard and Müller 2008). The driving forces of landscape transformation can be of natural origin such as volcanic eruptions, formation of river networks, fire disturbances, biogeomorphology, among others. However, the widespread and rapidly increasing human impact on the environment driving is leaving a significant human footprint on landscapes (Foley et al. 2005). Anthropogenic driving forces could be related to human population density, the relative accessibility of an area to humans, the availability of roadways, the density of transportation networks, and the level of technological development (Sanderson 2002).

Here, we are connecting the landscape approach and the ecosystem service cascade model (Haines-Young and Potschin 2010) with a pragmatic framework to conduct ecosystem or landscape assessments to understand the impacts of human activities. These landscape assessments need to incorporate a sufficient level of complexity to ensure that they represent the different patterns and processes acting within the region's social-ecological systems. Therefore, we are pragmatically applying the Driver-Pressure-State-Impact-Response (DPSIR) framework to identify the key characteristics of our model system: tropical mountain systems.

The DPSIR conceptual framework models human-environmental systems that includes a feedback approach which illustrates causal relationships of anthropic impacts (Burkhard and Müller 2008). The advantage of the DPSIR framework is that it operationalizes and links cause and effect relationships, as well as feedback between socio-ecological systems (Organization for Economic Cooperation and Development (OECD) 2003) to understand and sustainably manage environmental problems (Müller and Burkhard 2012). Within the DPSIR framework, driving forces will exert pressures, changing the state of the system (Nassl and Löffler 2015). This altered state could ultimately impact on ecosystem services and human well-being, which could lead to a societal response. The societal response in turn feeds back to all other components (Müller and Burkhard 2012). Understanding this complexity is fundamental for the development of policies and measures for landscape planning and management, as societal responses to overcome environmental impacts (Burkhard and Müller 2008).

Oddermatt (2004) was the first to conceptualize and implement the DPSIR framework in the context of mountain systems; however, an adaptation of such an approach to conduct ecosystem assessments was lacking for the tropical mountain system context (Berrio-Giraldo et al. 2021).

In this research, we propose an adapted version of the DPSIR framework based on Balzan et al. (2019), Müller & Burkhard (2012), and Santos-Martín et al. (2013) to identify the key characteristics of tropical mountain systems that should be represented in ecosystem assessments at a landscape scale. The proposed DPSIR framework is described in detail in Chapter 2. More integrative and proactive implementations are possible when conducting analysis of ecosystem services using a DPSIR framework (Kelble et al. 2013). This framework presents multiple similarities with the NCP framework used by the IPBES Platform.

Land cover and land use change: One of the most significant human-induced environmental impacts on the biosphere

Natural and anthropogenic processes occur on the land surface that alter the structure and composition of landscape elements over time (Foley et al. 2005). However, humans have been modifying natural landscapes for thousands of years (Turner et al. 2007). The transformation of land to meet the natural resource needs of humans, referred as to land cover and land use change (Gergel and Turner 2017; Lambin and Geist 2006) has modified a significant proportion of the Earth's surface (Sala et al. 2000; Vitousek et al. 1997). Transformation of the dominant habitat or vegetation type – referred to as land cover – and changes in the way people use the land – defined as land use (Turner and Gardner 2015) are probably the most significant and oldest of all human-induced environmental impacts on the biosphere and the first to attain global magnitude (Foley et al. 2005; Turner et al. 2007; Vitousek et al. 1997).

Today, virtually no land surface remains untouched by human activities, and less than 50% of the ice-free surface of Earth remains forested (Dinerstein et al. 2019; Luysaert et al. 2014). Moreover, recent estimates of land use change, based on high-resolution satellite imagery and long-term inventories, suggest that 32% of the global land was transformed from 1960 at a steady rate until 2005, when this trend decelerated worldwide (Winkler et al. 2021). Geographically diverging land use change patterns were detected during the last six decades, with afforestation and cropland abandonment in the global north, whereas deforestation and agricultural expansion dominated the global south. These geographic trends were mainly driven by the global trade of agricultural products (Winkler et al. 2021) (Figure 1).

Land use activities have provided food, water, and other essential living products, helping to improve our quality of life. But unsustainable expansion and overexploitation of land resources have significantly transformed the natural landscape, causing negative impacts on the Earth system (Cerretelli et al. 2018). The long-term impacts of land cover and land use change may be observed across a broad spectrum of environmental systems, including the atmospheric, hydrologic, geomorphologic, and ecologic systems (Newbold et al. 2015; le Quéré et al. 2018).

Unsustainable land use, driven by urban expansion, deforestation, and mainly agricultural intensification and expansion to provide food for an overgrowing human population (Foley et al. 2005), leads to land degradation (Luysaert et al. 2014; Peters et al. 2019). Consequently, the space for nature has been squeezed and the quality of ecosystems have deteriorated, leading to biodiversity loss and degradation of the services they provide (Cardinale et al. 2012; Millennium Ecosystem Assessment (MEA) 2005; Winkler et al. 2021).

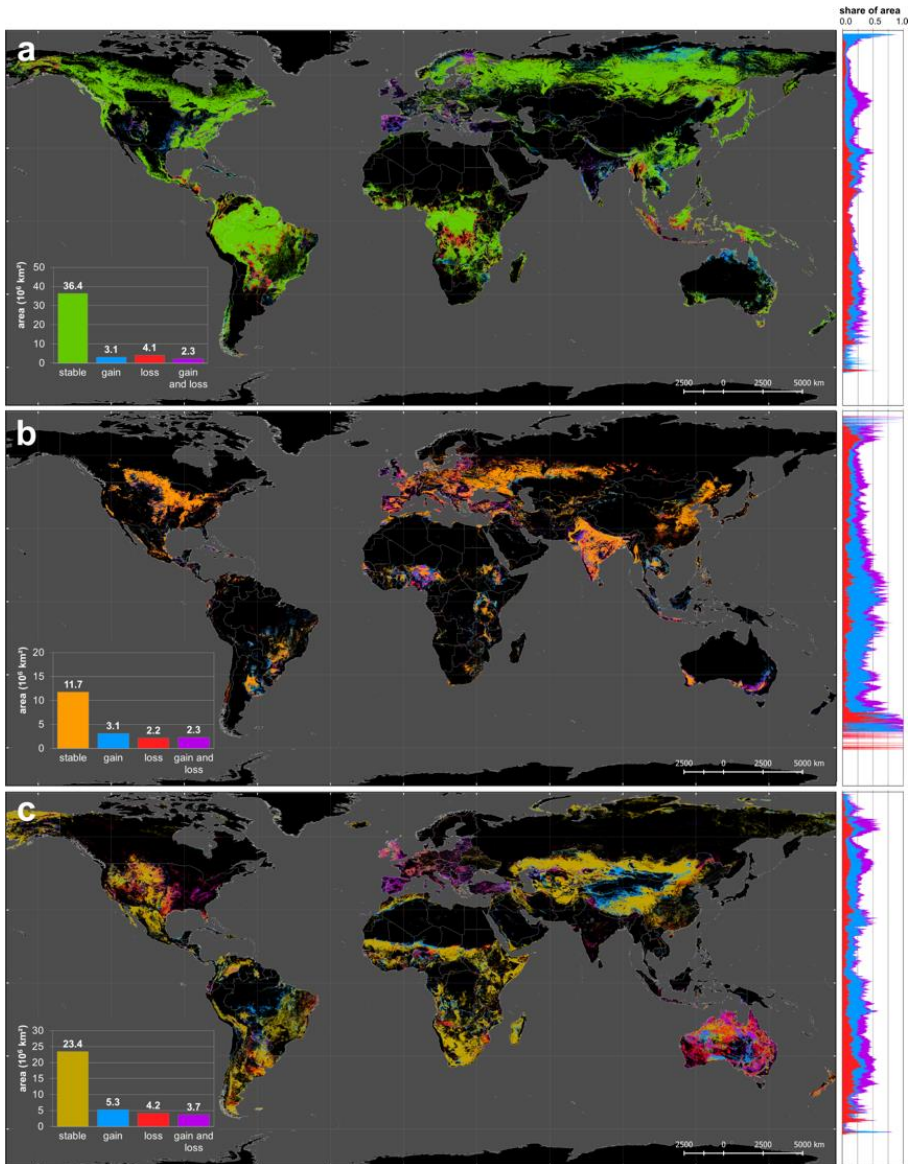


Figure 1. Spatial distribution of a) forest, b) cropland, and c) pasture/rangeland extent (stable area) and change (gain and loss) between 1960 and 2019. Area charts on the right show the stacked share of gains, losses, and multiple change area (on which both gains and losses have occurred) related to the total area under the respective land use change category along each geographic latitude (from Winkler et al., 2021).

Globally, mountains are increasingly being transformed by human activities, and montane forests are considered a top global conservation priority because of their high levels of clearing, vulnerability to climate change, and the vital services they provide to local and lowland inhabitants (Balthazar et al. 2015; Gaglio et al. 2017). Forest cover in Latin America continues to decline, and deforestation rates remain high (FAO 2015). During the last decade, the tropical Andes have lost 1% of their natural forest cover per year (Aide et al. 2013; Farley 2010; Portillo-Quintero et al. 2012; Sánchez-Cuervo et al. 2012) but at smaller scales, some regions are experiencing forest transitions or forest cover stabilization, especially in higher elevations (Aide et al. 2013). Therefore, the Andes are an important and compelling region to study the drivers and outcomes of local and regional land use change.

How the landscape concept and approach could help us to grasp the environmental impacts of land use and land cover change

Land change science has emerged as a fundamental component of global environmental change and sustainability research. This interdisciplinary field indicates that the modification of land due to anthropogenic factors has spatial and temporal interactions at the landscape scale (Turner et al. 2007). In addition, the sustainable management of this human-induced environmental impact should be appropriately framed to interconnect the social and natural dimensions of ecosystems (Lambin and Geist 2006). Sustainable management refers to the responsible and balanced management of the natural and human resources. It aims to ensure the preservation of the biodiversity, support local livelihoods, enhance resilience to climate change, and maintain the essential services provided by ecosystems and landscapes to surrounding regions (Wu 2012). Therefore, here we explore the definition of landscapes, as this provides the setting over which environmental problems unfold, and we describe the landscape approach as it provides the social-ecological systems' framework by which environmental issues can be tackled.

Alexander Von Humboldt proposed the first scientific definition of landscape 200 years ago. The Humboldtian conception of landscape was intended as a holistic view to understand the 'total character of a region' (Potschin and Bastian 2004). This conception was based on an aesthetic representation from the individual contemplation of nature, as proposed by German romantic idealist philosophy from the XVIII century, primarily represented by Schelling and Goethe (Potschin and Bastian 2004). But Humboldt added a materialist dimension to the concept that includes the actual appearance of nature, useful for identifying and comparing geographic areas and determining causes of combinations of its spatial composition and configuration (Corbera 2014). Furthermore, in his seminal book 'Cosmos', Humboldt used the landscape conception as a diagnostic tool to highlight the human footprint on environments. He was one of the first ecologists to point out the immense impact of the industrial revolution on the reduction and degradation of natural environments (Angelstam et al. 2019).

From Humboldt's vision, the term 'landscape' has been used in a wide range of different disciplines, art, and in practice, producing independent interpretations of the concept (Angelstam et al. 2019). Recently, the holistic approach to landscape has reemerged as an important research subject. The revalorization of this integrated view has resulted from the imbalance produced by the division of conceptual frameworks used by the natural and the social sciences to study landscapes (Tress and Tress 2001).

From the landscape ecology conception, 'the landscape is explicitly defined as an area that is spatially heterogenous in at least one factor of interest'. Thus, a specific spatial scale may not be universally applied. Rather, the emphasis in landscape ecology is to identify a scale that best characterizes relationships between spatial heterogeneity and the processes or response variable of interest (Turner and Gardner 2015). For the purpose of this thesis, I define the scale of the landscape as seen as by a human observer and I use the definition of landscape proposed in the ecosystem services' (ES) glossary by Potschin et al. (2018): 'A heterogeneous mosaic of land cover, habitat patches, physical conditions or other spatially variable elements viewed at scales relevant to ecological, cultural-historical, social or economic considerations'. According to this definition, the landscape implies a spatial scale that must be large enough (mostly larger than a field and smaller than a physiographic region) to encompass key environmental, economic, and social processes that determine the sustainability of a place of interest (Forman 2008). Following this notion, landscapes are spatial units in which society and nature interact and co-evolve and represent a pivotal place in research and the practice of sustainability science.

The challenge to translate knowledge about the state and trends of ecosystems – which is the basis of ecosystem services evaluations – to action that allows mitigation and adaptation to local to global challenges, as is envisioned by sustainable science, is immense, and requires multi-level governance based on knowledge and the sustainable use of concrete socio-ecological systems (SES). According to Berkes and Folke (1998), SES are a complex and adaptive set of different social, economic, ecological, and other components that interact, provide a comprehensive view of the complexity of environmental problems, and link the social and natural sciences. In other words, a SES is an ecological system that is intricately linked with and affected by one or more social systems (Anderies et al. 2004). Within this concept, the landscape approach pragmatically interconnects the human and nature systems through communicating evidence-based knowledge and incorporating the local perceptions about ecosystem services (Angelstam et al. 2019).

A landscape approach is broadly defined as a framework to integrate policy and practice for multiple land uses, within a given area, to ensure landscape sustainability which is defined as "the capacity of a landscape to maintain its basic structure and to provide multiple ecosystem services in a changing world of environmental, economic and social condition" (Wu 2012). It also aims to balance competing demands on land through the implementation of adaptive and integrated management landscape-specific ecosystem services (With 2019). These include not only the physical characteristic features of the landscape itself, but all the internal and external socio-economic and socio-political drivers that affect land use, particularly related to

conservation, forestry, and agriculture (Sayer et al. 2013). In other words, it is an interdisciplinary scientific approach to studying relatively large-scale socio-ecological systems that are increasingly influenced and determined by human activities.

According to With (2019), research is urgently needed to determine which measures can best serve as leading indicators of degraded landscape function and impeding state change within different types of landscapes, especially as many systems may soon be reaching a tipping point due to changes in environmental conditions, disturbance regimes, and land use, all of which are being exacerbated by climate change.

What are the key elements to understand land use and land cover trends in landscapes? The Forest Transition Theory.

The dynamics of land use change could be explained by the Forest Transition Theory (FTT). This theory describes a sequence over time where a forested region or country initially experiences a deforestation period before the forest cover eventually stabilizes and starts to increase. The FTT predicts a U-shaped curve in forest cover through time, with initial deforestation due to agricultural expansion and other human activities, followed by a reforestation and afforestation phase, when economic development leads to the abandonment of agricultural land or when forest scarcity leads to increases in planted forests (Mather 1992; Rudel et al. 2005). The forest transition theory also predicts that the drivers of deforestation change over time, from small-scale agriculture and logging to larger-scale commercial agriculture and industrialization, and eventually to urbanization and a shift towards more sustainable land use practices (Grau and Aide 2008).

Even though FTT has been examined worldwide, including tropical and temperate regions, forest transitions' outcomes are context-dependent and may or may not occur even if conditions are similar in comparable landscapes (Mather 1992; Rudel et al. 2005). Some examples suggest the economic development pathway may be of less relevance in developing country contexts, while studies in Latin America suggest that, in certain regions, forests are expanding in the highlands, as a consequence of land abandonment in less productive lands, to give way to agricultural intensification in fertile lowlands and flatlands (Aide et al. 2013). For instance, some studies found that one of the most important pathways to forest establishment in the highlands of Ecuador were associated with globalization and decisions by smallholders to use exotic tree species for plantations to try to restore land or provide economic diversification (Balthazar et al. 2015; Farley 2007; Grau and Aide 2008).

Additionally, recent studies in mountain tropical landscapes have identified that different socio-economic trajectories produce a variety of forest types in the regenerative stage of transition and this has implications for the provision of ecosystem services (Peters et al. 2023; Wilson et al. 2017). Understanding why, where and how forest transitions take place is of great interest for landscape planning, management and restoration (Wilson et al. 2019). However, this framework has been little studied in highland landscapes of northern Ecuador.

Causes, processes, and consequences of land use and land cover change predominantly determine the structure, functioning, and dynamics of most landscapes throughout the world. Land use and land cover change is driven primarily by socio-economic forces and is one of the most important and challenging research areas in landscape ecology, and in global ecology. More research efforts are needed to understand the causes, processes, and ecological consequences of land use and land cover change (Lambin and Geist 2006).

Decadal landscape changes imposed by economies, natural hazards and climate change, as well as ‘land use legacies’ (i.e., the types, extents, and durations of persistent effects of prior land use on ecological patterns and processes), need to be considered in the study of land use and land cover change. In addition, highly dynamic or chaotic landscapes may provide unique opportunities for studying land use and land cover change and their impacts on biodiversity loss and the provision of ecosystem services (Turner et al. 2007).

Approaches for Ecosystem services evaluations

To evaluate ecosystem services and their change over time, it should be considered that the spatial unit scale of analysis becomes the landscape. This spatial demarcation provides the basis to characterize spatial and temporal patterns of land use change and, in turn, assess if the capacity of ecosystems to provide ecosystem services to people have been degraded (Wu 2012).

Evaluating ecosystem services is generally supported by mapping techniques. The mapping of ecosystem services is the basis for identifying the state of an ecosystem and its services, and thus for proper planning (Burkhard and Maes 2017). The exponential development of technologies, especially remote sensing technologies (aerial photographs and satellite images) has made it possible to study processes at large spatial and temporal scales (Jones et al. 2013). The data resulting from these complex processes are analyzed through the use of geographic information systems that transform them into vectors, rasters, or digital models in the form of maps (Mace 2014). The maps through time allow the identification of movement in spatial patterns caused by changes in land use and land cover (LULC), conflict zones, where corridors or buffer areas for species can be established, in addition to documenting processes of forest transition in high Andean mountains (Balthazar et al. 2015; Gaglio et al. 2017; Hall et al. 2012).

The assessment of ecosystem services includes three approaches: ecological, economic, and social. Ecological evaluation measures the ecological functions or biophysical properties of the ecosystem in order to carry out technical interventions to recover and conserve ecosystem functions. Economic evaluation attempts to give a monetary value to ecosystem services in order to identify what type of services can be compensated, known as payments for environmental services. Social evaluation makes it possible to apprehend the awareness and perception that local residents have of ecosystem services in order to strengthen the decisions made about them (Balvanera et al. 2016).

Ecologic or biophysical assessments could be based on direct data obtained from primary information, such as observations, surveys, or field experiments. But also, indirect information could be integrated in ecosystem assessments through proxy indicators, socio-economic data, expert perceptions, process-based models and statistics (Balthazar et al. 2015; Vihervaara et al. 2017). Indicators and proxies are surrogates for mapping ecosystem services, and they are widely used in assessments, however, they give an estimated result of supply and demand for services (Eigenbrod et al. 2010).

On the other hand, the objective of applying social valuations is to understand and describe the background of the social value linked to nature. There are distinct ways to evaluate ecosystem services from the social aspect, but they are generally obtained from semi-structured surveys. Expert or local stakeholders' perceptions are used to evaluate the ecosystem services associated with distinct land cover and land use types and have been widely applied in different geographic contexts (Burkhard et al. 2009, 2012; Casado-Arzuaga, Madariaga, and Onaindia 2013; Madrigal-Martínez and Miralles-García 2019; Rojas 2016).

While economic valuations encompass the complexity of the natural environment and relate this to the economic capital, they use primary valuation or value transfer methods. This method assigns a monetary value to ecosystem services (Vihervaara et al. 2017). Despite the pros of accounting for the economic benefits that come from nature, this approach also has limitations. Some authors suggest that it poses a risk of imbalance between ecological and economic assessments, neglects non-use and socio-cultural values, and paves the way for the commodification of nature (Díaz et al. 2018). Therefore, a key challenge to be addressed is developing comprehensive assessment frameworks, in which biophysical, socio-cultural, and monetary values can be properly integrated (Martínez-Morales 2005).

RESEARCH PROBLEM

Land use trends in the tropical Andes

Tropical mountain systems are recognized as hotspots for biodiversity and habitat refugia in a warming world (Foster 2001; Gradstein et al. 2008) and are considered to be fundamental ecosystems because they supply vital ecosystem services to millions of upland and lowland inhabitants (Peters et al. 2019). They are of great ecological and socioeconomic importance as sources of drinking water, hydropower generation, and other regulating ecosystem services (Farley and Bremer 2017; Körner et al. 2005; Payne et al. 2017). Also, for local inhabitants, tropical mountain forests are sources of ‘wild foods’ and many other non-timber forest products (Van den Eynden, Cueva, and Cabrera 2003). Likewise, in many mountain areas, tourism is a special form of highland-lowland interaction and forms the backbone of regional and national economies (Martín-López et al. 2019).

However, increasing human populations, the expansion and intensification of agriculture, and the exploitation of natural resources have transformed tropical mountain ecosystems across the world. While there have been research efforts in the highlands of Ecuador (Balthazar et al. 2015; Hall et al. 2012; Vanacker et al. 2022), there is still a significant need for assessing the impact of land use change on biodiversity and ecosystem services, especially in the northern highlands where there are limited studies on this topic. Context-dependent trends, rapidly changing landscapes, policy relevance, and advancements in technology and methodology all point to the importance of continued research in this area. It is of vital importance that we understand how land use constrains biodiversity and ecosystem functions to determine the consequences of global change for mountain ecosystems (Peters et al. 2019; Vanacker et al. 2020, 2022).

The tropical Andean Mountain systems of Ecuador are characterized by spatial complexity, heterogeneity and landscape dynamism (Young, 2007), mainly shaped by intensive traditional agriculture. This activity has been practiced for centuries and still threatens its remnant biodiversity (Sarmiento 2002). However, recent complex land change dynamics have been documented (Aide et al. 2013; Gaglio et al. 2017; Guns and Vanacker 2013; Madrigal-Martínez and Miralles-García 2019; Young 2014). In some areas, native montane forests and paramos have mainly been converted into agricultural land and only remnant patches exist upland (Gaglio et al. 2017; De Koning, Veldkamp, and Fresco 1999; Tapia-Armijos et al. 2015); whereas in other highland regions, some significant areas of paramo have remained unchanged over the last decades, while native forests have declined. Moreover, other studies have demonstrated that plantations of non-native timber species had increased in the last decades, replacing high altitude paramo grassland (Balthazar et al. 2015; Farley 2007; Ross et al. 2017); thus, important trade-offs have resulted between ecosystem services provided by forest plantations with exotic species and native ecosystems in tropical mountain landscapes (Farley and Kelly 2004; Hall et al. 2012; Mosandl and Günter 2008).

These land transformation patterns are caused by a complex web of indirect demographic, socio-economic, cultural, and technological triggers that interact with biophysical features like elevation, topography, soils, and climate parameters (Lambin et al. 2001; Lambin et al. 2003; Nelson et al. 2006; Wilson et al. 2019; Young 2009); which operate in a synergistic manner across spatial, temporal, and organizational scales (Lambin et al. 2003; Millennium Ecosystem Assessment (MEA) 2005; Nelson et al. 2006). However, more research efforts are needed to understand the causes, processes, and ecological consequences of land use and land cover change in poorly studied mountain systems such the Northern Ecuadorian Andes.

It seems that in recent decades, the LULC dynamics in mountain systems, like the Ecuadorian Andes, are more context dependent and could be driven by distinct interacting factors, which vary across areas of the same region. Then, even though it seems that Andean landscape mosaics will continue to shift at least over the next couple of decades (Young 2009), predicting how and where trajectories of land change will be altered remains uncertain (Lambin et al. 2001).

Understanding future changes in these tropical mountain systems may be informed from describing LULC pattern-dynamics across environmental gradients and on different temporal scales. In addition, deciphering anthropogenic influences on biodiversity, ecological processes, and ecosystem services (Young 2009) will be of pivotal importance given the high vulnerability to climate change of highland landscapes like the Northern Ecuadorian Andes (Brandt and Townsend 2006).

These changes in land use strongly influence the capacity of ecosystems to provide services (Costanza et al. 2014; Millennium Ecosystem Assessment (MEA) 2005) since they affect the biological structure of ecosystems, mainly vegetation cover, which affects the main ecological functions such as energy and nutrient exchange (Ghaley, Sandhu, and Porter 2015), soil erosion, water recycling and biogeochemical cycles (Felipe-Lucia, Comín, and Bennett 2014). These changes can affect, in turn, the provision of multiple ecosystem services that include the provision of water and food, the production of timber and non-timber forest products, the provision of habitat for forest species, soil fertility, and climate regulation through carbon sequestration, among others (Liiri et al. 2012).

Studies suggest that natural ecosystems with minimal human disturbance provide fewer provisioning services; however, they support abundant regulating and supporting services; while systems with moderate human disturbances increased the delivery of provisioning services at the expense of regulatory and supporting services. However, when human disturbances are strong to cause land degradation, the capacity of the landscape to provide multiple ecosystem services is severely threatened (Braat and Brink 2010). Consequently, the management of land use and the restoration of ecosystems can act to improve or alter the ecological functions that, in turn, affect the capacity of ecosystems to generate ecosystem services (Fu et al. 2013). Therefore, the study of ecosystem services, land use changes and the links between them have strong implications for the restoration, management and conservation of landscapes (Maes et al. 2016; Palmer et al. 2004).

Understanding this complexity is fundamental for the development of policies and measures for landscape planning and management in highland ecosystems, where biodiversity conservation, sustainable use of natural resources, and the supply of essential ecosystem services (e.g., water or food) should be assured (Hosonuma et al. 2012; Madrigal-Martínez and Miralles-García 2019) not only for local inhabitants but also for downstream populations, thus leading to strengthened highland-lowland linkages (Grau and Aide 2008).

History of land use in the highlands of Ecuador

The landscapes of the Ecuadorian highlands are the result of a long-term interaction between people and their natural environment, the so-called socio-ecological systems, where agricultural and livestock activities have been key factors shaping landscape dynamics through time (Halliday and Glaser 2011). Early on, during the two thousand years preceding the Spanish conquest, these mountain ecosystems were the center of a flourishing agriculture, based in the production of traditional Andean crops, such as potatoes, beans, oca, white carrots, quinoa, mashua, among others, focused basically on self-consumption, which was complemented by the exchange of surpluses with residents of the lower altitudinal areas (De Noni et al. 1996; Ruiz Azurduy 2017).

When the Inca empire extended towards this equatorial latitude, the natural landscape was further transformed to maximize land area for agriculture; the Incas developed irrigation systems with channels following the contour of a tight network of terraces, such an approach prevented soil erosion and promoted water conservation (De Noni et al. 1996). Other highland areas, like paramos, were valued for their ceremonial use and as hunting places of wildlife for food consumption for earlier dwellers (Ruiz Azurduy 2017).

With the arrival of the Spanish conquest and colonization (more than 500 years ago) followed a demographic depression, which resulted in the abandonment of agricultural areas (Deler et al. 1983). In the centuries XVII and XVIII this agricultural landscape was recolonized and further transformed into grazing areas, especially in the paramo ecosystem, oriented to the mass rearing of sheep to support the textile industries which characterized the production system in this region of the Spanish colonies (Deler et al. 1983). This activity was developed for a long time without governmental and social control, which generated the degradation of natural resources as a result of overgrazing. Landscapes located nearby cities and small settlements were also modified by the sowing of cereals brought from the old continent such as wheat and barley that gave rise to a first cycle of over-exploitation (Deler et al. 1983; Hofstede et al. 2003)

When the textile industry declined in the eighteenth century, a new configuration of this production system resulted in the establishment of large farms, better known as haciendas, for cattle ranching. The haciendas were owned by local elites and religious orders, this production system was based on the virtual condition of servitude of numerous indigenous laborers (De Noni et al. 1996). The livestock in all its forms, from the corral to the immense herds in the páramos, became a permanent feature of the Andean agrarian landscapes. From 1900, the haciendas began a modernization

process, characterized by development of irrigation, import of livestock and selected seeds, which resulted in the establishing a remarkable dairy economy (Deler et al. 1983).

Yet, the strongest pressure on the highlands occurred in the mid-twentieth century, due to the exhaustion of the green revolution in productive zones, and the failure of the redistribution of the land after the application of the agrarian reform (Deler et al. 1983; De Noni et al. 1996). The agrarian reform mandated that large landholders were to give up a part of their land to indigenous laborers; this is how the minifundio agrarian system developed. However, the haciendas kept the best land for themselves, yielding only inhospitable land to the peasant farmers (De Noni et al. 1996). Minifundios (0 to 20 ha) accounted for more than 80% of the farm units but occupied only 20% of the arable land and were located mostly in places where it was hard to get a good return. The good flat land in the watershed was still managed by the haciendas for extensive cattle ranching (De Noni et al. 1996).

During the last second half of the twentieth century, the rural population increased dramatically; heavy population densities varying from 50 to over 200 persons per km² characterized the minifundios; this demographic pressure caused the expansion of the agricultural frontier upwards (De Noni et al. 1996). Steep slopes along with climate harsh condition portray ecosystems above 3000 masl, where the minifundios were located, this corresponds a marginal environment for food production, which has caused acute erosion problems along the Andes (De Noni et al. 1996). Also, during this period, some highland landscapes were modified for plantation of eucalyptus and pine trees for fuel and timber production whereas in other regions exotic trees were planted to restore deforested or degraded landscapes (Farley 2007; Hofstede et al. 2002).

At present, the major pressure for land use change is still the expansion upwards of the agricultural-livestock frontier caused by small scale farmers; but other human activities exert pressure on the highland ecosystems such as fires and burning, clearing of forests, introduction of exotic species, urban expansion, in addition to the local effects of climate change which together affect the structure and function of the ecosystem, putting at risk the goods and services that people need (Ruiz Azurduy 2017). This research aims to evaluate recent trends in land use change, from 1990.

Pedro Moncayo county – The landscape studied

The historic trend of landscape transformation described at a regional scale, along with its associated socio-economic and environmental problems, has been observed in the territory of Pedro Moncayo county. This county is located in the Andean province of Pichincha, and encompasses 332 km² distributed among five parishes. This region includes a variety of soils, and climates, as well as a fluvial system derived from the melting of glaciers of one of the most important snow-capped mountains (Cayambe) and from the highland ecosystems (Gobierno Autonomo Descentralizado Pedro Moncayo 2015). The Northern Ecuadorian Highlands have received contribution of volcanic eruptions on which volcanic soils of varying fertility have developed. Most of these soils are classified as Andisols and Mollisols, however, the presence of microclimates has affected the development of volcanic soils in particular sections where it is possible to find Entisols, Inceptisols and Aridisols (Moreno et al. 2022).

Due to its equatorial latitude and altitude, this county has low seasonal variability, with solar radiation and mean air temperature remaining almost constant throughout the year. However, diurnal temperature cycles are highly variable and can range between 0 and 20°C. This region is classified as pluvial and cold temperate according to the Ministry of Environment of Ecuador (Ministerio del Ambiente del Ecuador 2013). It has an average annual temperature of 14°C ($\pm 1,3$ SD) (Gobierno Autonomo Descentralizado Pedro Moncayo 2015). Seasonal variation of temperature is reduced, while precipitation is bimodal, with two wet seasons from February to May and September to November with a monthly average precipitation of 70 mm ($\pm 20,1$ SD). The dry season presents an average precipitation of 25 mm ($\pm 14,3$ SD) (Cáceres-Arteaga et al. 2018).

The territory has a wide altitudinal gradient ranging from 1900 to 4000 m.a.s.l. (Figure 2) and this landscape encompasses a mosaic of different natural ecosystems and distinct land uses which can be described following the altitudinal gradient (Gobierno Autonomo Descentralizado Pedro Moncayo 2015). The higher altitudinal zone (above 3300 m) is dominated by native ecosystems, represented by paramo (highland natural grassland) and highland montane forests (Ruiz Azurduy 2017). In the study area, native montane forest vegetation is represented by species such as *Oreopanax ecuadorensis*, *Piper nubigenum* and *Barnadesia arborea* (Solórzano 2020).

The middle altitudinal area (2800-3300 m) has been extensively used for non-mechanized agriculture and livestock over time, causing severe soil degradation (De Noni et al. 1996; Ruiz Azurduy 2017). The pasture is characterized by Pennisetum clandestinum and crop fields are dominated by maize (*Zea mays* L.) (Solórzano 2020). This crop is an important source of livelihood for the family economy and food security of small-scale farmers, it is cultivated in small lots (of up to one hectare) that mostly lack irrigation and are located on marginal soils including hillside which cause severe erosion problems (Boada and Espinosa 2016; Gobierno Autonomo Descentralizado Pedro Moncayo 2015). Although a common practice is to intercrop

maize with other cereals and legumes such as chocho (*Lupinus mutabilis*) or roots and tubers such as potato (*Solanum tuberosum*), a good proportion of these lots are not rotated with other crops. Thus, as proposed by Morris (1997), we refer this type of crop production system as a monoculture of maize.

Forest plantations with exotic species, mostly represented by *Eucalyptus globulus* and *Pinus radiata* and are primarily located scattered among the remnants of native forest at an altitude of approximately 2800 to 3200 m and also along the ravines throughout the territory. The lower lands are characterized by shrub-dominated dry ecosystems known as Andean dry forests in northern Ecuador (Figure 2). The most abundant species in this forest type are *Croton elegans*, *Opuntia pubescens* and *Acacia macracantha* (Villalba 2020).

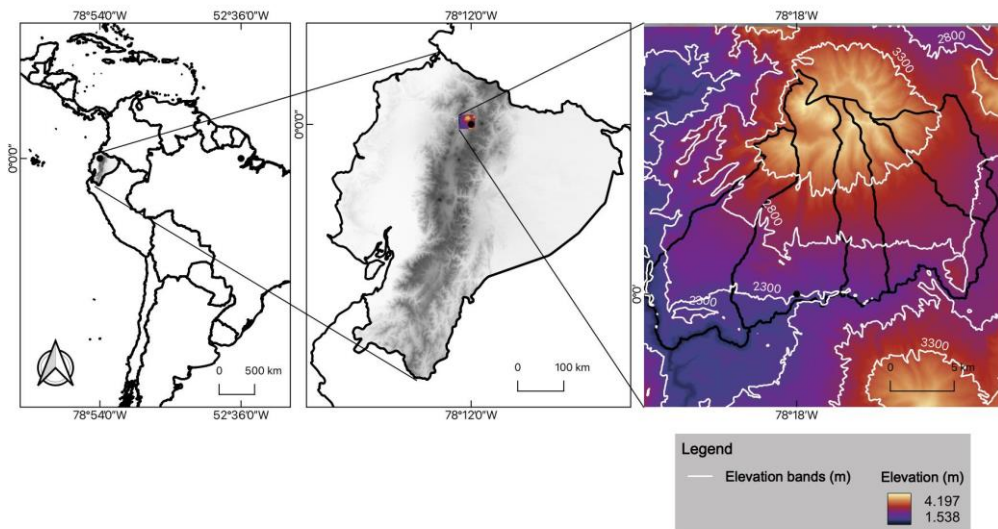


Figure 2. Location of Pedro Moncayo county, the studied landscape. Numbers represent the parishes within the county as follows: 1: Malchinguí, 2: Tocachi, 3: La Esperanza, 4: Tabacundo, 5: Tupigachi. (Data sources: ASTER Global Digital Elevation Model courtesy of NASA Earth Data. Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com).

At present, the economy of the region revolves around the production and export of flowers, mainly roses. In this context, the development of other productive activities such as small and medium-scale agriculture and livestock ranching, small industry, the artisanal sector, commerce, tourism, and transport is lower in terms of labor absorption, technology incorporation, and productivity (Ruiz Azurdúy 2017). These

conditions force families to migrate to other activities, such as day labor or precarious work, and to maintain their land with very low investment crops, and eventually to rent or sell the land to the agroindustry (Sawers 2005).

Flower cultivation is a land- and labor-intensive activity with high land productivity (that is, high market value of output per hectare). In 2004, flowers had the highest land productivity of any major crop exported from Ecuador, reaching \$9437 per hectare. However, the gains in income have been offset by growing health and environmental problems posed by the intensive use of pesticides in flower cultivation. All indications suggest that flower exports will continue to play a major and probably increasing role in Ecuador's economy (Sawers 2005). In fact, this industry is steadily expanding and this is causing land use changes in the territory; for instance, former important and traditional lands dedicated to livestock and food crop production, located in areas with an aptitude for agricultural production and with access to irrigation systems have been transformed into greenhouses for flower cultivation (GAD Municipal del cantón Pedro Moncayo 2021).

In this scenario, the structure of the land could have resulted in the loss of productive capacities and the weakening of systems dedicated to the production of food (Gobierno Autonomo Descentralizado Pedro Moncayo 2015). Additionally, pollution related to agricultural and floriculture production is considered an important factor affecting ecosystem services supply and delivery throughout the territory, to the detriment of food security and with the associated effects on well-being. Qualitative diagnostics of the state of natural resources have stated that soil, water, and native vegetation are under constant degradation (Ecociencia 2008). In addition, shifting former crop areas to flower cultivation may threaten the food sovereignty of the country in the medium and long term, if we consider that the peasant family economy has sustained in volume and quality the diet of most Ecuadorian families (Guarderas et al. 2022).

Finally, the local government of Pedro Moncayo county and the regional government and other institutions, are leading an initiative to establish a Conservation and Sustainable Use Area in the highlands of Pedro Moncayo county to protect high mountain ecosystems and the lacustrine system of Mojanda, thus maintaining the important ecosystem services that these ecosystems provide to local inhabitants, such as water provision and biodiversity conservation (Ruiz Azurduy 2017).

Research Justification

Overall, in highland landscapes of northern Ecuador the history of human settlements and the expansion of the agricultural frontier, which intensified in the last decades, may have seriously affected biodiversity and the provision of ecosystem services, leading to soil erosion and loss of soil fertility, decreased water and food supply and the reduction and fragmentation of mountain ecosystems to make way for pastures and monoculture systems (Ministerio de Ambiente del Ecuador 2016). In addition, montane forests are one of the least studied and most threatened ecosystems in the tropics. Likewise, the specific mechanisms through which human activities

affect species, biotic communities, and ecological functions have been little studied (Foster 2001).

In this region, soil degradation associated with anthropogenic effects, mainly involving deforestation and vegetation cover change, could be exacerbated by severe climatic conditions and rugged topography (Viña et al. 2004). Soil degradation is considered one of the most worrisome environmental problems facing mountain ecosystems, since it is estimated that between 48 and 50% of cultivated land is affected by soil erosion (Moreno et al. 2022). Given the great importance of mountain ecosystems for the regulation and maintenance of water resources and for supporting local food security, it is therefore of great importance to understand the factors that influence soil degradation and the implications of land use changes on biodiversity and soil ecosystem services (De Valença et al. 2017).

This scenario is exacerbated by the local effects of climate change; studies suggest that the productive areas of the canton are vulnerable to the drastic effects of climate, such as droughts, windstorms, hailstorms, and frosts. All of these elements are contributing to the loss of ecosystem services, mainly those related to the provision of water by the paramo's lake systems, and the loss of productivity and quality of agricultural systems distributed from 1880 m to 3340 m (GAD Municipal del cantón Pedro Moncayo 2021).

Managing ecosystems to ensure the provision of multiple ecosystem services is a critical challenge for applied ecology (Landis 2017) and, in this context, understanding the links between biological diversity, ecosystem functioning, and ecosystem service provision is key to meeting this challenge. The study of ecosystem services is fundamental for designing more sustainable environmental policies and landscape planning (Balvanera et al. 2014), could promote arguments for biodiversity conservation (Boeraeve et al. 2014), as well as for ecological restoration and protected area management, and for the sustainable management of agroecosystems that optimize the provision of ecosystem services for food security and, at the same time, contribute to biodiversity conservation objectives (Bastian et al. 2012).

RESEARCH QUESTION AND STRUCTURE OF THE THESIS

Questions, objectives and hypothesis

This project aimed to further the understanding of the impacts of land use changes on biodiversity and ecosystem services in tropical mountain systems of Northern Ecuador. I studied the territory of Pedro Moncayo county as a characteristic landscape of the Andean system of northern Ecuador. This landscape encompasses a mosaic of ecosystems with distinct climatic conditions and management regimes, arranged in gradients of land use intensity, where agricultural and livestock activities have been key factors shaping landscape dynamics through time in this territory (GAD Municipal del cantón Pedro Moncayo 2021; Guarderas et al. 2022). The motivation and rationale for choosing the territory of Pedro Moncayo county to carry out this research is related to the opportunity to integrate scientific research with technical information required to support territorial planning and development, given the close relationship between the Universidad Central del Ecuador and the Autonomous Decentralized Government of the Pedro Moncayo Municipality. It is important to highlight that since 2015 the UCE initiated a cooperation agreement with the Municipal Government of Pedro Moncayo to support this rural government with technical inputs to promote the sustainable development of the territory.

Within this context, this research raised the following main research question: What is the pattern of land use change in the northern Andes of Ecuador in the past two decades and how these changes impact on the biodiversity and ecosystem services? Acknowledging the diverse and context dependent human pressures on tropical mountain landscapes and recognizing the structural changes that occur after the conversion of native ecosystems to anthropic ecosystems, we hypothesized that: (1) the land use change will follow the patterns of native ecosystem loss, in the context of Forest Transition Theory, demonstrated for tropical systems and will exhibit different spatial and temporal patterns across altitudinal and administrative zones; and (2) the biodiversity will decline and the multifunctionality of the landscape will be disrupted after forest conversion to anthropic systems.

To answer the main research question and test the hypotheses, specific research questions were posed, while addressing this issue in the broader context of forest transition theory and the mechanisms and biophysical outcomes that have been associated with these transitions. These specific questions followed the proposed DPSIR framework and guided the development of an ecosystem assessment in the studied landscape. Table 1 details the specific questions posed, their connection to the DPSIR framework and the approach to conduct them.

Table 1. Specific research questions, the linkages to the DPSIR framework and the approaches

Specific questions	DPSIR component	Approach
(1) What are the LULC change patterns across geographical and biophysical settings, in terms of the rate, magnitude, and direction of those changes, emphasizing trends in native ecosystems as sentinel habitats, and	Drivers + Pressures: <i>LULC trends and driving forces</i>	Landscape oriented study using publicly available spatial data from LULC, socioeconomic, environmental.
(2) What combination of environmental and anthropic factors can best explain the different landscape transitions.		
(3) What is the impact of LULC change on soil biota and soil fertility?	State + Impact <i>LULCC impact on biodiversity and ecosystem services</i>	Field site-oriented research based on primary data collection
(4) What is the impact of LULC change on microclimate?		
(5) Does LULC change affects the capacity of ecosystem services' supply through time in the studied landscape?	Impact + ES assessments <i>LULCC impact to provide ES</i>	Landscape oriented study: Multiple ES assessments, based on experts' perceptions related to LULC types

In summary, our hypotheses include two areas of research—one focused on describing the trends and causes of land use change and the other focused on its consequences for ecosystem services—have been carried out separately. Analyzing them jointly requires approaches to understanding both socioeconomic and biophysical components in order to shed light on the conditions that lead to land use change as well as the effects of such change (Farley 2010). The development of the objectives of each chapter stems from the different specific questions posed in our research which follow two approaches:

1) The first approach included a landscape scale analysis whose objectives were to study the dynamics of land use change since 1990, understand the drivers of change, and finally conduct a spatially explicit evaluation of change in the supply of multiple ecosystem services, following the guidelines of Barton et al. (2020). A simple mapping method using qualitative information from experts to evaluate the capacity of the different LULCs to provide ecosystem services was chosen. This evaluation encompassed an integrated biophysical assessment of the supply of multiple ecosystem services at landscape scale, using spatially explicit mapping tools. This assessment was based on information from experts, who evaluated the capacity of each land use type with a specific assessment based on their knowledge and expertise to integrate it with the matrix model. However, according to Jacobs (2015) this

application of a matrix model invokes serious risks as it is often simplistic and lacks scientific underpinning. Therefore, our approach incorporates measures of confidence and reliability analysis of the expert scores based on recently reported methods in the literature (Madrigal-Martínez and Miralles-García 2019).

2) The second approach was to develop a case study where direct data collection and individual ecosystem services (e.g., microclimate regulation, maintenance of soil fertility as a proxy for food production for human consumption) were assessed. The case study compared the status of montane forests, considering them as the reference systems, with other characteristic land use types (planted forests, agricultural monocultures and pastures) of the assessed area. This approach intended to estimate the impact of conversion from native systems to anthropic ones, and therefore to advance knowledge using primary information.

Structure of the thesis

As described before, the conceptual framework of this thesis follows the DPSIR workflow. Our proposed DPSIR approach envisions the implementation of a tool to characterize the complexity of tropical mountain systems and conduct integrated ecosystem and ES assessments (Figure 3). Specifically, we tested the framework to assess the impact of landscape transformation on biodiversity and ecosystem services in a mountain landscape, located in northern Ecuador.

Then, the structure of the Chapters follows the framework as follows:

Chapter 2 presents the implementation of the initial phases (Drivers and Pressure boxes) of the framework in a characteristic landscape of the highlands of northern Ecuador. We conducted an integrated analysis of landscape changes and their driving forces. Our findings revealed significant patterns of landscape dynamics from 1990 to 2014, highlighting the increasing threat of permanently losing the already vulnerable native mountain ecosystems. Our findings suggest how complex land use transition and their explanatory drivers can assist local authorities and decision makers to improve sustainable resource land management in vulnerable landscapes such as the tropical Andes in northern Ecuador. This study was published in the journal " PLOS ONE, a fully Open Access journal, as a contribution to expand Open Science under the following title: 'Land use and land cover change in a tropical mountain landscape of northern Ecuador: Altitudinal patterns and driving forces.

Following the conceptual scheme of the thesis, **chapter 3** presents the third element (State) of the DPSIR framework. This chapter exhibits the results of a field study conducted in the upper elevation zone of our studied landscape, where the greatest extension of native forests was found, to assess the impact of forest conversion to three main anthropic systems (planted forests, pastures and agriculture fields). This study assessed the impact of land-use change on soil macroinvertebrate biota and chemical parameters of soil health. This study has been published in the Journal of Frontiers in Forest and Global Change.

Following the same approach (field study) described in the previous chapter, in **chapter 4**, we explored *in situ* methods to evaluate the impact of land use change on microclimate, which corresponds an important regulating ecosystem service. This

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

study captures the fourth element (Impact) of the proposed DPSIR framework. We found a climate buffering effect in native forests; this finding highlights the importance of conserving natural ecosystems for climate mitigation and adaptation in the context of global climate change. The article has been recently published in the *Journal of Mountain Research and Development* under the following title: ‘Land use affects the local climate of a tropical mountain landscape in northern Ecuador

In chapter 5, connecting the results of the landscape transitions presented in Chapter 1, we conducted a valuation of ecosystem services based on expert perception of the supply of ES provided by each land use type.

Finally, **chapter 6** summarizes and discusses the main findings and achievements of the thesis.

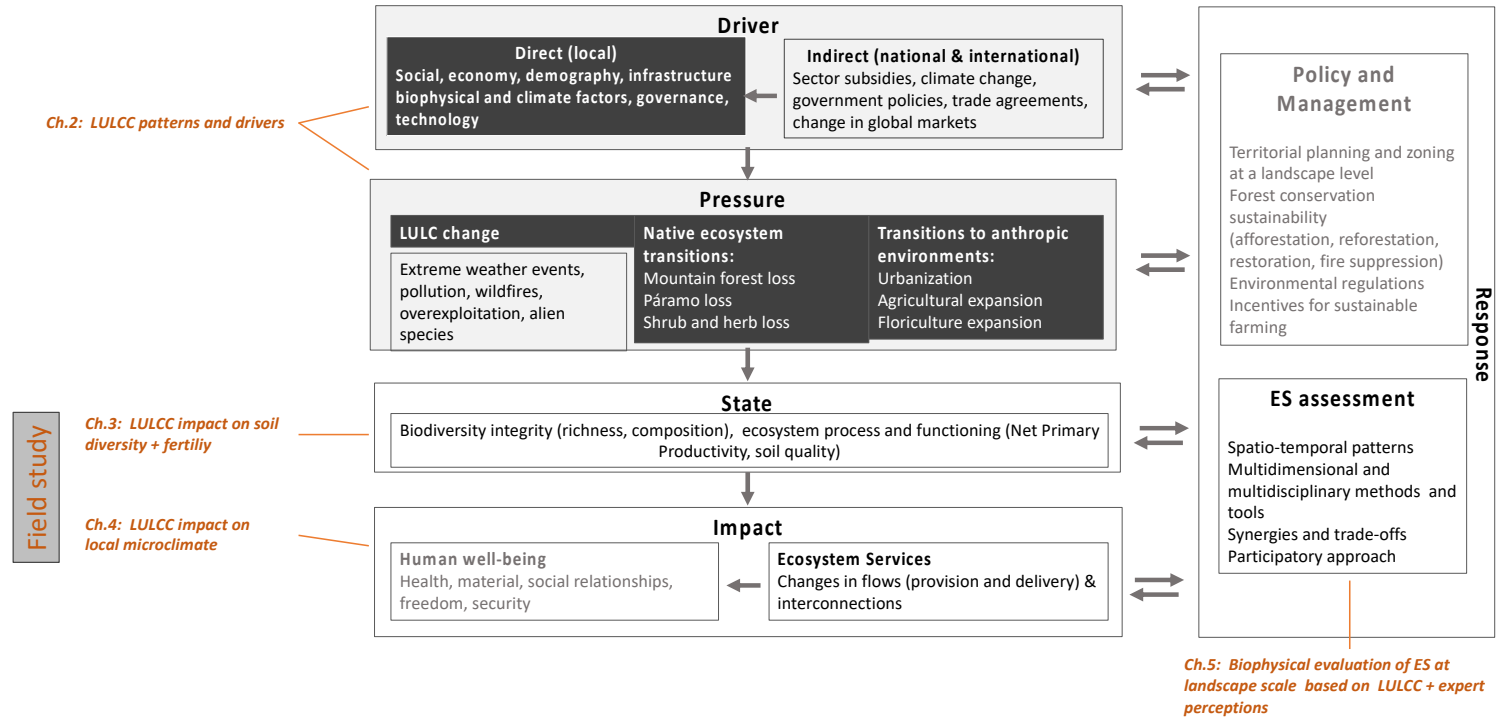


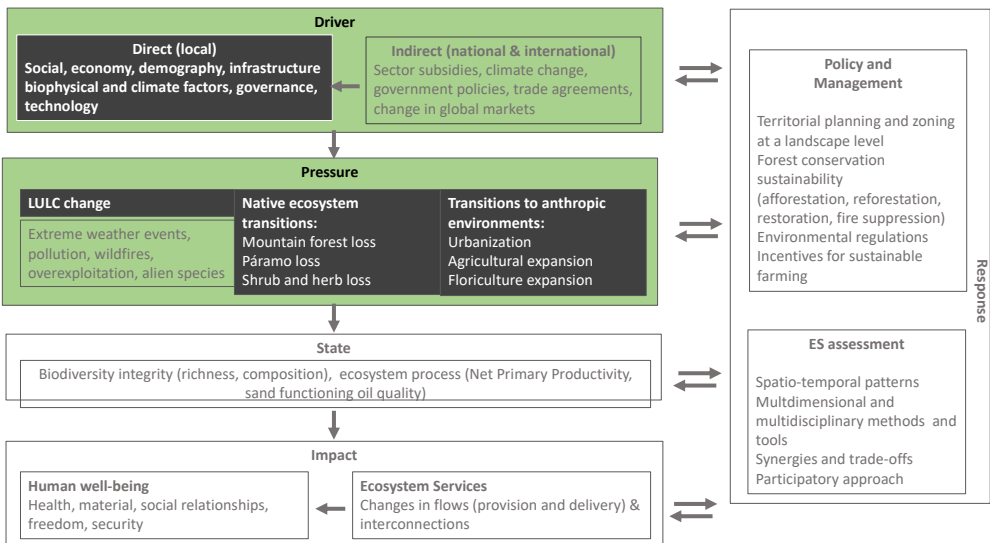
Figure 3. Organization of the PhD theses chapters in connection to the Driver Pressure State Impact Response (DPSIR) conceptual framework. Adapted from Guarderas et al.(2022).

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

2

Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces

This chapter addresses the first two elements of our DPSIR framework (Drivers and Pressures) by characterizing land use land cover (LULC) dynamics along elevation and geographic settings and by exploring the variables driving such landscape dynamics in a sensitive region of the northern Ecuadorian Andes.



This chapter is based on the published article:

Paulina Guarderas, Franz Smith, Marc Duf erne (2022). Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces. PLoS ONE, volume 17, number 7, pages 1-26. e0260191. <https://doi.org/10.1371/journal.pone.0260191>

Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces

Abstract

Tropical mountain ecosystems are threatened by land use pressures, compromising their capacity to provide ecosystem services. Although local patterns and interactions among anthropogenic and biophysical factors shape these socio-ecological systems, the analysis of landscape changes and their driving forces is often qualitative and sector oriented. Using the Driver-Pressure-State-Impact-Response (DPSIR) framework, we characterized land use land cover (LULC) dynamics using Markov chain probabilities by elevation and geographic settings and then integrated them with a variety of publicly available geospatial and temporal data into a Generalized Additive Model (GAM) to evaluate factors driving such landscape dynamics in a sensitive region of the northern Ecuadorian Andes. In previous agricultural land located at lower elevations to the east of the studied territory, we found a significant expansion of floriculture (13 times) and urban areas (25 times), reaching together almost 10% of the territory from 1990 to 2014. Our findings also revealed an unexpected trend of páramo stability (0.75 -0.90), but also a 40% reduction of montane forests, with the lowest probability (<0.50) of persistence in the elevation band of 2800-3300 m; agricultural land is replacing this LULC classes at higher elevation. These trends highlight the increasing threat of permanently losing the already vulnerable native mountain biodiversity. GAMs of socio-economic factors, demographic, infrastructure variables, and environmental parameters explained between 21 to 42% of the variation of LULC transitions observed in the study region, where topographic factors were the main drivers of change. The conceptual and methodological approach of our findings demonstrate how dynamic patterns through space and time and their explanatory drivers can assist local authorities and decision makers to improve sustainable resource land management in vulnerable landscapes such as the tropical Andes in northern Ecuador.

Introduction

Tropical mountain systems supply vital benefits to millions of upland and lowland inhabitants (Payne et al. 2017) through the provision of Ecosystem Services (ES) (Haines and Potschiand 2010; Millennium Ecosystem Assessment (MEA) 2005a) and represent a global hotspot of tropical biodiversity and habitat refugia (Peters et al. 2019). These areas are increasingly being transformed by human activities (Peters et al. 2019; Young 2009). Although the human activities in this region, including intensive traditional agriculture, have impacted its history of landscape patterns for centuries (Young 2009), recent transitions have also been documented (Aide et al. 2013; Gaglio et al. 2017; Madrigal-Martínez and Miralles-García 2019; Young 2014), changes to this landscape's natural cycles and heterogeneity is reducing the capacity of the system to provide multiple benefits to people and guarantee their long-term sustainability (Young 2009).

Deforestation and agricultural intensification are the dominant transitions in many Andean systems (Madrigal-Martínez and Miralles-García 2019). However, forest recovery due to agricultural de-intensification and transitions between crops, pastures, and secondary vegetation, in addition to urban and agro-industrial expansion have also been observed in these systems. In-depth multi-temporal change studies are required to better understand this complexity in order to balance biodiversity conservation with human needs (Aide et al. 2013; Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013).

These distinct patterns of land utilization by various human activities (land use), in addition to spatial changes of biophysical cover on the earth's surface (land cover) (Di Gregorio and Jansen 2005) observed in the Tropical Andes vary with demographic, socio-economic, cultural and technological factors (Madrigal-Martínez and Miralles-García 2019; Ross et al. 2017; Tapia-Armijos et al. 2015). Additionally, these drivers interact with biophysical features like elevation, topography, soil and climate parameters, operating across spatial, temporal, and organizational scales (Lambin et al. 2003; Millennium Ecosystem Assessment (MEA) 2005; Nelson et al. 2006). For example, increasing global demand for food and non-food crops can drive agriculture expansion onto more fertile and flat land (Aide et al. 2013; Farley 2007; Lambin et al. 2003), whereas natural ecosystem recovery has been observed in abandoned marginal agricultural land (Grau and Aide 2008; Rocha 2011; Young 2009).

Despite the documented useful insights into how different drivers can influence Land Use Land Cover (LULC) change in tropical mountain systems (Aide et al. 2013; Rodríguez Eraso et al. 2013; Tapia-Armijos et al. 2015; Young 2014), evidence from synthetical studies suggests that no universal link between cause and effect exists to explain deforestation and other LULC changes (Aide et al. 2013; Lambin et al. 2003; Young 2009). Different combinations of various proximate causes and underlying driving forces in varying geographical and historical contexts could affect landscape changes (Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013).

Understanding future changes in tropical mountain systems and their associated ES relies on ecosystem assessments to document LULC pattern dynamics across environmental gradients and different temporal scales (Brandt and Townsend 2006; Jones et al. 2013). Additionally, revealing interactive effects of distinct anthropogenic influences on landscape dynamics will be valuable for informing management (Young 2009), given the high vulnerability to climate change of highland landscapes like the Ecuadorian Andes (Vanacker et al. 2018). Conducting integrated ecosystem assessments for adaptive management is urgently needed in highland tropical ecosystems where biodiversity conservation, sustainable use of natural resources, and the supply of essential ES should be assured (Hosonuma et al. 2012; Madrigal-Martínez and Miralles-García 2019).

The Driver-Pressure-State-Impact-Response (DPSIR) framework links cause-effect relationships and feedback between human and natural systems (Organization for Economic Cooperation and Development (OECD) 2003) to understand and sustainably manage environmental problems (Müller and Burkhard 2012). Within the DPSIR framework, the anthropogenic impacts on ecosystems and their services can be described by social, demographic, economic, and other biophysical driving forces where these drivers exert pressures on the environment, affecting the state and condition of ecosystems (Santos-Martín et al. 2013). Understanding this complexity is fundamental for the development of policies and measures for landscape planning and management, as societal responses to overcome environmental impacts (Burkhard and Müller 2008).

Within this context, our study is unique in that it adapts the DPSIR holistic approach to the context of tropical mountain systems and implements the first elements of the framework to further complete an ES assessment in a sensitive region of the northeastern Ecuadorian Andes. The study region comprises a landscape with distinct climatic conditions and management regimes along its elevation gradient, where floriculture crops and urban centers are emerging in an agricultural matrix, posing more pressure on remnant native ecosystems and their services.

Specifically, we addressed two questions: (1) what are the LULC change patterns across geographical and biophysical settings, in terms of the rate, magnitude, and direction of those changes, emphasizing trends in native ecosystems as sentinel habitats, and (2) what combination of environmental and anthropic factors can best explain the different landscape transitions.

Materials and methods

Conceptual framework

In this study, we adapted the DPSIR framework, by (Balzan et al. 2019; Müller and The DPSIR framework has been widely applied in ecosystem assessments to evaluate the impact of environmental changes on human well-being (Balzan et al. 2019; Larrea et al. 2015; Millennium Ecosystem Assessment (MEA) 2005; Santos-Martín et al. 2013). Furthermore, since ecosystem assessments are based on scientific evidence,

they are considered key management tools for decision making processes and adaptive management at landscape scales (Nassl and Löffler 2015).

In the context of mountain systems, the DPSIR framework was initially conceptualized and implemented by Oddermat (2004). Recent initiatives have implemented this conceptual model for evaluating the state of mountain systems in distinct regions (Nassl and Löffler 2015), but an adaptation of such an approach to conduct ecosystem assessments was lacking for the tropical mountain system context (Berrio-Giraldo et al. 2021).

In this study, we adapted the DPSIR framework, by (Balzan et al. 2019; Müller and Burkhard 2012; Santos-Martín et al. 2013), to identify the key characteristics of tropical mountain systems that should be represented in ecosystem assessments at a landscape scale (Figure 4). In this context, driving forces will exert pressures, changing the state of the system (Nassl and Löffler 2015). This altered state could ultimately impact on human wellbeing and lead to a societal response. The societal response in turn feeds back to all other components (Müller and Burkhard 2012).

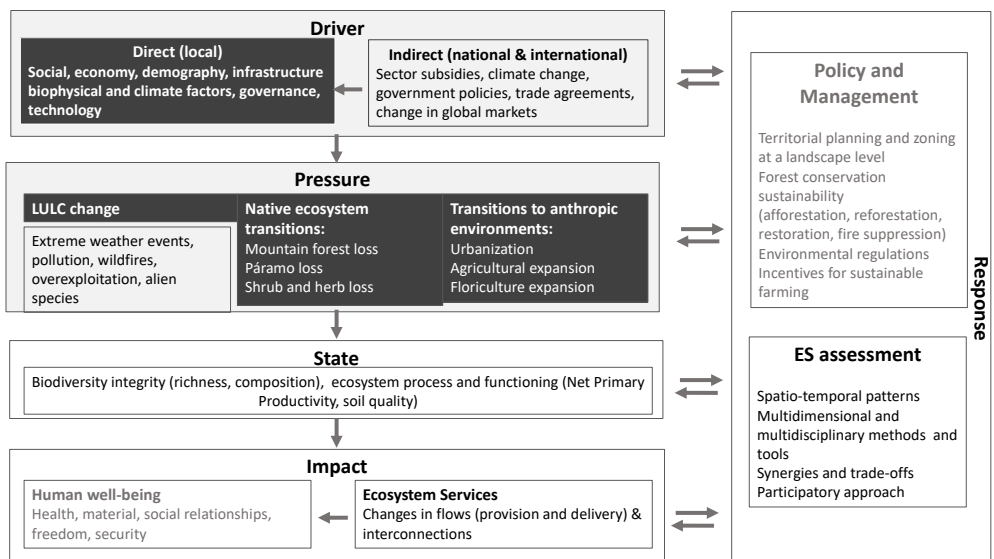


Figure 4. DPSIR framework for ecosystem assessments in tropical mountain systems. Arrows indicate causal relationships between driver, pressure, state, impact, and response (Adapted from (Balzan et al. 2019; Müller and Burkhard 2012; Santos-Martín et al. 2013).

Drivers are the underlying causes of environmental change, and we consider that both direct and indirect driving forces are shaping mountain landscapes in the tropics (Figure 4). Indirect drivers act by modifying the conditions of one or more direct drivers, while direct drivers explicitly influence the system (Müller and Burkhard 2012). We integrated the scale of the impact into the level of influence of the driving forces as follows: the direct drivers are considered as local forces (such as

demographic, economic, cultural, socio-political, governance and technological factors) (Figure 4), while the indirect drivers were forced as exogenous or external factors which operate at larger scales (Nassl and Löffler 2015). Then, indirect driving forces could include sector subsidies, government policies, trade agreements, change in global markets, and even climate change (Figure 4). Within the direct drivers, we considered it important to add the governance dimension, as proposed by (Berrio-Giraldo et al. 2021), to complement the DPSIR framework with the holistic conceptualization of the Socio-Ecological Framework (SEF) and to analyze the interaction between social and ecosystem processes (Ostrom 2009).

Pressure is the result of the interacting driving forces and generally represents a measurable human induced effect on the system – such as land use change, extreme weather events, pollution, wildfires, and overexploitation (Müller and Burkhard 2012; Nassl and Löffler 2015). In this article, we evaluated LULC change as the pressure element in the DPSIR approach. We operationalized LULC change considering two main landscape transitions: 1) the loss of native ecosystems and 2) the conversion to anthropic environments (Figure 4).

Pressures on the environment as a consequence of the driving forces could impact the state of the system. Here we described the state of tropical mountain systems in terms of their unique and vulnerable taxonomic and functional biodiversity (e.g., richness, composition, trophic groups) and their derived ecosystem properties (e.g., primary productivity, soil quality, vegetation cover, etc.) (Figure 4) (Santos-Martín et al. 2013).

Likewise, changes in the state of ecosystems impact on the provision and flow of ecosystem services and the associated benefits on people's quality of life (Figure 4). Tropical mountain systems are characterized by their contribution to essential ecosystem services such as water and food provision, carbon sequestration, landslide and erosion prevention, microclimate regulation, and the provision of multiple cultural services (Ruiz Azurduy 2017). The level at which the provision of ecosystem services changes as a result of environmental changes will also impact on the well-being of people (Santos-Martín et al. 2013).

The final step in the DPSIR framework corresponds to the response component, which is envisioned as the societal acknowledgment of the state of the system and their feedback to overcome the impacts due to human activities (Nassl and Löffler 2015). According to (Balzan et al. 2019), in the DPSIR framework the responses could be disaggregated into: 1) ES assessments and 2) policy and management where these aspects have been integrated into the DPSIR approach for this study (Figure 4). ES assessments should encompass multiple dimensions and disciplines to understand synergies, trade-offs, and interconnections of ES. These ES assessments should include participatory approaches and their scope should characterize geographical, biophysical, and temporal patterns. In tropical mountain systems, local and medium levels of territorial governance are key elements to implement policy and manage responses to overcome environmental issues. For instance, territorial planning and zoning schemes could organize a more balanced and multifunctional system of ES

provision and flow at landscape scales. In addition, initiatives for native forest sustainability could be fostered at the local and medium levels of governance. Environmental regulations and incentives for the sustainable use of natural resources could also be supported at the national level of governance.

Study area

Pedro Moncayo county is located in the western Andes of northern Ecuador (Figure 5). Pedro Moncayo is characterized by a wide elevation gradient (2400-4400 m) and a management regime that varies in intensity depending on the elevation (Gobierno Autonomo Descentralizado Pedro Moncayo 2015). The higher altitudinal zone (above 3300 m) is dominated by native ecosystems, represented by páramo and highland montane forests (Ruiz Azurduy 2017). The middle altitudinal area (2800-3300 m) has been extensively used for agriculture and livestock through time, causing severe soil degradation (De Noni et al. 1996; Ruiz Azurduy 2017), and the lower lands are characterized by shrub dominated dry ecosystems (Figure 5).

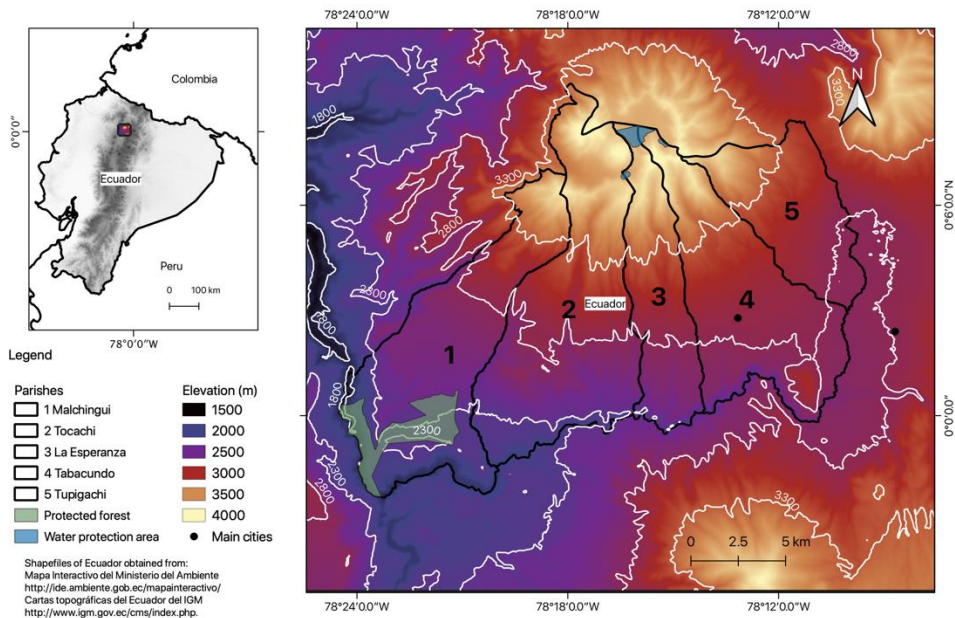


Figure 5. Study area of the Pedro Moncayo county in the highlands of northern Ecuador. (Data sources: ASTER Global Digital Elevation Model courtesy of NASA Earth Data. Made with Natural Earth. Free vector and raster map data @ naturalearthdata.com).

The studied territory has a total surface area of 339 km², which is divided into 5 parishes that have an east to west geographical arrangement, depicting the same elevation belts previously described (Figure 5). Each parish shows different levels of production development and population trends. For example, parishes located to the west portray a local economy based on subsistence agriculture and lower population growth, whereas the eastern parishes are attracting a growing population, have a more concentrated urban development, more irrigation systems, and harbor an expanding agro-industrial sector (Gobierno Autonomo Descentralizado Pedro Moncayo 2015).

Pedro Moncayo county is characterized by a typical climate of the tropical Andean region, with low annual variability but significant changes between night and day (Cáceres-Arteaga et al. 2018). For example, quarterly midday maximum temperatures could range from 14°C to 24°C and minimum night-time temperatures could range from 4°C to 17°C (Cáceres-Arteaga et al. 2018). In contrast, the precipitation pattern follows a bimodal peak of heavy rains concentrated from October to November and April to May, followed by a dry period of low precipitation from June to September; quarterly precipitation could range from 0 mm to 225 mm, and depending on the season the territory could shift to a different hydrological regime (Cáceres-Arteaga et al. 2018). For instance, from April to June the majority of the territory could have more than 200 mm of precipitation, whereas in the quarter of July to September most of the area receives less than 75 mm of precipitation (Cáceres-Arteaga et al. 2018).

Approximately 4% of the county's territory is designated as conservation or environmental management area, including the Jerusalem Protected Forest which occupies 1110 hectares of dry ecosystems in the county's lowlands, and the Mojanda Lacustric complex, protecting only 26 hectares of highland ecosystems and water sources (Figure 5) (Gobierno Autonomo Descentralizado Pedro Moncayo 2015).

Although at present the majority (58.1%) of the territory of Pedro Moncayo is dedicated to traditional agricultural activities – mainly growing cereals, maize and potatoes – the economy of the region is based on the production and export of flowers (mainly roses) using greenhouse infrastructures (Gobierno Autonomo Descentralizado Pedro Moncayo 2015); small and medium-scale agriculture and livestock ranching are lower in terms of labor absorption, technology incorporation, and productivity (Ruiz Azurduy 2017).

LULC datasets

To study landscape change through time in the study area, we used the official and publicly available LULC maps for four periods of time: 1990, 2000, 2008, and 2014 (<http://ide.ambiente.gob.ec/mapainteractivo/>). These are vector data produced by the Ministry of Environment (MAE) and the Ministry of Agriculture, Livestock, Aquaculture and Fisheries of Ecuador (MAGAP) in a mapping scale of 1:100,000 from mainly Landsat images (TM, 30 m). To obtain the LULC maps, a supervised classification method was carried out by a team of interpreters from MAE and MAGAP with training data of regions of interest (ROIs), using the maximum likelihood clustering algorithm of ENVI software (Ministerio del Ambiente (MAE)

and Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2015). The following overall accuracy values were obtained: 69%, 73%, 76%, and 85% for the years 1990, 2000, 2008, and 2014, respectively (Ministerio del Ambiente (MAE) 2016). More details on the processing and classification methods used by MAE and MAGAP can be found here (Ministerio del Ambiente (MAE) and Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2015).

The LULC official classification encompasses a 2-level hierarchical scheme, based on the International Panel on Climate Change (IPCC) classes in combination with a taxonomy agreed by the entities in charge of generating land cover information in Ecuador (Ministerio del Ambiente (MAE) and Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2015).

To ensure the quality of the MAE-MAGAP LULC data sources for the study area, a process of validating the official vector maps from the different study periods was carried out. To support this validation process, as proposed by (Madrugal-Martínez and Miralles-García 2019), distinct secondary sources of information were revised such as field points, Google Earth images, orthophotographs, and other official sources such as ecosystem coverage (<http://ide.ambiente.gob.ec/mapainteractivo/>), floriculture cadastral surveys, and other maps from the Ministry of Agriculture (<http://geoportal.agricultura.gob.ec/>). In addition, composite LANDSAT images from our study area, using radiometric enhancements and spectral band combinations, were also used (Gorelick et al. 2017). From the validation process, five main typologies were improved (Sreedhar et al. 2016). These included: planted forests, developed areas (populated zones), floriculture (areas represented by greenhouses), and natural water bodies. Following the methods proposed by (Jin et al. 2021), a point-based accuracy assessment was conducted using Google Earth as a verification source. After that, a confusion matrix was created using 600 random points obtained from a stratified sampling scheme over the altitudinal bands. The resulting overall accuracy of the edited maps ranged from 82 to 86%. The validation process using visual digitalization over the LULC official vector layers from the periods of interest and the accuracy assessment were conducted in QGIS 3.10 (QGIS Development Team. 2022).

For our LULC change analysis we used a modified categorization from MAE-MAGAP (Ministerio del Ambiente (MAE) and Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2015), we combined level 1 and 2 official LULC taxonomy (S1 Table). Briefly, we aggregated all the agricultural level 2 typologies into agricultural land, and as suggested by MAE-MAGAP (Ministerio del Ambiente (MAE) and Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2015) we included pasture in this LULC class since in the highlands of Ecuador there is a system of rotation from pasture to agricultural fields along the cropping cycles. In addition, we added floriculture crop as a separate typology from the developed LULC category, assuming that all greenhouses detected in the study region correspond to flower production based on the following facts: (1) The study area corresponds to the major center of floriculture production in the highland belt of Ecuador (above 2400 m), characterized by the implementation of greenhouse and irrigation technology mainly

developed for the export market (Knapp 2017; Sawers 2005); (2) according to the flower export cadastral (Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2010), the region of study encompasses thousands of greenhouses dedicated to flower production, occupying more than 1000 ha, and (3) the agricultural land in this region is characterized by a small-scale low input production system (Gobierno Autonomo Descentralizado Pedro Moncayo 2015). As a result, the identified LULC classes were 1) developed, 2) floriculture crop, 3) agricultural land, 4) planted forest, 5) shrubland and herbs, 6) native forest, 7) páramo, and 8) water bodies (S1 Table).

Land use and cover changes

First, we mapped and estimated the land area occupied by each LULC class through time and the percentage change (C %) in each land-use class was calculated by dividing the area difference between the latest and the base year of each class by the coverage area in the base year and multiplying by 100 (Madrigal-Martínez and Miralles-García 2019).

Then, LULC changes were estimated for three periods of analysis: 1990-2000 (T1), 2000-2008 (T2), and 2008-2014 (T3). To analyze the succession of LULC classes in these periods of analysis, we used discrete-time, finite-state, homogeneous (stationary) Markov chain models, which have been widely used to model LULC changes (Hamad, Balzter, and Kolo 2018; Kumar, Radhakrishnan, and Mathew 2014; Liping, Yujun, and Saeed 2018). The Markov chain probability Matrix was estimated using the markovchain R-package (Spedicato 2017) for five administrative zones (at the parish level) and across four elevation bands. By applying a Markov chain model for three periods of analysis to land use classes, it is possible to observe conversions between them when values are higher than 0.5. In contrast, the stability probability is observed when higher values are compared between the same LULC class, representing the probability of remaining in the same class in the consequent time period, given the present state of the class.

The spatial patterns of LULC change across administrative zones were obtained from an overlay procedure of the LULC maps with the polygons of parishes from the studied Pedro Moncayo county, which were downloaded from the official reference (<https://www.ecuadorencifras.gob.ec/clasificador-geografico-estadistico-dpa/>) (Instituto Nacional de Estadísticas y Censos (INEC) n.d.). In the same way, to understand the patterns of LULC change across elevation classes, first the Global Digital Elevation Model (ASTER GDEM) at a 30 m spatial resolution was downloaded from NASA's Earth Data website, was clipped to the study area and the resulting image was further reclassified according to elevation bands, with an interval of 500 m as proposed by (Jin et al. 2021; Meybeck et al. 2001). Then, the following four elevation bands <2300, 2300-2800, 2800-3300, >3300 m (Figure 5) were obtained for the study region. Finally, the LULC classification for each year was layered over both (1) the reclassified elevation map, and the (2) reclassified administrative map. Spatial data assimilation, processing, and overlaying analysis were conducted in R (R Core Team 2019).

Drivers of change

To understand which driving forces could explain LULC transitions in our study region, we selected a set of factors within our DPSIR framework (Figure 4) if they meet the criteria selection exactly as proposed by (Wang et al. 2015): ‘(1) Relevancy: indicators should reflect the underlying cause of environmental change. (2) Availability: the indicator data should be available, accessible, and consistent within the period of analysis. (3) Independence: indicators must be independent of each other to eliminate multicollinearity. (4) Representativeness: each indicator used in the model must represent a category or phenomenon of its own and must provide superior information to other indicators in a similar category’.

Criteria 1 was achieved by conducting a literature review to select a list of driving forces that have been documented to explain LULC change in tropical mountain systems (Aide et al. 2013; Lambin et al. 2003; Madrigal-Martínez and Miralles-García 2019; Nelson et al. 2006; Rodríguez Eraso et al. 2013; Young 2014). Data availability was the result of searching freely available and accessible databases both from national and international sources for the period of interest (Table 2). To meet criteria 3 and 4, we selected groups of drivers that represent different complementary phenomena to explain LULC changes (Table 2). We avoided multicollinearity within each group of drivers by conducting a principal component analysis (PCA) to discard highly correlated variables.

The result was a compiled dataset of 13 variables considered to be direct drivers, organized into the following groups: (1) socio-economic, (2) demographic and infrastructure factors, (3) topographic and (4) climate variables, in addition to (6) local governance decisions about landscape development that influence landscape transitions (Table 2, Figure 4).

In order to increase the number of units of analysis within parishes, all these variables were obtained at the spatial resolution of census area (Valle 2015). After the spatial data assimilation, processing and visualization necessary to obtain the drivers at the spatial unit of analysis, we carried out a reduction dimension procedure using PCA (Dormann et al. 2013) for each grouping of drivers. Within the PCA, correlated variables were screened for the total variation explained by the first principal axes, and used to remove correlated variables (Clark 2019). Coordinates of the principal components that accounted for more than 60% of the variation were then used as explanatory variables in a subsequent statistical model to reduce the dimensions of the multivariate matrix within each grouping of drivers.

Statistical analysis

We synthesized and incorporated the different groupings of drivers into a statistical model to improve LULC predictions and inform decision making by carrying out multivariate analysis using Generalized Additive Models (GAM). GAMs are an approach used extensively in environmental modeling and provide great scope to model complex relationships between covariates (Barton et al. 2020; Wood 2017).

We used GAM regressions to elucidate two types of transitions in our study area: 1) the probability of natural ecosystem loss, and 2) the probability of change to anthropic environments. The LULC trends evaluated as response variables within the first approach (Figure 4) were the probability of loss of native forest, páramo, and shrubs and herbs estimated through Markov chain analysis. Complementarily, the second approach tried to explain what drivers could cause the transitions towards developed areas, floriculture crops, and food crop and pastures (Figure 4). We did not include transitions to planted forests because this LULC element was shown to be very stable during the periods of analysis. As explained in the previous section, the explanatory variables for each GAM were the coordinates of the PCAs that explained more than 60% of the variation in the multivariate matrix of each driver grouping.

The computational methods for the GAM modeling were implemented from the Comprehensive R Archive Network (CRAN) repository ‘mgcv’ package (Hastie 2020). Since in our study, the response variable is a probability ranging from 0 to 1, we used the beta regression within the GAM family, as suggested by this type of data (Ferrari and Cribari-Neto 2004). For the smoothing basis function, we used the penalized cubic regression spline to lower computation cost and avoid overfitting; the smoothing parameter estimation was restricted maximum likelihood (‘REML’), typically used for smooth components viewed as random effects (Barton et al. 2020). After checking the results of different models using distinct methods for selecting the number of knots (default, cross validation, and manual adjustments), we selected the more conservative approach. We set the number of knots to three to be flexible enough to allow the models to fit simple curve relationships, preventing spline curves with complex overfitting estimates. Overfitting curves would have limited our ability to interpret and describe the mechanisms operating, in order to explain LULC changes from an ecological perspective. We presented the results of the GAMs with Partial Dependence Plots using the ‘mgcv’ R-package (Hastie 2020) to determine which variables best explained the variation in LULC change (Barton et al. 2020).

Results

Coverage area patterns and land-change dynamics through time

Agricultural land was the most representative LULC type in the study area, followed by shrubs and herbs (Figure 6). Both LULC types were very dynamic over the different periods of analysis: agricultural land ranged from 35 to 50% of the total area, and shrubs and herbs varied from 16 to 28% of the total area, depending on the period analyzed (Table 3).

2 Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces

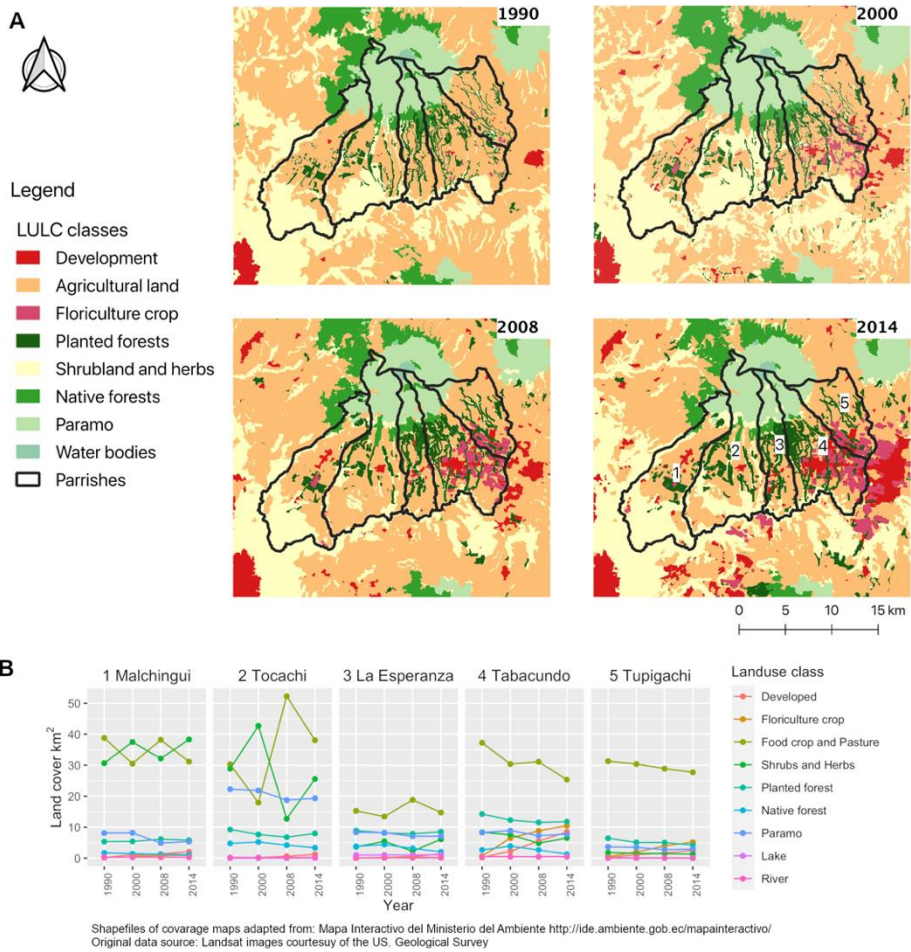


Figure 6. Land use land cover changes in Pedro Moncayo county through time. A. LULC maps throughout the periods of study (1990, 2000, 2008 and 2014). B. Land extent changes through time in Pedro Moncayo county by administrative zones (parishes).

Table 2. Direct driving forces are included as predictors in the Generalized Additive Model to explain probability of change of LULC transitions

Type	Name	Units	Description	Spatial resolution	Source
Socio-economic driving forces	Education index	N/A	Change of a compounded index of eight census indicators of education, with parish breakdown, between years	Census areas	Instituto Nacional de Estadísticas y Censos (Instituto Nacional de Estadísticas y Censos (INEC) 2020) (1990 & 2001, 2010, 2014*)
	Index of economic diversification of employment	N/A	Change of index of economic concentration of employment between years of study	Census areas	Instituto Nacional de Estadísticas y Censos (Instituto Nacional de Estadísticas y Censos (INEC) 2020) (1990 & 2001, 2010)
Demographic and infrastructure variables	Total population	Number of inhabitants	Change of total population between years of study	Census areas	Instituto Nacional de Estadísticas y Censos (Instituto Nacional de Estadísticas y Censos (INEC) 2020) (1990 & 2001, 2010)
	Distance to roads	Distance to nearest cities	km	Change of distance to roads or nearest cities between years of study	30 m
Climate factors	Maximum temperature	°C	Change of daily maximum air temperatures at 2 meters averaged over each month and summarized in a year	1 km	Chelsa datasets tmax, tmin, prec (1990, 2000, 2008) (Karger et al. 2017)
	Minimum temperature				
	Precipitation	mm	Change of monthly means of daily forecast accumulations of total precipitation at earth surface summarized in a year		
	Water availability irrigation	by	N/A	30 m	Digitation from Google images (2008)

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	Altitude	m	Height in relation to sea level		
Topographic	Aspect	degrees	Orientation of slope, measured clockwise in degrees from 0 to 360	30 m	ASTER Global Digital Elevation Model courtesy of NASA Earth Data
	Slope	%	Steepness or the degree of incline of a surface		
Governance decisions on production development	Parish typologies	N/A	Gradient of production development (1-5) based on policy decisions across administrative zones	Parish	Land use development plan of Pedro Moncayo county (2015) (Gobierno Autonomo Descentralizado Pedro Moncayo 2015a)

Overall, natural ecosystems – which are mainly represented by native forests and páramos – decreased from 1990 to 2014 (Table 3), there was a 40% and 16% decrease of native forest and páramo cover when comparing the first and last periods of study (Table 3); but, areas of páramo still represent an important part (13%) of the study territory in the last period of study. Natural water bodies (lakes and rivers) showed high persistence over time (Table 3).

Developed areas and floriculture crops continuously increased over time, and although they were poorly represented in the first period of analysis (less than 0.4% in 1990), by 2014 they represented almost 5% of the study area (Table 3), demonstrating a 26 and 13-fold increase from 1990 to 2014, respectively.

Table 3. Changes in land cover classification in Pedro Moncayo county from 1990 to 2014.

LULC TYPE	YEAR	1990		2000		2008		2014		2014-1990
		km ²	%	km ²	%	km ²	%	km ²	%	% Change
Developed		0.58	0.17	4.72	1.39	9.61	2.84	15.54	4.60	2569.55
Floriculture crop		1.19	0.35	9.44	2.79	14.06	4.16	16.75	4.95	1305.89
Food crop and pasture		152.92	45.20	122.58	36.23	169.29	50.04	137.03	40.51	-10.39
Planted forest		44.16	13.05	38.56	11.40	37.35	11.04	38.24	11.30	-13.42
Shrubs and herbs		73.33	21.68	94.74	28.00	53.40	15.78	77.75	22.98	6.02
Native forest		12.96	3.83	15.11	4.47	11.29	3.34	7.77	2.30	-40.03
Páramo		50.62	14.96	50.60	14.96	40.73	12.04	42.51	12.57	-16.03
Lake		1.48	0.44	1.52	0.45	1.52	0.45	1.66	0.49	12.29
River		1.04	0.31	1.06	0.31	1.04	0.31	1.04	0.31	0.09
Total		338.29	100.00	338.33	100.00	338.29	100.00	338.29	100	0.00

Landscape dynamics through time were not homogenous across the study area, instead they show a geographic pattern (Figure 6). Expansion of developed areas and floriculture crops occurred mainly in the southeastern part of the studied region (Figure 6). The greatest degree of loss of native forests and páramos occurred in the northeast (Figure 6), where there is almost no páramo left due to the expansion of agricultural land.

Transitions of native ecosystems

In general, as expected, the stability of native forests is decreasing through time across the entire territory (Figure 7), with the exception of the western parish where the probability of remaining in this LULC class increases through time – probably due to agricultural land abandonment (Figure 7). In contrast, areas located in the east tend to have lower values of stability through time and higher probabilities of changing to páramo and agricultural land; this pattern was more evident in the last period evaluated (2008-2014) (Figure 8). Additionally, this trend is more evident along elevation bands; where native forests located above 3300 m showed a lower probability of remaining as forest through the years (Figure 8) and in the 2800-3300 m altitudinal belt there is a high probability of converting native to planted forests, especially in the center of the territory (Figure 8).

Furthermore, shrubs and herbs show variable change throughout the study period (Figure 7).

In the majority of administrative areas, the stability of shrubs and herbs decreased (from values around 0.75 to values close to 0.25) in the second period of evaluation (2000-2008) and increased again in the last period (2008-2014). Across all elevation belts, this LULC class tended to follow a dynamic trend changing back and forth with the agricultural land; however, this pattern was not observed in the eastern parish at the elevation belt of 2800-3300 m, where the landscape seems to have a high probability of remaining as agricultural land (S1 Figure).

In contrast, páramo is the most stable among all the natural ecosystems evaluated, although a slight decrease in stability was observed from values above 0.90 to around 0.75 in the second period of analysis (2000-2008) (Figure 7), and the probability of remaining in the same land use class increased by the last period of analysis (2008-2014). Since this ecosystem is characteristic of highlands (above 3000 m) the transition probabilities were only observed for the two higher elevation belts evaluated and their stability seems to be increasing in the administrative zone located in the western part of the territory (S2 Figure).

Transitions to anthropic environments

Developed areas demonstrate a differential trend over time in the study area (Figure 9). In the western areas of the territory (Figure 9) the stability of this LULC class decreased in the second period of evaluation (2000-2008) and significantly increased again in the last time period (2008-2014). In contrast, the parishes located to the east exhibit a more stable probability of remaining as developed areas through time, probably due to their proximity to the larger towns (Figure 9). Since the territory studied is in general a rural area, there is a dynamic trend towards converting agricultural land to urban areas, which follows a geographic pattern (Figure 9).

To the east and center of the study area, floriculture crops have not been fully established because land use tends to change to agricultural land (Figure 9); in contrast, this LULC type located in the eastern parishes is more stable with values around 0.75 throughout the period of study (Figure 9).

Agricultural land is a very stable land use class throughout the study period in the administrative zones located in the center and eastern parts of the study area, with values ranging above 0.77 (Figure 9); the stability of this land use class in the west followed a dynamic trend through time: in the first period (1990-2000) it was lower than in the second period of analysis, and it increased again by the last period studied. In contrast, planted forests depict a very stable land use trend through time across the territory, their probability of remaining in the same land use class ranges from 0.6 to 0.90 (Figure 9).

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

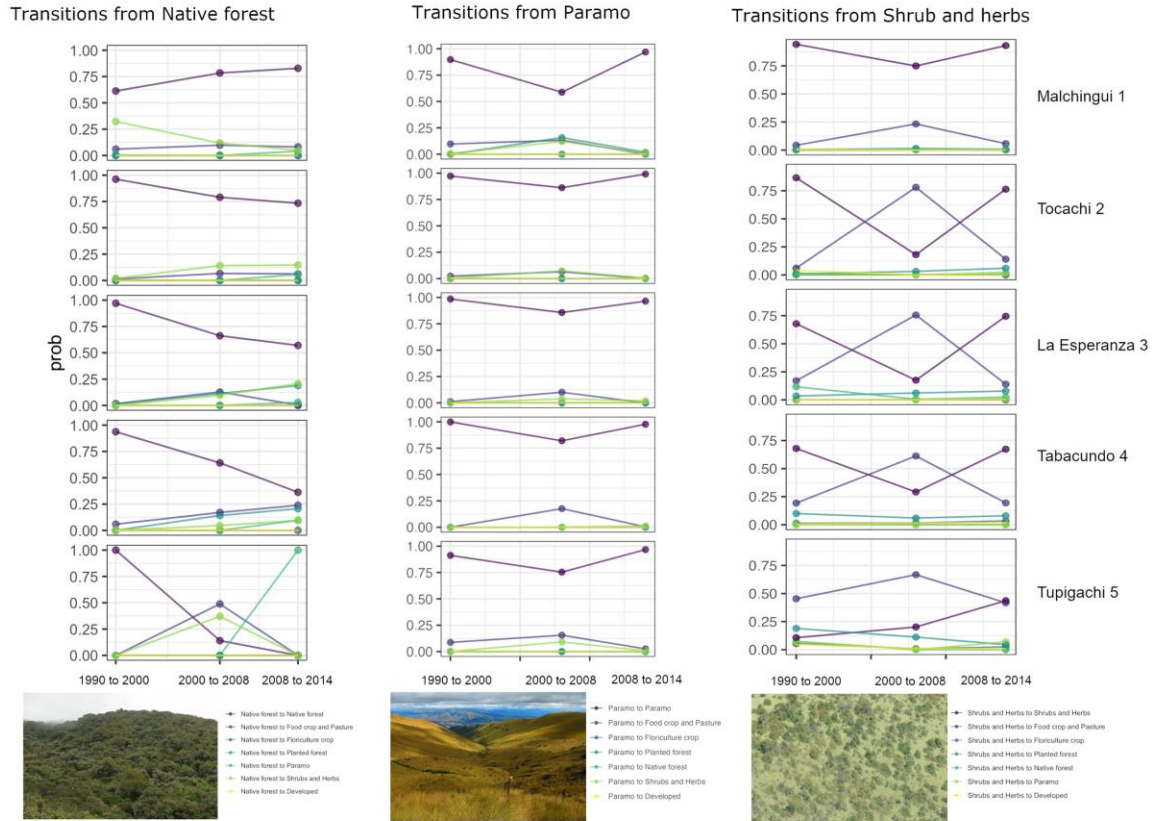


Figure 7. Transition probability of native ecosystems through time in Pedro Moncayo county, at the parish level. (The above photos are the original works of the authors).

2 Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces

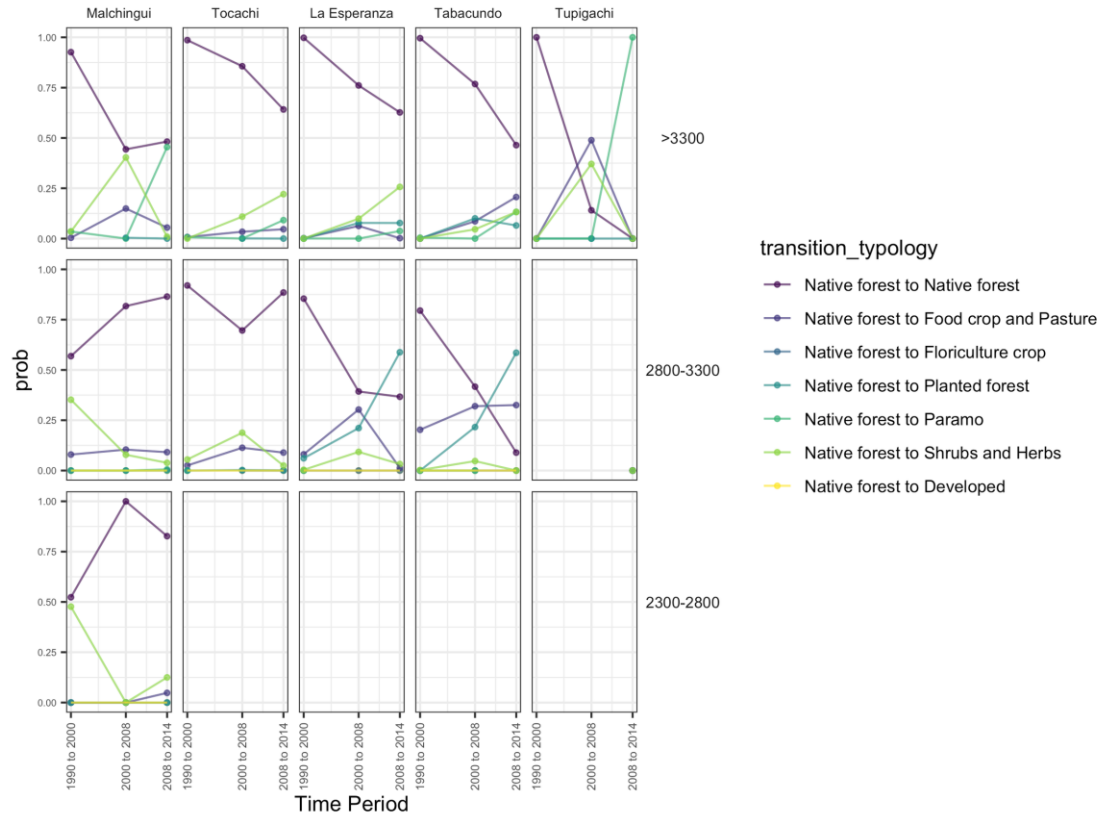


Figure 8. Transition probability of native forests through time in Pedro Moncayo county, by altitudinal bands at the parish level.

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

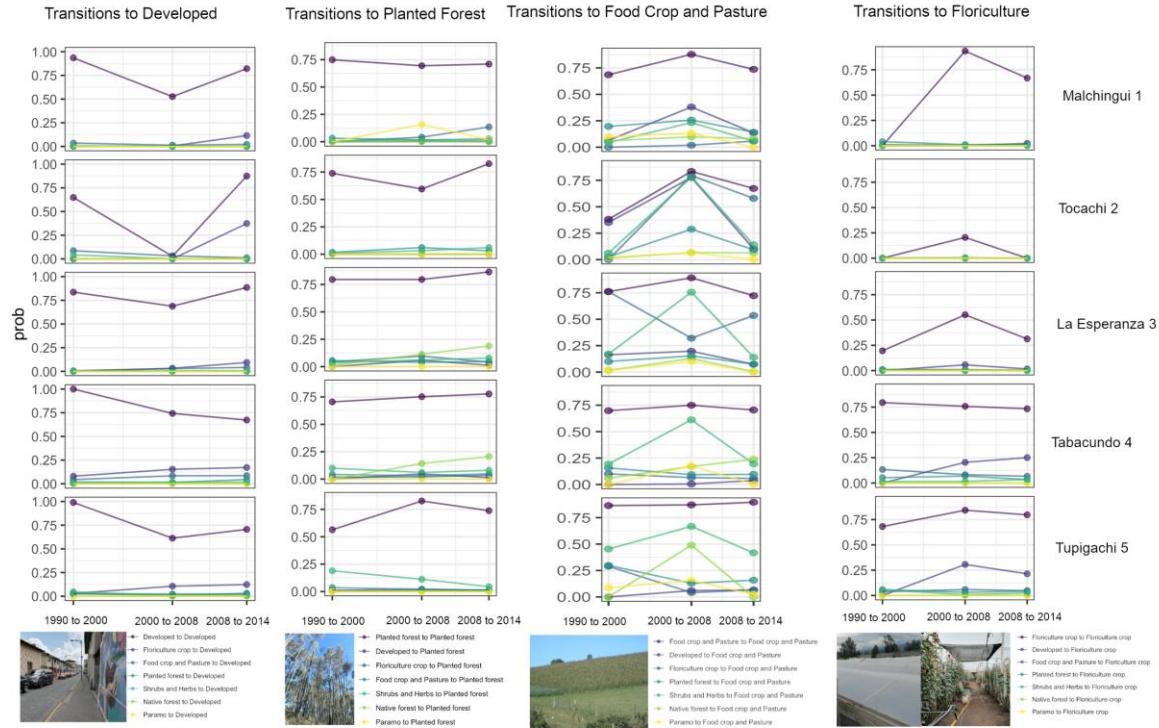


Figure 9. Probability of land use transition to anthropic environments in Pedro Moncayo county, at the parish level through time. The above photos depicting the developed area and the floriculture crops are reprinted from Guasgua (<https://zenodo.org/record/6231701#.YhVzVpPMLJ8>) under a CC BY license, with permission from (Jessica Guasgua), original copyright 2022. The other photos are the original works of the authors.

Drivers of change

The general results of the screening and dimension reduction process within each driver grouping obtained after conducting PCAs are briefly described as follows: within the socioeconomic drivers group, variables were not correlated and the first PC explained much of the variability (60%) in this matrix. Inside the topographic group, aspect was removed after data screening and the PC1 coordinates were selected for the further models, since they accounted for 61% of the variation. For instance, *tmax* was a correlated variable and it was extracted from the climate matrix, then both PC1 (representing irrigation and *tmin* variability) and PC2 (representing water availability by irrigation) were selected as predictor variables, as they together accounted for more than the 60% of the variation in the climate dataset. Finally, in the driver grouping that represents demography and infrastructure, distance to roads was removed and the coordinates from PC1 (distance to cities) and PC2 (population change) were included as predictors within this driver grouping because together they explained more than 60% of the variation.

The selected predictors or possible drivers of change to explain LULC transitions displayed different spatial distributions within the study area (S3 and S4 Figures), depicting a territory with contrasting patterns. The details of the spatio-temporal distribution of the drivers of change are presented in S3 and S4 Figures.

Table 4 describes the results of the different LULC transitions studied and their main explanatory variables; the GAMs demonstrated different results when explaining each LULC transition (Table 4). The lowest total variance (21.00%) corresponded to the native forest loss model and the largest value (41.80%) was for the agricultural expansion model. Overall, the most relevant parameters explaining LULC in the region were the topographic driver grouping (which incorporates elevation and slope), this driver grouping was highly significant for the majority of the transitions studied ($p < 0.001$, Table 4), with the exception of the shrub and herb loss. In contrast, the climate driver grouping PC1 (which mostly depicts the variation of precipitation and minimum temperature) was not significant in any model ($p > 0.05$).

For the native forest loss model, the most important groupings of drivers ($p < 0.001$) were the socioeconomic and topographic drivers (Figure 10, Table 4). For instance, páramo loss was only explained by the variation in elevation and slope (topographic PC1) (Table 4, S5 Figure). Figure 10 shows the GAM partial dependence plots for the native forest loss model and indicates that the probability of native forest loss increases as land aspect PC1 increases, in other words, when elevation and slope increases. In contrast, when the socioeconomic variables have low and high values the probability of forest loss increases, although the confidence interval for lower values in the socioeconomic drivers is higher.

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

Table 4. Summary of the results of the Generalized additive models to elucidate drivers of change for the six LULC transition models in Pedro Moncayo county.

Drivers	Native forest loss			Paramo loss			Shrub loss			Urbanization			Floriculture expansion			Agriculture expansion		
	p value	chi sq	edf	p value	chi sq	edf	p value	chi sq	edf	p value	chi sq	edf	p value	chi sq	edf	p value	chi sq	edf
Socioeconomic PC1	0.000	19.65	1.8	0.721	0.00	< 1	1.000	0.00	< 1	0.468	0.00	< 1	0.307	0.05	< 1	0.812	0.00	< 1
Topographic PC1	0.000	13.32	1.4	0.000	23.89	1.5	0.426	0.00	< 1	0.000	16.69	1.7	0.001	9.62	1.4	0.000	18.48	1.9
Climate factors PC1	0.889	0.00	1.0	1.000	0.00	< 1	1.000	0.00	< 1	1.000	0.00	< 1	0.774	0.00	< 1	0.814	0.00	< 1
Climate factors PC2	0.336	0.00	< 1	0.791	0.00	< 1	0.374	0.00	< 1	0.609	0.00	< 1	0.018	4.23	< 1	0.039	3.06	< 1
Demography & infrastructure PC1	0.547	0.00	< 1	1.000	0.00	< 1	0.000	17.02	1.76	0.000	26.71	1.8	0.936	0.00	< 1	0.000	15.21	1.3
Demography & infrastructure PC2	0.189	0.721	< 1	1.000	0.00	< 1	0.364	0.00	< 1	0.048	0.00	1.2	0.144	1.24	< 1	1.000	0.00	< 1
Parish governance	0.507	0	< 1	0.118	1.46	< 1	0.000	25.53	1.53	0.386		< 1	0.000	10.41	1.2	0.000	31.00	1.8
Deviance explained	21.00%			20.80%			39.90%			36.50%			25.00%			41.80%		
R-sq.(adj)	0.22			0.15			0.29			0.30			0.21			0.33		

2 Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces

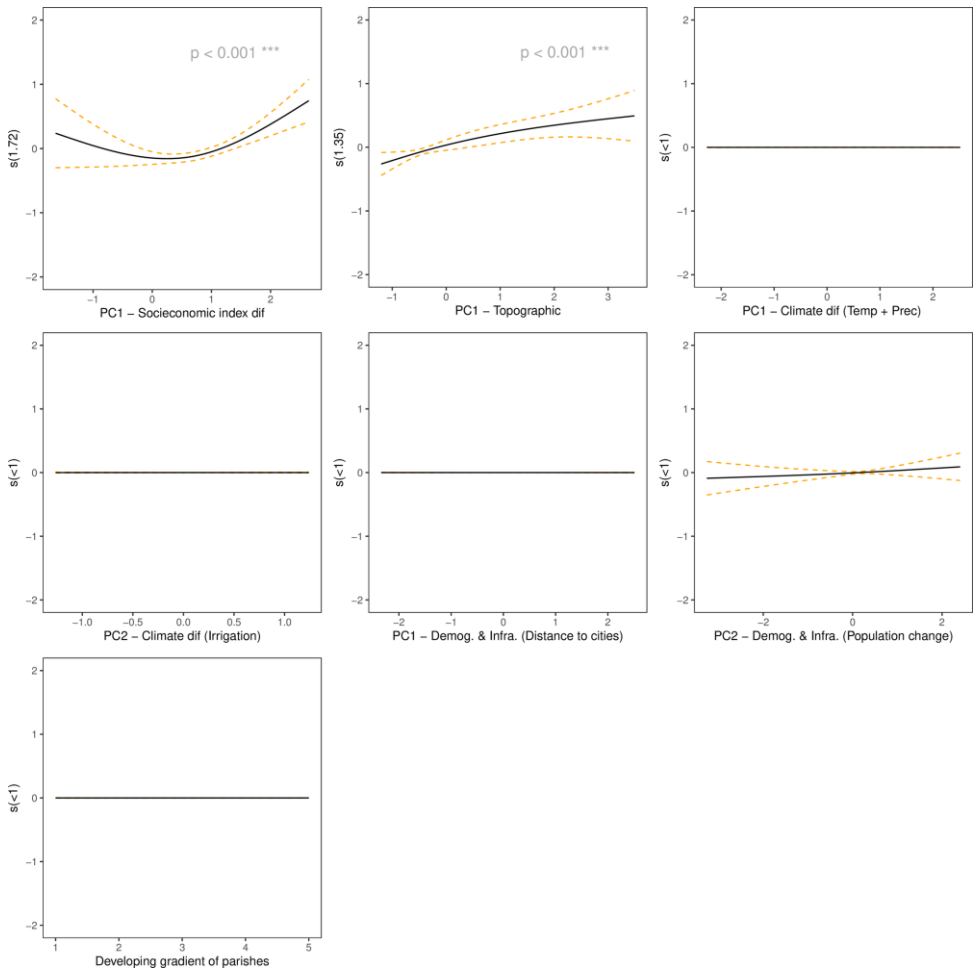


Figure 10. Generalized additive model partial dependence plots for native forest loss. Each plot shows a covariate and their partial dependence on probability of native forest loss in the context of the model. The y axis shows the mean of the probability of native forest loss and the x axis the covariate interval. The gray area represents the 95% confidence interval.

Some transition models were explained by similar driver groupings, such as shrub loss and agricultural expansion (Table 4). These also show a contrasting pattern in their response variables, in such a way that when an increase in agricultural areas was prevalent, there was a decrease in shrub and herb land (Figure 6). These models depicted the following driver groupings as significant parameters ($p < 0.001$): pressure drivers (PC1) and a variable that describes differences in the development of distinct administrative areas within the study area (Table 4).

S6 and S7 Figures show the GAM partial dependence plots for shrub and herb loss and agricultural expansion, respectively, and they reveal that high probabilities for these transitions are related to medium values of elevation and slope (topographic drivers). Additionally, when the main local cities are further away the probability of converting natural areas to agricultural land increases, and there is a linear increase in rates of change to agricultural land with the gradient of development at the parish level.

Variables leading to the highest change in the probability of transition to floriculture crops comprise the topographic driver grouping, the climate PC2, which includes water irrigation and the development gradient across parishes. Floriculture crops increase as elevation and slopes decrease. Complimentarily, when more water is available through irrigation, the probability of establishing floriculture crops increases (S8 Figure).

The urbanization transition model was explained by topographic, demographic, and infrastructure driver grouping PC1 ($p < 0.001$) (Table 4). Urban transition probabilities decrease significantly ($p < 0.001$) with altitude and slope, it also significantly decreases ($p < 0.001$) with the distance to city centers (demographic and infrastructure PC1), and with higher values of total population change (demographic and infrastructure PC2) (S9 Figure).

Discussion

This study demonstrates that a combination of environmental variables and human induced factors still have an impact on LULC transformations during the past several decades, despite a legacy of landscape transformation occurring in the Ecuadorian highlands (Deler et al. 1983; Ross et al. 2017) and supports findings in similar mountainous landscapes of Latin America (Aide et al. 2013; Gaglio et al. 2017; Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013). The study area of Pedro Moncayo represents a rural Andean landscape dominated by an agricultural matrix which contains important areas of shrubland and páramo, accompanied by patches of remaining native forest, consistent with other current landscapes in the Tropical Andes (Aide et al. 2013; Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013).

We found spatially explicit patterns of LULC transition across the study area, including a distinct deforestation pattern of native montane forests located below 3300 m.a.s.l. In addition, we found an unexpectedly high pattern of páramo stability for the majority of the studied territory, and a dynamic transition between agricultural land and shrubland. Likewise, we found an exponential increase in urban land and floriculture crops in the eastern part of the territory. This result is striking because of the small spatial scale where the changes occur; our study area encompasses only 334 km² compared to other landscapes studied in central Ecuador (Ross et al. 2017), the Peruvian Puna (Madrigal-Martínez and Miralles-García 2019) or Colombia (Rodríguez Eraso et al. 2013), where the extent of land is 10, 120, and 800 times larger, respectively than our studied territory.

We estimated a páramo loss of 16% from 1990 to 2014 in Pedro Moncayo county (Table 1), this result is consistent with the findings of loss (13%) in a nearby territory (Wigmore and Gao 2014). Although most of the studied territory depicted a relatively high pattern of páramo stability, as also described for a highland landscape of central Ecuador (Ross et al. 2017), our results also demonstrated a hotspot of páramo conversion to agricultural land concentrated in the northeast. In contrast, our results are strikingly different to the land cover patterns observed in other páramos in the region, where a more widespread agricultural use of páramo was observed (Camacho 2013; Garavito 2015). Another common transition reported for páramos in the Ecuadorian mountains is to exotic timber plantations (Farley 2007), yet this trend was not apparent for our studied territory.

We found a 40% montane forest loss from 1990 to 2014, and the Markov chain model demonstrated a very low probability of persistence of this ecosystem in the majority of Pedro Moncayo county (Figs 2 and 4). This is consistent with the general trend of deforestation and degradation of mountain forests in the Tropical Andes mainly explained by agricultural expansion (Tejedor Garavito et al. 2012). We also found that the highest chances of loss occur in the altitudinal band of 2800 to 3300 m (Fig 3). These findings are in accordance with those described for other representative highlands in central Ecuador (Ross et al. 2017); however, LULC change studies carried out in more isolated landscapes of central and southern Ecuador reported deforestation hotspots for lowland montane forests and afforestation transition in upper altitudinal areas (Gaglio et al. 2017; Tapia-Armijos et al. 2015); additionally, higher rates of deforestation were also observed in the lowland forest of Colombia, and in the Napo region along the northeastern Ecuadorean border (Rodríguez Eraso et al. 2013).

Mountain forests are considered one of the most threatened forest types in the tropics (Mosandl and Günter 2008), which are also highlighted as a global priority for conservation due to their relatively high biodiversity and high level of endemism (Pennington et al. 2010), and their vital role in the provision of different ecosystem services in the region (Anderson et al. 2011; Balvanera 2012). However, if the trends demonstrated by the Markov model are maintained for this territory, there is a high probability that the remnant montane forests will be permanently lost in a few years, posing a greater threat to the already vulnerable biodiversity (Ataroff 2003) and limiting the capacity of these ecosystems to provide services in the county, such as the provision and regulation of freshwater, "wild foods", and many other non-timber forest products (Brandt and Townsend 2006), as described for other latitudes (Costanza et al. 2014; Lawler et al. 2014; Millennium Ecosystem Assessment (MEA) 2005).

Along with this deforestation trend, we observed a dynamic and opposite transition between agriculture areas and shrubland, this pattern was more evident for the parishes located in the center of Pedro Moncayo county and along the elevation bands between 2300 to 3300 m. This pattern could demonstrate a gain of secondary vegetation, probably due to a temporal abandonment of agricultural areas, followed

by a net gain of agricultural land which has been observed in other Andean systems of Colombia (Rodríguez Eraso et al. 2013) and Central America (Wassenaar et al. 2007).

We found that urban areas are dramatically increasing in the eastern part of the territory (Figure 4, Table 1); we reported a 25-fold increase in urban cover from 1990 to 2014. This pattern follows the global trend of urban expansion (Mishra, Rai, and Rai 2020; Seto et al. 2011), but the rate of expansion is even faster than that reported for many cities around the world (Angel et al. 2011) and in small urban centers (Obaco and Díaz Sánchez 2018), raising questions of the sustainability of future development in the region. For example, higher probabilities of urban land expansion were explained by increases in population, proximity to urban centers, and occurred at lower elevations and slopes in previous crop land. This pattern has been observed in other regions of South America, where urban expansion is taking place largely on agricultural land (Seto et al. 2011), a zone characterized by areas of lower altitude and slope, which in the Andean zones corresponds to the more fertile valleys between mountains.

Another interesting finding was the exponential expansion of flower cultivation cover reported for Pedro Moncayo county (Table 1, Figure 5). We described a 13-fold increase in total land area of greenhouse floriculture from 1990 to 2014 (Table 1); this expansion was observed primarily in the eastern parishes of the territory (Figs 1-3), which are located contiguous to Cayambe county, another center for the development of this activity in Ecuador (Wigmore and Gao 2014). This region, situated in Pichincha Province in central Ecuador, has an equatorial location and has optimal sunlight conditions (long hours of daylight) and an ideal highland climate (abundant sunshine, warm days and cool nights), making it possible to produce some of the highest quality flowers in the world (Knapp 2017; Sawers 2005) and proximity to international airports and key infrastructure facilitates product export.

Our analysis suggests that in addition to the topographic variables, another driver that explains the floriculture expansion pattern is water availability by irrigation, depicted by the geographic pattern of irrigation in the lower eastern part of the studied territory. This creates a subsidy for growing crops which would have been limited by natural precipitation, as demonstrated by (Singh et al. 2020) to increase yield in many crops. This irrigation canal transports water from the glacier of a snow-capped mountain located in a contiguous territory, corresponding to the neighboring county (Cayambe). This water source only reaches the center of the territory and can distribute water to lower elevations, therefore providing a water irrigation subsidy to the area situated to south-east.

We found that topographic variables (elevation and slope) are the most important drivers for all LULC transitions. For instance, native ecosystem transitions (including the models to explain loss of native forest and páramo) and agricultural expansion were both significantly related to changes in elevation and slope, in such a way that the probability of native ecosystem loss and the probability of agriculture expansion increase with elevation and slope, until they reach a certain value where they level off

(native forest and páramo models) and even decrease (shrub and herb loss and agricultural expansion models). These complementary trends suggest that the major pressure on native ecosystems in this region of northern Ecuador is the continued expansion upwards of the agricultural-livestock frontier, similar to other Andean landscapes (Rodríguez Eraso et al. 2013; Ross et al. 2017). In addition, the expansion of urban areas and floriculture crops in the previous agricultural land, located at lower elevations of the eastern part of the territory, represents ongoing pressure for expansion of the agricultural frontier in highland areas. Even though we did not find evidence that climatic variation explained the LULC transitions, the effect of climate change could be stronger in the near future due to the extreme events predicted in the tropical Andes (Vanacker et al. 2018), affecting the capacity of highland ecosystems to keep providing key goods and services to people (Buytaert et al. 2011).

The trend of native ecosystem loss associated with higher elevation and slopes observed in this landscape of northern Ecuador could be attributed to its past patterns of land use, as summarized by (Hahs et al. 2009; Young 2009). The most drastic transformation and loss of native ecosystems in Andean landscapes occurred centuries ago and this was also expanded in the mid-twenty century by agrarian reform; current native ecosystems are only the remnant patches, localized at higher elevations and slopes (Brandt and Townsend 2006). However, the leveling off and further decrease in the probability of native forest loss at higher values of topographic variables could be explained by conservation measures adopted to restrict human activities in the upper mountain belt, such as the establishment of protected areas (Brandt and Townsend 2006; Ross et al. 2017; Young 2009) or implementation of national or local policies to limit agricultural expansion (Peters et al. 2019) that have prevented the loss of high mountain ecosystems in other Andean regions (Aide et al. 2013; Grau and Aide 2008).

Páramos and other high-elevation ecosystems (pristine native forest patches), which are ecosystems situated above 3500 m in the northern highlands of Ecuador, are currently more valued due to their importance in providing critical ecosystem services and, thus, in Ecuador have received special protection measures at the national (Asamblea Nacional de la República del Ecuador 2017; Asamblea Nacional del Ecuador 2004) and local level (Ministerio del Ambiente Agua y Transición Ecológica (MAATE) 2021).

Studies have found that environmental variables such as topography were better predictors of woody vegetation change, indicating that these variables place physical limits on the types of land-use practices that are feasible in a region (Aide et al. 2013; Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013). However, the trends were different from those observed in our study, in that these authors found that deforestation occurred in the lowlands, which are more appropriate for large-scale mechanized agriculture (Aide et al. 2013; Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013).

The dynamic transition trend between agricultural land and shrubland observed in our study could be attributed to natural reforestation succession at high elevations

(e.g., cooler temperatures, steeper slopes), which is consistent with other findings (Aide et al. 2013; Tapia-Armijos et al. 2015). In our study, this pattern was also associated with variation in population change, which could be attributed to population migration dynamics within the territory. Migrations of farmers from higher mountainous zones to urban concentrated areas have been widely documented in different regions of Latin America and are the drivers associated with natural reforestation in higher elevations due to agricultural land abandonment (Grau and Aide 2008). This finding is consistent with the local demography dynamics, where the urban population tripled from 1990 to 2010 (from 3,000 to 10,000 inhabitants) while the rural population has doubled (12,000 to 23,000 inhabitants) in the same period (Gobierno Autonomo Descentralizado Pedro Moncayo 2015), representing an increasing pressure on natural resources to sustain livelihoods in the region.

In places where this landscape transition has been reported, it has facilitated ecosystem recovery in the highlands, likewise this has allowed the provision of ecosystem services to be maintained for a growing urban population (Grau and Aide 2008). The dynamic conversion from agricultural land to shrubland in some highland areas of this landscape, explained by rural-urban migration, is consistent with the “Forest Transition Model” proposed by Mather (Mather and Needle 1998). In our study area the pattern was uneven; for instance, native forests are decreasing in some areas, while shrubland was expanding in other areas, describing a process of ecological succession before a fully recovered forest could occur. Maintaining and increasing native ecosystems in higher elevations and expanding urban and agricultural areas in the lowland and valleys raises new opportunities and challenges for conservation. However, the consequences of these spatial transitions have not been studied in depth (Grau and Aide 2008).

We have considered a comprehensive set of factors characterizing landscape conversion dynamics, however some limitations concerning the scope of the drivers used for this analysis should be considered. The underlying driving forces affecting land use transformations could also be attributed to production support policies geared towards the internal market and exports (Lambin et al. 2003; Ross et al. 2017), which were not included in our analysis. For example, the greenhouse floriculture expansion initiated in the 1990s has been cited as a response to favorable trade agreements and increased access to technologies from multiple sources and local entrepreneurship (Knapp 2017). Flower cultivation is a land- and labor-intensive activity with high land productivity (that is, high market value of output per hectare) (Sawers 2005). However, the gains in income have surely been offset by growing health and environmental problems posed by the intensive use of pesticides in flower cultivation (Sawers 2005) and irreversible change to landscape properties.

All indications suggest that flower exports will continue to play a major and probably increasing role in Ecuador’s economy (Sawers 2005); in fact, this industry is steadily expanding and causing land use changes in the territory; for instance, former important and traditional lands dedicated to livestock and food crop production, located in areas with the capacity for agricultural production and with access to irrigation systems have been transformed into greenhouses for flower

cultivation, posing a trade-off between agricultural production and environmental concerns, including the asserted need for global land use expansion, and the issues of rural livelihoods and food security (Gobierno Autonomo Descentralizado Pedro Moncayo 2015).

Despite possible drawbacks to the LULC datasets, such as the existence of classification errors and uncertainties (García-Llamas et al. 2019), its accessibility and availability at different time spans offers considerable advantages for studying land cover changes (Kroll et al. 2012), providing a consistent source of primary data facilitating the reproducibility of results. In addition, post-classification or editing process of vector maps, complemented with the images and analytical capabilities of Google Earth engine allows more accurate identification of distinct land use classes (Damtea et al. 2020).

Regardless of these limitations, we envisage that the proposed DPSIR framework and the practical implementation analysis of LULC transitions and their drivers, using official LULC maps and other freely available databases from distinct sources (demographic, climatic, topographic, etc.), could be replicated to understand environmental change in tropical mountain systems. These types of approaches are particularly important in areas of data scarcity and low technical capacities for the processing of remote sensing information required for land management and planning, which characterizes many distinct territorial levels of governance in tropical mountain systems and developing countries.

The assessment of local and regional patterns of current land use and past land cover conversion is the first step in developing sound land management plans that could prevent broad scale, irreversible ecosystem degradation (Mishra et al. 2020). This characterization of landscape patterns through time and the analysis of their proximate drivers of landscape change enhance our understanding of how landscape patterns might influence ecosystem services (Jones et al. 2013). Our findings would help distinguish important areas for conserving native ecosystems. In addition, our study highlights that research and landscape management, zonation and ecological recovery/restoration should be better integrated into land-use policy and conservation agendas at the local level (Mishra et al. 2020) to balance the multiple needs and benefits from ecosystems of a growing population in the rural landscape of northern Ecuador.

Conclusions

Our study proposes an adaptation of the DPSIR framework, as a tool to characterize the complexity of tropical mountain systems and conduct integrated ecosystem and ES assessments. After testing the initial phases of the framework in the highlands of northern Ecuador, we present the following conclusions: (1) we found a dynamic and clear geographical pattern of distinct LULC transitions through time. In a span of 24 years, the urban and floriculture zones increased substantially (by 25 and 13 folds, respectively to their original extent, which was less than 2 km² in 1999); these transitions were observed in the lower elevation bands localized to the east of the study region (less than 2800 m), mainly occupying previous agricultural land. Between 1990 and 2014, the native forests experienced a 40% reduction, with the lowest probability of persistence in the elevation band of 2800-3300 m, where agricultural land and planted forest are continually replacing this LULC class. Our findings also revealed an unexpected stability trend of paramo (0.75 -0.90) and a successional recovery of previous agricultural land to the west and center of the territory, which could be explained by agricultural land abandonment. (2) Our conservative results from the GAMs explained between 21 to 42% of the variation of the distinct LULC transitions observed in the study region. Different combination of human induced, and environmental variables were the explanatory driving forces, whereas topographic factors, resulted in the main drivers of change in this landscape. Interestingly, floricultural expansion was also explained by water availability by irrigation and the production gradient across parishes, whereas shrubland, urban and agricultural transitions can be explained by demographic and infrastructure driving forces, which could be related to urban-rural population dynamics that need further analysis. Future work will include implementing all the phases of the proposed DPSIR framework, which include a multitemporal Ecosystem Service evaluation of the studied landscape.

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2 Land use and land cover change in a tropical mountain landscape of northern Ecuador: altitudinal patterns and driving forces

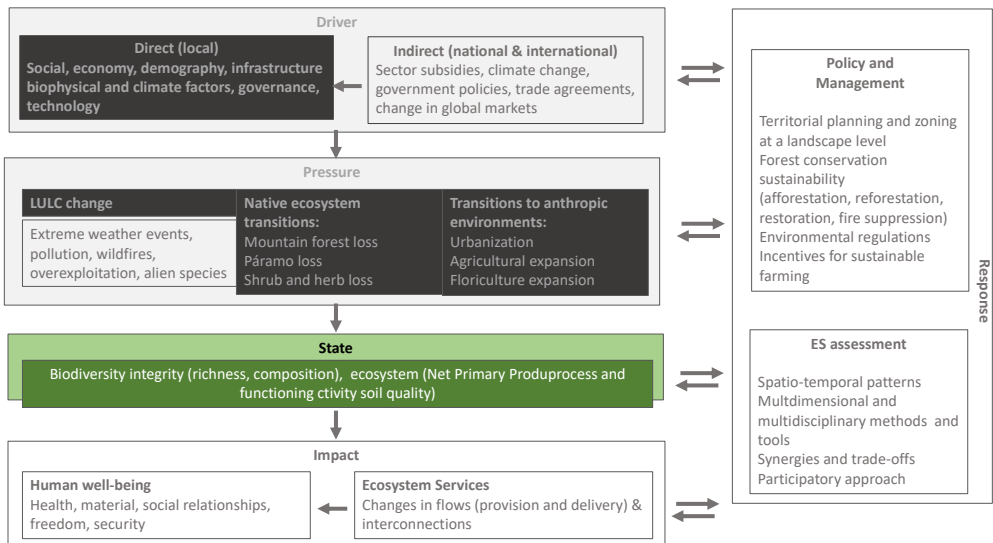
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Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

3

Native forest conversion alters soil macroinvertebrate diversity and soil quality in tropical mountain landscapes of northern Ecuador

Using the soil health framework, this chapter evaluates the impact of native forest conversion into anthropic systems (planted forests, pastures, and monocultures) on soil fertility and biodiversity conservation in the highlands of northern Ecuador. The State and Impact elements of the DPSIR framework are addressed.



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Native forest conversion alters soil macroinvertebrate diversity and soil quality in tropical mountain landscapes of northern Ecuador

Abstract

Land use changes cause soil degradation and loss of biodiversity, thereby affecting ecological processes and soil-associated ecosystem services. However, land use change impacts on soil health have received little attention in the highland landscapes of the tropics. In this research, using the soil health framework, we assessed the impact of native forest conversion to anthropic systems (planted forests, pastures, and monocultures) on two ecosystem services: biodiversity conservation and soil fertility in the highlands of northern Ecuador. The biological dimension of our assessment focused on the diversity, abundance, and biomass of soil macroinvertebrate communities as proxies to soil functions, whereas soil chemical parameters were used to describe the soil fertility. The soil invertebrate communities and soil chemical parameters were studied in topsoil samples using 25×25×10 cm monoliths, obtained from ten sampling sites randomly selected in each land use category. We hypothesized that native forests would present more diverse and even soil macroinvertebrate communities, and together with their soil chemical properties would indicate better soil quality than anthropic environments. Our results showed that the structure and composition of the edaphic macroinvertebrate communities significantly differed among the studied land use categories. As predicted, native forests presented greater values for richness, evenness and diversity of soil biota than did the other categories, demonstrating a significant loss of taxonomic biodiversity at order and genus levels. We also found a significant reduction of trophic diversity in native forests converted to anthropic environments. More trophic groups with greater abundances were found in native forests, where predators and detritivores stood out as dominant groups, indicating the good quality of the soil. The results from the soil chemical parameters also confirmed the distinction in soil health between native forests and anthropic environments. Our results highlight the risk associated with current trends of native forest loss and conversion to anthropic systems in high mountain ecosystems in the tropics, illustrating how these alterations could cause biodiversity loss and degradation of the chemical attributes of soil health. The findings of this research could contribute to the conservation and sustainable management of mountain agricultural landscapes in the study region.

Keywords: Soil diversity, soil health, native forest conversion, land use change, soil macroinvertebrates, soil ecosystem services, tropical mountain systems

Introduction

Considerable evidence demonstrates that the world's ecosystems are affected as a result of human activities Millennium Ecosystem Assessment, 2005; Díaz et al., 2006, with land use change being one of the most important factors that transforms terrestrial ecosystems (Foley et al., 2005; Winkler et al., 2021). Conversion of native forests to anthropic environments, such as agricultural land for food production or to planted forest for timber extraction, has generated alterations in vegetation cover and biodiversity for various biomes and continents, negatively impacting soils and their derived ecosystem services (Sylvain and Wall, 2011; Nielsen et al., 2015; Veldkamp et al., 2020; Zarafshar et al., 2020). Soil degradation attributed to land use conversion is a major problem in the tropics, affecting the overall resilience of the socio-ecological systems (Delelegn et al., 2017; De Valença et al., 2017).

Tropical mountain landscapes, such as the Ecuadorian Andes, are characterized by complex topography, severe intensity in weather conditions, and poor management practices (Farley, 2007). The long history of land use transformation in these landscapes, mostly shaped by agricultural and livestock activities, has caused severe soil degradation (Lema, 2016; Guarderas et al., 2022), affecting agricultural yield productivity, food security, and the overall delivery of vital ecosystem services (Suquilanda, 2008). In addition, today native montane forests occur only as remnant patches, and these fragile ecosystems are still highly threatened by land use changes (Gaglio et al., 2017; Guarderas et al., 2022). Thus, understanding the magnitude and trend of changes in soil quality due to land use conversion is pivotal to promote sustainable and productive landscapes in the Ecuadorian Andes (Nielsen et al., 2015).

Land use conversion can produce significant disturbances in the soil environment (Lukina et al., 2011; Sylvain and Wall, 2011; Comerford et al., 2013). Soil moisture, structure, aeration, pH, nutrient status, microbial biomass, enzymatic activities, and the structure of edaphic communities are largely altered due to land use changes and different soil management practices. Therefore, soil health could be severely affected by land use changes (Delelegn et al., 2017; Mann et al., 2019).

“Soil health, also referred to as soil quality, is defined as the continued capacity of soil to function as a vital living ecosystem that sustains plants, animals, and humans” (Natural Resources Conservation Service, 2022). According to Bünemann et al. (2018), the functions of living soil could be defined as the bundles of soil processes that underpin the delivery of ecosystem services. This integrated view transcends the productivity-oriented function of soils to wider frameworks that include the maintenance of environmental quality and biodiversity conservation. In addition, soil health is focused on the dynamic soil properties that can be strongly influenced by management and are mainly monitored in topsoils (0–25 cm) (Karlen et al., 2003). Soil health under different land uses can be assessed using indicators that measure the properties of soil or plants that provide clues about how well the soil can function. These indicators should interact synergistically and could encompass the physical, chemical, and biological attributes of soils (Karlen et al., 2003; Delelegn et al., 2017).

However, quantifying soil health is still dominated by chemical indicators, despite the growing appreciation of the importance of soil biodiversity (Lehmann et al., 2020).

The biological attributes of soil health are those associated with the soil biota, in other words, its biodiversity, food web structure, activity, and the range of functions it performs (Bünemann et al., 2018). However, the remarkable biodiversity harbored in soils has been poorly described, and even when taxonomic information is available, less is known about the functional roles of the great majority of these organisms within the ecosystems they occur (Eisenhauer et al., 2017).

The use of edaphic macrofauna as a soil indicator is considered an advantage because they are the first to manifest the changes that involve environmental disturbances (Cabrera, 2014). Soil diversity and macrofaunal biota play an important ecological role in the functioning of the soil environment and the belowground part of terrestrial ecosystems. They regulate nutrient cycles, organic matter, mineralization, modification of the soil structure, and water regime (Food Agriculture Organization of the United Nations, 2015). In addition, soil fauna is considered an appropriate bioindicator to measure soil quality due to its sedentary characteristics, permanence throughout the year, ease of measurement, and high sensitivity and rapid response to environmental stress. Monitoring soil macrofaunal communities, in combination with chemical and other biological soil properties, could improve the assessment of soil health in a more integrative manner (Cabrera, 2014; Lehmann et al., 2020).

Although the study of soil ecology is currently growing in the scientific literature (Brown et al., 2001; Decaëns et al., 2006; Nielsen et al., 2015; Eisenhauer et al., 2017), we need better insights into soil chemical parameters and biodiversity to determine the impacts on soil health in response to the altered environments (Food Agriculture Organization, 2015). This need is highlighted in tropical mountain landscapes where few studies have been conducted (Lema, 2016).

Therefore, using the soil health framework, our study was aimed at assessing the effect of land use change on soil fertility and soil biodiversity conservation in the highlands of northern Ecuador. We studied soils under native forests, as a reference system, to compare the biological and chemical attributes of soil with anthropic environments representative of the study area. These land use types include planted forests to agricultural land (characterized mainly by pastures and maize monocultures). Specifically, our objectives were as follows: (1) to contrast the structure and composition (diversity, abundance, and biomass) of the edaphic macroinvertebrate communities at order and genus levels, as well as by trophic groups, among land use types and (2) to compare their soil chemical properties. In addition, we aim (3) to assess how the soil chemical parameters could affect soil macroinvertebrate communities among land use types, by applying different multivariate analyses. We hypothesized that native forests would present more diverse and more even soil communities, and their soil chemical properties would indicate better soil fertility attributes than soils under anthropic environments.

Materials and Methods

Study Area

The study area includes an agricultural landscape located in the mountainous area of northern Ecuador, which is located in La Esperanza parish of Pedro Moncayo county (longitude -78.25716 , latitude 0.08222), covering an area of 13 km^2 (Figure 11). This region is classified as pluvial and cold temperate according to the Ministry of Environment of Ecuador (Ministerio del Ambiente del Ecuador 2013). It has an annual mean temperature of 14°C ($\pm 1,3 \text{ SD}$) (GAD Municipal Pedro Moncayo 2015). Seasonal variation of temperature is reduced, while precipitation is bimodal, with two wet seasons from February to May and September to November with a monthly average precipitation of 70 mm ($\pm 20,1 \text{ SD}$). The dry season presents an average precipitation of 25 mm ($\pm 14,3 \text{ SD}$) (Cáceres-Arteaga et al. 2018). The study sites exhibit an altitudinal range that varies between 3000 and 3600 m.a.s.l. and the landscape is dominated by managed ecosystems, where 33.13% is represented by agricultural land, 23.28% by pastures, 21.92% by planted forests with exotic species, and 21.67% by native forests (S2 Table) (GAD Municipal Pedro Moncayo 2015; Ministerio del Ambiente del Ecuador 2016). Agriculture activities in this region consist of small-scale low input production systems, with poor management practices.

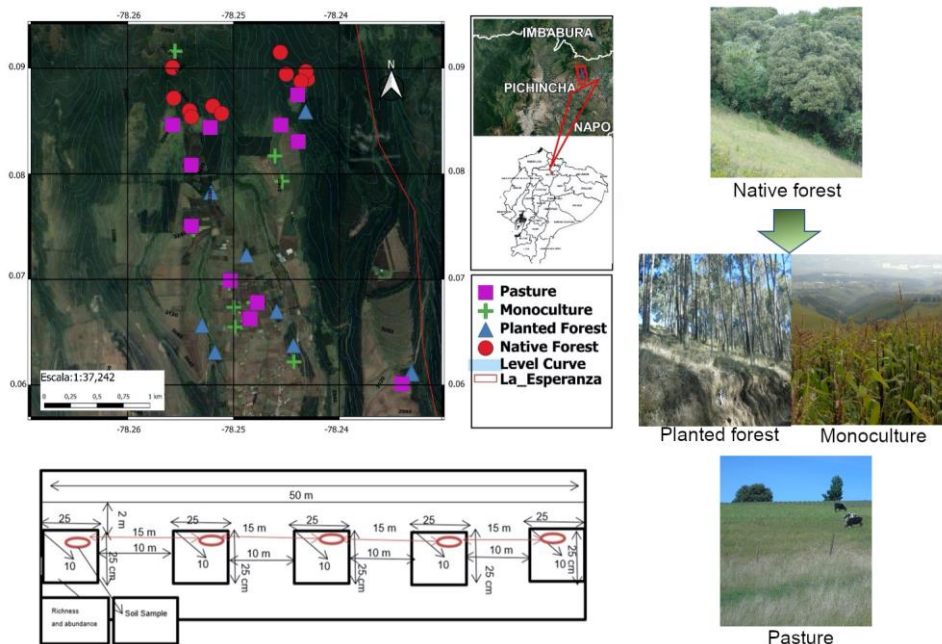


Figure 11. Study site location, representation of land use categories and diagram of the soil sampling scheme.

Sampling design

We used a variation of the methodology of Fertility and Tropical Soil Biology (Baillie et al. 1990; De Valença et al. 2017) to investigate the effect of land use on the diversity of edaphic macrofauna and the physical-chemical parameters of soil quality among four land use systems: 1) native forest, 2) planted forest, 3) pasture, and 4) maize monoculture (Ministerio del Ambiente del Ecuador, 2013; GAD Municipal Pedro Moncayo, 2015) (S2 Table) (Ministerio del Ambiente del Ecuador 2013). The natural forest was used as a reference system.

The study region presents a spatially explicit pattern of soil types that includes Entisols, Mollisols, and Inceptisols (Ministerio de Agricultura y Ganadería 2017). To control for this variable that could affect the results, the sampling design focused on the Inceptisol soil type only, which represents more than 60% of soils in the study area. This soil order is generally fertile, young, less weathered, and varies in depth from 1 to 2 m and according to clay mineralogy. Inceptisols are considered high-activity clay soils (Veldkamp et al. 2020). The soil texture of the study sites corresponds to loam.

Ten sampling sites were randomly selected in each land use category, with a distance of at least 50 m from each other. Within each site, five monoliths (25×25×10 cm) were obtained with a separation of 10 meters along a 2×50 m transect. Prior to the excavation of the monolith, the leaf litter and the existing vegetation cover above the soil layer were discarded. To control the possible effects of elevation across land use types, we established replicates along the altitudinal range (Figure 1). However, due to the historical patterns of land use transition in our study area, we could not find replicates for native forest at lower elevation. We conducted two field sampling trips to cover the rainy season, one in November 2018 when we conducted 4 transects of each land use category, and the other sampling trip was carried out in February 2019, covering 6 transects of each land use category.

Diversity of soil macroinvertebrates

In each monolith (Figure 1), all visible organisms (>2 mm) of soil invertebrates were collected. Then, all the specimens were divided into arthropods and worms according to their type, weighed (balance accuracy 0.001 g), and transported to the laboratory for counting and identification. Then, the arthropod specimens were stored in a 50 ml plastic jar with 70% alcohol, while worms were preserved using 4% formalin. The collection of specimens is part of the research permit No. 007–2018-RC-AD-FLO-FAU-DPAP-MA, granted by the Environmental Authority of Ecuador.

The collected specimens were sorted and taxonomically identified up to the genus level, using specialized keys (Kitching 2000; Leibensperger 2016; McGavin 2000; Merritt RW 1996; Triplehorn et al. 2005). The abundance and biomass of soil macrofauna was averaged among the 5 samples obtained along each transect and reported at the taxonomical level of order and genus, while the biodiversity measures were summed up among the subsamples within each transect (De Valença et al. 2017).

In addition, each specimen was classified in its corresponding trophic group (predators, herbivores, omnivores, detritivores, parasites/hematophagous), as proposed by (Cabrera 2014; McGavin 2000; Soliveres et al. 2016) (S3-4 Tables).

Soil chemical parameters

For the study of soil chemical parameters, surface soil samples (0 to 10 cm) were collected with a borehole every 10 meters along each transect. The soil sampling was carried out after removing the leaf litter and the surface vegetation layer. Then, the samples within the same transect were thoroughly mixed to obtain 40 composite samples, representing all the sites from the different land use types. From each composite sample, 500 cm³ were extracted, placed in plastic bags and taken to the Soils Laboratory of the Central University of Ecuador for further analysis. In the lab, the following chemical parameters were obtained: organic carbon, nutrients (Ca, P, K, N), and pH. The pH was measured with a potentiometer in aqueous solution, ratio 1:2.5. Organic carbon was obtained by Walkley-Black wet combustion, while %N was estimated by the Kjeldahl method and P by the colorimetrically-modified Olsen method with a photocolormeter. Nutrients (K, Ca) were measured by atomic absorption spectrophotometry, using the PerkinElmer Analyst, the extraction solution was sodium bicarbonate (NaHCO₃) 0.5 N at a pH of 8.5 (Dominati et al. 2010; Lukina et al. 2011).

Statistical Analysis

The estimated richness of edaphic macroinvertebrates at the genus level was measured with the nonparametric estimators Chao 1, Bootstrap and Jackknife 1 (Jiménez-Valverde and Hortal 2003; Villarreal et al. 2006) using EstimateS, version 9.1 (Colwell 2013). According to (Magurran, 2004), the agreement of results obtained from different estimators that use conservative to flexible approaches demonstrates a robust sampling effort. Sampling completeness was considered as the percentage of observed relative to the estimated richness (Colwell et al 1994).

We used the Hill numbers approach, also known as true diversity, as a framework for a reliable estimation of alpha diversity of soil macrofaunal communities at the order and genus level (Chao et al. 2014). This approach provides generality and flexibility in controlling the effects of common and rare taxa in biodiversity quantification. We estimated the three orders of diversity within this approach: $q=0$, $q=1$, and $q=2$, which are equivalent to species richness, Shannon diversity, and Simpson diversity, respectively (Jost 2006; Moreno 2011).

To test if the alpha diversity measures and soil chemical properties differ between land use categories, we conducted analyses of variance after verifying the parametric assumptions using the Levene and Shapiro-Wilk tests. When the assumptions were not met, Kruskal-Wallis tests were carried out. If significant differences were detected in the analyses of variance, post hoc tests were conducted using Tukey's method. To test if the abundance, biomass, and richness of the most represented trophic groups

presented divergences among land use categories we applied Kruskal-Wallis tests and the post hoc Wilcoxon rank sum test with continuity correction for non-parametric comparisons. All analyses of variance were conducted using JASP 0.16.3 software (JASP Team 2020).

The structure of the edaphic macroinvertebrate communities was described by rank abundance curves at the genus level, expressed in logarithm base 10 for each land use category and plotted with GraphPad Prism 8.0.1 (GraphPad Software 1995). These plots highlight differences in evenness amongst assemblages. Steep curves signify assemblages with higher dominance, while shallower slopes imply the higher evenness of the community (Whittaker, 1972; Whittaker et al., 2001). As reported by Magurran (2004), ordination analysis is a very simple and intuitive meaningful method of representing differences amongst samples and communities, which describes beta diversity in terms of compositional change. Therefore, ordination methods were conducted for the beta diversity comparison of the edaphic macrofauna communities across land use categories. Firstly, abundance data was transformed using the “total” option in the `decostand` function within the `R-vegan` library, then the Bray-Curtis dissimilarity index was estimated (Villarreal et al. 2006). This index varies between 0 and 1, where 0 represents identical communities and 1 depicts communities that do not share any genus. The resulting dissimilarity matrix was used to perform principal coordinates analyses (PCoA), which were plotted for sites and genera. Finally, to determine if there were significant differences between the edaphic macrofaunal communities, multivariate analysis of variance with 999 permutations were carried out using the `adonis` function, with land use as the explanatory variable. Likewise, the soil chemical parameters were analyzed through principal components analysis (PCA) to describe general patterns of the soil environment across land uses (De Valença et al. 2017).

To understand if the edaphic macroinvertebrate communities could be explained by the soil chemical parameters recorded across land uses, we applied canonical correspondence analysis (CCA) and redundancy analysis (RDA). In the CCA, the relative abundance of soil macroinvertebrate fauna, at genus level, was used as the biological matrix while the continuous parameters of soil quality accounted for the environmental matrix. For the RDA, the diversity metrics based on Hill numbers (richness, Shannon, and Simpson) made up the biological matrix and, similarly to the CCA, the explanatory environmental dataset corresponded to the chemical parameters of the soil.

For both the CCA and the RDA, the variables with the most significant influence on the edaphic macroinvertebrate community were chosen using a stepwise model based on the “`ordistep`” function. In addition, the variance inflation factors (VIFs) were estimated for each of the soil chemical variables, when showing VIF values <10 the noncollinearity in the matrix of environmental variables was demonstrated and maintained for the final analysis. The variables selected in this way were included in the final model to test whether the variation of the matrix of biological variables could be explained more by the soil chemical variables than expected by chance. All

multivariate analyses were performed with `vegan` and were plotted with `ggplot` packages in R (Hammer et al. 2001; Oksanen et al. 2019).

Results

Community composition of soil macroinvertebrates by land use categories

We collected 1,776 individuals of edaphic macrofauna, representing 50 genera, 42 families, and 21 orders (Table 5). From these, the most represented orders were Coleoptera (beetles, 31%), followed by Haplotaxida (earthworms, 29%), and Diplura (two-pronged bristletails, 10%). Other less abundant groups included: Isopoda (woodlice), Araneae (spiders), Lithobiomorpha (stone centipedes), Diptera (flies), and Scholopendromorpha (centipedes), which represented less than 10 percent of the total abundance of soil macrofauna registered (Table 5).

Compared to the reference system, diversity of macroinvertebrate communities at the level of order was notably reduced in pastures and monocultures (Table 5). From the 18 different orders found in native forests, only 8 were registered in monocultures and 12 in pastures. Planted forest shared the most orders observed in the reference system (Table 5).

Regarding abundance, most of the more-represented orders of soil macroinvertebrates exhibited higher values in the soils from native forests, ranging from 2 to 40 times higher than the abundance found in the anthropic environments (Table 5). Some noticeable exceptions were the abundance of Haplotaxida (earthworms) and Coleoptera (beetles), which were two to three times higher in pastures (13.44 ind/m²) and monocultures (9.84 ind/m²) than in the other land use categories (Table 5).

According to the shape of the rank abundance curves, the communities at the level of genus found in native and planted forests were richer and presented shallower slopes, then, were more even than the pasture and monoculture communities. Soil macrofaunal communities in pastures and monocultures were dominated by few taxa (Figure 12). Another notable difference between the communities at this taxonomic level was their composition; only 8 genera were shared between all land use types. In pastures and monocultures, the most dominant genera were *Eisenia* sp. Malm, 1877, *Lumbricus* sp. Linnaeus, 1758, *Naupactus* sp. Dejean, 1821, and *Heterogomphus* sp. Guérin-Ménéville, 1851, which are classified under the orders of Coleoptera and Haplotaxida, described above. In native forests, the most represented genera were *Holojapyx* sp. Silvestri, 1910, *Forficula* sp., and *Naupactus* sp.; while in the planted forests, *Armadillidium* sp. Latreille, 1804, *Holojapyx* sp., and *Fufus* sp. dominated the soil macrofauna community (Figure 12).

Table 5. Abundance (mean \pm standard error) of soil macroinvertebrates at order level across different land use categories.

TAXA	LAND USE OF SOIL							
	Native Forest		Planted Forest		Monoculture		Pasture	
	indv. m ⁻²	SE	indv. m ⁻²	SE	indv. m ⁻²	SE	indv. m ⁻²	SE
Coleoptera	7.04	\pm 1.81	4.88	\pm 1.25	4.88	\pm 1.81	12.48	\pm 3.14
Haplotaaxida	2.88	\pm 1.36	1.52	\pm 0.95	9.84	\pm 4.26	13.44	\pm 2.86
Diplura	5.04	\pm 2.29	3.2	\pm 0.81	0	0	0.08	\pm 0.08
Isopoda	1.44	\pm 0.42	4	\pm 1.60	0	0	0	0
Araneae	1.52	\pm 0.32	3.12	\pm 0.87	0.08	\pm 0.08	0.08	\pm 0.08
Dermaptera	3.2	\pm 1.11	1.04	\pm 0.62	0.16	\pm 0.10	0.08	\pm 0.08
Lithobiomorpha	2.4	\pm 1.46	0.64	\pm 0.35	0.24	\pm 0.17	0.16	\pm 0.10
Scolopendromorpha	2	\pm 0.71	0.24	\pm 0.17	0	0	0.16	\pm 0.10
Diptera	0.72	\pm 0.32	0.32	\pm 0.24	0.4	\pm 0.21	0.64	\pm 0.28
Trombidiformes	1.76	\pm 0.62	0.08	\pm 0.08	0	0	0	0
Julida	0.8	\pm 0.31	0.08	\pm 0.08	0.08	\pm 0.08	0.08	\pm 0.08
Hymenoptera	0.24	\pm 0.17	0.08	\pm 0.08	0.24	\pm 0.17	0	0
Lepidoptera	0.24	\pm 0.24	0.08	\pm 0.08	0	0	0.24	\pm 0.17
Stylommatophora	0.4	\pm 0.17	0.08	\pm 0.08	0	0	0.08	\pm 0.08
Tylenchida	0.48	\pm 0.34	0	0	0	0	0	0
Opilion	0.32	\pm 0.13	0.08	\pm 0.08	0	0	0	0
Orthoptera	0.16	\pm 0.11	0.16	\pm 0.10	0	0	0	0
Blattodea	0.08	\pm 0.08	0.08	\pm 0.08	0	0	0	0
Hemiptera	0	0	0	0	0	0	0.08	\pm 0.08
Scorpion	0	0	0.08	\pm 0.08	0	0	0	0
Trichoptera	0	0	0	0	0.08	\pm 0.08	0	0
Mean Abundance	30.72	\pm 1.80	19.76	\pm 0.52	16	\pm 1.80	27.6	\pm 1.06

Diversity of edaphic macrofauna across land use categories

The non-parametric richness estimators at genus level (Chao 1, Jackknife and Bootstrap) used in the present study revealed a high degree of completeness of the sampling effort for all land use categories (S10 Figure). Although the asymptote was not reached, the level of completeness exceeded 67%, being the sampling in the native forest (more than 76% for all non-parametric estimators) the one that obtained the best results to estimate richness at genus level.

Edaphic diversity metrics at genus level (richness, Shannon, and Simpson) showed statistical differences across land use categories (Figure 13). Mean richness ranged from 8 (± 2 SE) in monocultures to 22 (± 2 SE) genera on average in native forests. The highest richness values were observed in native forests which were statistically different from the other categories (ANOVA $F(3,36)=9.047$, $p=0.001$; Figure 13). A similar statistical pattern was observed for the Hill numbers: Shannon ($q=1$) (ANOVA $F(3,36)=14,121$, $p=0.001$, $p<0.001$) and Simpson ($q=2$) (ANOVA $F(3,36)=10,508$, $p=0.001$; Figure 13).

The macrofauna assemblages (beta-diversity) differed significantly across land use categories (PERMANOVA, pseudo- $F=5.0721$, $p=0.001$; Figure 14), demonstrating a clear pattern between forested and non-forested sites. This pattern was illustrated by the 2-dimensional ordination plot (PCoA; Figure 14).

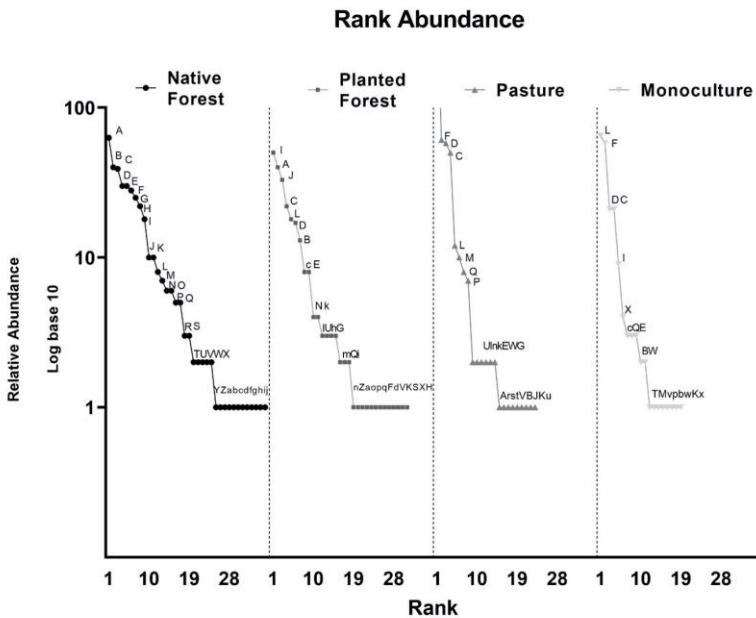


Figure 12. Rank-abundance curve in logarithm10 of edaphic macrofauna at genus level across land use categories. (A) *Holojapyx* sp., (B) *Forficula* sp., (C) *Naupactus* sp., (D) *Heterogomphus* sp., (E) *Lithobius* sp., (F) *Eisenia* sp., (G) *Scolopendra* sp., (H) *Trombicula* sp., (I) *Armadillidium* sp., (J) *Fufus* sp., (K) *Julus* sp., (L) *Lumbricus* sp., (M) *Aspidolea* sp., (N) *Cheiracanthium* sp., (O) *Meloidogyne* sp., (P) *Arachnocampa* sp., (Q) *Eleodes* sp., (r) *Naesiotus* sp., (S) *Phalangium* sp., (T) *Aphididae* sp., (U) *Cyrtotrachelus* sp., (V) *Euconulus* sp., (W) *Passalus* sp., (X) *Stomoxys* sp., (Y) *Tegenaria* sp., (Z) *Allonemobius* sp., (a) *Blatta* sp., (b) *Ctenus* sp., (c) *Dermestes* sp., (d) *Ensifera* sp., (e) *Gasterophilus* sp., (f) *Gonipterus* sp., (g) *Leiobunum* sp., (h) *Loxosceles* sp., (i) *Sitophilus* sp., (j) *Synoeca* sp., (k) *Enicmus* sp., (l) *Agriotes* sp., (m) *Calliphora* sp., (n) *Agrotis* sp., (o) *Chactas* sp., (p) *Cimex* sp., (q) *Drosophila* sp., (r) *Aphrastus* sp., (s) *Centrotus* sp., (t) *Cydia* sp., (u) *Melyris* sp., (v) *Cecidomyia* sp., (w) *Hydropsyche* sp., (x) *Trypoxylon* sp.

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

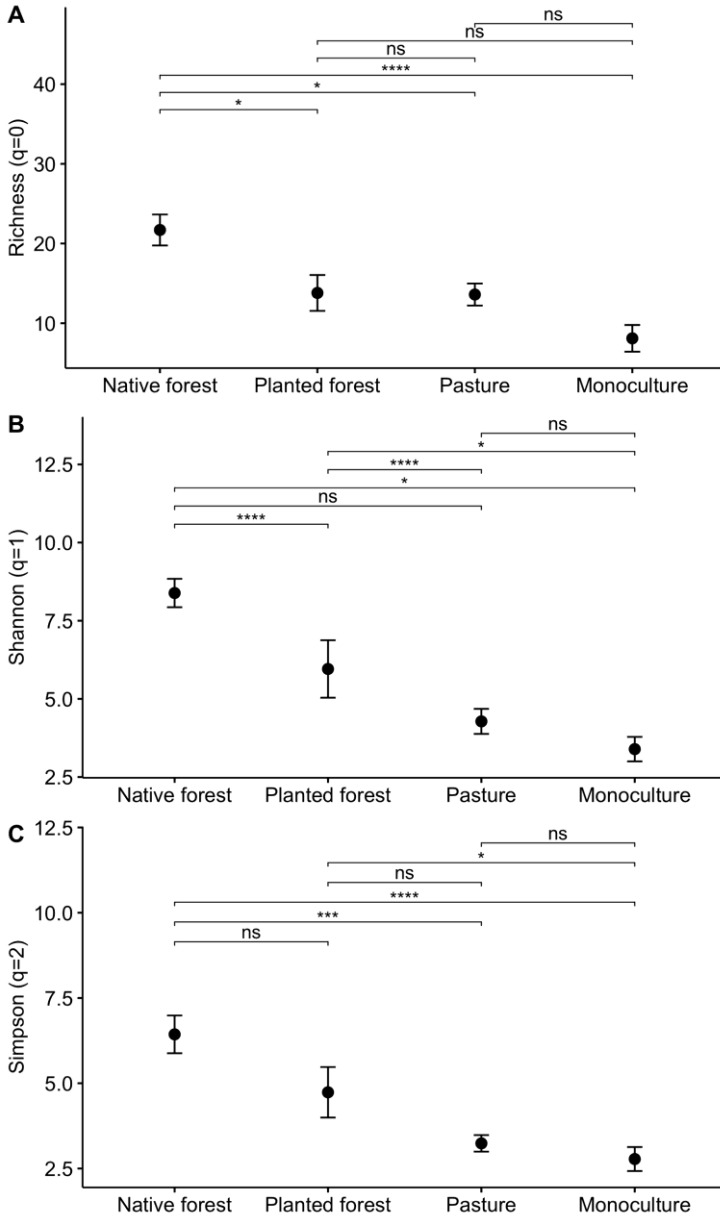


Figure 13. Average of Hill numbers: richness (A), Shannon (B), and Simpson (C) of soil macroinvertebrates at genus level across the land use categories. Error bars based on standard error of the mean. Asterisks illustrate the power of the levels of significance of the statistical tests: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; **** $p \leq 0.0001$ and ns represents $p > 0.05$.

The community composition patterns observed in the rank-abundance curves between land use categories were similar to the results obtained in the PCoA (Figure 14A-B). For instance, native and planted forest assemblages of soil macrofauna were represented by a large number of taxonomic groups, which were observed closer together in the PCoA ordination space, and *Lithobius* sp., among others. Monoculture and pasture sites were better characterized by less taxonomic groups, highly distinctive by the abundance of earthworms (*Eisenia* sp. and *Lumbricus* sp.) (Figure 14A-B). The first axis of the PCoA depicts the variability of soil fauna assemblages across land use categories (Figure 14A-B). Native and planted forests are clustered together in one side of the First PC, whereas monocultures and pastures are grouped on the other side of this axis.

Trophic group patterns of soil macroinvertebrates

Detritivores, predators, and herbivores were the most represented trophic groups in the edaphic macrofaunal communities (Figure 15A). However, there were differences in relative abundance, biomass, and richness between the land use categories. In general, relative abundance and richness by trophic group presented similar patterns between native and planted forests (Figure 15A,C). However, the most abundant trophic group in native forests were predators, exhibiting significantly higher values than pastures and monocultures ($H(3)=26.218$, $p<0.01$; Figure 15A). On the other hand, the edaphic macrofaunal communities in pastures and monocultures were similar to each other and dominated by detritivores (Figure 15A), but for this trophic group the mean abundance in pastures was significantly different from native and planted forests ($H(3)=9.740$, $p<0.05$; Figure 15A). Moreover, herbivore abundance did not show significant differences among land uses

Different patterns from those described for relative abundance were observed when analyzing biomass of trophic groups (Figure 15B), showing a marked dominance by detritivores, followed by an important component of herbivores in all systems, particularly in monocultures and pastures (Figure 15B). However, only detritivores in planted forests showed significantly lower values than the other land uses ($H(3)=12.068$, $p<0.01$) (Figure 15B).

Finally, richness exhibited different results across land use categories (Figure 15C). A significantly greater number of genera within the predators ($H(3)=26.218$, $p<0.001$) was found in native and planted forests. Detritivore richness was significantly lower in planted forests and monocultures than in native forests ($H(3)=10.546$, $p<0.05$; Figure 15C).

3 Native forest conversion alters soil macroinvertebrate diversity and soil quality in tropical mountain landscapes of northern Ecuador

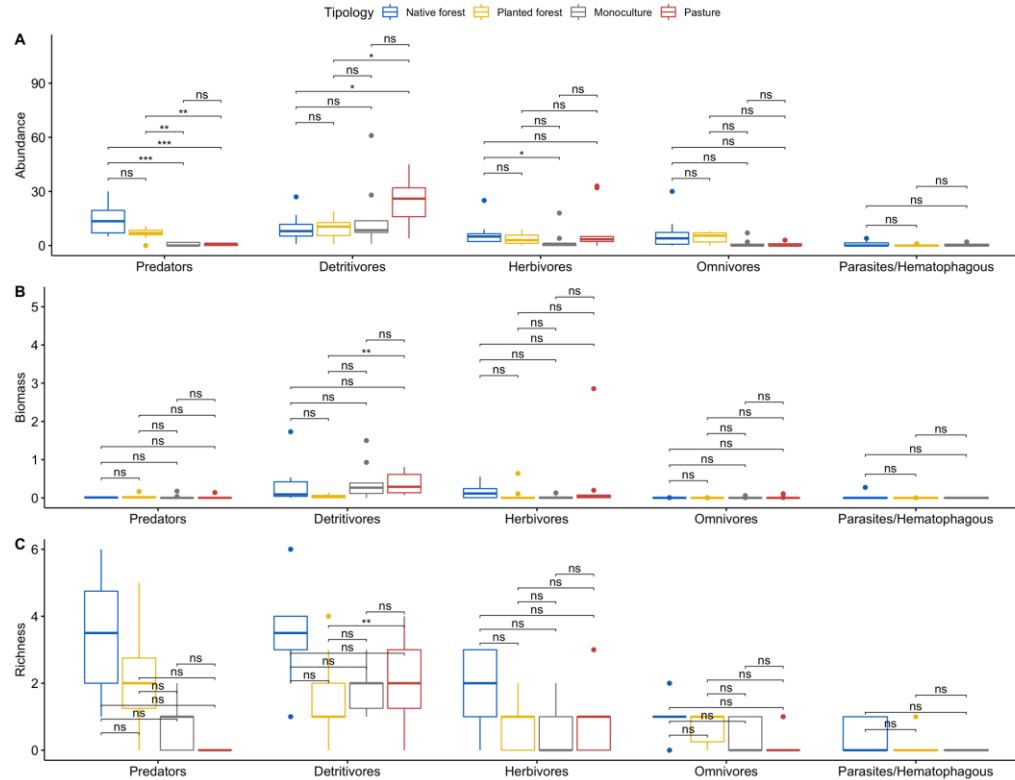


Figure 15. Multiple boxplots for (A) abundance, (B) biomass, and (C) richness for trophic groups of soil macroinvertebrates by land use category. Asterisks illustrate the power of the levels of significance of the statistical tests: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$ and ns represents $p > 0.05$.

Soil chemical parameters

Soil chemical properties showed significant differences across land use categories. In general, organic carbon, pH, and the content of nutrients (N, Ca, and K) were significantly higher in the native forest compared to anthropic environments, although the average values of pH and P did not show differences between pastures and native forests (Table 6). In contrast, P was the only parameter that was significantly higher in monocultures. All the soil chemical parameters studied were similar in planted forests and monocultures (Table 6).

Principal component analysis of the soil chemical properties showed clear groupings based on land use categories (Figure 16). Most of the variation explained by the soil chemical parameters was represented in the first principal component axis (PC1, 58.58%), a clear pattern of clustering of sites within each land use category was observed on this axis. Native forests clustered in the right side of the biplot, where high values of C, N, and Ca were also found. Pastures were represented in the central region of the plot. In contrast, monocultures and planted forests depicted a grouping pattern in the left side of the biplot, coinciding with strikingly high values of P in their soils. The biplot of the PCoA demonstrated a positive correlation between organic carbon, Ca, and N, while a strong negative correlation was observed among these variables with P. These association patterns of soil structure variables were clearly related to PC1. Complementarily, an important part of the variability of the multivariate dataset was explained by PC2 (16.88%), which captured the variation of pH, C:N ratio, and micronutrients (especially K) (Figure 16) among sites.

3 Native forest conversion alters soil macroinvertebrate diversity and soil quality in tropical mountain landscapes of northern Ecuador

Table 6. Chemical parameters of soil fertility (mean \pm standard error) by land use categories.

Land use	Organic carbon		N		P (ln)		K (ln)		Ca		pH	
	%	SE	%	SE	mg/kg of soil	SE	cmol _c /kg	SE	cmol _c /kg	SE		SE
Native Forest	8.92a ^A	± 0.46	0.84a	± 0.04	2.45a	± 0.15	1.29a	± 0.26	16.81a	± 1.41	6.43a	± 0.19
Planted Forest	3.99bc	± 0.37	0.38b	± 0.03	24.44b	± 7.37	0.47b	± 0.03	9.89b	± 0.62	5.9b	± 0.08
Mono-culture	2.69c	± 0.45	0.25b	± 0.04	79.71bc	± 17.57	0.62b	± 0.11	7.09b	± 0.75	5.74b	± 0.21
Pasture	4.86b	± 0.71	0.46b	± 0.77	9.22bab	± 9.22	0.64b	± 0.10	9.91b	± 1.52	5.97ab	± 0.07

Values of P and K were transformed to natural logarithm (ln).

^A Lowercase letters in the same column indicate significant differences between land use systems ($p < 0.05$).

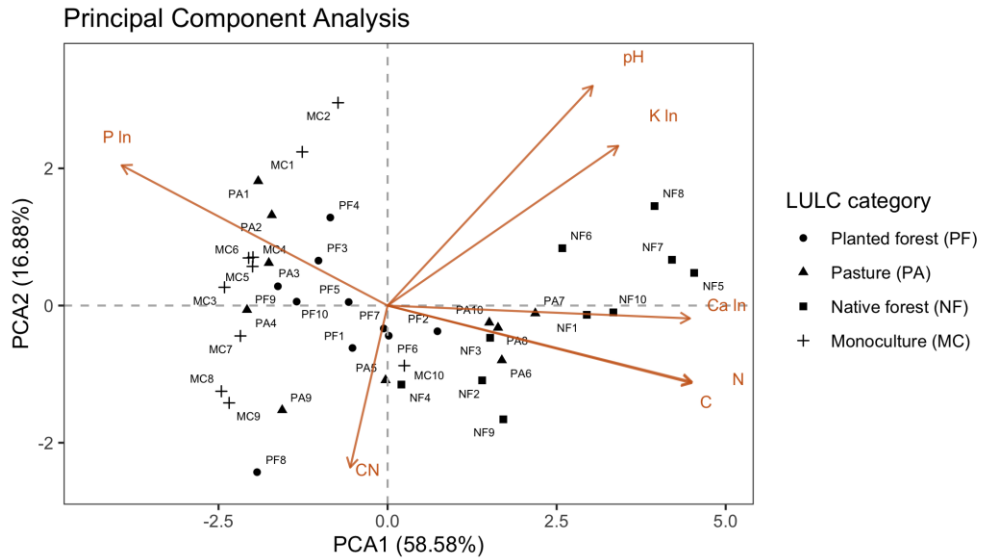


Figure 16. Principal components analysis of soil chemical parameters by land use category.

Relationship between the soil macroinvertebrate community and soil parameters

The canonical correspondence analysis demonstrated that the inertia that was successfully constrained by the explanatory variables was 28%. From this percentage, constrained inertia associated with CCA1 was 53% and CCA2 was 28%. Both axes significantly explained (ANOVA $p < 0.002$) the variation in relative abundance of the soil macroinvertebrates at genus level. Therefore, there is a good representation of the relationship between biological variables and soil chemical parameters. According to the results of the ANOVA of the CCA, the main soil chemical parameters that influenced the structure of the edaphic macroinvertebrate community were organic carbon ($p < 0.001$), followed by pH, and K ($p < 0.01$). In addition, this analysis also identified that C:N and P significantly ($p < 0.05$) explained some of the variation in the matrix of the relative abundance of soil macrofauna analyzed (Figure 17, S5 Table).

The redundancy analysis demonstrated that soil chemical parameters significantly explained 27% (ANOVA $p < 0.05$) of the variation of diversity metrics of the soil macrofauna community. The values of inertia associated with RDA1 and RDA2 were 25.606 and 1.313, respectively. The main chemical parameters that influenced the diversity of the edaphic macroinvertebrate community were organic carbon ($p < 0.01$) and pH ($p < 0.05$) (Figure 18, Supplementary Table 5).

3 Native forest conversion alters soil macroinvertebrate diversity and soil quality in tropical mountain landscapes of northern Ecuador

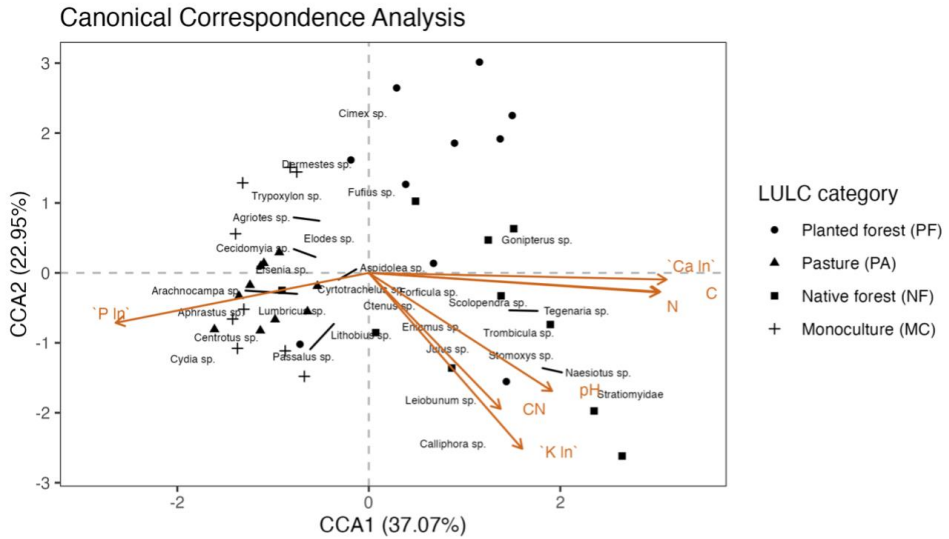


Figure 17. Canonical correspondence analysis of the soil chemical parameters and the relative abundance of the edaphic macroinvertebrate community. Significant parameters: ***Org carbon, **pH, K(ln), *C:N, P(ln). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

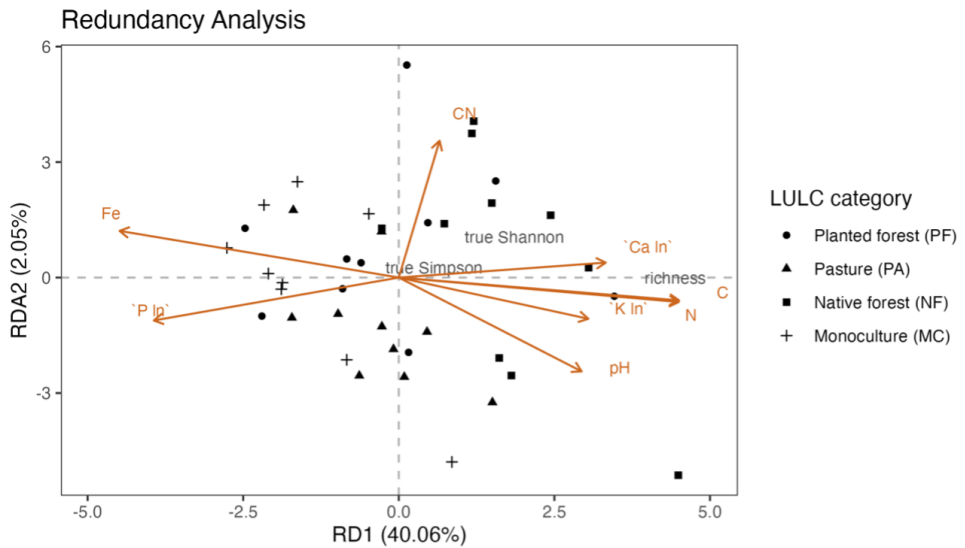


Figure 18. Redundancy analysis of the soil chemical parameters and diversity of edaphic macroinvertebrate community. Significant parameters: * *Org carbon, *pH. * $p < 0.05$, ** $p < 0.01$.

Discussion

Our findings suggest that the conversion of native forests to anthropic environments, especially to agricultural land (pastures or crops), causes biodiversity loss and degrades soil fertility. These results are in line with other studies conducted in tropical mountain systems (De Valença et al. 2017; Delelegn et al. 2017; Zhang et al. 2017; Pérez et al.¹). Biodiversity loss was evident when structure and community composition of soil macrofauna were compared amongst land use categories. As we expected, native forests showed significantly higher values of alpha diversity metrics than pastures and monocultures. However, our reference system presented soil macrofaunal assemblages as diverse as those found in planted forests, a result that was not expected. Moreover, our study demonstrated taxonomic diversity depletion at genus and order levels as a result of native forest conversion to agricultural land. The length of the abundance range curves of soil macroinvertebrates registered in native and planted forests almost doubled those found in pastures and monocultures. Strikingly, from the 18 distinct orders of soil macroinvertebrates found in native forests only half were found in pastures and even less in monocultures. Additionally, our findings from the PCoA showed differences of soil community composition across land use categories. Native and planted forests depicted similar communities, which differed from those found in pastures and monocultures, a result also reflected in the permutation analysis of variance using distance matrix, where the aforementioned finding was statistically verified.

Differences in the structure and community composition of soil macrofauna among land uses demonstrated in our study would likely be related to the degree of human disturbance in managed ecosystems (Lukina et al. 2011; Sylvain and Wall 2011). A change in vegetation structure, such as the total or partial removal of its biomass due to land use conversion, can produce significant disturbances in the physical, chemical, and biological properties of soil (Ruiz et al. 2010; Solórzano 2020; De Valença et al. 2017). In turn, changes in the soil ecology could alter habitat conditions and resource availability for different groups of soil dwellers, who are sensitive to changes in their environment (Rousseau et al. 2013). For example, the similarities observed between native and planted forests' soil fauna could be explained by the low level of physical disturbance in these land use types. Generally in the highlands of northern Ecuador, exotic species (*Eucalyptus* sp. and *Pinus* sp.) were planted mainly to restore deforested and/or degraded landscapes – and to a lesser extent for commercial purposes (Farley 2007). Therefore, after their establishment, vegetation cover and the associated litter production do not substantially change in planted forests, a condition that is shared with native forests. Studies have shown that vegetation cover and litter

¹ Perez, A., Acosta-Lopez, C., Buitrón, S., Guarderas, P. (2022). 'Land use changes alters the diversity and composition of soil bacteria in an Andean landscape of northern Ecuador', Microbiology Society. (submitted)

production are the main factors that control the composition and distribution of soil fauna (Guangbin and Xiaodong 2007; Zhou et al. 2022). In forested soils, these factors may have provided habitats to evade natural enemies and more resources to thrive (Guangbin and Xiaodong 2007; Shrewsbury and Raupp 2006).

Moreover, in this study, the less-disturbed systems – which correspond to native and planted forests exhibited high overall taxonomic diversity in addition to richness of predators, represented by centipedes (Lithobiomoppha, Scolopendromorph) and spiders (Aranea). Previous work in tropical systems (Cabrera and López 2018; Halffter and Arellano 2002) have demonstrated that soils protected from surface disturbance, such as forest and fallows, favor the development of taxonomically and functionally diverse macroinvertebrate communities (De Valença et al. 2017). These stable ecosystems are characterized by low soil disturbance, representative root biomass and soil plant cover, in addition to abundant leaf litter – providing complex topsoils where balanced food webs and abundant predators can thrive (Manhães et al. 2013; De Valença et al. 2017).

Our results from pastures and monocultures demonstrate a simplification pattern in soil community composition. High abundance and biomass of one trophic group (detritivores), mainly represented by some beetles (Coleoptera) and earthworms (Haplotaxida), depict soils under agricultural land in our study region. Intensively managed agricultural land, characterized by tillage, the application of pesticides and fertilizers, soil compaction, and the harvest of plant biomass have caused simplification of edaphic communities (Menta 2012; Thiele-Bruhn et al. 2012). In these disturbed systems, species capable of withstanding stress predominate and rare taxa decrease or disappear (Brown et al. 2001; Decaëns et al. 2006). This result could be explained by the ability of some soil species (especially earthworms) to tolerate the disturbance associated with land preparation, planting, and even contamination caused by pesticides (Araneda 2016; Eisenhauer et al. 2017; Halffter and Arellano 2002; De Valença et al. 2017). Another complementary explanation of the high representation of detritivores in agricultural land could be related to higher inputs of manure and higher biomass of plant roots available to decomposers of soil organic matter (Ernst and Emmerling 2009).

Another interesting result, related to the biological attributes of soils, was the lack of ants or termites in all topsoils studied across land use categories in the highlands of northern Ecuador. These arthropods are the most commonly cited examples of soil engineers across all biomes (Lavelle et al. 2014). This result could be related to altitudinal limitations of these groups in our study sites (Brussaard et al. 2013), although this cannot yet be proven by our data.

Our findings related to soil chemical parameters of the topsoil layer (0-10 cm) demonstrated a strong degradation of soil fertility as a result of native forest conversion to anthropic environments. As expected, we found significantly higher values in many chemical properties that characterized healthy soils (total C, total N, nutrient availability) in native forests compared to anthropic environments. Only phosphorus was found in less quantity in native forests, while in monocultures and

planted forests this nutrient had a significant greater value. This result coincides with the study of Escobar et al. (2017) that states that finding P in high quantities is expected in the soil of monoculture systems. Agricultural systems with a large amount of phosphorus added by mineral fertilization tend to accumulate this nutrient as a function of the time that the soil has been used for cultivation (Delelegn et al. 2017). Furthermore, the lower values of soil chemical parameters observed under the agricultural sites would likely be explained by a lack of soil cover, high levels of tillage disturbance, an accelerated rate of soil organic matter decomposition, and increased erosion (Delelegn et al. 2017).

In addition, we found that pH was highest in native forest soils. This result is in line with the studies by (Urrego 1996; Veldkamp et al. 2020), where topsoils under natural forests exhibited higher pH than other land use categories. Moreover, our findings are consistent with the study conducted by Heitkamp et al. (2014) in the Central Andes. They demonstrated that the decrease in vegetation cover, as a result of forest conversion to rangeland systems, enhanced soil weathering and leaching rates, which in turn cause soil acidification. Distinct natural and anthropic processes lead to decreased soil pH (Goulding 2016). However, in the agricultural land of our study region, a combination of these factors may explain the observed lower pH values. The opening of the system (more water percolating in the soil profile), disrupted biological cycles (lower return of Ca in the topsoil through litterfall) and nitrogen fertilization, containing acidifying products, might be the major driving factors for the acidification pattern detected in monocultures (Hao et al. 2020).

Our results highlighted a wide variation in the fertility parameters of pasture sites. Half of them had patterns similar to those observed in native forests, and although the rest of the sites resembled the conditions present in monocultures, the mean values showed significant differences for some soil chemical properties evaluated (total C, total N, and soil organic matter) compared to monocultures. These differences could be attributed to the history of land use, where soils recently converted to pastureland would present better conditions of soil fertility. Other contributing factors would be related to differences in grass root biomass, levels of disturbance by tillage, and the addition of nutrients from organic wastes of livestock in the system. Mann et al. (2019) demonstrated that grass and mixed perennial-annual cropped fields presented higher levels in physico-chemical and biological parameters of soil quality than more intensely managed fields like undiversified grain and vegetable crops.

We did not observe differences in soil chemical properties between plantations with exotic tree species (like *Eucalyptus* spp.) and the degraded monoculture sites. These two land uses presented significant lower values in most the chemical soil properties (organic carbon, N, K, Ca and pH) than native forest, suggesting a strong degradation on soil fertility. Regarding the effect of native forest conversion to plantations with exotic tree species (like *Eucalyptus* spp.) on soil properties, different investigations present contrasting findings. Some studies suggest a positive impact in degraded and treeless lands by increasing litter input on the soil surface (Yitaferu et al. 2013). On the other hand, many other studies demonstrated the high demand for soil nutrients of *Eucalyptus* plantations as a result of the combined effect of fast growth and the

inability to fix nitrogen (Zegeye et al. 2011), causing detrimental effects on soil properties (Coca-Salazar et al. 2021; Liang et al. 2016). Our results are consistent with the latter findings. This would imply that reforestation efforts using exotic plants does not contribute to improving soil fertility (Liang et al. 2016; Veldkamp et al. 2020).

The divergent results of topsoil macrofauna diversity and soil chemical properties among land uses is remarkable. However, the effect of land use change on the soil biota and the soil chemical properties showed some differences. Although native forests stood out for presenting a greater diversity of soil biota and significantly higher values for chemical quality variables than the other land use typologies studied, the edaphic communities in the reference sites presented similarities with those found in planted forests. It appears that taxonomic diversity and composition in the soils studied are determined by a combination of factors, where acidification, soil nutrients, vegetation cover and litter production seem to be relevant. Although, as vegetation cover and litter production were not measured directly, it is necessary to incorporate these variables to better understand the driving factors that influence the dynamics of edaphic communities in response to altered environments of Andean landscapes.

Our results from the CCA and the RDA showed that a significant amount of variation of the community composition and diversity of soil macroinvertebrates was explained by soil chemical parameters. These results demonstrated a connection between biological attributes and chemical properties of topsoils, which likely affect soil health (De Valença et al. 2017). On one side, the CCA showed that relative abundances of different genera of soil macrofauna were significantly affected by pH, organic matter, C:N, and phosphorus. We observed distinct soil assemblages associated with high levels of pH and organic matter, attributes that characterized native forests. In contrast, high levels of phosphorus were associated with communities characterized by earthworms mostly found in monocultures and pastures, which was in line with the findings of other Andean systems (De Valença et al. 2017). Furthermore, RDA demonstrated that all diversity metrics (richness, Shannon, and Simpson) of soil macrofauna were significantly explained by pH and C. The first axis of both multivariate analyses demonstrated a clear distinction between forested and agricultural sites, and represented pH and nutrient variations, whereas the second axis was mostly defined by C:N, which was not explained by land use, suggesting a variation present in all land use categories.

Our findings are consistent with many studies that have reported that soil abiotic conditions interact with soil biodiversity (Bardgett and Van Der Putten 2014; Tibbett et al. 2020). In this study, the orders Lithobiomorpha and Scolopendromorpha, which belong to the class Chilopoda, have higher mean abundances in the native forest than in the other typologies. This typology in turn has high values of organic matter, organic C and N. Therefore, it can be inferred that the presence of chilopods demonstrates the good quality of the soil in the native forest. In contrast, we found higher abundance and biomass of earthworms associated with more acidic soils (pastures and monocultures), this result differs from the well-documented reduction

of earthworm abundance with a decrease in soil pH (Urrego 1996; Veldkamp et al. 2020). However, this contrasting result, especially in pastures, could be explained by the species composition among earthworms. Generally, topsoil communities are dominated by epigeic earthworms, who feed on plant litter and are less affected by pH (Duddigan et al. 2021). Since the taxonomic resolution of our research was at the genus level, a further identification at the species level could better elucidate this issue. Moreover, we found that high values of phosphorus concentration on soils (characteristic of agricultural land) were negatively correlated to pH. According to (Le Bayon and Milleret 2009), earthworm abundance and composition could directly or indirectly influence C, N and P dynamic. Earthworms are keystone soil organisms in regulating nutrient cycling by their feeding and burrowing activities, as well as by their metabolism and metabolic wastes. But these possible interactions need further study. The higher soil fertile conditions in pastures may be mediated by the presence of earthworms.

Likewise, land use change could affect soil chemical and biological interactions in different ways, leading to cascading effects on other elements of the system. For instance, belowground communities are tightly linked to aboveground communities through multiple trophic interactions, at different scales and across the whole range of ecological processes that ultimately govern ecosystem functioning (Eisenhauer et al. 2017). (Veldkamp et al. 2020) suggest that deforestation leads to drastic changes in inputs of litter organic residues, which may modify the soil microclimate, its biological activity, and decomposition rates. Differences in microclimates between native forests and the other land uses were recorded by (Guaman and Guarderas 2022), which may affect ecological processes taking place in topsoils (Gehlhausen, Schwartz, and Augspurger 2000; Montejo-Kovacevich et al. 2022). However, further integrated approaches that incorporate climate variations and other environmental parameters are needed to understand the cascading relationship between biodiversity, ecological functions, and the provision of soil ecosystem services (Leibensperger 2016). Notwithstanding, we argue that shifts in soil community structure and biodiversity loss, generated by anthropogenic land use may be mostly related to the changes of habitat structure (e.g. tree density, canopy cover), microclimatic conditions (e.g. temperature, humidity, light intensity and incidence), and the disruption of ecological interactions among species (Gehlhausen et al. 2000; Košulič, Michalko, and Hula 2016).

In our study we controlled for the soil taxonomy (Inceptisols) and soil texture (mostly loams), therefore, we envisioned that our findings would mostly uncover the effects of land use changes on soil quality parameters. However, the proportion of variance that is not explained by our study could be attributed to differences in land use history and variability of other topographic variables such as slope or aspect across our study sites (Lavelle et al. 2014). Although our sampling design incorporated altitudinal variation throughout the study area, replicates of native forests were not found at lower elevations due to land use history patterns. However, the similarities between native forest and planted forest, especially in the diversity and composition of soil macrofaunal communities, suggest that an altitudinal range

of hundreds of meters is not a determining factor in high mountain areas above 3000 m.a.s.l.

Our findings, consistent with other studies (Lavelle et al. 2014), also propose the irreplaceable value of native forests as biodiversity reservoirs. This study contributes to expanding the soil biodiversity knowledge in mountain landscapes of Ecuador, especially in remnant forests where few studies have been undertaken. However, our analysis focused on the taxonomic diversity of soil macrofauna at order and genus levels, therefore more effort is required to elucidate the belowground species biodiversity, which has not yet been fully described (Eisenhauer et al. 2018; Phillips et al. 2019).

Landscape management implications

The findings of this research could contribute to the conservation and sustainable management of mountain agricultural landscapes in the study region. This should involve management for restoring ecological processes and ecosystem services at the plot and at the landscape scale, by integrating plants and soil biota characteristic of native forests, as well as diminishing soil disturbance practices in agricultural systems (The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2018).

For instance, there are clear indications that managing agroecosystem diversity within farms by higher amendments, promoting soil organic matter and beneficial soil fauna will improve soil quality, assuring the maintenance of crop productivity and support for vital ecosystem services (Letourneau et al. 2011). However, an important guiding principle of landscape restoration implies the definition of conservation and ecosystem service' outcomes (Reed et al. 2013). For example, our results demonstrated that planted forests appear to support similar assemblages of soil macrofauna as native forests, but limited soil fertility. Thus, a restoration initiative framed in the soil health framework would imply improving both biodiversity conservation and soil fertility in degraded agricultural land. Therefore, it should emphasize the use of native plants and soil fauna occurring in the region landscape.

Another complementary approach involves spatial arrangement and connectivity at the landscape scale (Lavelle et al. 2014). Studies have suggested that the ecological quality of a homogenous matrix in an agricultural landscape could be highly enhanced by the addition of seminatural elements (Lavelle et al. 2014). For instance, setting aside relatively undisturbed natural systems such as native forests and connecting them with agricultural land through corridors may provide sources of soil biodiversity which could recolonize depleted soils under agricultural management (e.g., soil vegetation and macrofauna) (Nieminen et al. 2011). In addition, the spatial arrangement of pastures, which demonstrated better soil quality, alongside monoculture plots can support the recovery of soil macrofauna populations.

As described by Lehman et al (2020), the terminology, concept and operationalization of soil health are still evolving to address concerns over biodiversity, water quality, climate, recreation, and human and planetary health

beyond humans. Likewise, appropriate soil health indicators should involve biological, chemical and physical properties to measure soil multifunctionality and should be integrated into informative soil-health indices, which are still under development. We are aware that our research only evaluated two dimensions of the soil health approach: soil fertility and biodiversity conservation. However, we envision that the inclusion of soil invertebrates, as biodiversity indicators, in combination to chemical attributes could contribute to expand the use of the soil health approach in soil assessment and management to attempt longer-term sustainability challenges related to multiple ecosystem services.

Conclusions

This study shows clear differences in soil chemical properties and in the structure and composition of edaphic macrofaunal communities between anthropic land use categories and the reference natural system. Biodiversity loss was evident when structure and community composition of soil macrofauna were compared amongst land use categories. As we expected, native forests showed significantly higher values of alpha diversity metrics than pastures and monocultures. However, our reference system presented soil macrofaunal assemblages as diverse as those found in planted forests, a result that was not expected. Then, the biodiversity dimension of our assessment demonstrated a clear pattern between forested and non-forested sites.

Our findings related to soil chemical parameters of the topsoil layer (0-10 cm) demonstrated a strong degradation of soil fertility as a result of native forest conversion to anthropic environments. As expected, we found significantly higher values in many chemical properties that characterized healthy soils (total C, total N, nutrient availability) in native forests compared to anthropic environments. However, for this dimension we did not detect the patterns of forested and non-forested sites found for soil invertebrate diversity.

A significant amount of variation of the community composition and diversity of soil macroinvertebrates was explained by soil chemical parameters. These results demonstrated a connection between biological attributes and chemical properties of topsoils, which likely affect soil health. However, because soil invertebrate communities did not change between native and planted forest, even when chemical parameters of soil fertility were significantly different between them, suggests that other driving factors should be playing a more important role than soil chemical parameters in the establishment of the invertebrate communities in these highland

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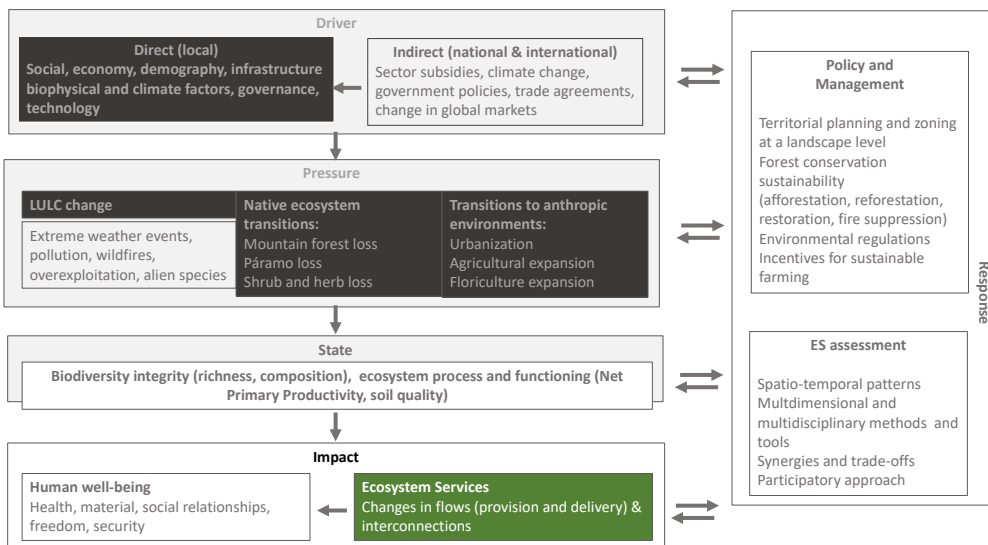
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4

Land use affects the local climate of a tropical mountain landscape in northern Ecuador

This chapter explores the variations of local climate across land use types in the study landscape located in the northern Ecuadorian highlands, addressing the Impact element of DPSIR framework. In addition, it examines the role of native ecosystems on microclimate regulation on microclimate regulation



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Land use affects the local climate of a tropical mountain landscape in northern Ecuador

Abstract

Changes in land use affect biodiversity and the biophysical structure of ecosystems, causing negative impacts on ecosystem services, such as climate regulation. However, there are few studies that evaluate the effect of land use changes on the local climate, particularly in tropical mountain systems like the Andes. Therefore, this study compares four land use types (native forest, planted forest, maize monoculture and pasture) in a mountain landscape in northern Ecuador as a proxy to assess the impact of land use change on local climate regulation. We estimated gap fraction with photographic techniques, and recorded temperature and relative humidity using dataloggers set at two heights (0 m and 1 m) above ground level across the land use types. As we expected, native forests provided a more stable microclimate, demonstrating significantly lower temperatures and higher relative humidity values than the other land use types. This effect on microclimate was significantly explained with highest temperatures at intermediate gap fraction levels. In addition, we observed that native forests provided a buffer effect on the variations in mesoclimate; only in this land use type there was an evident reduction in local temperature over the range of mesoclimate; whereas local temperature variations registered on human altered systems (planted forests and pastures) were significantly explained by the mesoclimate variation, with the exception of monocultures that exhibited a mismatch between the two scales of climate. These results highlight the importance of native forest for microclimate regulation, an ecosystem service which can act synergistically with other biodiversity other conservation goals to sustainably manage landscapes in Andean mountain systems.

Key words: ecosystem services; land use change; mesoclimate; microclimate; vegetation cover.

Introduction

Land use change is a major threat to the integrity of ecosystems because it affects their biophysical structure, taxonomic and functional diversity, ecological processes (Cardinale et al. 2012b) and, therefore, alters their ability to provide ecosystem services (Costanza et al. 2014). In this context, ecosystem transformation significantly influences the regulation of macroclimate, mesoclimate and microclimate, acting at different spatial scales (Sahagún and Reyes 2018).

Climate regulation of ecosystems goes much further than carbon sequestration through biogeochemical processes (Foley et al. 2003). Mesoclimate (defined as the climate which scale extends from tens to hundreds of kilometers) and local climate (which occurs at scales of less than 0.1 km) are also regulated by ecosystems through biophysical processes that intervene in the equilibrium of energy and water on the planet's surface (West et al. 2011). Local climate can be described as the climatic differences between forests, crops, and bare soil, at various depths in a plant canopy, at different depths in the soil, on different sides of a building. Forest stands act as biophysical thermoregulators of the microclimate, since they modify evapotranspiration and albedo (Valladares 2006). If a natural ecosystem is deforested, this system will absorb less radiation; however, the climate will be drier because net radiation will be released in large amounts as sensible heat (Foley et al. 2003; West et al. 2011).

Therefore, changes in vegetation and soil coverage strongly influence the temperature and humidity of the surrounding air (Meir et al. 2006; Chapin et al. 2008) and, generally, the effects on the local and regional climate exceed the recorded variation in air temperature at a global scale, due to the increase in greenhouse gases in the atmosphere (Costa and Foley 2000).

The study of the modification of general microclimatic conditions, such as temperature, relative humidity, evapotranspiration and wind speed, in addition to the environmental conditions of the soil (temperature and humidity), as a result of changes in vegetation cover provides relevant information for the management, conservation and restoration of ecosystem services (Briceño et al. 2010).

Amaya-González et al (2019) suggest that the microclimate of each layer (air, canopy and soil) changes due to land use transformation. Correspondingly, Guntiñas (2009) found that in agricultural soils, plowing and periods in which the soil is without vegetation increase aeration, modify the climate of the upper soil layer (humidity and temperature) and, frequently, accelerate the velocity of decomposition of edaphic organic matter, affecting the provision of soil ecosystem services (Amaya et al. 2019). Likewise, these changes will have implications for the quality and sustainability of the pedosphere (Valladares 2006).

The study of microclimates has recently aroused renewed interest as it connects global climate change with local weather conditions, in addition to predicting the responses and physiological distributions of species in the context of environmental change (Sears et al. 2011).

The Andean landscape of Ecuador encompasses a mosaic of ecosystems with different management regimes arranged in different land use types (Pru Foster 2001), where native mountain ecosystems have been reduced to small remnants, historically affected by the conversion of land cover to agricultural land (Cardinale et al. 2012). The impact of land use change on the local microclimate of the high Andean landscapes has been little evaluated (Faye et al. 2014), despite the important implications of climate variation on food production and food sovereignty in high Andean ecosystems (IPCC 2017).

For this reason, in this study we investigated four land use types (native forest, planted forest, pasture and monoculture) representative of the study area in an Andean landscape of northern Ecuador as a proxy to understand the effect of land use change on the local microclimate; native forest was used as a reference to make comparisons between land use types.

We expect the native forest to present more stable microclimatic conditions with lower temperatures and higher relative humidities compared to the other land use types. These effects could be explained by differences in gap fraction, which is distinct between land use types. We also expect the microclimatic variation recorded in this study to follow the pattern of variation recorded at a mesoclimatic scale, evidencing seasonal changes, with a distinct buffering effect of native forests.

Methods

Study area

This research was carried out in the Andean landscape of the community of Guaraquí in La Esperanza parish ($0^{\circ}4'19.2''$ N, $78^{\circ}15'50.4''$ O) of Pedro Moncayo county, located in the Pichincha province of Ecuador, between 3075 and 3516 masl (Figure 19).

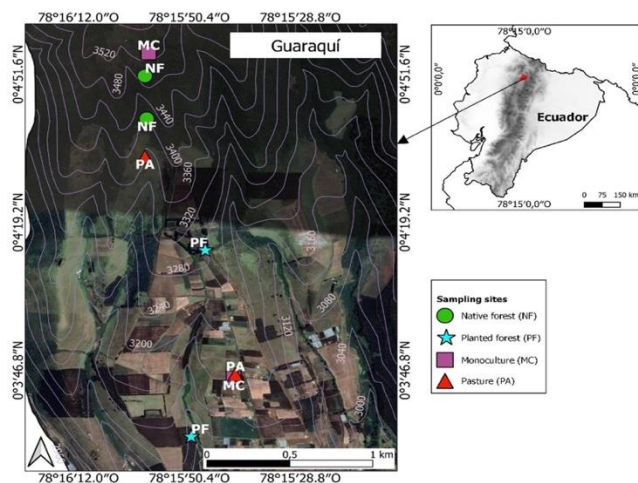


Figure 19. Location map of the study area with the sampling sites. SRC: WSG 84.

The study area has a climate typical of the high Andean region of northern Ecuador, with a bimodal peak of high precipitation that occurs from April to May and October to November; the dry period takes place July to September (Cáceres-Arteaga et al. 2018). It has a cold temperate climate, with average annual temperatures that vary from 8°C to 13°C and average annual precipitation ranging from 750 mm to 1250 mm (Gobierno Parroquial Rural La Esperanza 2015).

This mountain landscape encompasses native ecosystems such as the páramo grassland and evergreen high montane forest of the western Andes (Ministerio del Ambiente de Ecuador 2014) and includes other land use types modified by human activities (Ministerio del Ambiente de Ecuador and Ministerio de Agricultura, Ganadería 2014), such as planted forests, pastures and monocultures (Figure 19). In the study area, native forest vegetation is represented by species such as *Oreopanax ecuadorensis* Seem., *Piper nubigenum* Kunth. and *Barnadesia arborea* Kunth., while planted forests are dominated by *Eucalyptus globulus* Labill. and *Pinus radiata* D. Don. The pasture is characterized by *Pennisetum clandestinum* Hochst. and crop fields are dominated by maize monocultures (*Zea mays* L.) (Solórzano 2020).

Field phase

Because this research is part of a project that integrated several components to understand the effect of land use change on biodiversity and various ecosystem services, we used 2x50 m transects as a frame of reference for the project and, we installed a pair of dataloggers in the center of two transects per land use typology to evaluate microclimate patterns across land uses (Briceño et al. 2010). We used Hobo U23-001-Pro-V2 dataloggers (Onset Computer Corporation, Bourne, USA) to register temperature and relative humidity in two layers: air and soil (Faye et al. 2014); these variables were recorded at an interval of 5 minutes (Faye et al. 2017).

The air layer dataloggers were placed on wooden stakes at a height of one meter and were protected with 20 cm² of white plastic to reduce solar radiation heating; the plastic roof was placed 5 cm higher than the logger (Amaya et al. 2019). The soil layer loggers were placed on the same wooden stake at 0 m. Loggers were left in situ, and data was recorded from April to November (8 months) to cover the rainy and dry season of 2019.

To relate canopy vegetation cover to the microclimatic variation across land use typologies, we used the canopy gap fraction, defined as the fraction of open sky that is not obstructed by vegetation, which represents the amount of light radiation reaching the lower stratum of a forest (Gonsamo et al 2010). To obtain this proxy, a Sony WX500 compact camera with Zeiss F/6.4 lens with 30× optical zoom and a GPS Essentials compass were used, following the methodology proposed by (Beckschäfer 2015).

Gap fraction depends on the proportion of direct and diffuse radiation reaching the ecosystem, which could be affected by latitude, season, time of day, as well as atmospheric characteristics such as transmissivity and cloudiness of the site (Valladares 2006). Then, all photos were taken from 8 to 10 AM (Garrido et al. 2017), on cloudy days in June 2019, which corresponds to the end of the rainy season. In

addition, five photographs were taken with the camera oriented north, capturing distinct directions: north, northeast, southeast, southwest, and northwest; these photos were taken where the pair of dataloggers were installed and in four more points along the transect. Also, because the study area is located in the equator, no latitudinal variability is expected among sites.

Photographs were taken at a height of 1m from the ground, as it is a representative height to study the microclimate in the low stratum of native forests (Garrido et al 2017), which correspond to our reference system; accordingly, we standardized this height to be able to make comparisons across land use types, using the digital camera placed horizontally on a tripod at 1 m from the ground (Valladares 2006) (S11 Figure).

Data analysis

Since our study registered the microclimatic variability from April to November 2019, for comparisons we pooled the data from the sensors within each land use type and summarized the data in monthly averages, obtaining eight months ($n=8$) for each of our microclimatic variables: mean temperature, mean relative humidity and minimum night temperature. Prior to conduct analysis of variance (ANOVA) to compare each microclimatic variables across land use types and between the two datalogger placement heights with respect to the ground, the homogeneity and homoscedasticity of the data were verified using Shapiro-Wilk and Levene tests, with a 95% confidence interval. Once significant differences were found, the Tukey test was used to obtain the exact pair-wise comparisons between land use types with a confidence interval of 95%.

For the gap fraction analysis, the Hemispherical 2.0 macro tool of the ImageJ program was used (Beckschäfer 2015), which calculated the ratio between the number of white pixels (sky) and the total number of pixels (white plus black, the latter representing vegetation) in the binary images (Gonsamo et al 2010). Mean, maximum and minimum values of gap fraction were also obtained for each land use type.

The daily variation over the months was plotted for temperature and relative humidity by pooling the data from dataloggers within land use types and from both heights (0 and 1 m). We disaggregated these data into minimum, maximum and average values for each hour, representing a curve for each of the study months; in addition, we summarized these data in a smooth curve that showed the general trend of each variable.

ANOVAs and Pearson correlations between average temperatures and average relative humidities recorded in the four land use types were carried out using the computer software JASP version 0.12.2 (JASP Team 2020).

To understand the potential drivers of microclimate variation across land use types, we fitted a Generalized Additive Model (GAM) to explain the variation in monthly mean temperature as a function of gap fraction, datalogger placement height and relative humidity. The logit transformation was used for both explicative variables as they are proportions (Warton and Hui 2011).

Finally, to find out whether the mesoclimate has an effect on the variation of the local climate registered across land use types, for each land use type we fitted another GAM of monthly means in local temperature as a function of mesoclimate temperatures and precipitation. Mesoclimate data (temperature and precipitation) from the study area were downloaded from the Terra Climate gridded database (Abatzoglou et al 2018) (<https://www.climatologylab.org/terraclimate.html>), using the climateR package (DOI: 10.5281/zenodo.2672843).

The computational methods for the GAMs were carried out using the mgcv package version 1.8-34 (Wood 2011). Likewise, the daily and monthly trends, as well as all Figures comparing microclimatic variables across land use types, were generated in R version 3.6.2 (R Core Team 2020), using the ggplot2 package version 3.3.3 (Wickham 2016).

Results

Gap fraction

The gap fraction varied between 5.99% and 100% across land use types, while the average values were between 20.54% and 100% (Table 7). The lowest values were reported in native forest (5.99%), followed by planted forest (9.02%), while the highest values were recorded in pasture (100%) (Table 7).

Table 7. Microclimatic variables (gap fraction, temperature, and relative humidity) grouped by replicates that were performed by land use type and grouped for the two heights (0 m and 1 m).

Sampling site	Gap fraction (%)			Temperature (°C)			Relative humidity (%)		
	Max	Min	\bar{x}	Max	Min	\bar{x}	Max	Min	\bar{x}
Native forest	86.82	5.99	20.54	27.21	1.89	8.94	100	27.07	91.78
Planted forest	48.91	9.02	30.57	28.52	4.92	11.1	100	17.92	79.75
Monoculture	91.71	62.03	80.03	37.62	-1.5	11.91	100	1	81.68
Pasture	100	100	100	42.03	-3.04	10.75	100	1	78.31

Note: Microclimatic variables are reported with their respective average (\bar{x}).

Comparison of microclimatic variables by height (0 m and 1 m) between the different types of land use.

Monthly mean temperature and monthly mean relative humidity differed significantly between the different land use types, (ANOVA, S6-S7 Table), yet no significant effects were found for height (0 m and 1 m) or the interaction between height and land use type.

As shown in Figure 20A, the average temperature recorded in the native forest presented significantly lower values than all other land use types (p Tukey ≤ 0.001), both in the data obtained at 0 m (8.93°C) and 1 m above the ground (8.89°C). In pasture, the average temperature reached 10°C, which was marginally lower than the temperature recorded in monocultures and planted forests, which varied between 11°C and 13°C, therefore no significant difference was found between the average temperatures for monoculture and planted forest (p Tukey > 0.05) (Figure 20A).

However, in the microclimatic variables averaged between the replicas for each of the land use types (Table 7), the highest temperatures were recorded in pasture (42.03°C) and monoculture (37.62°C). The lowest temperatures, -3.04°C and -1.5°C, were found in pasture and monoculture, respectively.

Figure 20B shows that the average relative humidity recorded in the native forest had statistically higher values than all other land use types (p Tukey ≤ 0.001), both at 0 m (95.6%) and 1 m (89.5%), while the relative humidity values registered in planted forests, monocultures and pastures varied between 70% and 95%, without significant differences between them (p Tukey ≥ 0.05).

The ANOVA that compared the monthly minimum nocturnal temperature (S8 Table) between the different land use types and the interaction between the land use types and the two heights (0 m and 1 m) revealed significant differences ($F=27.014$; $p\leq 0.001$ and $F=2.890$; $p=0.044$).

As shown in Figure 20C, the monthly minimum night temperatures recorded in monoculture and pasture presented lower values than the rest of the land use types at both heights (0 m and 1 m). Similarly, there was a greater variation in temperature at 0 m in the monoculture and pasture.

Significant effects of gap fraction explaining the variation (50%) of monthly mean temperature were demonstrated with the GAM ($F=13.33$, $p<0.001$); whereas relative humidity did not seem to have an effect on monthly mean temperature (Figure 21, Table 8). Figure 21 clearly demonstrates the distinct clustering of land use types along the Y axis; where the lowest gap fractions were observed within native forests, followed by planted forests, monocultures and pastures. Monthly mean temperature showed a hump-shaped relationship with gap fraction (Figure 21).

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

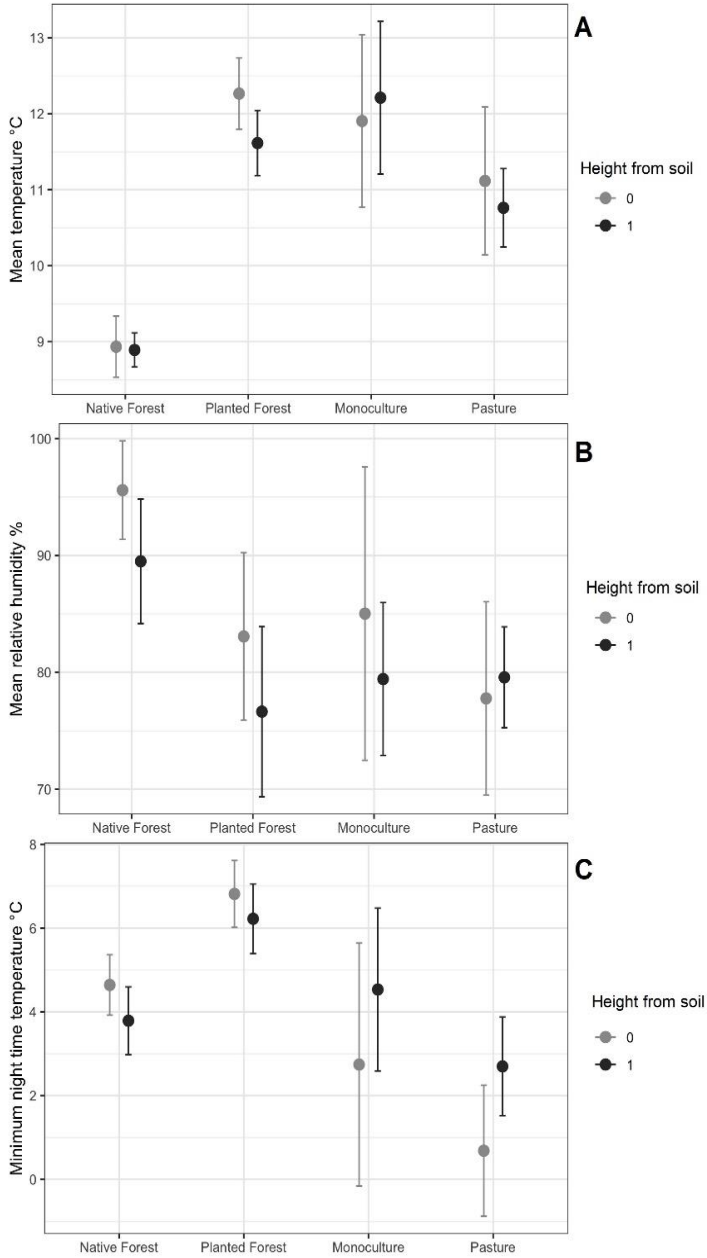


Figure 20. Monthly mean temperature (A), monthly mean relative humidity (B) and monthly minimum night time temperature (C) in the four land use types at two heights with respect to the ground level (0 m and 1 m). The error bars represent the 95% confidence interval (n=8 for each land use type at each layer).

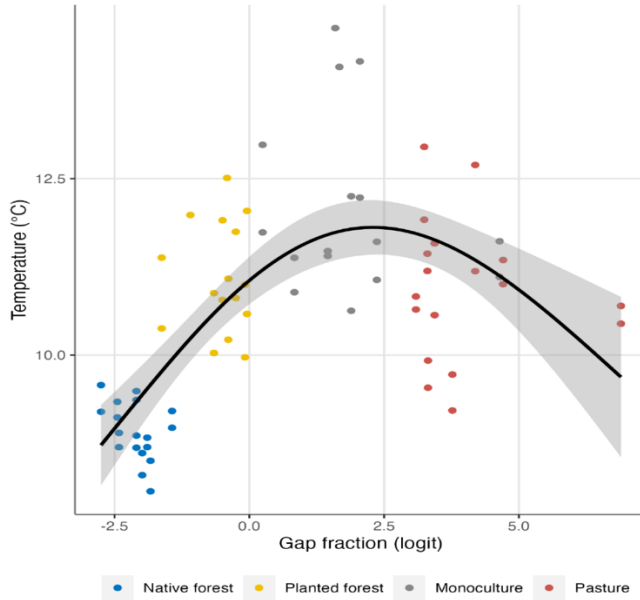


Figure 21. Generalized Additive Model of monthly mean temperature as a function of gap fraction (logit-transformed) and for the two heights (0 m and 1 m) (n= 16 for each land use type).

Table 8. Generalized additive model of monthly mean temperature as a function of gap fraction, monthly mean relative humidity and height of the datalogger from the ground for the four land use types taken together. The model deviance explained is 50.40%; the adjusted R² is 0.48.

Explanatory variable				
Approximate significance of smooth terms		P value	F ratio	edf
s(Gap fraction)		<0.001***	30.66	1.94
s(Monthly mean relative humidity)		0.392	0.00	<1
Parametric coefficients	Estimate	SE	t value	P value
Intercept	10.54	0.19	56.63	<0.001***
Height	0.30	0.26	1.17	0.246

Note: s(x), smooth function of x variable; edf, effective degrees of freedom; SE, standard error.

* P < 0.001

Monthly variation of microclimatic variables and its relationship with mesoclimate

The temporal variation of the mesoclimate and microclimate temperatures across land use types is represented in Figure 22 and S11 Figure. Across land use types, we noted a decreasing trend of temperatures from April to August and an increasing pattern from September to November 2019 (S6 Table); this pattern was also observed at the regional scale (using the TerraClimate data) (Figure 22A). The lowest humidities were recorded in August and September in all four land use types (S11 Figure).

The local temperature during the entire study period was lower for the native forest compared to the mesoclimate data, which contrasts with the patterns observed across the other land use types (Figure 22A). The planted forest and monoculture exhibited higher local temperature values than those representing the mesoclimate temporal variation in temperatures (Figure 22A), while pastures followed a highly similar trend to the mesoclimate (Figure 22A).

A greater mismatch between the microclimate and mesoclimate is evident for monocultures during all sampling months (Figure 22A). The GAM of monthly local temperature shows that mesoclimate temperature explains a significant amount of variation in the local climate in pastures ($F=5.47$, $p=0.019$) and planted forests ($F=2.98$, $p=0.046$). This effect was marginally not significant in native forests ($F=2.3$, $p=0.067$), whereas the microclimate within the monoculture was not explained by mesoclimate (Figure 22B, Table 9). The only significant explanatory variable of mesoclimate was temperature (Figure 22B, Table 9); while precipitation did not explain the variation in monthly mean local temperature within any land use type (Table 9).

Table 9. Generalized Additive Model of monthly mean local temperature as a function of mesoclimate temperatures and mesoclimate precipitation for the four land use types.

Explanatory variables	Native forest			Planted forest			Pasture			Monoculture		
	P value	F ratio	edf	P value	F ratio	edf	P value	F ratio	edf	P value	F ratio	edf
s(Mesoclimate temperature)	0.067	2.3	0.99	0.046*	2.98	10.5	0.019*	5.47	1.3	0.407	0.00	<1
s(Mesoclimate precipitation)	0.818	0.0	<1	0.6131	0.00	<1	0.358	0.00	<1	0.391	0.00	<1
Model statistic												
Deviance explained (%)	47.80			54.10			68.10			0.00		
Adjusted R^2	0.39			0.46			0.61			0.00		

Note: s(x), smooth function of the x variable; edf, effective degrees of freedom.

* $P < 0.05$

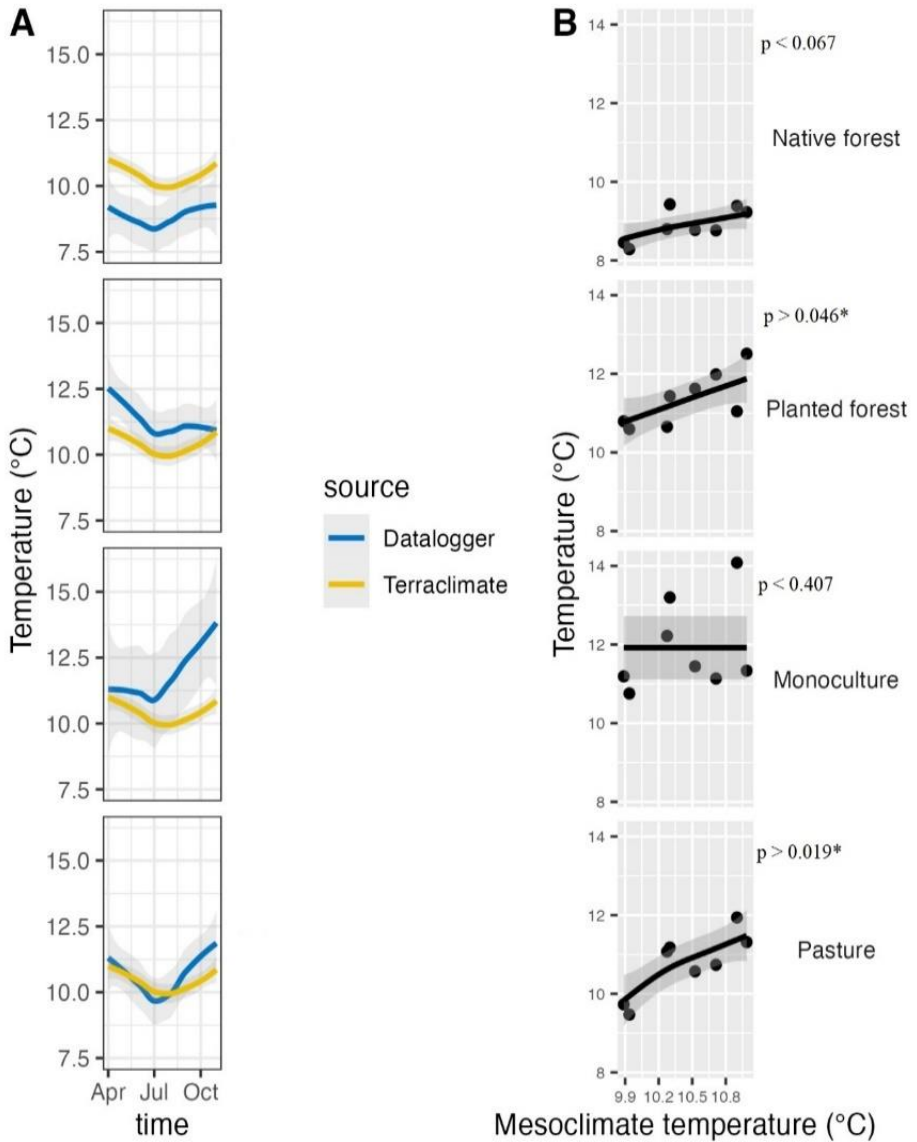


Figure 22. Mesoclimate effect on monthly mean local temperature. (A) Monthly mean temperatures recorded by dataloggers (blue line) and obtained from the TerraClimate grid (yellow line). (B) Generalized Additive Model of monthly mean local temperature as a function of mesoclimate temperatures for the four land use types (n=8 for each land use type).

Daily variation of microclimatic variables

Figure 23A shows that the lowest daily temperatures were evident in August (pasture: 4.71°C, native forest: 5.55°C, monoculture: 5.61°C and planted forest: 7.75°C) from 3:00 to 6:00, without being less than 0°C, while the highest daily temperatures were recorded in September (monoculture: 22.44°C, pasture: 20.36°C, planted forest: 16.92°C and native forest: 15.86°C) from 11:00 until 13:00; only in the planted forest was the highest temperature recorded during the rainy season in April (17.32°C) at 11:00. Figure 23A also shows that the maximum temperature was recorded from 13:00 in native forest and from 11:00 in the other land use types.

Figure 23B shows that the highest relative humidity was reported during the rainy season in May in the native forest (99.28%), monoculture (98.56%) and planted forest (98.28%) from 4:00 to 6:00, which was different from the pasture that registered 96.14% relative humidity in November at 4:00. The lowest relative humidity was obtained during the dry season in August and September in the four land use types (native forest: 62.5%, monoculture: 52.38%, planted forest: 48.63% and pasture: 45.47%) from 10:00 to 14:00; however, in monoculture, a low value was also recorded in July (51.09%) at 7:00.

Correlations between microclimatic variables in each of the land use types

S9 Table shows that there are no statistically significant correlations between the microclimatic variables (temperature vs. relative humidity) recorded in each of the land use types. However, a low negative correlation was evident only in the native forest ($r=-0.206$; $p=0.445$).

Discussion

In this study, we found that land use can have a significant impact on the local climate in mountain landscapes in the Andes, as was demonstrated globally (Meir et al. 2006; Chapin et al. 2008) and in other tropical regions (Osborne et al 2004). As we expected, native forests generate a particular microenvironment, providing more stable weather conditions, which were significantly different from the other land use types (e.g. planted forests, monocultures and pastures). Similar results were found for lowland and montane tropical forests along the western and eastern slopes of the Ecuadorian Andes (Montejo-Kovacevich et al 2020).

4 Land use affects the local climate of a tropical mountain landscape in northern Ecuador

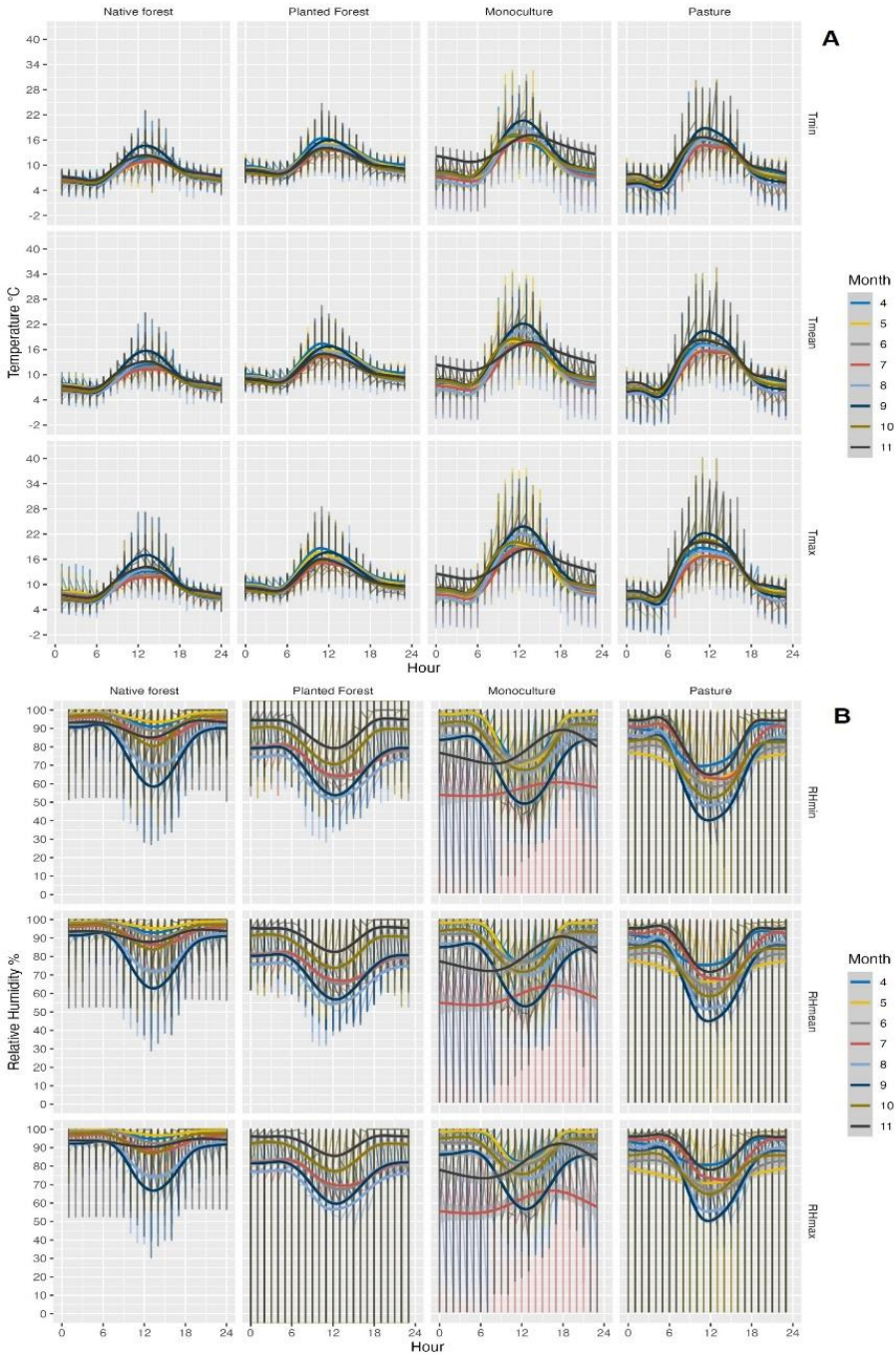


Figure 23. Maximum, medium and minimum daily temperature variation (A) and maximum, medium and minimum daily variation in relative humidity (B) recorded for each hour in the four types of land use during the sampling months.

Specifically, the native forests demonstrated a significant cooling effect where the temperature was on average 2°C lower than that recorded in pasture and 3°C lower than in the planted forest and monoculture. It differed from the rest of the land use types in the daily timing of maximum and minimum temperatures, as well as in the microclimatic variations, which were less intense. Likewise, relative humidity in the reference system was 12% higher than in the other land use types.

These microclimatic differences could be attributed to the influence of vegetation cover (Briceño et al 2010) observed in native forests, affecting albedo and evaporative cooling (Valladares 2006; Duveiller et al 2018). As we demonstrated, gap fraction significantly explains the variation in temperature observed across land use types, suggesting that changes in vegetation cover could impact radiative and non-radiative biophysical properties that may, in turn, affect the local climate (Duveiller et al 2018). However, a hump-shape relationship was detected, where temperature rises as the openness of the canopy vegetation increases in a gradient from native forest to monoculture, but it decreases when pastures are accounted. This result can be explained by the low canopy vegetation cover of the agricultural land, which can cause a nocturnal cooling effect that decreases the high diurnal temperatures. In addition, due to the temporal variation of the growing and harvesting cycle of the main crop (maize), a high temporal variation in the canopy gap fraction would be expected, however, this monthly variation was not accounted in our study, as we registered this variable in June, when the plants reached more than one meter high, interacting with the solar radiation.

Additionally, we argue that the lower temperature and higher relative humidity found in native forests could be explained by vertical stratification, as suggested by Duval and Campo (2017), the upper stratum captures most of the solar radiation during the day, then the average percentage of gap fraction reaching to the lower stratum is less than 10%.

Likewise, Montejó-Kovacevich et al (2020) found that within tropical forests there are microclimatic differences along the vertical stratification, where the lower stratum presents a 2°C reduced temperature and relative humidity 11% higher than the upper stratum, generating less diurnal heating and little nocturnal cooling.

In contrast, the planted forest, despite recording a relatively low gap fraction (approximately 30%), did not show a cooling effect compared to the reference system. This land use type is dominated by eucalyptus and pine trees that can have very extended canopies (Huber et al 2010), but it lacks vertical structure (Solórzano 2020). In addition, the dominant trees are introduced species that grow rapidly and require large amounts of water, producing a dry microclimate; that is, high temperatures and low humidity either in dry or rainy seasons (Huber et al 2010), thus explaining the local climate observed in this land use type (Figure 23). Likewise, the microclimatic conditions recorded in the two other anthropically altered environments (monoculture and pasture) could be explained by a lack of vertical forest structure and vegetation cover to attenuate the surface climate.

The cooling effect of the native forest was also evident when the local microclimate was compared with the regional climate; only in this land use type there was an evident reduction in local temperature over the range of mesoclimate. As demonstrated by Briceño et al (2010) and Duval and Campo (2017), the vegetation cover characteristic of forests stabilizes microclimatic variations and works as a buffer for mesoclimatic changes. Furthermore, according to Huber et al (2010) the lack of vegetation cover and vertical stratification could result in a higher significant relationship between mesoclimate and microclimate in human-altered systems, as seen in the trends observed in pastures and planted forests (Figure 22B). A similar pattern was reported by Valladares (2006) in grassland, where less variation between mesoclimate and microclimate was detected due to low attenuation caused by the 0.20 m high vegetation cover over the ground.

Similarly, our results demonstrate marginally lower temperatures in pastures compared to those observed in planted forest and monoculture. In this regard, Senra (2009) suggests that under adequate management conditions the use of 50% to 70% pasture by livestock allows the herbaceous cover to reduce high evaporation and high soil temperatures, in addition to decreasing other negative impacts on soil properties such as compaction, erosive effects of raindrops on the surface, run-off and wind erosion. In contrast, Costanza et al (2014) argue that the presence of cattle, even if it is minimal, causes wear on soils and vegetation in the long term, which causes effects contrary to those already mentioned such as lower water capture and low evaporation in the soils. Our results for relative humidity in the pasture do not differ from the values of planted and monoculture forests, depicting the latter scenario. In addition, this could explain the ability of the studied pasture to exhibit extremely high and low temperatures compared to the other land use types (Table 7).

On the other hand, the monoculture presented a mismatch with the temporal mesoclimate pattern, which could be attributed to the cycle of the main crop. Extreme values of temperature and relative humidity (maximum and minimum) were recorded in this land use type during the harvesting season (June to September) and the beginning of the growing period of maize (November to October) in Northern Ecuador (Boada and Espinosa 2016). We specially detected a greater alteration of the microclimatic variables in September, when the soil lacks vegetation cover after the harvest and coincides with the dry season (Gobierno Autónomo Descentralizado de Pichincha 2015). This trend was also apparent in the agricultural landscape studied by Faye et al (2017).

In addition, the microclimatic variation of monoculture could also be explained by factors such as conduction and convection that affect the recording of climatic variables (Maclean et al 2021). When the surface is uncovered, without cultivation, the direct effect of the solar radiation causes high soil temperatures and the datalogger would also record the surface temperature through conduction. Maclean et al (2021) also suggest that air flow at 1 m from the ground can modify the heat exchange of the datalogger by convection, causing high microclimatic variation.

The daily microclimatic trends showed higher variation in monoculture and pasture than in the other land use types. These results corroborate the temporal fluctuation patterns observed throughout the year in the same land use types. We also observed similarity across land use types in the occurrence of daily microclimatic peaks during the year. The four land use types exhibited the highest diurnal temperatures and lowest diurnal relative humidities in September (Figure 23); which corresponds to the months with the most extreme values of the dry season in the climatic regime of the study area (Cáceres-Arteaga et al (2018).

Furthermore, to understand the variation in the monoculture microclimate, tillage practices that exist in mountain agriculture may also have an impact on the local and global climate (Gutiñas 2009). Tillage causes the loss of soil organic matter, mostly carbon, which is released as CO₂ to the atmosphere (Reicosky and Saxton 2007). According to the Food and Agriculture Organization (2020), intensive tillage is responsible for 10% of all greenhouse gas emissions. Thus, Ruiz et al (2015) argue that it is necessary to eliminate tillage and promote polycultures to mitigate climate change. In addition, Gutiñas (2009) suggests that the lack of restoration, the constant use of tillage, and the unsustainable management of monocultures and pastures in Andean landscapes would generate irrecoverable losses in ecosystem services such as climate regulation and soil quality.

The tropical Andes is a region severely affected by human activities and extremely vulnerable to climate change (Gonda 2020); the ongoing warming and changes in precipitation patterns (Ranasinghe et al 2021) are threatening the capacity of these mountain landscapes to provide vital ecosystem services (Gonda 2020). Therefore, our results highlight the importance of maintaining and restoring native forests in this vulnerable region, as it was demonstrated in regional (Montejo-Kovacevich et al 2020) and global studies (De Frenne et al 2019). The buffering effect within native forests could be implemented as preventive, mitigating and adaptive measures in the face of global warming (De Frenne et al 2019).

Although the averaged microclimatic variables recorded in this study for monoculture are not so extreme, they reflect the high variation and intensity with which they reach the soil, giving rise to strong seasonal changes in the studied landscape (Figure 22B). This demonstrates the importance of integrating agricultural land in mitigation and adaptation plans for climate change, as they occupy an important extension on the earth's surface, especially in the tropics (Cardinale et al 2012; Senior et al 2017).

Limitations

As demonstrated by Montejo-Kovacevich et al (2020) differences in microclimatic conditions could be attributed to changes in elevation. In this study, to control the possible effects of elevation on microclimate variation across land use types we established replicates at two different altitudes within our target elevation range (Figure 19). However, due to the historical patterns of land use transition in our study area, we could not find a replicate for native forest at lower elevation. In addition,

variation in the attributes of the dominant plant species in each system could also influence the results, and this factor should be included in future studies.

In addition, the observational approach used in the present study to understand the potential effect of a land use transition on the local climate is based on comparisons between neighboring zones with similar conditions but contrasting vegetation cover, this could be affected by the sensors and loggers utilized. Maclean et al (2021) suggest that maximum temperatures may increase due to physical factors such as conduction and convection that affect the heat exchange processes of the dataloggers used. Although we replicated the methodology proposed by Faye et al (2014) to reduce the effect of direct radiation and reduce convective heat exchange on the dataloggers, such as placing solar shields at a distance of 5 cm above the sensors to allow natural air flow and reduce heat exchange by convection, other factors proposed by Maclean et al (2021) may artificially influence the observed differences by the measurement technique used. Then, future microclimate studies should use temperature sensors with a polished metal surface coating, as metals have lower absorption of solar radiation than plastics Maclean et al (2021).

De Frenne et al (2019) also point out that these problems are more likely to occur in datalogger records at 1 m high. In our study, datalogger placement height was not a significant variable in the GAM fitted to explain mean temperature; also our analysis of variance did not detect significant effects of height on local mean temperatures, relative humidity or minimal nocturnal temperatures when data was summarized as monthly means. However, existing differences between minima (and potentially maxima) between 0 and 1 m could be blurred out in the monthly averages.

Conclusions

Based on the results of this study, we conclude that the local microclimate in the studied Andean landscape will vary according to land use; native forests provided a more stable microclimate, demonstrating significantly lower temperatures and higher relative humidity values than the other land use types.

This difference could be attributed to the vegetation cover and vertical stratification of the native forest, demonstrated by the low gap fraction, which stabilizes microclimatic variations within the forest and acts as a buffer to mesoclimatic changes. Only the microclimate recorded in the planted forest and pasture followed the same mesoclimatic pattern. In contrast, the monoculture exhibited a mismatch with the temporal mesoclimate pattern, which could be due to the crop cycle and physical factors such as conduction and convection that affect the recording of climatic variables.

Thus, our results demonstrate the importance of better management of intervened land use types in a tropical mountain landscape, since the increase of planted forests, monocultures and unsustainable pastures would reduce the microclimatic regulation capacity of the landscape as a whole. The protection of native forests is also relevant

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Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

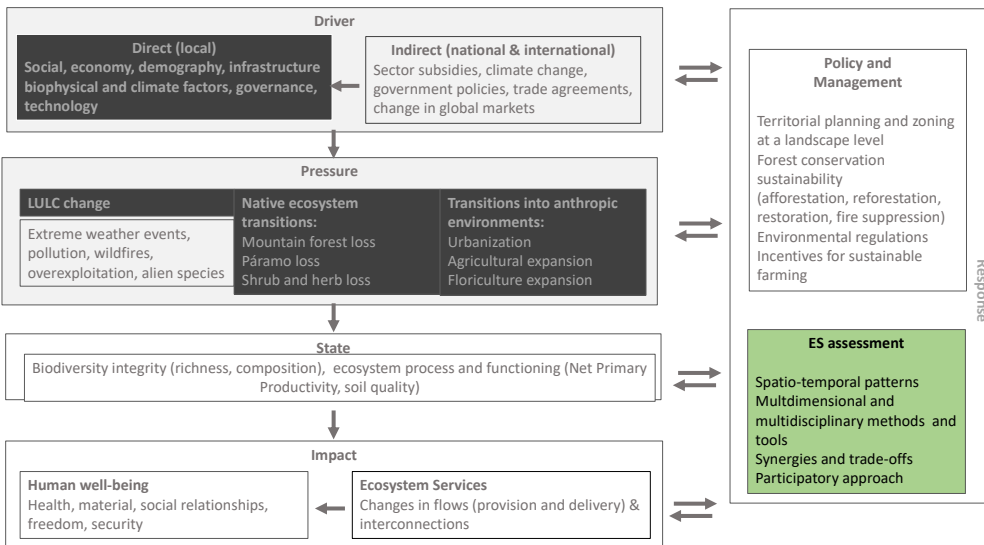
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5 The impact of land use change on the provision of ecosystem services in a montane landscape of northern Ecuador

5

The impact of land use change on the provision of ecosystem services in a montane landscape of northern Ecuador

This chapter describes changes in composition and configuration of the study landscape in two periods of analysis (1990 and 2014) to further assess their effects on the provision of ecosystem services over time.



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The impact of land use change on the provision of ecosystem services in a montane landscape of northern Ecuador

Abstract

To contribute to the understanding of landscape ecology in the northern Andes of Ecuador, this research aims to evaluate changes in landscape composition and its effect on the provision of ecosystem services in Pedro Moncayo county. In addition, we describe patterns of landscape configuration over time. A characterization of spatial patterns was performed using landscape metrics (land use coverage and number of patches of each land use type) for the years 1990 and 2014 from maps obtained from official sources, and the capacity of the landscape to provide ecosystem services was evaluated through the assessment of expert perceptions. The two components were integrated into maps for each period and comparisons of ecosystem service supply were carried out within parish administrative units. The results showed that during the period evaluated, a fragmentation trend and complex landscape composition transitions were detected: a) dynamic trends through time between agricultural land and shrubland, b) increase in land use for urban and commercial provisioning services, c) decrease in natural forest and d) stability of the paramo ecosystem. The valuation of the capacity of the landscape to provide multiple ecosystem services, obtained from experts determined that natural areas (native forest and páramo) present a greater variety and higher values of ecosystem services than the human-dominated land use types. Finally, the distribution of ecosystem services in the territory showed that in the areas where natural areas occur (north of the territory and southwest), a higher valuation of regulating and cultural services was obtained. Briefly, the landscape of Pedro Moncayo during the 24 years of study (1990-2014) experienced transitions between land uses with defined geographical dynamics that resulted in the decrease of food provision services and the increase of areas with urban infrastructure in the east of the territory. This research may contribute as a technical input in the planning and management of the local territory.

KEYWORDS: spatial patterns, ecosystem services, land use change, ecosystem service mapping, transitions, expert valuation.

Introduction

Land use change, defined as the conversion of natural ecosystems for human purposes (Gergel and Turner 2017), has significant impacts on the natural environment, human societies, and their interactions (Foley et al. 2005; Lambin et al. 2001), by altering the structure, processes and functions of ecosystems and landscapes (Wu 2012). Ecosystem function is generally defined in terms of the condition or performance of the system, in other words, its capacity to produce, regulate, or maintain one or more services, especially in relation to human needs (De Groot 2006; With 2019). Because the diversity and spatial arrangements of landscape elements are intimately connected to ecosystem functions (Lovell and Johnston 2009), land use changes may significantly impact on the provision of essential ecosystem services (ES) (Millennium Ecosystem Assessment (MEA) 2005), especially in sensitive landforms such as mountain ecosystems (Martín-López et al. 2019).

At a global scale, mountain ecosystems have been severely altered by land use changes (Balthazar et al. 2015; García-Llamas et al. 2019) and the remaining tropical mountain ecosystems are considered a top global conservation priority because they exhibit high levels of vulnerability to climate change (Payne et al. 2017; Peters et al. 2019), support a range of biodiversity (Gradstein et al. 2008) and provide critical ecosystem services to local and downslope users (Balthazar et al. 2015; Hall et al. 2012; Madrigal-Martínez and Miralles-García 2019; Vanacker et al. 2020). For instance, they are of great ecological and socio-economic importance as sources for drinking water, hydropower generation, and other regulating ecosystem services (Payne et al. 2017). For local inhabitants, tropical mountain forests are also sources of ‘wild foods’ and many other non-timber forest products. Likewise, in many mountain areas, tourism is a special form of highland-lowland interaction and forms the backbone of regional and national economies (Martín-López et al. 2019).

Although at regional and national scales tropical mountain regions depict high rates of deforestation, at smaller scales diverse and intricate landscape dynamics have been documented (Madrigal-Martínez and Miralles-García 2019; Peters et al. 2023). Currently, some highland landscapes in the Tropical Andes have experienced rapid deforestation rates (Rodríguez Eraso et al. 2013; Tapia-Armijos et al. 2015); whereas other regions are facing forest recovery, – known as ‘forest transitions’ (Aide et al. 2013; Farley 2010; Wilson et al. 2019). A recent analysis to explain patterns of land use land cover (LULC) change in the northern Ecuadorian Andes demonstrated a complex and dynamic geographical pattern of LULC transitions through time (Guarderas et al. 2022). Deforestation of remnant native forest and agricultural expansion still occur in higher elevations, while urbanization and floriculture development significantly shaped the eastern lower elevation belt of the territory (Guarderas et al. 2022). However, other native ecosystems such paramo demonstrated high stability through time. These dynamic trends highlight the importance to assess their effect on the capacity of the landscape to provide ecosystem services through time (Foley et al. 2005). The highland landscapes of northern Ecuador are thus an

interesting area to study the consequences of local and regional land use change dynamics on the provision of ecosystem services

As landscapes are increasingly being transformed and used for a variety of ecological, societal and economic functions (Vitousek et al. 1997), the importance of their multifunctional role is more evident (With 2019). Therefore, landscape management requires a means of identifying and resolving the conflicts that inevitably arise in response to competing interests and valuation of ecosystem services (De Groot 2006). In that sense, the mapping of ecosystem services, by using quantitative and qualitative data in combination with landscape metrics to assess land use land cover change, is an important tool to evaluate the impacts of human activities on the capacity of the ecosystems to provide a diverse array of essential benefits that humans obtain from nature (Burkhard et al. 2009, 2012; Burkhard and Maes 2017; Jacobs et al. 2015).

From the conceptualization of ecosystem services as a key element for the connection between natural and human systems, the cascade model is a paradigm that proposes a relationship arising from the configuration and composition of the landscape, its ecological functions, and the ecosystem services that derive from them, to offer benefits to people. This comprehensive approach uses a spatial context and interconnects the social appreciation of a service and its intervention and action within the structure and natural dynamics of the ecosystems present in the landscape (Haines-Young and Potschin 2010). All these will facilitate the understanding of the ecosystem services that the landscape provides, which allows better decisions to be made regarding the sustainable use and management of a selected territory (Zachringer et al. 2017). So far, few evaluations that include spatially explicit land use data with social science exist for the high Andean ecosystems in Northern Ecuador.

In this context, understanding the interconnections between human activities, land use change, and natural systems is key to achieve sustainable outcomes that benefit both people and nature. Therefore, this research aims to evaluate how different landscape trends affect the landscape's capacity to provide multiple ecosystem services for a highland landscape of northern Ecuador. Specifically, we aim to: 1) describe the changes in composition and configuration of the studied landscape by administrative zones in the two periods of analysis (1990 and 2014) that may affect landscape function and 2) relate spatio-temporal variations in landscape patterns and the capacity of the landscape to provide ecosystem services through time (Balthazar et al. 2015; Burkhard et al. 2009) through expert perceptions (Madrigal-Martínez and Miralles-García 2019).

Methods

Spatio-temporal patterns of landscape change

For landscape data, land use coverage maps of the canton of Pedro Moncayo for two periods (2009 and 2014) (Guarderas et al. 2022) were included in this research. The original source of information for the maps was the Ministry of Environment of Ecuador. These maps were in vector format with a spatial resolution of 30 meters. The geometries were corrected and changed from vector to raster format with the same resolution using the QGIS 3.22.4 program.

Landscape composition was characterized by land use coverage and the proportion in km² occupied by each land use type within the map. On the other hand, landscape configuration, defined as the spatial arrangement of land cover types on the landscape (With 2019), was assessed by the number of land cover patches within the landscape, so this landscape attribute could also be described in terms of their level of fragmentation (Burkhard and Maes 2017; Teixeira Duarte et al. 2018). To estimate landscape metrics, we used the Landscape Ecology Statistics (LecoS) add-on in the QGIS software (QGIS Development Team. 2022). According to (Jones et al. 2013), landscape structure could influence changes in the ecosystem services (ES) supply. The description of the different landscape metrics chosen are presented in Table 10.

Table 10. Landscape metrics chosen to describe components of landscape structure

Components of Landscape Structure	Metrics	Formula	Interpretation
Composition	Landscape Proportion	$LAND = P_i \frac{\sum_{j=1}^n a_{ij}}{A}$	Measures the proportion in km ² occupied by each land use type within the map. Values range from 0 to 1.
Configuration	Number of Patches	Vector/Raster $NP = N$	Count of the units (n) of patches that make up each land use type. Values range from 0 to n.

From: McGarigal, 2014 and Teixeira et al. (2018)

Expert perceptions of the capacity of ecosystems (land use types) to provide ecosystem services

The selection of experts involved a combination of academic, researchers, and practitioners based on the following criteria selection: (1) Expertise and Qualifications: Experts should possess relevant expertise and qualifications in the field of study related to the ecosystem services being assessed. They should have a strong scientific background and experience in conducting research, analysis, or monitoring related to ecosystem dynamics, biodiversity, or specific ecosystem services of interest. (2) Knowledge of the Study Area: Experts should possess knowledge about the ecological characteristics, biodiversity, land use history, and

socio-economic factors that influence ecosystem services in the area. (3) Interdisciplinary Perspective: Experts from various fields, such as ecology, economics, social sciences, or land management. (4) Research Experience: Experts should have a track record of conducting relevant research or studies on ecosystem services are valuable contributors to the assessment.

A structured survey was conducted to determine the social perception of the provision of ES. Due to the Covid-19 health emergency, the survey (S10 Table) was carried out using the Survio online platform. A group of facilitators, who were trained in the concepts and the information to be collected in the survey, assisted the development of the online surveys through video calls with the participants, who had agreed to be interviewed in a previous communication. The survey collected information of social interest regarding environmental goods and services in a qualitative manner (Balvanera 2012). The survey did not include confidential information or personal data, thus ensuring confidentiality and anonymization of the information from the source. In addition, the protocol included a presentation of the objective of the survey and other relevant information, prior to the acceptance of participation in the survey. The survey was organized in two parts: a) information about the respondent and b) the perception of respondents regarding the demand and supply of ES provided by the ecosystems of the canton of Pedro Moncayo. The questions included in the survey are presented in S10 Table and the types of ES that were evaluated are shown in Table 11. The ES supply part was focused on questions designed to give a value from 0 to 5 according to the capacity for the ES for each land use type, where 0= does not recognize the ecosystem service; 1= very low capacity, 2= low capacity, 3= medium capacity, 4= high capacity, and 5= very high capacity (Burkhard et al. 2012).

Table 11. Ecosystem services provided by the landscape to be evaluated.

Type of ecosystem service	Ecosystem service evaluated
Provisioning services	Cultivated food Livestock and small animal husbandry Wild animals for consumption and medicinal plants Timber for construction and fuel Cultivation of ornamental plants Water for consumption
Regulating services	Local climate regulation (temperature and humidity) Erosion control and soil fertility support Flood prevention
Cultural services	Environmental education Ecotourism Source of local ecological knowledge

Adapted from (Haines-Young and Potschin 2018; Martínez-Rodríguez and Viguera 2017).

Additionally, images were placed next to each land use and ecosystem service to better illustrate the questions for the online participants in the survey (Castro et al., 2014). We included the same land use classes (see Table 12) used by Guarderas et al. (2022). A numerical code was included to indicate their representation in the results.

This article focuses on the analysis of the impact of land use change on the capacity of ecosystems to provide services, in other words, the supply-side of ES. To accomplish this goal, we integrated in QGIS 3.26: a) the average data of the experts' perceptions with b) the land cover maps of the canton obtained by Guarderas et al. (2022), thus relating the landscape composition trends with the ES assessment. Finally, the spatial distribution of the ecosystems' capacity to provide services for each study period (1990 and 2014) are presented in continuous valuation maps represented by quantiles (Burkhard et al. 2009; Madrigal-Martínez and Miralles-García 2019).

Table 12. Land use type. Code, class and description.

N	Type	Description
1	Urban	Land covered by concrete, including road networks, residential, industrial, commercial buildings and other infrastructure. Overall, this land use type is characterized by urban areas.
2	Agriculture	Area under agricultural cultivation. Primarily represented by maize (<i>Zea mays</i>) crops in combination with intercrop rotation practices with other cereals and legumes such as chocho (<i>Lupinus mutabilis</i>) or roots and tubers such as potato (<i>Solanum tuberosum</i>).
3	Pasture	Land or a plot of land used for grazing. The pasture is characterized by <i>Pennisetum clandestinum</i> .
4	Planted forest	Anthropically established tree plantations, mainly exotic species, represented by <i>Eucalyptus globulus</i> and <i>Pinus radiata</i> .
5	Shrubs and herbs	Areas with a substantial component of non-tree native woody and herbaceous species, with spontaneous growth. This land use type has a high representation of species of the Asteracea family, where <i>Gynoxis sodoroi</i> is the dominant species.
6	Native forest	Tree ecosystem, characterized by the presence of trees of different native species, varied ages and sizes, with one or more strata. In the studied region this land use type is mainly represented by species such as <i>Oreopanax ecuadorensis</i> , <i>Piper nubigenum</i> and <i>Barnadesia arborea</i> .
7	Páramo	High Andean tropical vegetation characterized by grassland species such as <i>Cortaderia</i> spp., <i>Calamagrostis</i> spp., etc. This land use type also includes fragments of native forest typical of the area.
8	Water bodies	Surface and associated volume of static or moving water. <i>This class was not assessed for the supply of ES</i>

Adapted from Guarderas et al. (2022)

. The ES supply perception section was processed in the ES matrix format proposed by Burkhard et al (2009) and improved by Burkhard et al. (2012). The main matrix was constructed from the average of responses that had a scale of values from 0 to 5, discarding outliers by interquartile range to increase confidence and to be able to classify the values in a new indicator by rank according to their ability to offer the service: 0-0.83= no offer; >0.83-1.67= very low offer; >1.67-2.50= low offer; >2.50-3.34= medium offer; >3.34-4.17= high offer and >4.17-5.00= very high offer. Each range of values within this supply valuation scale of the systems' ability to provide services was labeled with a specific color, which is seen in Table 4.

Subsequently, a sensitivity analysis was performed that consisted of evaluating the uncertainty and variability of the experts' perception data, following the recommendations of Madrigal-Martínez and Miralles (2019). For the uncertainty analysis, the standard error (SE) was used to elaborate two additional matrices: the first corresponds to the positive sensitivity matrix (mean+SE) and the second consists of the negative sensitivity matrix (mean-SE). In contrast, for the variability analysis the standard deviation (SD) was considered. When this value is less than 2, the variability of responses was low and can be classified as: very low (SD<1) and low (SD>1 and <2) variability (Madrigal-Martínez and Miralles, 2019). The purpose of this analysis was to measure the percentage of category agreement with respect to the expert average matrix.

Finally, after obtaining the average matrix for each ecosystem service evaluated from each land use type, we estimated the value for each ecosystem service category by a process of summation of the scores corresponding to each type of ES. The result was a summary matrix by service (provisioning, regulating, and cultural) converted into an attribute Table to be integrated into the land cover and land use maps in the QGIS 3.22.4 program. The union of the structural composition component and the perception of experts resulted in spatial distribution maps where the spatio-temporal variation of the ES supply was described (Burkhard et al. 2009). Due to the relevance for the landscape evaluated, we decided to separately analyze the services of cultivated food and water provision for consumption. Thus, these maps were analyzed individually, while retaining their initial weights of 0-5 (Burkhard et al. 2009, 2012).

Results

Ecosystem service matrix scores, sensitivity, and variability analysis.

Thirty-four experts answered the survey. The average age of the respondents was 45 ± 10.6 , 61.7% were men and 38.3% were women. In general, they reported their background interests as having a very high interest 44.11% (n=15) and a high interest 38.23% (n=13) in conservation issues. Respondents directly identified that the land use system or type that provides the most ES was páramo with 67.6% (n=23), followed by native forest 23.5% (n=8). The average expert scores for provisioning, regulating, and cultural ES are presented in Table 13, and the results of the sensitivity

analysis of the expert scores are presented in Table 14. The details of the quantity of consulting experts, the outliers identified, and the contributing answers for each LULC/regulating ES pairs are systematized in S11 Table.

The average perceptions of experts (Table 13) demonstrated that páramos and native forests afforded the highest potential for both regulating and cultural ES (4.56-5). Planted forests and shrublands gave intermediate values for regulating ES (3,47). Shrublands obtained a high potential for preventing erosion and improving soil fertility (3.44) and preventing alluvium (3.70). Forest plantations were rated to have a high potential to produce timber (5), in addition, this land use obtained a high value for microclimate regulation (3.71) and flood prevention (3.93) (Table 13). On the other hand, agricultural land and pastures had high potential for crops (5) and livestock services (4.83), respectively. Finally, areas dedicated to floriculture crops and urban infrastructure had a low and very low potential for almost all environmental services (Table 13).

Table 13. Ecosystem services matrix according to experts' perceptions. The matrix illustrates the average scores for provision, regulating, and cultural ES.

0-0.83	No relevant potential supply	1	Urban
>0.83-1.67	very low potential supply	2	Agriculture
>1.67-2.50	low potential supply	3	Herbs and shrubs
>2.50-3.34	medium potential supply	4	Pasture
>3.34-4.17	high potential supply	5	Planted forest
>4.18-5.00	very high potential supply	6	Native forest
		7	Páramo

Systems	Provisioning services						Regulating services			Cultural services		
	Food crops (Fc)	Livestock and small animal husbandry (Lsa)	Wild animals and medicinal plants (WaMp)	Timber and fuelwood (Tf)	Ornamental plants (Op)	Drinking water (Dw)	Microclimate regulation (Mr)	Prevent erosion and support soil fertility (PeSsf)	Landslide prevention (Lp)	Environmental education (Eed)	Ecotourism (Ect)	Source of local Knowledge (Lap)
1	1,97	1,48	1,00	0,75	3,00	0,76	0,83	0,79	1,00	1,16	1,00	1,16
2	5,00	3,15	1,65	1,00	3,74	0,73	1,82	2,21	1,63	2,38	2,41	2,62
3	2,65	4,83	1,97	0,73	1,45	1,10	1,43	2,47	2,35	1,82	1,82	2,09
4	1,48	1,52	2,91	1,82	1,65	1,79	3,12	3,44	3,70	2,97	2,82	3,03
5	1,97	1,56	2,47	5,00	1,79	1,68	3,71	3,09	3,93	2,91	2,91	2,68
6	1,10	0,94	5,00	2,38	0,84	3,47	5,00	4,56	5,00	5,00	5,00	4,80
7	1,13	1,09	4,79	1,00	0,74	5,00	5,00	4,84	4,44	5,00	4,61	5,00

A sensitivity analysis was carried out to evaluate the variability and uncertainty in the ES matrix scores. Cells highlighted with a purple border show changes in the range of ratings when comparing the average matrix with the positive sensitivity matrix (Table 14A) and when comparing the average matrix with the negative sensitivity

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matrix (Table 14B). The comparison between the sensitivity matrices A and B (Table 14) and the average ES matrix indicated 65% and 67% overall agreement of cells in equal classes of the potential supply, respectively. The minor differences supposed an increment or decrement of one level in the potential supply scale. Agricultural cultivation had the greatest changes in the scoring scale for ES provision in all three categories, although the changes demonstrated an increase towards the immediate upper range in the scoring scale (Table 14A). The shrubland system presented the greatest changes when comparing the average matrix with the negative sensitivity matrix (Table 14B). Native forest and páramo were the most consistent systems when analyzing the positive and negative sensitivity matrices, especially in the evaluation of regulating and cultural services (Table 14A and 5B).

Table 14. Descriptive statistics for the sensitivity analysis of the ecosystem services (ES) matrix (A,B). The ES sensitivity matrix A shows the average expert scores plus the standard error. The ES sensitivity matrix B presents the average expert scores minus the standard error. The cells with a purple outline denote a one-level class variation in the potential supply.

0-0.83	No relevant potential supply	1	Developed
>0.83-1.67	very low potential supply	2	Agriculture
>1.67-2.50	low potential supply	3	Herbs and shrubs
>2.50-3.34	medium potential supply	4	Pasture
>3.34-4.17	high potential supply	5	Planted forest
>4.18-5.00	very high potential supply	6	Native forest
		7	Páramo

Systems	Provisioning services						Regulating services			Cultural services		
	Fc	Lsa	WaMp	M	Op	Dw	Mr	PeSf	Lp	Eed	Ect	Lap
1	2,22	1,68	1,00	0,83	3,33	0,87	0,94	0,89	1,00	1,33	1,00	1,34
2	5,00	3,45	1,83	1,00	4,03	0,81	2,08	2,46	1,78	2,65	2,69	2,90
3	2,93	4,91	2,21	0,81	1,65	1,15	1,62	2,72	2,75	2,05	2,04	2,34
4	1,64	1,72	3,20	2,07	1,90	2,00	3,37	3,68	3,91	3,26	3,11	3,30
5	2,24	1,79	2,72	5,00	2,07	1,89	3,86	3,32	4,09	3,19	3,19	2,93
6	1,28	1,08	5,00	2,71	0,96	3,76	5,00	4,75	5,00	5,00	5,00	4,88
7	1,19	1,25	4,86	1,00	0,84	5,00	5,00	4,90	4,54	5,00	4,81	5,00
Systems	Provisioning services						Regulating services			Cultural services		
	Fc	Lsa	WaMp	M	Op	Dw	Mr	PeSf	Lp	Eed	Ect	Lap
1	1,72	1,29	1,00	0,67	2,67	0,66	0,72	0,69	1,00	0,99	1,00	0,98
2	5,00	2,85	1,46	1,00	3,44	0,66	1,57	1,95	1,43	2,12	2,13	2,33
3	2,36	4,75	1,73	0,66	1,26	1,04	1,25	2,22	2,25	1,59	1,60	1,83
4	1,33	1,31	2,62	1,58	1,39	1,59	2,86	3,20	3,50	2,68	2,54	2,76
5	1,71	1,33	2,22	5,00	1,52	1,46	3,56	2,85	3,68	2,64	2,64	2,43
6	0,92	0,80	5,00	2,05	0,72	3,18	5,00	4,37	5,00	5,00	5,00	4,72
7	1,07	0,93	4,71	1,00	0,64	5,00	5,00	4,77	4,19	5,00	4,41	5,00

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

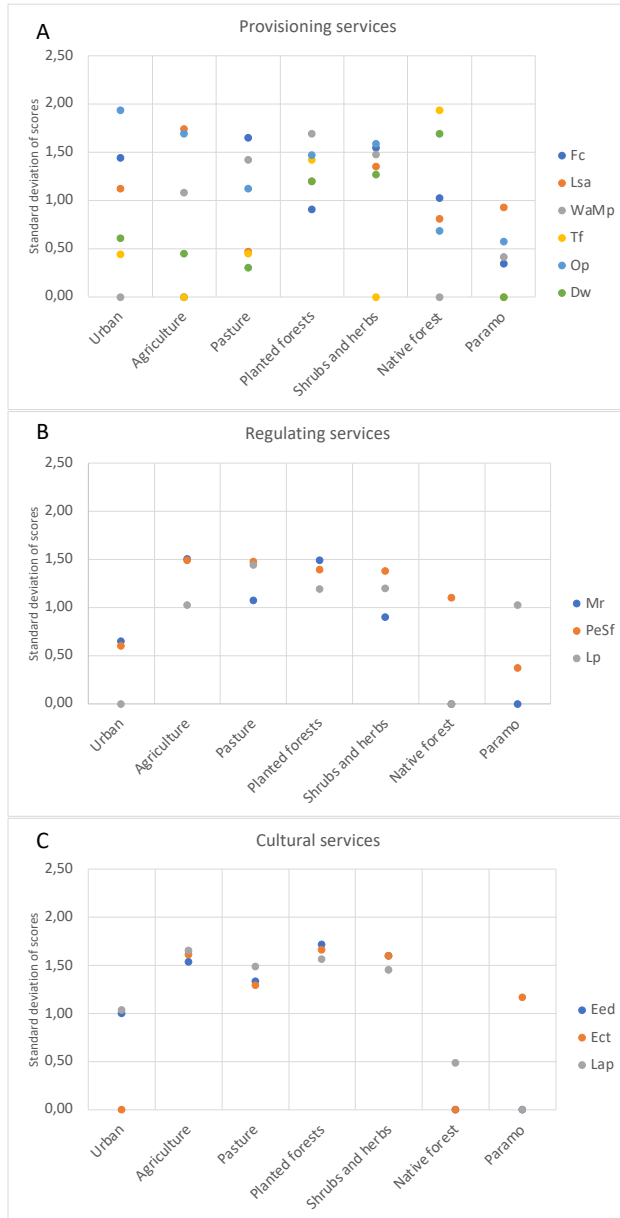


Figure 24. Standard deviation of experts' perceptions of ecosystem services (ES) for each land use type. A) Provisioning services. Classes and abbreviations: Fc: food crops, Lsa: livestock and small animal husbandry, WaMp: wild animals and medicinal plants, Tf: timber and firewood, Op: ornamental plants, Dw: drinking water. B) Regulating services. Classes and abbreviations: Mr: microclimate regulation, PeSf: prevent erosion and maintain soil fertility, Lp: landslide prevention. C) Cultural Services. Classes and abbreviations: Ect: ecotourism, Lap: local knowledge and appreciation, Eed: environmental education.

The results of the uncertainty analysis of the experts' responses are depicted in Figure 24. In general, the experts' perceptions were within a range of variability below 2 standard deviations. The greatest variability was found for the estimation of provisioning services, especially in the systems (see Table 11) with the greatest human activity (urban infrastructure and agricultural cultivation). There was 19.04% unanimity in the scores assigned and 27.4% had very low variability.

Landscape patterns

Composition

The landscape proportion metric helped to better determine the change in land use types in relation to the extent of the parish territory occupied (Figures 2). In general, agricultural areas and shrub and herb areas were the most representative land use categories in the parishes located in the west (parishes 1-2) of the analyzed landscape, while parishes located in the east (parishes 4-5) presented higher proportions of pastures instead of shrubs and herbs (Figure 25). The páramo ecosystem did not experience major changes of an increase or decrease of territory. Native forest decreased in extent and even disappeared in one parish (Figure 25). Planted forest remained relatively stable, with the parishes of La Esperanza and Tabacundo occupying a considerable proportion of the territory. Shrubland stands out in Malchinguí, increased in La Esperanza, and decreased in Tocachi. Pasture experienced the greatest fluctuations in terms of increase and decrease in the different parishes.

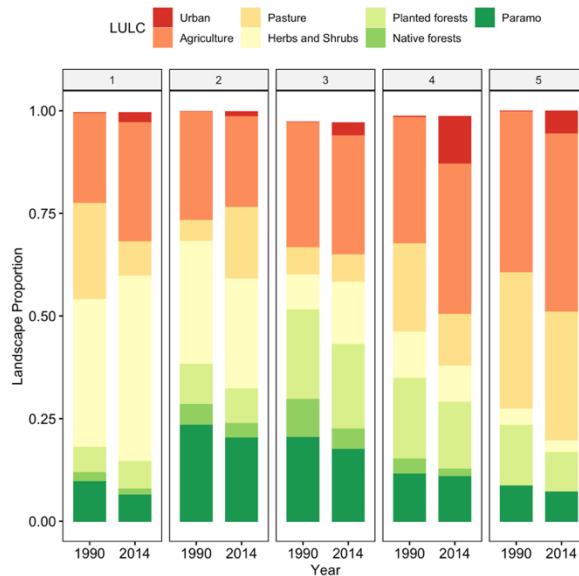


Figure 25. Landscape proportion of the different land use typologies in Pedro Moncayo County for 1990 and 2014 by parishes. Parish coding: 1= Malchingui, 2= Tocachi, 3= La Esperanza, 4= Tabacundo, 5= Tupigachi.

Agricultural cultivation covered the largest proportion of the landscape in most parishes and in both years. Finally, urban and infrastructure occupied the smallest proportion of territory in all parishes, but stands out because it has been increasing, especially in Tabacundo (Figure 25).

Configuration

This landscape attribute was analyzed by the number of patches (Figure 26). The number of patches increased in all administrative zones over the years in urban areas and pastures (Figure 26). The increase in this landscape metric for urban areas ranged from 6 to 20 times and for pastures the increase ranged from 2 to 6 times in the different parishes (Figure 26). On the other hand, the number of patches for the other land use types had different temporal patterns according to the location of the administrative zones. The parishes located in the east of the territory exhibited an increase (from 17 to 65%) in the number of agricultural patches, whereas for native forests this region presented a decreased in the number of patches from 45% to almost 100% (Figure 26). For instance, páramo seems to remain stable, however it exhibited a two to three-fold increase in two administrative areas (Figure 26). Likewise, different parishes presented a differential increase in the number of patches in relation to shrub and herbs (Figure 26).

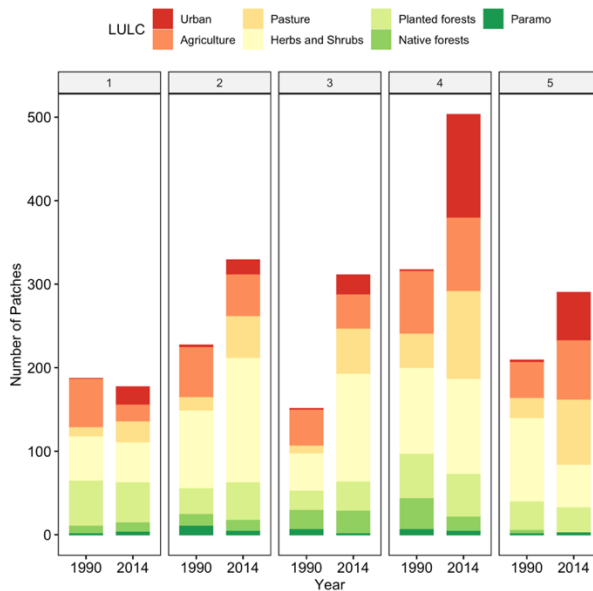


Figure 26. Number of patches by parish in Pedro Moncayo county in 1990 and 2014. Parish coding: 1= Malchingui, 2= Tocachi, 3= La Esperanza, 4= Tabacundo, 5= Tupigachi

Spatial and temporal variation in the provision of ecosystem services

Figures 27-31 present the spatial and temporal variation in the supply capacity of ecosystems to provide different types of ES in Pedro Moncayo. In the case of provisioning services, a decrease in the capacity of the evaluated territory to provide these services was observed when comparing the 1990 map with the year 2014, in particular for the parishes of Tabacundo and Tupigachi.

The northern part of the county remains constant with an average valuation (11.2-14.5), while in the central and southern part of the parishes located in the west of the canton (Malchinguí and Tocachi) presented spatial changes in the distribution of the provisioning services over time (Figure 27). Due to the relevance of the services of water supply for consumption and the provision of cultivated food, maps were generated that describe the spatio-temporal patterns for these two services, which can be seen in Figures 28 and 29.

It was observed that most of the territory has an intermediate to high valuation for the provision of cultivated food. With the exception of the northern part, which is where the páramos and high mountain forests are located, in addition to the Mojanda lake system, which remained stable in the analysis period. When comparing the two study periods, the provision of cultivated food had a change in spatial distribution (Figure 28). In 1990, the area located below where the forests and páramos are located (see Figure 28), of Malchinguí parish presented a higher valuation for this service, while by 2014 the areas that showed greater capacity to provide this service were located in lower areas (Figure 28). Likewise, a change in the spatial distribution of the provision of cultivated food was observed in the parishes located to the east. In 1990, crop production areas were more consolidated and located in higher areas, while by 2014 there was a redistribution to different areas of the territory (Figure 28).

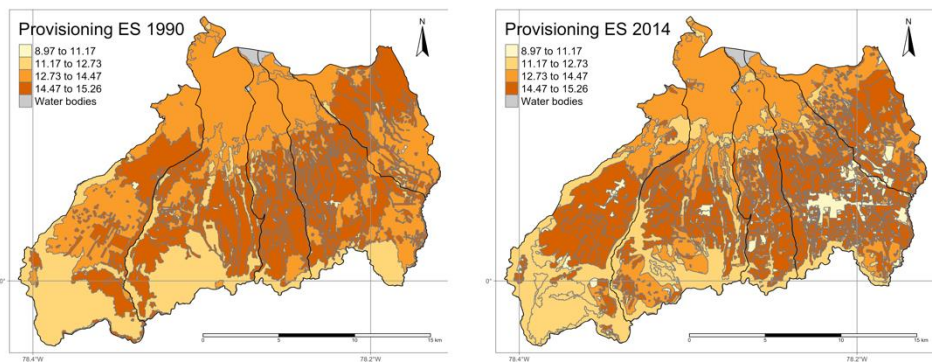


Figure 27. Map of the capacity of Pedro Moncayo's ecosystems to provide provisioning services.

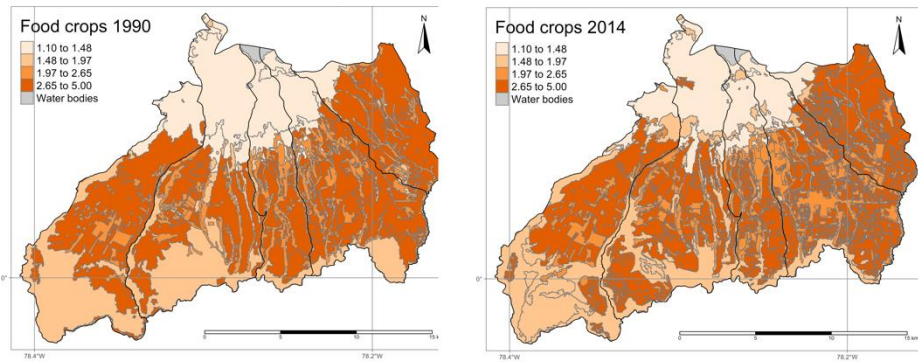


Figure 28. Map of the capacity of Pedro Moncayo’s ecosystems to provide provisioning services - cultivated food.

The valuation of the water supply in Pedro Moncayo canton also decreased over time. According to the experts’ perceptions, the highest score for drinking water provision was given to the páramos and forests (see Figure 29), which are located in the northern part of the territory. In addition, the places where agricultural crops are located or urban areas do not have any value for water provision (Figure 29).

Figure 30 presents the assessment of the capacity of the territory of Pedro Moncayo to provide regulating services. The páramos, native forests, and shrublands are the systems that have the highest valuation. When comparing the two study periods, a change in the spatial trends of the distribution of these services can also be seen. In La Esperanza the valuation of this type of service has increased since the forests occupy more space in this parish. However, in the east and the center of the territory the values are almost null for this type of ES (Figure 30).

In the same way, cultural services have a higher valuation in the northern and southern ends of the canton, but it is striking that in some central parts they are valued, although to a lesser extent (Figure 31).

5 The impact of land use change on the provision of ecosystem services in a montane landscape of northern Ecuador

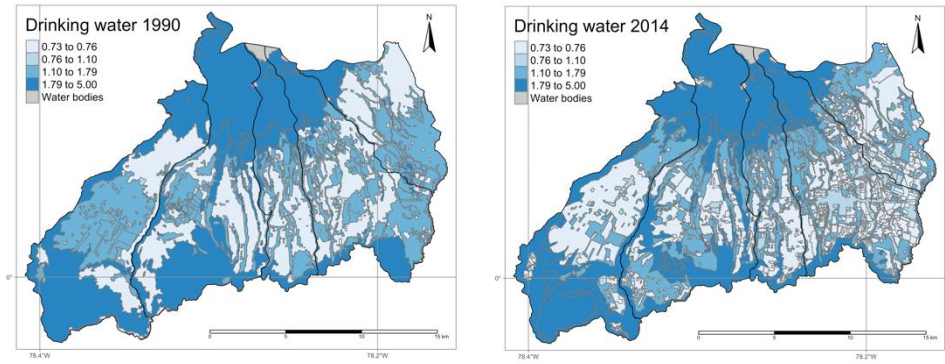


Figure 29. Map of the capacity of Pedro Moncayo's ecosystems to provide provisioning services – Drinking water.

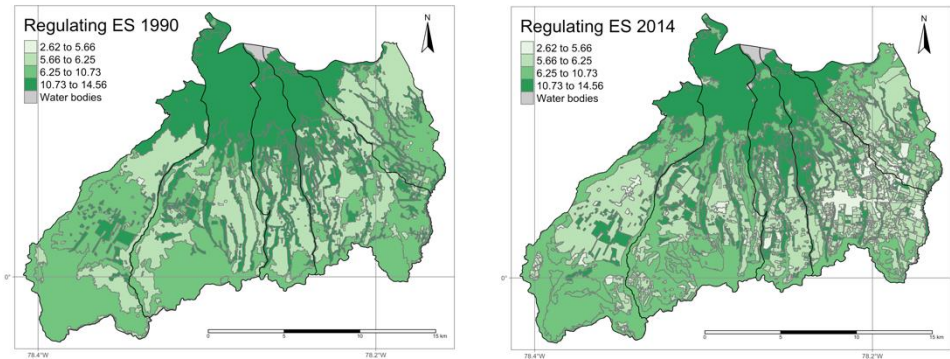


Figure 30. Map of the capacity of Pedro Moncayo's ecosystems to provide regulating services.

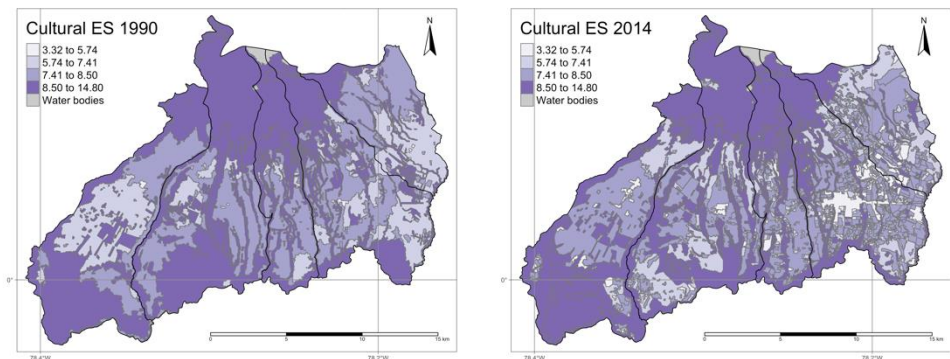


Figure 31. Map of the capacity of Pedro Moncayo's ecosystems to provide cultural services.

Discussion

Patterns of spatio-temporal change of landscape composition and fragmentation in the canton of Pedro Moncayo

The landscape changes that the territory of Pedro Moncayo experienced from 1990 to 2014 were characteristic of other mountain systems of the Andes (Gaglio et al. 2017; Rodríguez Eraso et al. 2013; Ross et al. 2017). The observed patterns in terms of composition, already described by Guarderas et al. (2022), can be summarized in the following transitions: a) dynamic trends through time between agricultural land and shrubland, that could be explained in the context of rural-urban migration and land abandonment, b) increase in land use for urban and commercial provisioning services (agriculture, livestock, floriculture), c) decrease in natural forest and d) stability of the paramo ecosystem. This latter finding differs from the patterns of land use change documented in the central highlands of Ecuador, where páramo is threatened by forest plantations of exotic species and the advance of the agricultural frontier (Balthazar et al. 2015; Farley 2007, 2010; Gaglio et al. 2017; Hall et al. 2012). In addition, the urban expansion pattern that was observed mainly in the eastern zone of the territory, follows global trends in the demand for urban areas at the expense of agricultural land (Mishra, Rai, and Rai 2020; Obaco and Díaz Sánchez 2018; Ortiz-Báez et al. 2023).

When analyzing the landscape in terms of configuration, we found a prevalent trend of fragmentation among most land uses, represented by an increased number of patches through time. This trend is consistent with the findings of Tapia-Armijos et al. (2015), who studied landscape dynamics in the highlands of southern Ecuador. The fragmentation pattern was more noticeable in the eastern part of the study area, represented by an urban-dominated zone, which is also the center of floricultural expansion of the country (Guarderas et al. 2022). In contrast, the paramo among all parishes and the shrubland in the western part of the landscape presented very few patches, which numbers were maintained or even decreased over time. The stability and lack of fragmentation of paramos were also described by Ross and his collaborators (2017) in a mountain landscape from central Ecuador; they argue that this pattern is explained by the difficult access to high altitude areas to implement agricultural activities. However, according to Rojas (2016) the explanation for a similar trend, observed in Chilean highlands, would be the result of *in situ* conservation actions. Indeed, in the study area the Paramos, together with the lake ecosystems located above 3500 m, receive special protection measures at the national and local level (Ministerio del Ambiente Agua y Transición Ecológica (MAATE) 2021). In addition, the lowland dry ecosystems, represented by shrubland in the western part of the landscape, are part of the Jerusalem Protected Forest (GAD Municipal del cantón Pedro Moncayo 2021).

Furthermore, our findings reveal that montane native forests are the least represented land use type in the study area, and it also documents fragmentation trends, especially in the parishes located in the east. Habitat loss and fragmentation of

mountain native systems are prevalent in the Andes (Tapia-Armijos et al. 2015). A combination of drivers, especially the national agrarian reforms that were implemented in the second half of the 20th century, as mentioned by Ross et al. (2017), caused a serious loss and deterioration of montane forests in Ecuador, which has resulted in this ecosystem being represented only by remnants of forest.

Capacity of the landscape to provide ecosystem services

Overall, experts' perceptions of the ES offered by the landscape demonstrated clear patterns associated with land use types. For instance, natural systems are best for providing multiple ES. The average responses of the experts' perception scores showed that regulating and cultural ecosystem services are prevalent in natural systems such as páramo and native forests, a medium-high supply in shrubland and forest plantations, and a low to very low supply in the human-dominated land use types such as urban areas, agricultural cultivation, and pastures. As expected, the supply of cultivated food was highly valued in cropland. In contrast, the urban area offers few services but requires most of them. These results are consistent with findings from other studies conducted in Latin America (Gaglio et al. 2017; Madrigal-Martínez and Miralles-García 2019; Rodríguez Eraso et al. 2013; Ross et al. 2017; Vanacker et al. 2018), and around the world (Burkhard et al. 2012; Palomo et al. 2014). Although natural ecosystems can offer a more diverse array of ES, according to experts, it is unknown if these systems are in an optimal state or condition to deliver ES to their maximum capacity (Madrigal-Martínez and Miralles-García 2019; Rojas 2016; Romo 2022). For this reason, it is strongly suggested that a mapping of ES should be analyzed over time.

Although the relationship between landscape composition and its capacity to provide ecosystem services has been raised and tested in this research and in different landscapes through the concept of landscape capacity (Burkhard et al. 2009), the possible effects of landscape configuration, in particular landscape fragmentation, on ES outcomes have not been fully elucidated (Mitchell et al. 2015). Our study did not quantify a direct association between fragmentation and the provision of ecosystem services, but the fragmentation trend detected among the different land use types over time, could compromise the delivery of ES in the studied landscape.

Some studies suggest that ecosystem service supply depends on the presence of particular species, ecosystems, or ecological processes that are often negatively affected by fragmentation. For instance, fragmentation of forests due to the expansion of the agricultural and urban frontier, or from logging, opening of roads and other human disturbances can alter the composition of plant species in the landscape, negatively affecting water quality regulation, carbon sequestration, among other ecosystem services (Edwards et al. 2014). On the other hand, fragmentation can also improve access to the ecosystems, thus favoring the flow of some goods and services to local communities (Peres and Lake 2003; Trombulak and Frissell 2000).

Spatial and temporal variation in the provision of ecosystem services

Regarding the maps that describe the capacity of Pedro Moncayo territory to provide ES in the two study periods, clear trends were detected both spatially and temporally. In the eastern region of the study area, a marked offer of commercial services related to urban expansion was observed. In contrast, regulating and cultural services presents a higher score in the southwestern part of the territory, and the higher elevation areas of all the parishes, where the Mojanda lake system is located.

In relation to changes over time in the distribution of the ES, we observed a decrease in the provision of food, which is consistent with other biophysical valuations (Balthazar et al. 2015; Vanacker et al. 2020), precisely where an extension of the urban infrastructure was found, in the east of the territory. In addition, by 2014 a decrease in the continuity of the agricultural matrix that was characteristic of the first study period (1990) was evident. As demonstrated by other studies, in particular those that analyze urban-rural gradients, urban expansion is displacing important areas of food provision for populations in the inter-Andean valleys (Obaco and Díaz Sánchez 2018). Political decisions have a determining role in the spatio-temporal patterns and dynamics of land use changes in a territory (Ross et al. 2017).

We indirectly detected trade-offs and synergies between different types of services that were consistent over time. For instance, regulating and cultural ecosystem services vary similarly across land use types. The highest weighting for both types of ES were detected in natural areas (paramo, montane forests and shrubland), but these natural land uses obtained the lowest values for the majority of the provisioning ES; while the opposite trend was observed in agricultural land. This is closely related to the dynamics of ES provisioning detected, which, although it was not directly analyzed in this study, is related to the phenomena described elsewhere (Hall et al. 2012; Madrigal-Martínez and Miralles-García 2019; Martín-López et al. 2014; Romo 2022). Thus, as Rojas (2016) suggests, different land use types will provide ecosystem services differentially, and the multifunctionality could be managed at a landscape scale.

The consequences of the spatial-temporal changes of land use on ES outcomes would be related to the history of land use and planning of each territory (Balthazar et al. 2015). As of 2019, the canton of Pedro Moncayo – which is mainly an agricultural landscape, because 55% of its territory is dedicated to this activity (GAD Municipal del cantón Pedro Moncayo 2021) – plans to expand its agroecological production. The idea for the future is to develop agricultural practices in the territory towards an agroecological transition, as described by Palomo et al. (2013), where the sustainability of agricultural ecosystems for food production can be maintained, using environmentally friendly practices, to simultaneously favor the maintenance of agricultural ecosystems and regulating and cultural services. However, Guarderas et al. (2022) suggest that the rapid urban and floriculture expansion observed may pose a risk to the capacity of this landscape to maintain the supply for food and other provisioning ecosystem services. Therefore, sustainable agriculture with an

agroecological approach could expand in the territory only with strong political decisions and economic and technological incentives coming from various levels of territorial governance to support local stakeholders' networks (Boeraeve et al. 2020; Duru et al. 2015; Hatt et al. 2016).

The spatial distribution of cultivated foods suggests that this service could be increasing as a response to population growth (Foley et al., 2005). A growing population, and its subsequent territorial expansion, requires greater agricultural production to supply itself. Given the low agricultural productivity in the territory, the most common outcome will be expansion into other spaces, putting pressure on the natural areas of the territory. This effect was visualized by Burkhard et al. (2012) in central Germany, which they describe as typical of the growth of cities. Another important factor that may explain this pattern, and which was not addressed in the present study, is the loss of agricultural areas due to the pressure on land use for the expansion of the production of ornamental flowers for export (Guarderas et al. 2022).

Limitations

Despite limitations of using quantitative and indirect information, based on experts' perceptions, to assess the capacity of ecosystems to provide services (Campagne et al. 2017; Jacobs et al. 2015), our results presented low variability and uncertainty among the experts' opinions to characterize the landscape, suggesting a robust result. Moreover, this method is frequently used for ES valuations, especially in a scenario of lack of data, which is characteristic of developing countries (Burkhard et al. 2012; Madrigal-Martínez and Miralles-García 2019). However, quantitative data from different sources such as censuses, estimates from on-site studies, satellite data, or modeling should be the next step to corroborate the patterns detected by this methodology (Burkhard et al. 2009); some studies have even combined different sources obtaining consistent results (Balthazar et al. 2015; Gaglio et al. 2017; Romo 2022). Another limitation of the experts' valuation of ES (Burkhard et al. 2009) is related to other context related environmental variables associated with landscape (Palomo et al. 2014). However, these limitations were resolved with the use of landscape metrics to better understand the changes produced in the studied landscape, a recommendation taken from the study by Rojas (2016) that uses a similar approach.

Although this research presents the results from the supply-side of ES, a future approach should include an ES valuation from the point of view of the demand-side to provide a complete understanding of the capacity of the landscape to provide ecosystem services (Burkhard et al. 2012). Even so, studies such as these are a useful early warning of the changes in spatial distribution of ES, for subsequent use in territorial planning (Balthazar et al. 2015; Burkhard et al. 2009; Burkhard and Maes 2017; Gaglio et al. 2017).

Conclusions

1) The experts' perceptions provided reliable information with low variability for the estimation of the capacity of ecosystems (defined in this study as types of land use) of Pedro Moncayo canton. These estimates made it possible to identify that natural ecosystems (páramos, native forests, and shrublands) have greater capacity to provide multiple services, expressed both in the variety of services offered and in their high valuation. These systems are characterized by providing mainly regulating and cultural services, but also provide water for human consumption which is a supply service most demanded by the local population. However, the human-dominated land uses have an almost-zero supply of ES. In an intermediate range are the agricultural areas that exclusively provide provisioning services, to the detriment of regulating services.

2) The landscape metrics used allowed the detection of changes in the landscape structure and configuration of the territory of Pedro Moncayo between 1990 and 2014. Complex land use composition and fragmentation trends were detected (with the exception of páramo)

3) In relation to the temporal change in the distribution of ES in the territory, clear patterns of distribution were detected both spatially and temporally. A decrease in the provision of food could be seen, precisely where an extension of the urban infrastructure is visualized, in the east of the territory. In addition, there was a marked offering of commercial services related to human growth. On the other hand, the southwestern part of the territory obtained a higher valuation in regulating services and cultural services, particularly in the Malchinguí parish and the high areas of all the parishes, where the Mojanda lake system is located.

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6

Discussion and perspectives

This chapter analyzes the importance and relevance of the major findings of this thesis. I state the answers to the research questions and hypotheses, then, I explore the findings in the light of the concepts and paradigms exposed in the introduction and, finally, I explore potential improvements in future studies on land use patterns.

Answering the research question and testing the hypothesis

This dissertation provides new insights into the landscape dynamics in tropical mountain systems by answering the following research question:

What was the pattern of land use change in the northern Andes of Ecuador during the past two decades and how these changes impact on the biodiversity and ecosystem services?

By implementing an adaptation of the DPSIR framework for tropical mountain systems and conducting an ecosystem assessment in the territory of Pedro Moncayo county, we furthered our understanding of the impacts of land use changes on mountain systems of Northern Ecuador. Based on our findings, we documented the complex landscape dynamics that have occurred in the last twenty years and revealed the factors that drive land use transitions in this region. Additionally, the results showed the effects of converting native forest into anthropic environments on local biodiversity and ecosystem services and summarized how land use change affects the capacity to supply ecosystem services.

This section summarizes the major findings of the ecosystem assessment conducted in the studied landscape and compares them with the stated hypotheses:

1. Although we detected a pattern of native forest loss, as stated by our first hypothesis: *the land use change will follow the patterns of native ecosystem loss, in the context of Forest Transition Theory, demonstrated for tropical systems*, we also found that other native ecosystems such as páramos and shrublands showed other patterns. In the territory studied, the páramos have remained stable, without a major reduction in the face of the threat of expansion of the agricultural frontier, as is evident in other areas of the Andean region (Gaglio et al. 2017). On the other hand, our study documented an alternation between the expansion of the agricultural zone and the shrublands, explained by rural-urban migration, consistent with the regeneration of former agricultural lands that have been abandoned (Rudel et al. 2005), which is also described in other Latin American landscapes in the context of the ‘Forest Transition Model’. In addition, we detected that the rapid urbanization pattern documented worldwide (Seto et al. 2011), together with the expanding extension of land dedicated to the production of ornamental flowers for export, are occurring at lower elevations at the expense of crop land. These changes potentially represent a food security challenge in this agrarian-dominated territory with limited capacity to compensate for these losses (van Vliet et al. 2017).
2. A key result of this research demonstrated *land use change in the studied territory presented different spatial and temporal patterns across altitudinal and administrative zones*. We found clear geographic and altitudinal patterns of

land use change in the studied landscape. Significant expansion of floriculture and urban areas was observed on previous agricultural land located at lower elevations in the east of the studied territory. Higher elevations contain more natural environments, where páramo demonstrated an unexpected trend of stability, but a reduction of montane forests was persistent in the elevation band of 2800-3300 m as agricultural land is replacing this LULC class at higher elevations. These trends highlight the increasing threat of permanently losing the already vulnerable native mountain biodiversity (Chapter 2).

3. This research also corroborated the second hypothesis: *ecosystem services have decreased over time along with land use change in a highland landscape of northern Ecuador*. In relation to the temporal change in the distribution of ecosystem services in the study area, clear patterns of distribution were detected both spatially and temporally. A decrease in the provision of food was observed precisely where urban infrastructure has been extended, in the east of the territory. In the eastern sector of the studied landscape, a dominance of the supply of commercial services related to urban activities and flower production for the export market was observed, while in the southwestern part of the territory, particularly in Malchinguí parish where the Mojanda lake system is located, in addition to higher elevations of all the parishes, there was a higher representation of regulatory services and cultural services (Chapter 5).
4. Finally, with the development of our field study we were also able to corroborate our third hypothesis. *Biodiversity, ecological functions, and ecosystem services have been affected by native forest conversion to anthropic systems in the studied landscape*.

Results showed that native forests had higher values for richness, evenness, and diversity of soil macroinvertebrate communities than the other land use categories, demonstrating a significant loss of taxonomic biodiversity at order and genus levels. We also found a significant reduction of trophic diversity in native forests converted to anthropic environments. More trophic groups with greater abundances were found in native forests, where predators and detritivores stood out as dominant groups, suggesting a higher quality of the soil. The results from the soil chemical parameters confirmed the distinction in soil health between native forests and anthropic environments. Our results highlight the risk associated with current trends of native forest loss and conversion to managed systems in high mountain ecosystems in the tropics, illustrating how these alterations could cause biodiversity loss and degradation of the chemical attributes of soil health (Chapter 2).

In relation to our study of microclimate regulation, native forests provided a more stable microclimate, demonstrating significantly lower temperatures and higher relative humidity values than the other land use types. This effect on microclimate was significantly explained by the highest temperatures at intermediate gap fraction levels, as a proxy for vegetation cover differences among land uses. In addition, we observed that native forests provided a buffer effect on the variations in mesoclimate, whereas local temperature variations

registered on human altered systems (planted forests and pastures) were significantly explained by the mesoclimate variation, except for monocultures that exhibited a mismatch between the two scales of climate. These results highlight the importance of native forest for microclimate regulation, an ecosystem service which can act synergistically with other biodiversity conservation goals to sustainably manage landscapes in tropical Andean Mountain systems (Chapter 3).

Connecting the theoretical framework with our major findings

Implementation of the proposed ecosystem service model and DPSIR framework in the highlands of northern Ecuador

As was explored in Chapters 1 and 2, we consider that the practical implementation of the DPSIR framework is a good alternative for conducting ecosystem assessments that could be replicated in tropical mountain landscapes. It consists of a framework and a tool that integrates the conceptual foundations of the landscape as the core spatial element where social dynamics interact with natural systems (Wu 2012).

Also, in agreement with Müller and Burkhard (2012) we argue that the DPSIR framework encompasses the ecosystem service cascade from Haines-Young and Potschin (2010). In this comprehension, the ‘state’ element of the framework is linked to the cascade component of ecosystem functions to deliver the ecosystem services that people require for their livelihoods (Müller and Burkhard 2012). We explored these connections in our case study, where direct observations and measures conducted in the field allowed us to assess the impact of land use change (or native forest conversion to anthropic environments) on soil biodiversity, soil fertility (Chapter 3), and microclimate regulation (Chapter 4).

According to this framework, the state element is described by several biophysical structures (landscape elements) and processes (ecosystem properties) that represent the natural capital of a landscape, which may be impacted by internal or external factors (drivers) that would change the state of system (Nassl and Löffler 2015). In our assessment, the state of the mosaic of ecosystems, represented by land use and cover types included in the landscape, can be understood by the changes and pressures that have been brought about by driving forces mainly of a socio-economic nature at the local, regional, and global level. The spatio-temporal landscape characterization and the analysis of the driving forces that explained the patterns were explored in Chapter 2. In addition, to uncover the spatial distribution of multiple ecosystem services and its temporal variation we combined experts’ perceptions of the capacity of land uses to provide services with the configuration of the landscape in two periods of analysis (Chapter 5).

Proposing a DPSIR framework for tropical mountain systems enhances our understanding of these unique and fragile environments, supports evidence-based decision-making, and facilitates the sustainable management and conservation of these valuable ecosystems. The ecosystem service approach included in the DPSIR conceptual model used in this research provides a useful framework for assessing the impacts of land use change on ecosystems. The integration of these conceptual approaches can provide valuable insights into the drivers and pressures impacting the ecosystem services, monitor the state of the ecosystem over time, assess the impacts of changes, and develop response strategies to mitigate negative impacts on the ecosystem services. Tropical mountain ecosystems are highly complex, with a

diverse range of plant and animal species and intricate ecological interactions (Gradstein et al. 2008) which may limit the efficacy of the application of these approaches. The ecosystem service approach may oversimplify the complex relationships between species and their environment, leading to incomplete or inaccurate assessments of ecosystem health.

Another potential limitation of this approach relates to the perception that the ecosystem service approach prioritizes human well-being over the intrinsic value of nature, emphasizing an anthropocentric view of nature. In the studied landscape the value of natural ecosystems, as spaces of multiple benefits including biodiversity conservation, was not evident to many local stakeholders due to the long history of landscape transformation, the struggle for land rights and the dependency of land resources to sustain livelihoods of marginalized rural- indigenous Andean communities (Himley 2009). Therefore, we believe that our results highlight the intrinsic value of native systems as a source of local biodiversity that can contribute to the well-being of high mountain communities in northern Ecuador.

In addition, the ecosystem service approach has been criticized for its potential ecological implications. For example, emphasizing a flow-based perspective focuses on the productivity of the system, prioritizing short-term gains over long-term ecological sustainability. This latter perspective, also referred as a stock-based, assesses the health and resilience of the ecosystem by looking at the stock of natural resources and the ability of the ecosystem to regenerate and adapt to change over time (Barnaud and Antona 2014; Schröter et al. 2016). We argue that the spatio-temporal analysis of the landscape's capacity to provide multiple services (Chapter 5), based on the perception of experts, contributes to the study of the resilience of the system. However, a subsequent economic valuation of ecosystem services could be nurtured by mechanisms that integrate the discount rate in order to produce estimates of the long-run value of natural stocks as durable assets with the ultimate goal of assessing the long-term sustainability of ecosystems (Fenichel et al. 2016).

Furthermore, in tropical Andean mountain ecosystems land use is often intricately linked to social and cultural practices. The ecosystem service approach may overlook these cultural complexities and fail to adequately consider the social impacts of land use change; unless there is an adequate representation of 'Cultural' ecosystem services in the system (Cheng et al. 2019; Díaz et al. 2018). According to Angelstam et al. (2019), a landscape approach is needed to understand the system's context and dynamics that should be used as a tool for planning and decision making in a territory. In this context, we argue that the proposed DPSIR framework also meets this practical requirement to help develop sound land management plans that could prevent broad scale, irreversible ecosystem degradation. This phase was initially implemented by sharing our major findings with local authorities and stakeholders. However, this initial exercise (which corresponds to the formal academic phase of the Doctoral studies) should, subsequently, be integrated into a holistic valuation, which in turn, leads to the implementation of decision-making processes to foster the sustainable

land management with all the elements describe in the NCP approach (Pascual et al. 2017).

It is evident the need for this research to follow a dynamic process that interlinks the scientific information with the phase of policy and decision-making (Díaz et al. 2018) from a critical realism posture that could even transcends to a post-normal scientific framework (Francis and Goodman 2010). Then, a further step of the assessment should recognize and consider different knowledge systems, including indigenous and local knowledge systems, which can be complementary to the findings presented in this research, bridging a plurality of knowledge sources and types together for knowledge co-production and co-management (Armitage et al. 2011; Chapman and Schott 2020). This further integration is embodied in the conceptual framework of nature's contribution to people, which although from my point of view is very similar to the DPSIR framework used in this research, however, the NCP's approach explicitly evidences certain elements that are not so visible in the DPSIR framework, such as the importance of the governance systems, the dialogues between different knowledge systems and the connections between different spatial and temporal scales (Díaz et al. 2018; Pascual et al. 2017), which could be advantageous in comparison with the conceptual model used in this research.

Overall, the valuation of the benefits that humans derive from nature are context-dependent, which involves a diverse array of views, values and different knowledge systems, then, this approach helps establishing a common ground for research that will require the explication and discussion of underlying values (Hermelingmeier and Nicholas 2017). The fact that this conceptualization is embedded in the Constitution of Ecuador means that there is an obligation to include this as part of the ecosystem management framework.

Land use dynamics in mountain landscapes of northern Ecuador in the context of Forest Transition Theory -FFT (Chapter 2)

On a global scale, land surface transformations that resulted from human activities have clear geographic patterns and follow the forest transition paradigm (Mather and Needle 1998). Processes of afforestation and agricultural decline have been documented in the global north, while deforestation and agricultural expansion dynamics dominate trends in landscapes located in the global south (Winkler et al. 2021). Currently, at a national level, Ecuador depicts an early transition stage, with high forest cover and deforestation rates (Hosonuma et al., 2012), however, at subnational level, various patterns and pathways have been described in the context of the FFT (Balthazar et al. 2015; Farley 2007; Grau and Aide 2008; Peters et al. 2023).

Our study of land use and land cover change in northern Ecuador also allowed us to document diverse and complex transitions that do not necessarily conform to the general patterns described for the Global South or at the national level (Hosonuma et al. 2012). Although montane native forests do follow the decline trends recorded in

the tropics of the world, the dynamics of other native ecosystems such as páramos and shrublands showed other patterns. In the territory studied, the páramos have remained stable, without a major reduction in the face of the threat of expansion of the agricultural frontier, as is evident in other areas of the Andean region (Gaglio et al. 2017). In addition, in the studied landscape (Pedro Moncayo county), although forest plantations were introduced decades ago on degraded land to foster regulating services, we did not find the expansion trend of planted forests with exotic species replacing páramos, as the landscape transformation described for the highlands in central and southern Ecuador. These latter afforestation patterns were explained, within the FTT approach, by land acquisition for the production of timber products, both at an industrial and community level (Balthazar et al. 2015; Farley 2007; Farley and Kelly 2004); however, these trends were not evident from our results.

On the other hand, our study documented an alternation between the expansion of the agricultural zone and the shrublands, which could be explained by rural-urban migration, consistent with the regeneration of former agricultural lands that might have been abandoned (Rudel et al. 2005), which is also described in other Latin American landscapes in the context of the ‘Forest Transition Model’ (Aide et al. 2013; Mather and Needle 1998). In addition, we detected that the rapid urbanization pattern documented worldwide (Seto et al. 2011), together with the expanding extension of land dedicated to the production of ornamental flowers for export, are occurring at lower elevations at the expense of crop land – posing a food security challenge in this agrarian-dominated territory with limited capacity to compensate for these losses (van Vliet et al. 2017). We also argue that these landscape transformations represent an ongoing pressure for expansion of the agricultural frontier in highland areas. In summary, at subnational level, landscapes in tropical mountains of Ecuador are context-specific and undergo complex landscape transformations, not only described by deforestation patterns; there is also evidence that some areas have started to transition towards reforestation. Therefore, the scales of analysis play an important role in unraveling the spatio-temporal trends that occur in a landscape (Raudsepp-Hearne et al. 2010; Wu 2012). Testing the Forest Transition Theory in the highland landscapes of Ecuador shed lights for understanding the dynamics of land use change in these regions that may help to identify sustainable land use practices and refine the theory. This with the ultimate goal to help inform policies and management strategies that balance the needs of conservation and development in the region (Peters et al. 2023).

Limitations on the land use land cover change analysis and driving factors

Although our study analyzed the patterns of land use change, our approach did not include a direct interpretation of data from satellite images. Rather, the focus of our study was to use publicly available maps and databases that allowed us to characterize changes in the landscape over time. These LULC national maps, however, were generated by a team of geographers from official institutions of Ecuador, through a

supervised classification method, using primarily LANDSAT images from different years at a spatial resolution of 30m (Ministerio del Ambiente (MAE) 2016; Ministerio del Ambiente (MAE) and Ministerio de Agricultura Ganadería y Pesca (MAGAP) 2015). The map classification process was followed by an accuracy assessment analysis (Forestry Department 2009; Simonetti, Beuchle, and Eva 2011) and the overall accuracy obtained for the official LULC maps of different years ranged from 69% to 85%.

To refine the official vector maps, our study implemented a thorough editing process from the different study periods by using distinct secondary sources of information as suggested by Madrigal Martinez (2019). After that, a point-based accuracy assessment was conducted following the methods proposed by (Jin et al. 2021). Specifically, a custom survey in Open Foris Collect Earth tool was used to gather reference data for map accuracy assessment (Bey and Alfonso Sanchez-Paus Diaz 2015; FAO 2016). A random stratified sampling method of 600 points with pixels of 30 x 30 m as spatial assessment unit were chosen for the accuracy assessment. We used the highest spatial resolution available from Google Earth archives (4,27 m), as reference data, to estimate accuracy for the 2008 and the 2014 maps and the resulting overall accuracy was 82 to 86%, respectively. A lack of high spatial resolution satellite data for 1990 and 2001 of the studied landscape prevented the accuracy assessment of these periods.

Despite possible drawbacks to the LULC official datasets utilized for land use change analysis regarding, quality, interpretation, accuracy assessment, timeframe and context (García-Llamas et al. 2019), their accessibility and availability at different time spans offers considerable advantages for studying land cover changes (Kroll et al. 2012), providing a consistent source of primary data facilitating the reproducibility of results. These types of approaches are particularly important in areas of data scarcity and lower technical capacities for the processing of remote sensing information required for land management and planning, which characterizes many distinct territorial levels of governance in tropical mountain systems and developing countries (Guarderas et al. 2022).

However, future analyses in any geographical context, even more so in sensitive territories such as tropical mountains, should be based on the use of satellite image platforms and freely accessible spatial databases, as those offered by new geospatial processing services at planetary scale (Gorelick et al. 2017). We consider that the further training of professionals in the geomatic sciences with these types of analysis capabilities will greatly facilitate the development plans and territorial planning towards sustainable territorial development, which is so needed in developing countries. Therefore, future assessments studies should include the effects of data quality on their results as it can produce important biases in the overall interpretation and decision-making support.

Regarding the analysis of drivers of change in the landscape, we found that topography (elevation and slope) was the most important explanatory variable for all LULC transitions. Native ecosystem transitions and agricultural expansion were both

significantly related to changes in elevation and slope. This finding suggests that the major pressure on native ecosystems in this region of northern Ecuador is the continued expansion upwards of the agricultural-livestock frontier, like other tropical Andean landscapes (Rodríguez Eraso et al. 2013). Other drivers such as population changes, irrigation systems, and rural-urban migrations, among others, were also identified as interactive driving forces of land transformation patterns which could affect the ecological integrity of the ecosystem or landscapes (Aide et al. 2013; Lambin et al. 2003; Young 2009). Our analysis considered a comprehensive set of factors characterizing landscape conversion dynamics; however, they describe only local forces. The underlying driving forces affecting land use transformations could also be attributed to production support policies geared towards the internal market and exports (Lambin et al. 2003; Ross et al. 2017), which were not included in our analysis and need further inspection.

The analytical methods utilized to reveal possible driving forces and explain the variation on the landscape transformation patterns in our studied system represent an innovative inferential and compelling model that seeks to uncover the relationships between factors driving dynamics in ecological systems and thereby predict them in quantitative terms. Briefly, we used the transition probabilities obtained in Markov chain analyses and integrate them into another very powerful statistical model (General Additive Model), currently in use by ecologists (Wood 2017), to reveal drivers of change or limiting factors for land use land cover dynamics. While our models explained between 21 and 48 percent of the variation in landscape dynamics found in our study, we argue that it is a good first approximation for understanding the system, given that the GAM models used were quite conservative, incorporating the minimum number of knots to fit a curve to avoid overfitting problems in the models. However, it is important to acknowledge the limitations and uncertainties associated with conducting research on land use change in tropical mountain systems, these limitations may arise due to the complexity of the system, data availability, and methodological challenges to interpret land cover and land use information in the studied landscape.

Impacts of land use change on biodiversity and ecosystem services (Chapters 3 and 4)

Assessing the impact of land use change on biodiversity and ecosystem services along a gradient of land use intensity is a valuable approach for understanding the ecological consequences of human activities (Wu 2013). In the study landscape, we identified native forests at one end of the gradient. These remnant forests have currently minimal human impact and retain their original vegetation, biodiversity, and ecological functions; we consider these areas as reference sites to compare them to a range of land use types, including planted forests, pastures and cropland, where the gradient culminates in our assessment. However, conducting such an assessment along a gradient of land use intensity have some potential drawbacks: Land use change is

often accompanied by multiple drivers and factors, making it challenging to attribute observed changes in biodiversity and ecosystem services solely to land use intensity. Likewise, short-term assessments may not capture the long-term consequences accurately, and the full extent of the impact may be underestimated or not fully understood. Conducting comprehensive assessments of biodiversity and ecosystem services requires significant data collection efforts, including species surveys, ecological measurements, and socio-economic data. Data availability and accessibility can pose challenges, particularly in remote or understudied regions. Limited or incomplete data can constrain the accuracy and robustness of the assessment, potentially leading to incomplete or biased conclusions (With 2019).

Impacts on soil biota and soil fertility

We conducted a field study to assess the impact of land use change on biodiversity, microclimate regulation, and soil-associated ecosystem services. This study revealed important data for tropical mountain ecosystems and constituted an interesting academic exercise to implement an *in situ* evaluation of the ‘state’ element under the DPSIR framework. Additionally, this research extended our understanding of the human impact on understudied organisms and systems such as soil fauna and soil ecosystems in tropical mountain landscapes. According to Newbold et al. (2015), the impact of native ecosystem conversion into human dominated systems on biodiversity loss is enormous; however, as these assessments were conducted using data-rich biodiversity groups, a broader biodiversity characterization that includes inconspicuous taxa is required to assess the impact of land use change. In addition, literature reviews have concentrated on the global status of species, whereas the long-term security of many ecosystem functions and services – especially in changing environments – are likely to depend upon local biodiversity. In this context, this study contributes to extend our knowledge of the impact of land use change on soil macroinvertebrate communities in the Tropical Mountain ecosystems of the Andes.

Likewise, I regard the operationalization of the concept of soil health for this assessment and including a biodiversity dimension fosters a comprehensive sustainable solution for their degradation (Lehmann et al. 2020). This study incorporated both biodiversity (soil invertebrate communities) and fertility dimensions of the soil health approach for conducting an ecosystem assessment. The comparison of the soil biota between the native forest, as a reference “intact” ecosystem, and the modified anthropic environments (planted forests, pastures, and monocultures) revealed a significant biodiversity loss at distinct taxonomic levels and trophic groups, as well as compositional turnover. These results are consistent with other studies conducted in tropical mountain systems (Cao et al. 2017; Delelegn et al. 2017; De Valença et al. 2017).

Additionally, our evaluation of soil fertility using chemical parameters of soil – as a proxy to assess the effect of land use change on the ecosystem service of maintaining productivity for food cultivation – revealed a significant degradation of soil fertility

in anthropic systems, as reported in the literature (Veldkamp et al. 2020). The higher pH values detected in native forest soils in relation to the soils under crops or under pastures, could suggest liming agricultural soils. However, we rather argue that a combination of distinct natural and anthropic processes may explain the observed lower pH values. The decrease in vegetation cover, as a result of forest conversion to anthropic systems, could enhance soil weathering and leaching rates, which in turn can cause soil acidification. The opening of the system (more water percolating in the soil profile), can disrupt biological cycles (lower return of Ca in the topsoil through litterfall) and nitrogen fertilization, containing acidifying products, might be the major driving factors for the acidification pattern detected in monocultures (Hao et al. 2020).

Although the soil taxonomy map for Ecuador, obtained from the geoportal of the Ministry of Agriculture, describes the soils in the study area as Inceptisols, it is more likely that these soils correspond to Andisols (Moreno et al. 2022). Its location above 3000 meters above sea level, its probable volcanic origin, its high composition of organic matter and dark coloration strongly suggest that they were misclassified. The Food and Agriculture Organization of the United Nations (FAO) defines Andisols as black soils of volcanic origin that are typically found in mountainous areas. These soils are an essential source of food, as well as sustaining valuable ecosystems in the mountain ranges, Andean forests, and páramos, which they provide nutrients and allow them to regulate their water cycle. Given its relevance for ecosystems such as Andean forests and páramos, and for growing food Soil conservation, ecosystem protection and sustainable food production are transcendental issues for humanity at this time.

Although the *in situ* study contributes to the body of knowledge of the impacts of land use change on ecosystem services, I am aware that an integrative assessment incorporates other dimensions such as climate change, human health, and water quality, among others (Bünemann et al. 2018; Lehmann et al. 2020), which were not included in our assessment. Other elements are required to have a more integrative view of the ecosystem; such as vegetation cover, litter production, enzymatic activity, and elements that relate to other ecosystem services such as carbon sequestration, erosion prevention, etc. Likewise, the biological dimension within the assessment could be studied by molecular techniques such as stable isotopes, metagenomics and high-throughput sequencing to distinguish the taxonomic composition of different groups of soil biota (Lehmann et al., 2020). But it is important to stress the relevance of obtaining direct information on the abundance and biomass of organisms, which molecular techniques do not provide, to better understand the connections between the soil biota and its soil ecosystem functionality (van den Hoogen et al. 2019).

Overall, this thesis empirically evaluated the impact of land use on biodiversity, focused on soil invertebrates (Chapter 3). However, other important elements in the system such as soil microorganisms, the vegetation that covers the soil (Diaz et al. 2007; Lavorel et al. 2011), as well as all biological activities such as respiration, enzymatic activity and functional attributes could provide a better understanding of the interlinkages between biodiversity and ecosystem services (Delelegn et al. 2017;

Potthast et al. 2012). These aspects are currently being studied to complement and further expand the scope of this research.

Impacts on regulating ecosystem services

Regarding the comparison of microclimatic variables between land uses using *in situ* measurements, we detected a significant buffering effect of native forests, demonstrating lower temperatures and greater relative humidity. Our results also suggest that local climate variation (operating at scales of tens of square kilometers) can be explained by the regional climate (at tens of square kilometers), but this association could only be observed for two types of land use: in pastures and planted forests. Although the microclimate in the native forests presented a pattern similar to the regional climate, the temperature values were much lower throughout the recording period and did not show statistically significant trends. These results reinforce the importance of forests and green spaces, in general, as microclimatic refuges. These refugia can provide cooler temperatures, higher humidity, and other favorable conditions compared to the surrounding landscapes, thus, assessing the loss or fragmentation of these refugia, can have implications for biodiversity conservation, ecosystem resilience, and human well-being (Montejo-Kovacevich et al. 2020). Moreover, the microclimatic differences detected between different land use types may be attributed to alterations of surface properties, such as albedo, roughness, and evapotranspiration. These effects have been documented after changes in vegetation cover due to deforestation, urbanization, afforestation and agriculture expansion (Valladares 2006; West et al. 2011).

Land use change can have significant implications for ecological systems, including changes in species composition, habitat fragmentation, and altered ecological processes. Microclimate plays a crucial role in shaping these ecological responses (Faye et al 2014). In fact, the high abundance of decomposing organisms in agricultural areas compared to native forest systems described in chapter 4, may be precisely due to the higher temperatures recorded in agricultural areas, which may favor ecological functions such as soil decomposition. Understanding the impact of land use change on microclimate is vital for addressing climate change mitigation and adaptation strategies, urban planning, natural resource management, and conservation efforts. It can provide insights into the localized consequences of land use decisions and helps inform policies and practices aimed at sustainable land use and climate-resilient landscapes (De Frenne et al 2019).

On the other hand, differences in microclimatic conditions could also be attributed to changes in elevation (e.g. Montejo-Kovacevich et al. (2020). In this study, we established replicates at two different altitudes within our target elevation range to control for the possible effects of elevation on microclimate variation across land use types. However, due to the historical patterns of land use transition in our study area, we could not find a replicate for native forest at lower elevation. In addition, variation in attributes of the dominant plant species associate with each land use type could also influence the results. This factor should be included in future studies.

Furthermore, our results may have been influenced by physical factors such as radiative heating, conduction and convection that affect the heat exchange processes of the dataloggers used. Therefore, future microclimate studies should use temperature sensors with a surface coating to reduce the absorption of solar radiation (Macleán et al. 2021). Changes in vegetation cover such as in deforestation exposes the underlying soil to direct sunlight. Soils generally have lower albedo values than forested areas, particularly if they contain darker components such as organic matter or minerals. Exposed soils absorb more solar radiation, leading to increased heating of the surface and potentially higher surface temperatures. Higher temperatures can accelerate the drying of the remaining vegetation and soils, further reducing the overall albedo and exacerbating the warming effect. The impact of deforestation on albedo can have broader implications for the local and regional climate. Changes in albedo can influence the energy balance, temperature patterns, and precipitation regimes (Osborne et al 2004).

Finally, in addition to soil fertility and microclimate regulation, there are a number of other important ecosystem services to be studied in the context of land use change in the highlands of Ecuador (Chapter 3 and 4). These include the soil's ability to store water, erosion, landslide prevention, and the ability to produce food, operating on spatial scales of 10s to 100s of kilometers. Again, it is important to point out that these research aspects are also being empirically carried out as complementary projects to the present doctoral thesis to help clarify the functional importance of a landscape in providing multiple ecosystem services. In ecosystem service research, climate change has received less scientific attention than land-use change, despite the fact that its impact is rapidly increasing worldwide particularly in tropical mountain ecosystems. Synergistic effects of land-use change and climate change on ecosystem services in mountains in both the present and future are largely underexplored (Martín-López et al. 2019).

Changes in the ecosystem's capacity to provide services in the highlands of northern Ecuador (Chapter 5)

The implementation of landscape-scale assessments of the capacity of ecosystems to provide ecosystem services has been documented in multiple case studies (Burkhard et al. 2012; Madrigal-Martínez and Miralles-García 2019). However, few evaluations have been carried out in the Northern Ecuadorian Andes. This research suggests that spatio-temporal dynamics in land use and land cover are associated with changes in distribution of the provision of ecosystem services in the studied territory. These changes were evident below 10s of kilometers of continuous habitat and manifested over decadal time scales, underscoring the importance of studying ecosystem service provision on landscape scales across decades. Although this study does not quantify the direct relationship between different types of ecosystem services, it was possible to indirectly demonstrate the presence of synergies between regulation services and cultural services that occur in native ecosystems, the same ones that are maintained in areas of higher elevations.

This study used the perceptions of experts as a broad methodology used to assess the capacity of ecosystems to provide services, constituting a first look at assessing the capacity of the system to provide ecosystem services, similar to a hypothesis formulation phase (Burkhard et al. 2009, 2012; Jacobs et al. 2015). Future integration of quantitative data from on-site studies, censuses and remote sensing data modeling will help complete understanding of changes across a regional territory.

For the purpose of this assessment, the supply side of provisioning ecosystem services was addressed. While assessing this aspect is valuable, there are several drawbacks and limitations to consider. Assessing the supply side of provisioning ecosystem services tends to focus primarily on quantifying the biophysical aspects of service provision, such as the quantity or availability of a specific resource. This focus may overlook other important dimensions of ecosystem services, such as their quality, reliability, or the social and cultural aspects associated with their use. It is essential to consider a broader range of factors to fully understand ecosystem service provision (Burkard et al 2012). It should be noted that this study focused on evaluating the capacity of terrestrial systems to provide ecosystem services. In this sense, freshwater ecosystems were not evaluated and require future work.

Moreover, the perceptions matrix should contrast the perceptions of experts and local stakeholders, who have important knowledge of the services in a landscape. It is essential to carry out further integrated assessments considering the biophysical aspect as well as the economic and social components of a regional territory (Martínez-Morales & Miguel (2005). These two latter dimensions provide further research horizons to build on the results of our assessment.

The next step after this formal phase of doctoral research should should incorporate local context, stakeholder perspectives, and a range of indicators and methods to capture the multidimensional nature of ecosystem service provision. Additionally, engaging in participatory processes and considering diverse values and knowledge systems can enhance the robustness and relevance of ecosystem service assessments.

7

Final remarks and recommendations

In this chapter, I summarize the main recommendations for land management practices to promote biodiversity conservation and ecosystem services provision in tropical mountain systems, especially the territory of the canton of Pedro Moncayo and other Andean landscapes from northern Ecuador.

Recommendations for landscape planning and sustainable management in tropical Andean ecosystems

Based on the findings of this research, I suggest some landscape management options to balance the objectives of ecosystem and local biodiversity conservation with the sustainable use of natural resources in the canton of Pedro Moncayo. The proposed measures mainly involve nature-based solutions (Seddon et al. 2020) for conserving or restoring ecological processes and ecosystem services at the landscape (defined as an heterogeneous mosaic of land cover, habitat patches, physical conditions or other spatially variable elements viewed at spatial scales of 10s to 100s of square kilometers) and at the plot scale (a managed area that can vary between tens of square meters to units of square kilometers):

- Based on the biodiversity and ecosystem services provision of intact native ecosystems documented in this study, I advise setting aside a representative portion of each native ecosystem. The New Global Framework for Managing Nature Through 2030 suggests that conserving between 20 and 30% of each native ecosystem as a reasonable compromise to ensure functionality and representation of the local biodiversity to sustain ecosystem services (UN Convention on Biological Diversity (CBD) Secretariat 2021). In this context, the conservation category within the territorial zoning of the canton should consider the spatial representation of each native ecosystem in the territory. The benefits provided by nature are dependent on the climatic setting, altitude and gradients of use – and thus should be explicitly considered for regional planning in tropical Andean socio-ecological ecosystems.
- To halt deforestation, an urgent decision should include an explicit Municipal ordinance for the protection and recovery of montane forests in the county. Although the establishment of the “Mojanda” Water Resources Reserve in 2021 (Ministerio del Ambiente Agua y Transición Ecológica (MAATE) 2021) was an important decision in favor of the long-term conservation of the páramo ecosystem to ensure fresh water supply - a vital ecosystem service for the local inhabitants - more effort is needed for the protection and recovery of montane forests in this administrative zone. The Mojanda Reserve covers 61 km² and is located from the contour line of 3300 to 4200 masl. Within the the Reserve boundaries, some of the remaining montane forests patches are included, however, some complimentary spatial-explicit measures should be taken for the recovery of the montane forests at lower altitude, specifically in the altitudinal band from 2800 to 3300 m.a.s.l.
- The proposed Municipal ordinance for the protection and recovery of montane forests could be incorporated in the territorial planning of the forthcoming Land Use and Development Plan of the county (GAD Municipal del cantón Pedro Moncayo 2021). I suggest extending the conservation zone to lower elevations, at least 200 meters in elevation along the contour line that corresponds to the lower boundary of the reserve.

- Restoration measures with native plant species should complement the suggested conservation declaration. I advise that active reforestation actions be carried out in the areas identified as shrub and herbaceous in the altitudinal band from 2800 to 3300 m.a.s.l. Results from this research indicate this type of land use corresponds to former montane forests in a state of succession after agricultural land abandonment, which could be explained by the effect of rural-urban migration (i.e. in the context of the Forest Transition Theory). According to Solórzano (2020), the dominant species in the native forest patches for this region of Ecuador include: *Oreopanax ecuadorensis*, *Piper nubigenum*, *Gynoxys acostae*, *Vallea stipularis*, *Barnadesia arborea*, *Myrsine andina*, *Piper barbatum*; these species could be tested to implement reforestation actions, using native species.
- Conservation and restoration corridors with native species (With 2019) should also be established in the ravine zones along an altitudinal gradient to promote connectivity of native ecosystems located in the upper elevation area and the flow of ecosystem services to meet the needs of the local population, located at lower elevations.
- The proposed corridors with relatively undisturbed natural elements could also enhance the connectivity with the agricultural matrix, providing sources of local biodiversity, including soil communities, which could recolonize depleted soils under agricultural management. In addition, the spatial arrangement of pastures, which demonstrated better soil quality, alongside monoculture plots can support the recovery of soil macrofauna populations.
- At the plot scale, I suggest integrating plants and soil biota characteristic of native forests, as well as diminishing soil disturbance practices in agricultural systems as part of an integrated ecosystem restoration plan. Some implemented conservation and management actions in tropical mountain systems suggest the adoption of agroforestry. For instance, one specific recommendation advise that agricultural land holdings should require at least 10 per cent under tree cover to ensure soil and water restoration and climate moderation (UN Convention on Biological Diversity (CBD) Secretariat 2017). These tree managed strips could contribute to reduce forest degradation from fuelwood extraction and promote fuelwood, timber harvesting and other tree products from planted rather than natural forests.
- As defined in the Development and Land Use Plan of the Canton of Pedro Moncayo, the agricultural-livestock production zone should be concentrated at elevations below 2800 masl (GAD Municipal del cantón Pedro Moncayo 2021). However, production system should be strengthened and migrate towards a more sustainable system by implementing pasture recovery, integrated crop–livestock forestry systems, biological nitrogen fixation, planted forests, agroecological farms, no-tillage systems and manure treatment (UN Convention on Biological Diversity (CBD) Secretariat 2017). According to the results of this research, this type of land use and production

planning should also explicitly consider climate, altitude, and previous land use practices to ensure ongoing provision of ecosystem services and resilience relevant to tropical Andean ecosystems.

- The conservation and restoration measures should define specific outcomes which should be accompanied by technical monitoring to evaluate the effectiveness for maintaining and/or restoring the local biodiversity and their associated ecosystem services.
- It is strongly suggested that the conservation and restoration strategies that be implemented recognize the trajectory of land use, the need for the use of natural resources by local communities and emphasize the co-production of solutions that balance the sustainable use of local biodiversity, with conservation. These strategies should also improve options for livelihoods and buffering of detrimental impacts of climate change.
- The agro-industrial flower production, which is entrenched in the studied landscape, should become more sustainable and environmentally friendly, while also improving the social and economic well-being of local communities. Nature-based solutions could be implemented to improve the sustainability of flower agroindustrial production. Some practical solutions toward this end include integrating trees into flower production and implementing organic farming, both activities could help improve soil fertility and reduce the use of fertilizers and pesticides, in addition to improve the quality of the flowers. Moreover, water use is critical for sustainable flower production; implementing practices such as drip irrigation, rainwater harvesting, and water recycling can help reduce water use and improve water quality. This is to reduce dependence on water subsidies from outside the territory (such as the water from the Cayambe glacier, transported through the Cayambe-Pedro Moncayo irrigation canal), as it competes with the primary objective of this water source, which is for the sustained production of food for the sector.
- The DPSIR and ES conceptual framework used in this research for the local government of Pedro Moncayo can be applied for ecosystem assessment in territories of other decentralized governments at the parish, county, and municipal levels. Additionally, this practical implementation experience could help build a national framework for the management of ecosystem service provision and biodiversity conservation in Ecuador. Such a national framework is essential to safeguard the country's rich biodiversity, promote sustainable development, enhance climate change resilience, ensure legal and policy coherence, meet international commitments, and recognize the rights of indigenous peoples and local communities. Its implementation requires a coordinated effort involving, different institutions, multiple stakeholders, and a solid legal framework that harmonizes national needs with international commitments on biodiversity conservation and sustainable use of natural resources. In addition, this national framework would need the support from the academia to conduct comprehensive assessments of Ecuador's

biodiversity and ecosystem services; this includes identifying priority areas for conservation, mapping ecosystems, and assessing the state and trends of biodiversity and ecosystem services. Precisely, the main contribution of the present research aims to use scientific research and data to inform decision-making processes.

- The Constitution of Ecuador enshrines a number of principles related to the State's responsibility in guaranteeing of the provision of ecosystem services, human well-being and the harmony between nature and society. In the context of the results of this research, it is evident that the State has a Constitutional responsibility to protect and conserve biodiversity, uphold the rights of nature, guarantee the provision of ecosystem services and promote sustainable development. According to the results of this research, the high montane forest, which in the official nomenclature corresponds to the 'Bosque Siempreverde Montano Alto de la Cordillera Occidental de los Andes', requires imminent *in situ* conservation actions. The National Environmental Authority, in this sense, should directly support the local government to ensure its protection. Moreover, the results of this research point to soil degradation and local climate instability in managed systems within the Andean landscapes of Northern Ecuador. In that sense, the State has a responsibility to ensure the provision of essential services such as climate regulation, soil fertility, among others at the local and national scale. This requires the protection and restoration of ecosystems that contribute to the delivery of these services. The State should establish concrete activities for overseeing and coordinating biodiversity conservation and ecosystem service management efforts among different institutions and levels of governance. These strategies should assure resources to enforce regulations, monitor progress, and coordinate actions to promote sustainable management practices and integrate ecosystem service considerations into decision-making processes.

Final reflections

I argue that an important task to address the current environmental problems, such as the direction of land use changes and their further impacts on biodiversity loss, ecosystem degradation and lack of resilience to climatic variability is to foster generalist thinking and training. Prevailing conceptual frameworks and paradigms to study the connections between systems, such as the Socio-Ecological Systems framework, Ecosystem Service Cascade Model, One Health approach, NCP scheme, among others, may only be answered by an integrated view and multidisciplinary work. The policy demands, *vis-à-vis* the Ecuadorian Constitution, also warrant a more integrated approach to environmental management, biodiversity conservation, and human development. Such a task should be guided by generalist researchers who can move within and across scientific domains to connect ideas and improve scientific

outcomes, such as the integration of biodiversity research, climatic, geologic and soil sciences, spatial analyses, and socio-economic evaluations. Thus, researchers need to gain more general knowledge, cross-disciplinary skills, and training across multiple disciplines. Building capacity for socio-ecological research in developing countries in Latin America is particularly acute, where there are enormous challenges for biodiversity conservation, environmental management, fostering socio-economic development while protecting cultural and traditional heritage. In line with the interdisciplinary focus of ecosystem assessments and ecosystem services evaluations under the DPSIR framework, we consider that our research contributes to further the theory and integrate tools of data analysis, to move forward in this much-needed generalist thinking to foster environmental and sustainability science.

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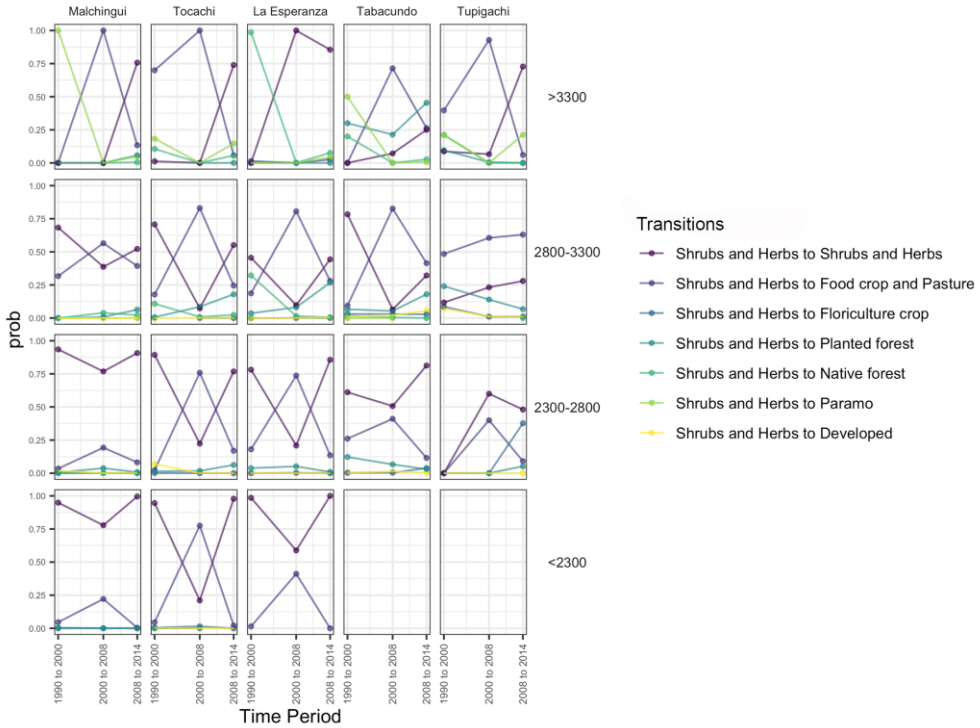
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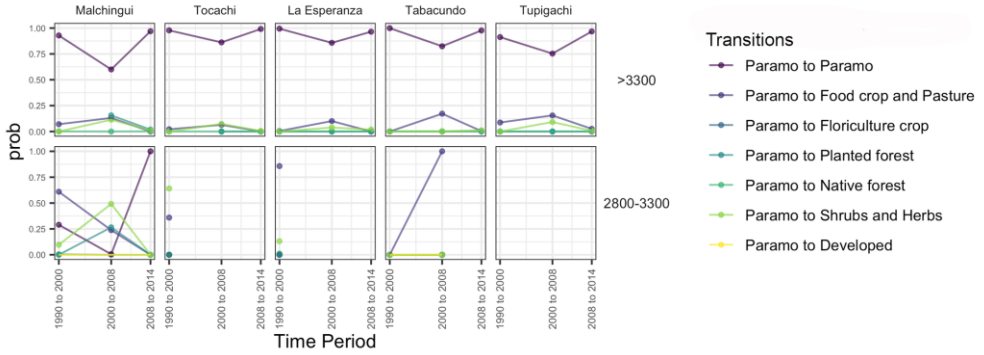
Supplementary information

Chapter 2

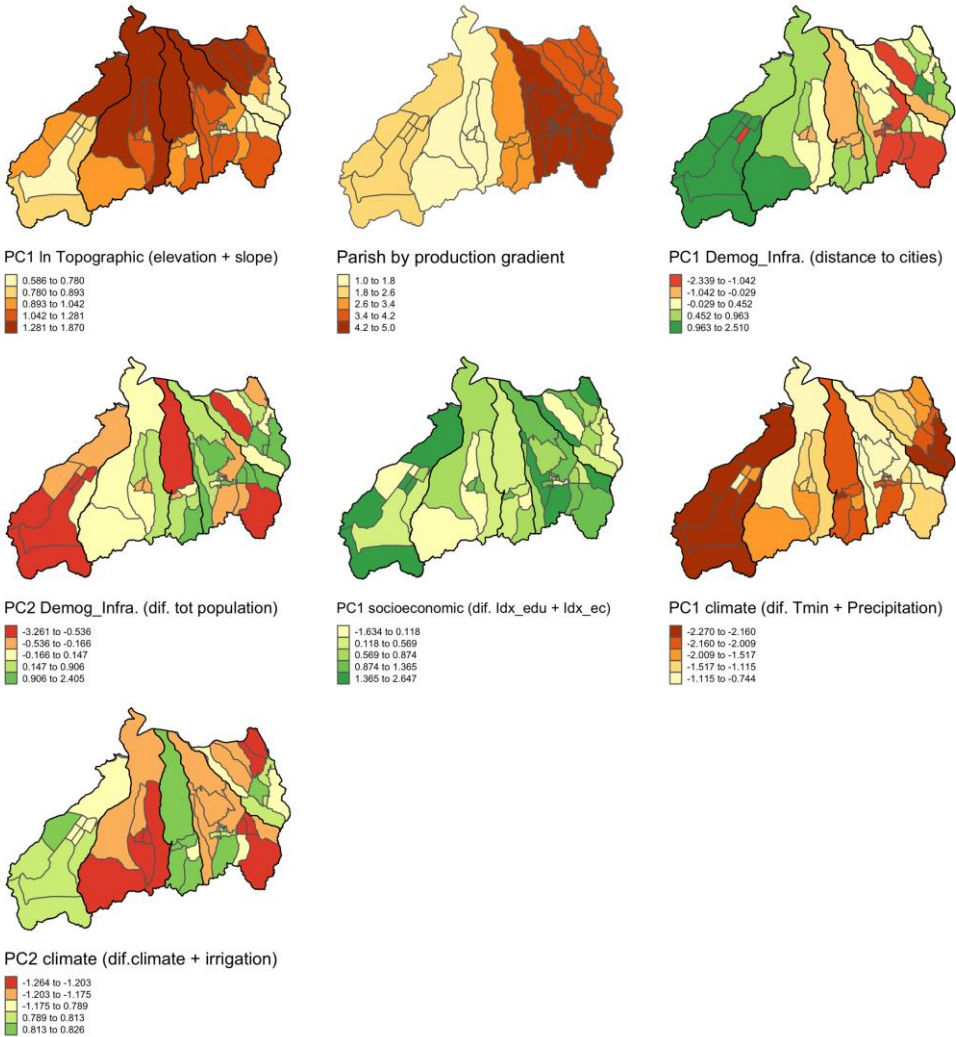
S1 Figure. Transition probability of shrubs and herbs through time in Pedro Moncayo county, by altitudinal bands at the parish level.



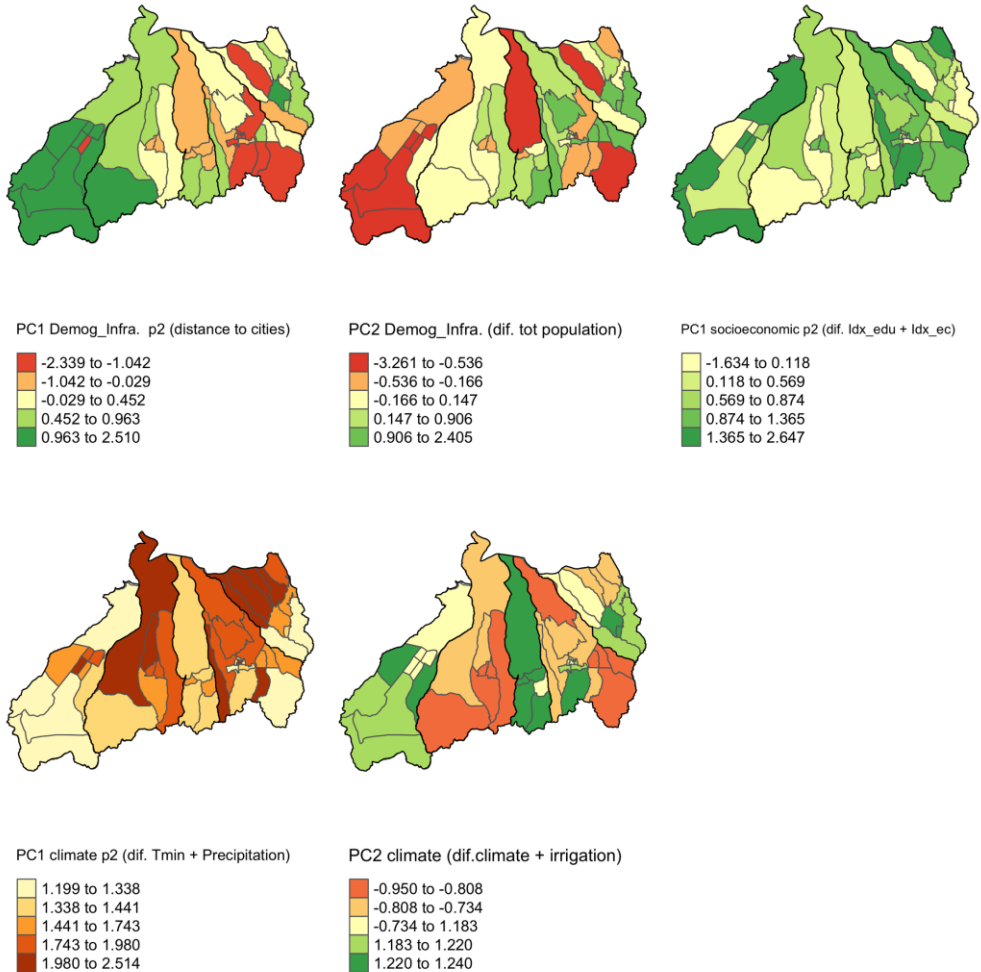
S2 Figure. Transition probability of páramo through time in Pedro Moncayo county, by altitudinal bands at the parish level.



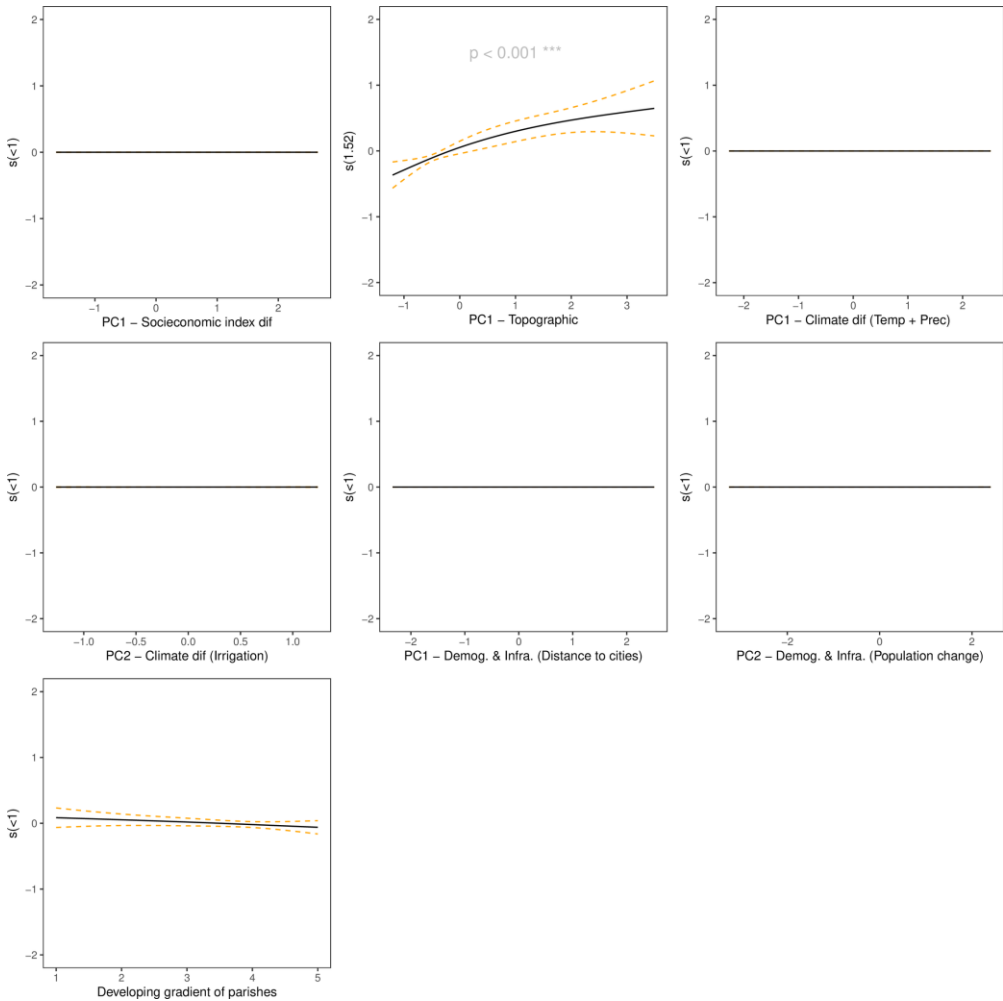
S3 Figure. Spatial distribution of each driver grouping for the first period of analysis. Each map represents the PC1 from the Principal Component Analysis carried out for each driver of change grouping from period 1 (1990 and 2000).



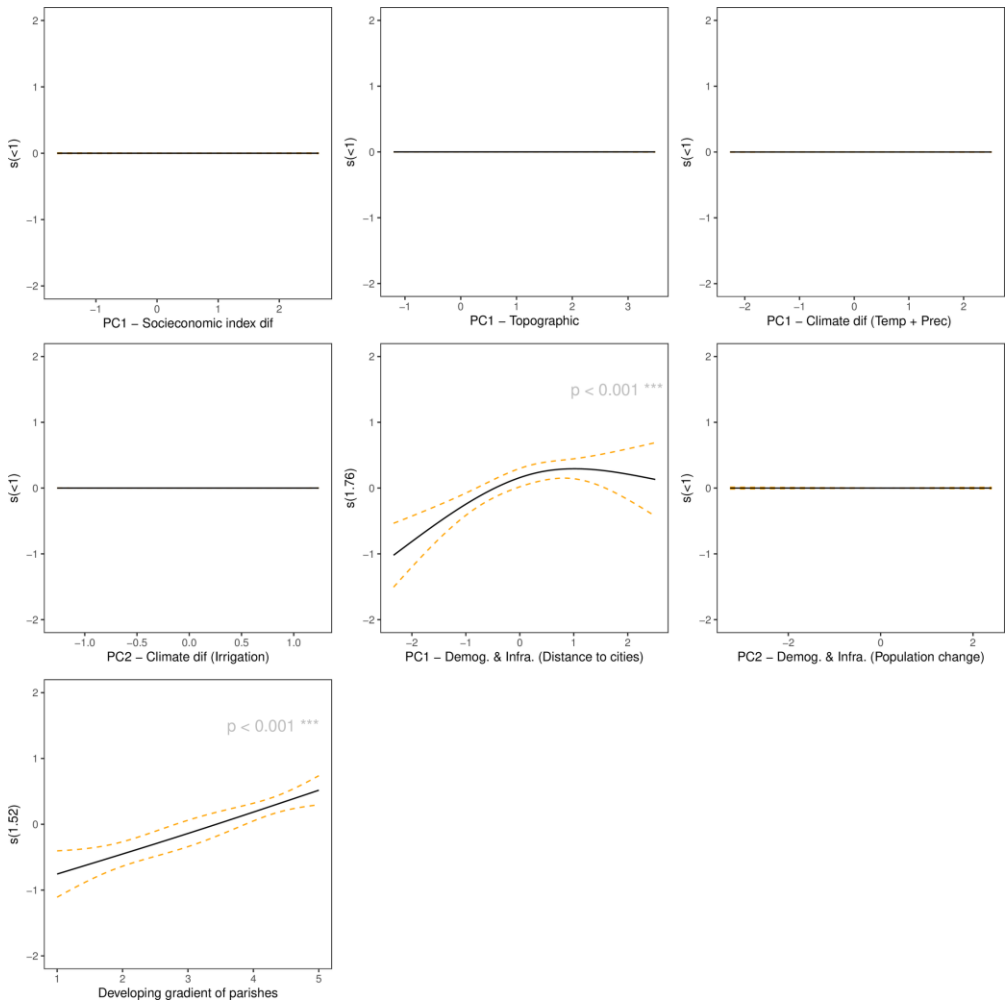
S4 Figure. Spatial distribution of each driver grouping for the second period of analysis. Each map represents the PC1 from the Principal Component Analysis carried out for each driver of change grouping from period 2 (2000 and 1990).



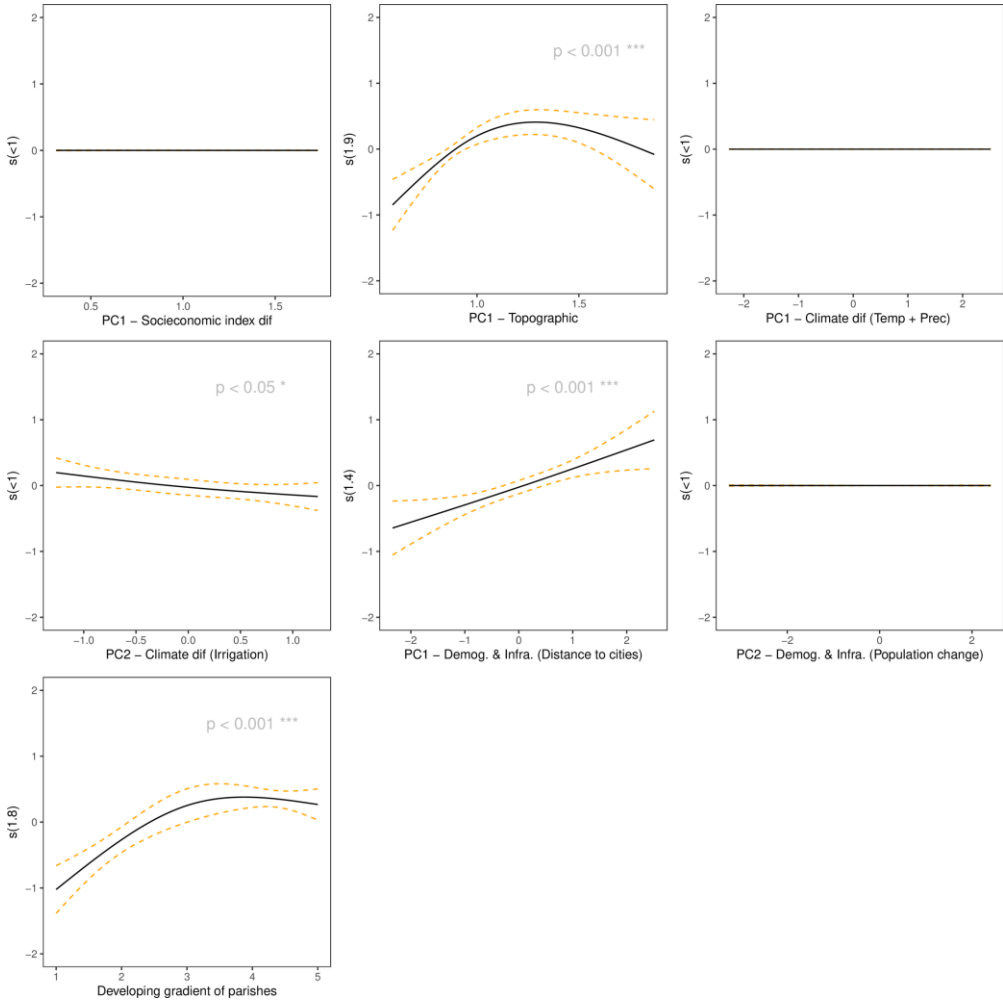
S5 Figure. Generalized additive model partial dependence plots for forest páramo loss. Each plot shows a covariate and their partial dependence on probability of páramo loss in the context of the model. The y axis shows the mean of the probability of native forest loss and the x axis the covariate interval. The gray area represents the 95% confidence interval.



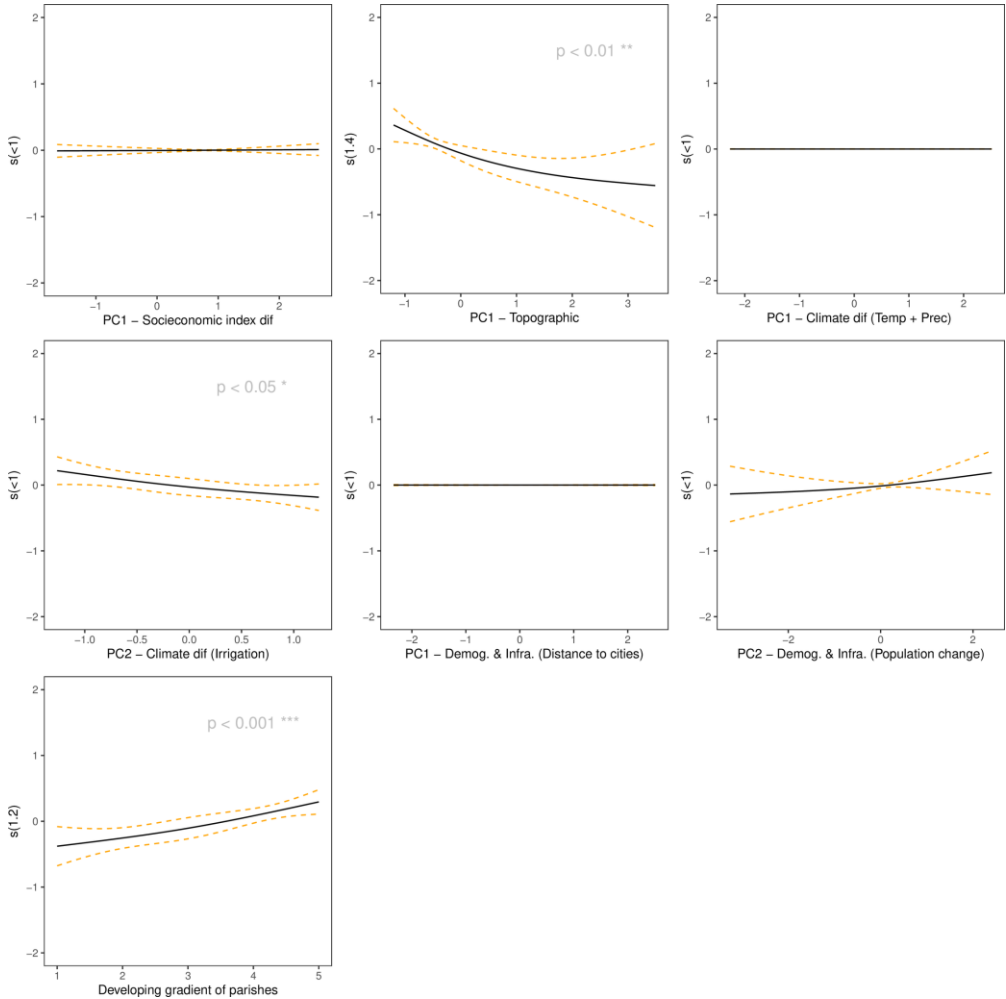
S6 Figure. Generalized additive model partial dependence plots for shrubland loss. Each plot shows a covariate and their partial dependence on probability of shrubland loss in the context of the model. The y axis shows the mean of the probability of shrubland loss and the x axis the covariate interval. The gray area represents the 95% confidence interval.



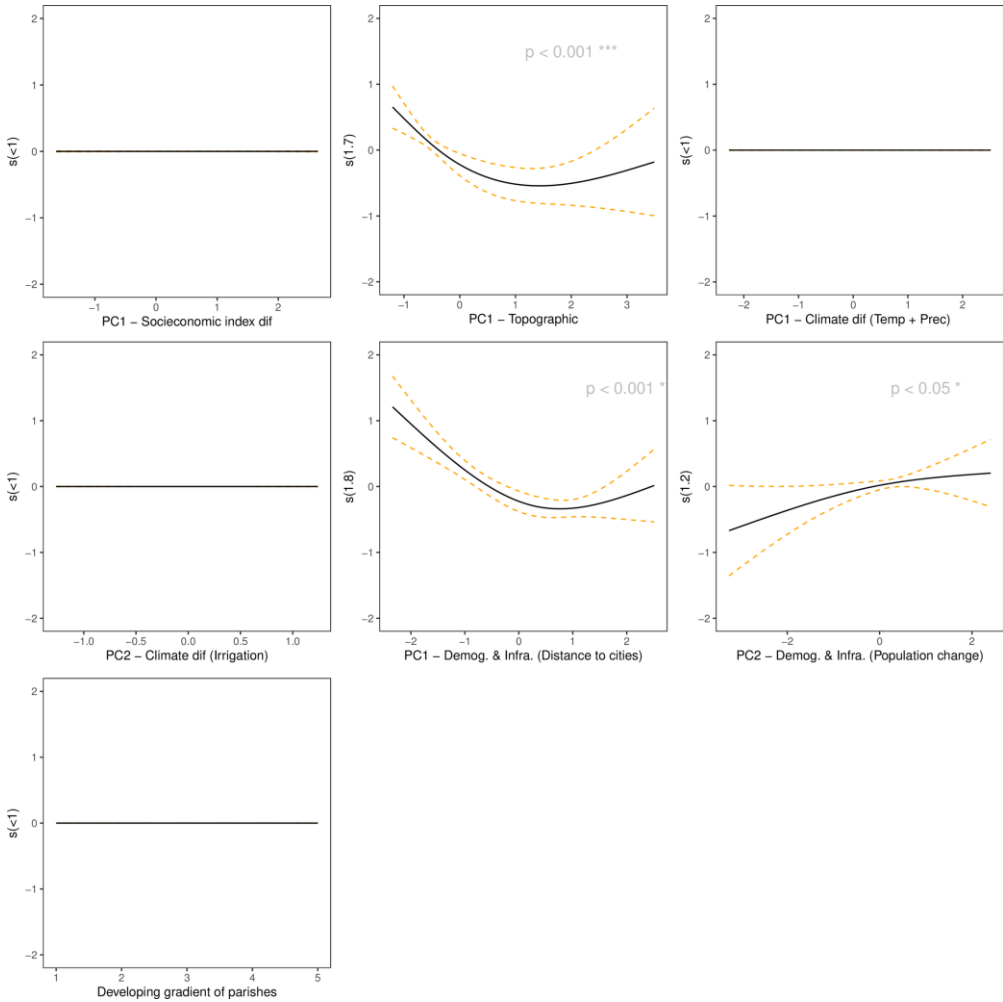
S7 Figure. Generalized additive model partial dependence plots for agricultural transition. Each plot shows a covariate and their partial dependence on probability of agricultural expansion in the context of the model. The y axis shows the mean of the probability of agricultural expansion and the x axis the covariate interval. The gray area represents the 95% confidence interval.



S8 Figure. Generalized additive model partial dependence plots for floriculture transition. Each plot shows a covariate and their partial dependence on probability of floriculture transition in the context of the model. The y axis shows the mean of the probability of floriculture transition and the x axis the covariate interval. The gray area represents the 95% confidence interval.



S9 Figure. Generalized additive model partial dependence plots for urban transition. Each plot shows a covariate and their partial dependence on probability of urban transition in the context of the model. The y axis shows the mean of the probability of native forest loss and the x axis the covariate interval. The gray area represents the 95% confidence interval.

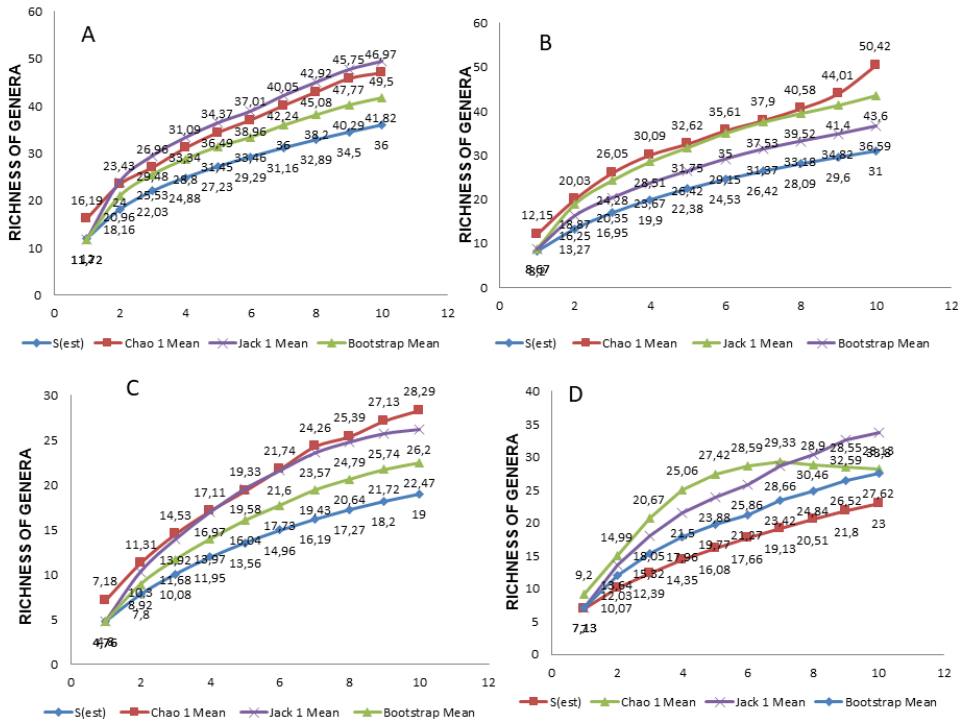


S1 Table. Land Use Land Cover (LULC) classification scheme used to assess LULC change analysis.

N	Class	Description
1	Developed	Land covered by concrete, including road networks, residential, industrial and commercial buildings and other infrastructures
2	Floriculture crop	Areas characterized by green house infrastructures dedicated to grow flowers
3	Agricultural land	Area under agricultural cultivation and planted pastures, or that are within a rotation cycle between them.
4	Planted forest	Anthropically established tree plantations mainly with exotic species
5	Shrubs and Herbs	Areas with a substantial component of non-tree native woody and herbaceous species, with spontaneous growth
6	Native forest	Tree ecosystem, characterized by the presence of trees of different native species, varied ages and sizes, with one or more strata.
7	Paramo	High Andean tropical vegetation characterized by dominant non-tree species that include fragments of native forest typical of the area.
8	Water bodies	Surface and associated volume of static or moving water.

Chapter 3

S10 Figure. Accumulation curve for edaphic macrofaunal genera collected in the land use, (A) Native Forest, (B) Planted Forest, (C) Crop, (D) Pasture.



S2 Table. Clasificación de la cobertura y uso del suelo de la Esperanza.

USE OF LAND LEVEL I	USE OF LAND LEVEL II	DESCRIPTION
FOREST	NATIVE FOREST	Arboreal ecosystem, primary or secondary, regenerated by natural succession with the presence of native trees, of different ages, sizes and strata. Wet black soil with a loamy texture. Human influence is unknown.
	PLANTED FOREST	Tree mass of forest species, established by humans. Tree species of pine and eucalyptus.
AGRICULTURAL LAND	CROP	Land dedicated to agricultural crops, whose vegetative cycle can be seasonal, last from 1 to 3 years or be longer than 3 years. These can be harvested one or more times. Humid soil, very dark gray and a loamy sandy field texture. Production of corn, alfalfa, barley, potato.
	PASTURE	Herbaceous vegetation dominated by introduced species of grasses and legumes, used for livestock.

S3 Table. Classification of edaphic fauna into functional groups.

Funtional Group	Description	Common name
Detritivores	Intervene in the decomposition of organic matter, they are responsible for the shredding of plant and animal remains that make up the litter.	Earthworms, Snails, Mealybugs, Termites
Predators	Consume various invertebrates, modify the equilibrium of their populations and the balance between these and the available resources of the ecosystem.	Centipedes, Millipedes, Spiders, Knee-legged spider, False scorpions, Earwigs
Herbivores	They feed on the living parts of plants and control the amount of plant material that enters the soil.	Beetles, Bed bugs and leaf hoppers, Butterflies and caterpillars, Crickets and grasshoppers
Omnivores	Consumers of all types of material of plant or animal origin	Cockroaches, Ants
Parasities/hematophages	An organism that lives on or within a host organism and feeds at the expense of the host.	Flies and mosquitoes

S4 Table. List of edaphic macrofauna species and functional group.

Order	Family	Genera	Species	Functional Group
Haplotaxida				Detritivores
Haplotaxida	Lumbricidae	Lumbricus	<i>Lumbricus terrestris</i>	
Haplotaxida	Lumbricidae	Eisenia	<i>Eisenia foetida</i>	
Orthoptera				Hervivores
Orthoptera	Gryllidae	Ensifera	<i>Ensifera sp.1</i>	
Orthoptera	Gryllidae	Allonemobius	<i>Allonemobius sp. 1</i>	
Scolopendromorpha				Predators
Scolopendromorpha	Scolopendridae	Scolopendra	<i>Scolopendra ciniculata</i>	
Araneae				Predators
Araneae	Agelenidae	Tegenaria	<i>Tegenaria sp. 1</i>	
Araneae	Ctenidae	Ctenus	<i>Ctenus sp. 1</i>	
Araneae	Cyrtacheniidae	Fufius	<i>Fufius ecuadorensis</i>	
Araneae	Eutichuridae	Cheiracanthium	<i>Cheiracanthium sp. 1</i>	
Araneae	Sicariidae	Loxosceles	<i>Loxosceles laeta</i>	
Blattodea				Omnivores
Blattodea	Blattidae	Blatta	<i>Blatta orientalis</i>	
Coleoptera				Detritivores
Coleoptera	Scarabaeidae	Aspidolea	<i>Aspidolea fuliginea</i>	
Coleoptera	Dermestidae	Dermestes	<i>Dermestes maculatus</i>	
Coleoptera	Scarabaeidae	Heterogomphus	<i>Heterogomphus bouceizii</i>	
Coleoptera	Passalidae	Passalus	<i>Passalus punctiger</i>	
Coleoptera				Hervivores
Coleoptera	Curculionidae	Aphrastus	<i>Aphrastus taeniatus</i>	
Coleoptera	Curculionidae	Cyrtotrachelus	<i>Cyrtotrachelus sp. 1</i>	
Coleoptera	Tenebrionidae	Eleodes	<i>Eleodes pos. omiscoides</i>	
Coleoptera	Curculionidae	Enicmus	<i>Enicmus transversus</i>	
Coleoptera	Curculionidae	Gonipterus	<i>Gonipterus sp. 1</i>	
Coleoptera	Melyridae	Melyris	<i>Melyris oblonga</i>	
Coleoptera	Curculionidae	Naupactus	<i>Naupactus xanthogonibus</i>	

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

Coleoptera	Curculionidae	Sitophilus	<i>Sitophilus sp. 1</i>	
Coleoptera	Elateridae	Agriotes	<i>Agriotes sp. 1</i>	Omnivores
Dermaptera				Predators
Dermaptera	Forficulidae	Forficula	<i>Forficula auricularia</i>	
Diplura				Omnivores
Diplura	Japygidae	Holojapyx	<i>Holojapyx diversius</i>	
Diptera				Detritivores
Diptera	Calliphoridae	Calliphora	<i>Calliphora sp. 1</i>	
Diptera	Mycetophilida	Arachnocampa	<i>Arachnocampa sp. 1</i>	Hervibores
Diptera	Cecidomyiidae	Cecidomyia	<i>Cecidomyia sp. 1</i>	
Diptera	Drosophilidae	Drosophila	<i>Drosophila sp. 1</i>	
Diptera	Oestridae	Gasterophilus	<i>Gasterophilus sp. 1</i>	Parasities/Hematophages
Diptera	Muscidae	Stomoxys	<i>Stomoxys sp. 1</i>	
Mosca	Diptera	Stratiomyidae		Predators
Hemiptera				Omnivores
Hemiptera	Membracidae	Centrotus	<i>Centrotus cornutus</i>	
Hymenoptera				Predators
Hymenoptera	Vespidae	Synoeca	<i>Synoeca surinama</i>	
Hymenoptera	Crabronidae	Trypoxylon	<i>Trypoxylon sp. 1</i>	
Hymenoptera	Aphelinidae	Aphididae	<i>Aphididae sp.1</i>	Omnivores
Hymenoptera	Cimicidae	Cimex	<i>Cimex sp. 1</i>	Parasities/Hematophages
Isopoda				Detritivores
Isopoda	Armadillidiida	Armadillidium	<i>Armadillidium vulgare</i>	
Julida				Hervibores
Julida	Julidae	Julus	<i>Julus terrestris</i>	
Lepidoptera				Omnivores
Lepidoptera	Noctuidae	Agrotis	<i>Agrotis sp. 1</i>	
Lepidoptera	Tortricidae	Cydia	<i>Cydia sp. 1</i>	Hervibores
Lepidoptera	Gelechiidae			
Lithobiomorpha				Predators
Lithobiomorpha	Lithobiidae	Lithobius	<i>Lithobius forficatus</i>	
Opiliones				Predators

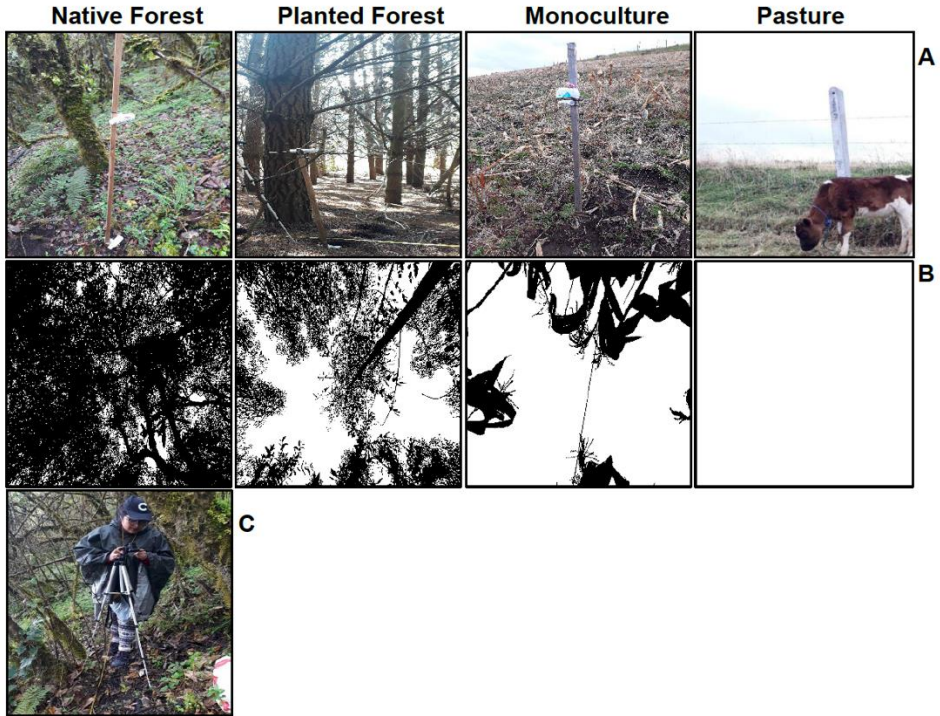
Opiliones	Sclerosomatida	Leiobunum	<i>Leiobunum rotundum</i>	
Opiliones	Phalangiiidae	Phalangium	<i>Phalangium opilio</i>	
Scorpiones				Predators
Scorpiones	Chactidae	Chactas	<i>Chactas gestroi</i>	
Stylommatophora				Detritivores
Stylommatophora	Euconulidae	Euconulus	<i>Euconulus sp. 1</i>	
Stylommatophora	Bulimulidae	Naesiotus	<i>Naesiotus quitensis</i>	
Trichoptera				Detritivores
Trichoptera	Hydropsychid	Hydropsyche	<i>Hydropsyche sp.1</i>	
Trombidiformes				Predators
Trombidiformes	Trombiculidae	Trombicula	<i>Trombicula sp. 1</i>	
Tylenchida				Parasities/Hematophages
Tylenchida	Heteroderidae	Meloidogyne	<i>Meloidogyne incognita</i>	

S5 Table. Resultados del CCA, análisis entre las tipologías de suelo de los parámetros físicos químicos del suelo y las variables de diversidad de la comunidad de macroinvertebrados edáfico

Model CCA Macrofauna Diversity and Soil Environment				
	Df	Chi square	F Pr (> F)	
Model	10	1.6190	1.5488	0.001 *
Residual	29	3.0315		
Signif. codes:	0 '**' 0.001 '*' 0.01 " 0.05 '.' 0.1 ' ' 1			
Model CCA Macrofauna Diversity and Soil Environment (by terms)				
	Df	Chi square	F Pr (> F)	
pH	1	0.20647	1.9752	0.012 *
Organic Carbon	1	0.21526	2.0592	0.002 **
Organic Material	1	0.11189	4.1178	0.345
N	1	0.10220	0.9777	0.471
Tip	3	0.60054	1.9150	0.001 *
P(ln)	1	0.17279	1.6530	0.019 *
Ca(ln)	1	0.08802	0.8421	0.676
K(ln)	1	0.12183	1.1654	0.266
Residual	29	3.03146		
Signif. codes:	0 '**' 0.001 '*' 0.01 " 0.05 '.' 0.1 ' ' 1			
Model CCA Macrofauna Diversity and Soil Environment (by axis)				
	Df	Chi square	F Pr (> F)	
CCA1	1	0.52726	5.0440	0.001 *
CCA2	1	0.26207	2.5070	0.189
CCA3	1	0.20423	1.9537	0.575
CCA4		0.17561	1.6799	0.778
CCA5		0.11891	1.1375	0.994
CCA6		0.09308	0.8904	1.000
CCA7		0.08054	0.7704	0.999
CCA8		0.06288	0.6015	1.000
CCA9		0.05674	0.5428	1.000
CCA10		0.03769	0.3605	0.999.
Residual	29	3.03146		
Signif. codes:	0 '**' 0.001 '*' 0.01 " 0.05 '.' 0.1 ' ' 1			

Chapter 4

S11 Figure. (A) Photographs of the four land use types studied; (B) photographs taken in the four land use types to obtain the gap fraction; (C) example of taking photographs to obtain the gap fraction with the help of a tripod at 1 m from ground level.



Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

S6 Table. ANOVA for the monthly mean temperature in the four land use types at two heights with respect to the soil level (n= 8 for each land use type at each layer).

ANOVA - Average T (°C)

Cases	Sum of squares	df	Mean square	F	p
Types	92.842	3.000	30.947	48.176	<.001
Height	0.719	1.000	0.719	1.120	0.295
Types * Height	1.351	3.000	0.450	0.701	0.556
Residual	35.331	55.000	0.642		

S7 Table. ANOVA for the monthly mean relative humidity in the four types of land use at two heights with respect to the soil level (n=8 for each land use type at each layer).

ANOVA - average RH (%)

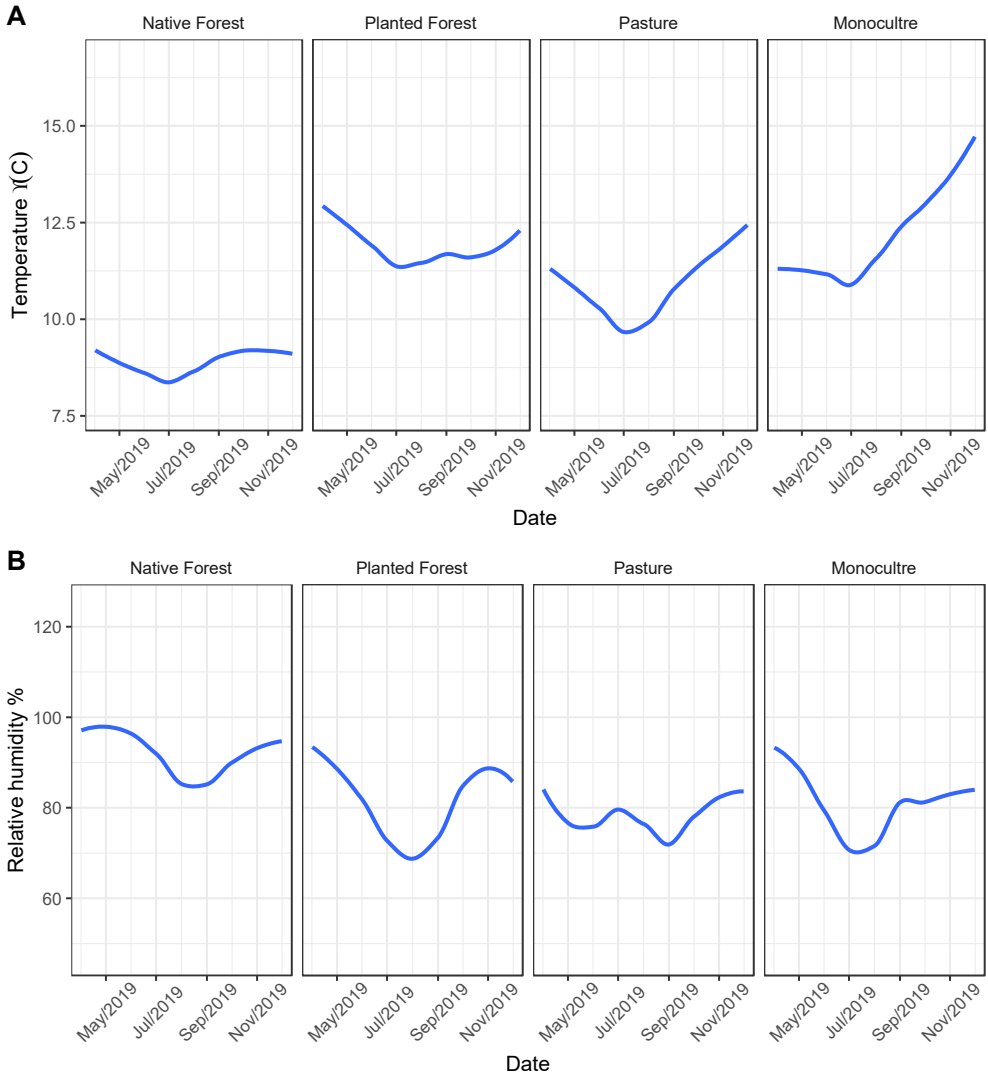
Cases	Sum of squares	df	Mean square	F	p
Types	1792.677	3.000	597.559	7.300	<.001
Height	255.580	1.000	255.580	3.122	0.083
Types * Height	269.135	3.000	89.712	1.096	0.359
Residual	4338.157	53.000	81.852		

S8 Table. ANOVA for the monthly minimum night temperature in the four land use types at two heights with respect to the ground level (n=8 for each land use type at each layer).

ANOVA - min night T (°C)

Cases	Sum of squares	df	Mean square	F	p
Types	209.671	3.000	69.890	27.014	<.001
Height	3.450	1.000	3.450	1.333	0.253
Types * Height	22.428	3.000	7.476	2.890	0.044
Residual	142.296	55.000	2.587		

S12 Figure. Monthly mean temperature (A) and monthly mean relative humidity (B) during the study period between the different types of land use: NF=Native Forest, PF=Planted Forest, PA=Pasture and MO=Monoculture. Dispersion of climatic variables with 95 % confidence interval (gray shade) (n=8 for each land use type).



Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

S9 Table. Correlations between monthly mean relative humidity (RH) and monthly mean temperature (T) recorded in the four land use types (NF=Native Forest, PF=Planted Forest, M=Monoculture, PA=Pasture) (n=16 for each land use type).

Pearson Correlations	Pearson's r	P
Average NF RH (%) - Average NF T (°C)	-0.206	0.445
Average PF RH (%) - Average PF T (°C)	0.501	0.068
Average M RH (%) - Average M T (°C)	0.045	0.874
Average PA RH (%) - Average PA T (°C)	0.105	0.698

Chapter 5

S10 Table. Expert perception survey on the capacity of ecosystems to provide services. Focused on the territory of the Pedro Moncayo canton.

UNIVERSIDAD CENTRAL DEL ECUADOR
FACULTAD DE CIENCIAS BIOLÓGICAS
CARRERA DE CIENCIAS BIOLÓGICAS Y AMBIENTALES

OBJETIVO DEL ESTUDIO

Analizar la percepción social de los bienes y servicios que proveen los distintos ecosistemas del cantón Pedro Moncayo para el bienestar de las comunidades.

CONCEPTOS

Los servicios ambientales o ecosistémicos son aquellos beneficios que se obtienen del ecosistema para mejorar la salud, la economía y la calidad de vida del ser humano. Existen tres categorías.

Los servicios de aprovisionamiento: son aquellos recursos naturales que son esenciales para la supervivencia de las personas. Por ejemplo: el agua, los alimentos, la madera, entre otros.

Los servicios de regulación: El mantenimiento de la calidad del aire y del suelo, el control de las inundaciones y enfermedades o la polinización de cultivos son algunos ejemplos de este tipo de servicio que proporcionan los ecosistemas.

Los servicios culturales corresponden a los beneficios no materiales que las personas obtienen de los ecosistemas. Por ejemplo: los beneficios espirituales, recreativos y educacionales.

ENCUESTA DE PERCEPCIÓN SOCIAL DE LOS SERVICIOS ECOSISTÉMICOS:

Parroquia en la que vive:

Tabacundo

Malchinguí

La Esperanza

Tocachi

Tupigachi

No resido en el Cantón Pedro Moncayo

¿Barrio o comuna dónde reside?

¿Cuántos años reside en su barrio o comuna?

¿Qué edad tiene?

¿Cuál es su género?

Primaria

Linkages between biodiversity and ecosystem services: an assessment of land use change along altitudinal and climatic gradients in the highlands of northern Ecuador

Secundaria (Bachiller)
Tercer nivel (Carrera técnica y tecnológica)
Tercer nivel (Carrera universitaria)
Cuarto nivel (Maestría, doctorado)
Ninguna de las anteriores

¿Cuál es su nivel de Educación?

Primaria
Secundaria (Bachiller)
Tercer nivel (Carrera técnica y tecnológica)
Tercer nivel (Carrera universitaria)
Cuarto nivel (Maestría, doctorado)
Ninguna de las anteriores

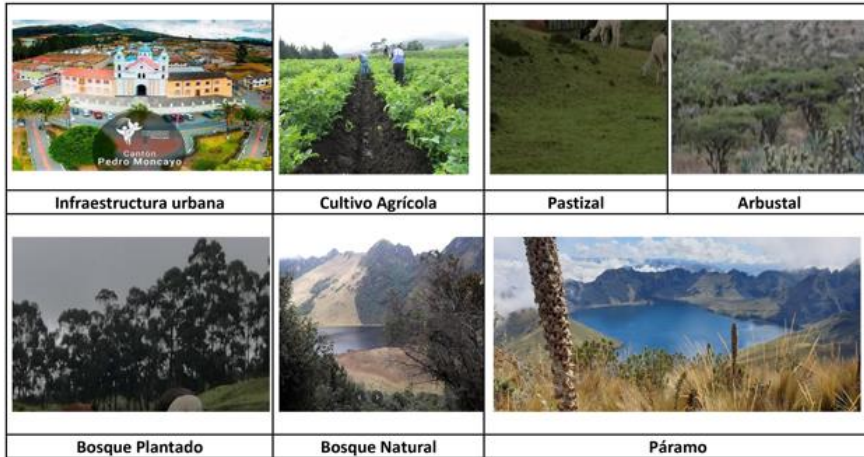
¿Cuál es su situación laboral?

Empleado/a u obrero/a del Estado, Gobierno, Municipio, Consejo Provincial, Juntas Parroquiales
Empleado/a u obrero/a privado
Jornalero/a o peón
Patrono/a
Socio/a
Cuenta propia
Trabajador/a no remunerado
Empleado/a doméstico/a.
No Trabaja
Otro

¿Con qué rama o sector se relaciona el negocio o empleo donde trabaja?

Agrícola- Ganadero
Forestal
Florícola
De comercio/ Servicios
Administración Pública (nacional, cantonal, parroquial, etc.)
Ciencia/ Conservación
Otro

Esta sección es informativa



En la imagen principal se encuentran los diferentes sistemas presentes en el Cantón y en las imágenes de selección (abajo del texto) están los diferentes servicios de APROVISIONAMIENTO que proporcionan. Escoja ¿Cuál cree usted que es el servicio ecosistémico más importante?



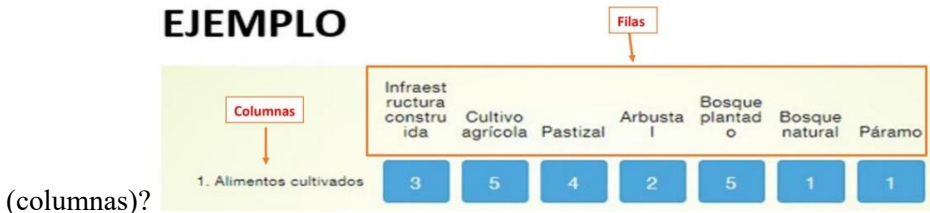
Alimentos Cultivados

Plantas y animales silvestres como alimento

Plantas ornamentales

Percepción sobre los SERVICIOS DE APROVISIONAMIENTO. Indique ¿Cuál de estos sistemas (filas) tiene mayor capacidad para proporcionar cada servicio

EJEMPLO



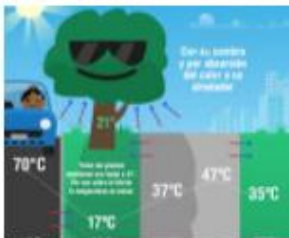
En cada casillero indique el nivel de importancia de 1 a 5, siendo 1 NO IMPORTANTE y 5 EXTREMADAMENTE IMPORTANTE (Ponga un 0 en caso de que no reconozca el servicio ambiental). Como el ejemplo presentado arriba

	Infraestructura construida	Cultivo agrícola	Pastizal	Arbustal	Bosque Plantado	Bosque Natural	Páramo
1. ¿En qué sistema (filas) se puede sembrar más Alimentos cultivados?							
2. ¿En qué sistema (filas) se puede Criar más ganado y animales menores (insectos, etc)?							
3. ¿En qué sistema (filas) se puede encontrar más animales silvestres para consumo y plantas medicinales?							
4. ¿En qué sistema (filas) se puede extraer más madera para construcción y combustible?							
5. ¿En qué sistema (filas) se puede sembrar más plantas ornamentales?							
6. ¿Qué sistema (filas) produce más agua para beber?							

Esta sección es informativa

			
Infraestructura urbana	Cultivo Agrícola	Pastizal	Arbustal
			
Bosque Plantado	Bosque Natural	Páramo	

En la imagen principal se encuentran los diferentes sistemas presentes en el Cantón y en las imágenes de selección (abajo del texto) están los diferentes servicios de REGULACIÓN que proporcionan. Escoja ¿Cuál cree usted que es el servicio ecosistémico más importante?



Regulación climática
(temperatura y humedad)



Control de la erosión y
mantenimiento de la fertilidad
del suelo



Prevención de aluviones
(deslizamiento de la tierra)

Percepción sobre los SERVICIOS DE REGULACIÓN. Indique ¿Cuál de estos sistemas (filas) tiene mayor capacidad para proveer los diferentes servicios ambientales (columnas)?

EJEMPLO

	Infraestructura construida	Cultivo Agrícola	Pastizal	Arbustal	Bosque plantado	Bosque natural	Páramo
9. Regulación climática local (temperatura y humedad)	1	3	2	4	3	5	5

En cada casillero indique el nivel de importancia de 1 a 5, siendo 1 NO IMPORTANTE y 5 EXTREMADAMENTE IMPORTANTE (Ponga un 0 en caso de que no reconozca el servicio ambiental). Como el ejemplo presentado arriba (Recuerde llenar todos los casilleros).

	Infraestructura construida	Cultivo agrícola	Pastizal	Arbustal	Bosque Plantado	Bosque Natural	Páramo
7. ¿Qué sistema (filas) regula mejor la temperatura y la humedad ambiental?							
8. ¿Qué sistema (filas) es el que mejor evita la erosión y ayuda a mantener el suelo fértil?							
9. ¿Qué sistema (filas) es el que mejor previene los deslizamientos de la tierra?							

Esta sección es informativa

			
Infraestructura urbana	Cultivo Agrícola	Pastizal	Arbustal
			
Bosque Plantado	Bosque Natural	Páramo	

En la imagen principal se encuentran los diferentes sistemas presentes en el Cantón y en las imágenes de selección (abajo del texto) están los diferentes servicios CULTURALES que proporcionan. Escoja ¿Cuál cree usted que es el servicio ecosistémico más importante?



Recreación

Ecoturismo

Percepción sobre los SERVICIOS CULTURALES. Indique ¿Cuál de estos sistemas (filas) tiene mayor capacidad para proporcionar cada servicio (columnas)?

EJEMPLO



En cada casillero indique el nivel de importancia de 1 a 5, siendo 1 NO IMPORTANTE y 5 EXTREMADAMENTE IMPORTANTE (Ponga un 0 en caso de que no reconozca el servicio ambiental). Como el ejemplo presentado arriba.

	Infraestructura construida	Cultivo agrícola	Pastizal	Arbustal	Bosque Plantado	Bosque Natural	Páramo
17. ¿De qué sistema se obtiene más información para hacer educación ambiental?							
18. ¿Qué sistema(fila) es el mejor para realizar ecoturismo (estética, amenidad del paisaje y observación de fauna silvestre)?							
19. ¿De qué sistema se obtiene más conocimiento ecológico local?							

¿ De todos los sistemas que evaluó ¿Cuál cree usted que abastece mayor cantidad de servicios ambientales en el cantón Pedro Moncayo?

- Infraestructura urbana
- Cultivo Agrícola
- Pastizal
- Arbustal
- Bosque Plantado
- Bosque Nativo
- Páramo

Gracias por su Colaboración

S11 Table. Outliers from experts' perceptions on the capacity of the ecosystems to provide services

Initial respondents												
	Provisioning services						Regulating services			Cultural Services		
Land use types	Ac	Ca	AsPm	M	Po	A	T y H	E yF	Al	Ea	E	Cl
1	34	34	34	34	34	34	34	34	34	34	34	34
2	34	34	34	34	34	34	34	34	34	34	34	34
3	34	34	34	34	34	34	34	34	34	34	34	34
4	34	34	34	34	34	34	34	34	34	34	34	34
5	34	34	34	34	34	34	34	34	34	34	34	34
6	34	34	34	34	34	34	34	34	34	34	34	34
7	34	34	34	34	34	34	34	34	34	34	34	34
Outliers												
1	0	1	14	2	0	0	4	1	12	3	13	3
2	3	0	3	14	0	4	0	0	1	0	0	0
3	0	5	0	4	1	13	4	0	0	0	0	0
4	5	1	0	0	0	0	0	0	0	0	0	0
5	0	0	0	4	0	0	3	0	0	0	0	0
6	4	3	5	0	3	0	7	0	7	6	4	4
7	11	2	6	13	3	0	4	3	1	5	1	7
Final number of experts included												
1	34	33	20	32	34	34	30	33	22	31	21	31
2	31	34	31	20	34	30	34	34	33	34	34	34
3	34	29	34	30	33	21	30	34	34	34	34	34
4	29	33	34	34	34	34	34	34	34	34	34	34
5	34	34	34	30	34	34	31	34	34	34	34	34
6	30	31	29	34	31	34	27	34	27	28	30	30
7	23	32	28	21	31	34	30	31	33	29	33	27