Land use land cover dynamics through time and their proximate drivers of change in a tropical mountain system: a case study in a highland landscape of northern Ecuador

Land use transitions and drivers of change in a highland landscape of northern Ecuador

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Abstract

Tropical mountain ecosystems are threatened by land use pressures, reducing the capacity of ecosystems to provide a large diversity of benefits to people and to be able to achieve them in the long term. The analysis of land use pressures is often superficial and very general, although they are characterized by numerous interactions and strong differences in their local dynamics. We used a variety of freely available geospatial and temporal data and methods to assess and explain patterns of land use land cover (LULC) change, focusing on native ecosystem dynamics, in a sensitive region of the northern Ecuadorian Andes. Our results demonstrate a dynamic and clear geographical pattern of distinct LULC transitions through time, explained by different combination of socio-economic factors, pressure variables and environmental parameters, from which ecological context variables, such as slope and elevation, were the main drivers of change in this landscape. We found that deforestation of remnant native forest and agricultural expansion still occur in higher elevations located, while land conversion toward anthropic environments were observed in lower elevations to the east of the studied territory. Our findings also reveal an unexpected stability trend of paramo and a successional recovery of previous agricultural land to the west and center of the territory which could be explained by agricultural land abandonment. However, the very low probability of persistence of montane forests in most of the studied landscape, highlights the risk that the remnant montane forests will be permanently lost in a few years, posing a greater threat to the already vulnerable biodiversity and limiting the capacity ecosystem service provisioning. The dynamic patterns through space and time and their explanatory drivers, found in our study, could help improve sustainably resource land management in vulnerable landscapes such as the tropical Andes in northern Ecuador.
Introduction

Tropical mountain systems supply vital ecosystem services to millions of upland and lowland inhabitants [1,2], but are increasingly being transformed by human activities [3,4]. Tropical Andean mountain ecosystems are global hotspots of tropical biodiversity and habitat refugia [4,5] and are threatened by agricultural expansion and intensification, urbanization, pollution, mining, among other human activities, reducing the capacity of these ecosystems to provide a large diversity of benefits to people and guarantee their long-term sustainability.

Although the millennial human presence in the Andean mountain systems has impacted the history of landscape patterns in this region, mainly shaped by intensive traditional agriculture, which has been practiced for centuries [6], recent land-change patterns have been documented in this region [7–10], demonstrating varying patterns of landscape dynamism and heterogeneity [11]. Deforestation and agricultural intensification are the dominant transitions in many Andean systems [8,9], but forest recovery due to agricultural de-intensification and transitions between crops, pastures, and secondary vegetation have also been observed in these systems, yet in-depth multi-temporal change approaches are required to better understand this complexity in order to balance biodiversity conservation with human needs [7,9,12].

Distinct land use and land cover conversion (LULCC) patterns observed in the tropical Andes vary along demographic, socio-economic, cultural and technological factors that interact with biophysical features like elevation, topography, soils and climate parameters [3,13–15], operating across spatial, temporal, and organizational scales [13,14,16]. For example, increasing global demand for food and non-food crops can drive agriculture expansion in more fertile and flat land [7,17–19], where natural ecosystem recovery has been observed in abandoned marginal agricultural land [3,19,20].
Despite the documented useful insights on how different drivers can influence LULCC on specific landscape mosaics in tropical mountain systems, evidence from synthetical studies suggests that no universal link between cause and effect exists to explain LULCC, especially deforestation in tropical systems, where different combinations of various proximate causes and underlying driving forces in varying geographical and historical contexts could affect landscape changes [17,21].

Part of the key to understanding future changes in tropical mountain systems may come from better understanding LULCC pattern-dynamics across environmental gradients and along different temporal scales, in addition to deciphering the interactive effects of distinct anthropogenic influences on these kinds of processes [3], which could be exacerbated, given the high vulnerability to climate change of highland landscapes like the Ecuadorian Andes [22].

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 (eg. water or food) should be assured [23,24] not only for local inhabitants but also for downstream populations[19].

This study is unique in that it uses a variety of geospatial and temporal data and methods to assess and explain patterns of LULCC in a sensitive region of the northeastern Ecuadorian Andes, which comprises a landscape with distinct climatic conditions and management regimes along its elevation gradient, where floriculture crops and urban centres are emerging in an agricultural matrix, posing more pressure to remnant native ecosystems and their services.

The objective of this paper was to assess the role of different drivers on LULCC in a highland landscape of Northern Ecuador from 1990 to 2014, using the Driver-Pressure-State-Impact-
Response (DPSIR) framework [25]. To achieve this objective, we addressed two specific questions: (1) what are the LULCC patterns across geographic and biophysical settings through time, emphasizing in trends on native ecosystems as sentinel habitats, specifically how landscapes are being transformed over time, in terms of the rate, magnitude and direction of those changes and (2) what is the combination of environmental and anthropic factors that better explain the different landscape transitions.

Materials and methods

Study area

Pedro Moncayo county is located in the western branch of the Andes in northern Ecuador (Fig 1). This county is characterized by a wide elevation gradient (2400-4400 m a.s.l) and a management regime that varies in intensity depending on the elevation [26]. The higher altitudinal zone (above 3300 m) is dominated by native ecosystems, represented by paramo and highland montane forests [27]. The middle altitudinal area (2800-3300) has been intensively used for agriculture and livestock through time, causing severe soil degradation [27,28] and the lower lands are characterized by a shrub dominated dry ecosystems (Figs 1 and 2).

Fig. 1. Location of study area (Pedro Moncayo county).

The studied territory has a total surface area of 339 km², which is divided into 5 parishes that have an east to west geographic arrangement, depicting the same elevation belts previously described (Fig 1), however show different levels of production development and population trends; 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 it harbors an expanding agro-industrial sector [26].
Pedro Moncayo is characterised by a typical climate of the tropical Andean region, with low annual variability but significant changes between night and day [29], in addition because of its elevation gradient, quarterly midday maximum temperatures could range from 14°C to 24°C and minimum nighttime temperatures could range from 4°C to 17°C [29]. 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 extension of the territory could shift to a different hydrologic regime [29]. 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 [29].

Approximately 4% of the county’s territory is under conservation or environmental management, 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 (Fig 1) [30].

Although, at present the majority (58.1%) of the territory of Pedro Moncayo is dedicated to traditional agricultural activities mainly for growing cereals, maize and potatoes, the economy of the region is based on the production and export of flowers (mainly roses) using greenhouse infrastructures [30]; small and medium-scale agriculture and livestock ranching are lower in terms of labor absorption, technology incorporation and productivity [27].

**LULC datasets**

Official Land Use Land Cover (LULC) maps from the Ministry of Environment of Ecuador (MAE) of four periods of time: 1990, 2000, 2008 and 2014 were used to generate polygon vector
from Landsat (TM) images with a spatial resolution of 30 meters and a temporal resolution of 16 days [31]. The LULC official classification encompasses a 2-level hierarchical scheme, based on the IPPC classes in combination with a taxonomy agreed by the entities in charge of generating land cover information in Ecuador [31]. Despite possible drawbacks to the LULC datasets, such as the existence of classification errors and uncertainties [32], its accessibility and availability at different time spans offer considerable advantages for studying land cover changes [33].

Five typologies not well represented in the official LULC dataset for the study region were digitised to improve map accuracy [34]. These included: planted forests, developed areas (populated zones), horticulture (areas represented by greenhouses) and natural water bodies.

Composite LANDSAT images from our study area were obtained from the periods of interest (1990, 2000, 2008 and 2014) using the Code Editor of Google Earth Engine [35]. Results of the digitation process were overlapped over the LULC official vector layers from the periods of interest and further rasterized. Digitation, rasterization and overlapping analysis were conducting in QGIS 3.10 [36].

For our LULC change analysis we used a modified categorization from MAE-MAGAP [31], we combined level 1 and 2 official LULC taxonomy (S1Table). Briefly we aggregated all the agricultural level 2 typologies into agricultural land, and as suggested by MAE-MAGAP [31], we included pasture to 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, because the study area corresponds to the major center of floriculture production for the export market in Ecuador [37,38], we added floriculture crop, as a separate typology from the agricultural land.

As a result, the identified LULC classes were 1) developed, 2) floriculture crop, 3) agricultural
Land Use and Cover changes

Firstly, 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 [24].

Then, LULC changes were estimated for three periods of analysis: for 1990-2000 (T1), 2000-2008 (T2) and 2008-2014 (T3). Furthermore, 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 [39–42]. The Markov Chain probability Matrix was estimated, using the markovchain R-package [43] 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 [44]. In the same way, to understand the patterns of LULC change across elevation classes, first the National Digital Elevation Model at a 30 m spatial resolution [45] was clipped to the study area, after that, the resulting image was further reclassified according to elevation bands, with an interval of 500 m [46,47], resulting in the following four elevation bands <2300, 2300-2800, 2800-3300, >3300 (Fig 1); these
groupings take into consideration the mean medium of relief surface roughness, type of forests and the presence of urban areas [46]. 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 the R environment [48].

**Drivers of change**

To understand what predictors could explain the LULC dynamics we tested a set of five group of variables that have previously been reported as possible drivers of change [7,12] and were described in the conceptual framework that interconnects: Driving forces – Pressure – State – Benefits / Impacts- Response adopted by the European Environment Agency [25]; a scheme also used by the Ministry of the Environment of Ecuador as a tool to guide the formulation and adjustment of policies to foster biodiversity conservation in Ecuador [49]. Within this approach, we compiled a dataset of 13 variables of LULCC ranging from (1) socio-economic, (2) topography, (3) anthropic pressures to natural ecosystems, (4) climate and (6) governance decisions toward landscape development (Table 1).

In order to increase the number of units of analysis within parishes, all these variables were obtained at the spatial resolution of census area [50]. After all the spatial data assimilation, processing and visualisation necessary to obtain the drivers at the spatial unit of analysis, we carried out a reduction dimension procedure using Principal Component Analysis [51] of the drivers of change to summarize the distinct variables within the grouping drivers, all these procedures were completed using R software (version 3.2.3) [48]. Correlated variables were screened for the total variation explained by the first principal axes, and used to remove correlated variables [52]. 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.
| Type                  | Name                                    | Units | Description                                                                                                                                                                                                 | Spatial resolution | Source                                                                                          |
|----------------------|-----------------------------------------|-------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------|------------------------------------------------------------------------------------------------|
| Socio-economic       | Education index                        | NA    | Change of a compounded index of eight census indicators of education, with parish breakdown, between years of study                                                                                   | Census areas       | Instituto Nacional de Estadísticas y Censos [53] (1990 y 2001, 2010, 2014*)                   |
|                      | Index of economic diversification of   | NA    | Change of index of economic concentration of employment between years of study                                                                                                                          | Census areas       | Instituto Nacional de Estadísticas y Censos [53] (1990 y 2001, 2010)                         |
|                      | employment                              |       |                                                                                                                                                                                                           |                    |                                                                                                |
| Pressure drivers     | Total population                        | Number of inhabitants | Change of total population between years of study                                                                                                                                                    | Census areas       | Instituto Nacional de Estadísticas y Censos [53] (1990 y 2001, 2010)                         |
|                      | Distance to roads                        | km    | Change of distance to roads or nearest cities, between years of study                                                                                                                                     | 30 m               | Cartography - Instituto Geográfico Militar and digitation from Landsat images (1990, 2000, 2008) |
|                      | Distance to nearest cities               |       |                                                                                                                                                                                                           |                    |                                                                                                |
| Climate factors      | Maximum Temperature                     | °C    | Change of daily maximum air temperatures at 2 metres averaged over each month and summarized in a year                                                                                                    | 1 km               | Chelsa datasets tmax, tmin, prec (1990, 2000, 2008) [54,55]                                  |
|                      | Minimum Temperature                      |       |                                                                                                                                                                                                           |                    |                                                                                                |
|                      | Precipitation                           | mm    | Change of monthly means of daily forecast accumulations of total precipitation at earth surface summarized in a year                                                                                       |                    | Chelsa datasets tmax, tmin, prec (1990, 2000, 2008) [54,55]                                  |
|                      | Water availability by Irrigation        | NA    | Availability of water from the main irrigation system                                                                                                                                                     | 30 m               | digitation from Google images (2008)                                                         |
| Ecological context   | Altitude                                | m     | height in relation to sea level                                                                                                                                                                          |                    |                                                                                                |
|                      | Aspect                                  | degrees | orientation of slope, measured clockwise in degrees from 0 to 360                                                                                                                                         | 30 m               | Digital Terrain Model (SRTM) - Instituto Geográfico Militar                                  |
|                      | Slope                                   | %     | Steepness or the degree of incline of a surface                                                                                                                                                          |                    |                                                                                                |
| Production development | Parrish typologies                     | NA    | Gradient of production development (1-5) based on policy decisions across administrative zones                                                                                                           | parrish            | Land use development plan of Pedro Moncayo county (2015) [26]                               |
**Statistical analysis**

We synthesized and incorporated the different grouping 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 modelling and provide great scope to model complex relationships between covariates [56,57]. We used GAM regressions to elucidate two types of transitions in our study area: 1) the probability of natural ecosystems loss, and 2) the probability to change towards anthropic environments. The LULC trends evaluated as response variables within the first approach were the probability of loss of native forest, paramo and shrubs and herbs; complementary, the second approach tried to explain what drivers could cause the transitions towards developed areas, floricultural crops and food crops pastures. We did not include transitions toward planted forests because this LULC demonstrated 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 PCA that explained more of the 60% of the variation in the multivariate matrix.

The computational methods for the GAM modelling were implemented from the cran repository ‘mgcv’ package [58], since in our study the response variable is a probability ranging from 0 to 1, we used the GAM family as a Beta Regression, as suggested by this type of data [59]. For the smoothing basis function, we use 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 [56]. 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 models, setting the number of knots in three to be flexible enough to allow the models to fit simple curve
relationships and preventing spline curves with complex overfitting estimates, which would have limited the interpretation ability from the ecological perspective. We presented the results of the GAMs with Partial Dependence Plots (PDP) using the ‘mgcv’ R-package [58] to determine which variable best explained the variation in LULC change [56].

Results

Coverage area for each year
Agricultural land was the most representative LULC type in the study area, followed by shrubs and herbs (Fig 2). Both LULC types were very dynamic over the different periods of analysis, agricultural land ranged from 35 to 50% of the total area, depending on the period of analysis (Table 2), and shrubs and herbs varied from 16 to 28% of the total area, depending on the period analyzed (Table 2).

Overall natural ecosystems, which are mainly represented by native forests and paramos, decreased from 1990 to 2014 (Table 2), there was a 40% and 16% decrease of native forest and paramo cover when compared the first and last periods of study (Table 2); but, by the last period of study, areas of paramo still represent an important part (13%) of the study territory. Natural water bodies (lakes and rivers) showed high persistence over time (Table 2).

Developed areas and floricultural crops were continuously increasing 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 2), demonstrating a 26 and 13 times fold of increase from 1990 to 2014, respectively.
Table 2. Changes in land cover classification in Pedro Moncayo county from 1990 to 2014

| LULC Type                  | YEAR | 1990 km² | 1990 % | 2000 km² | 2000 % | 2008 km² | 2008 % | 2014 km² | 2014 % | 2014-1990 Change km² | 2014-1990 Change % |
|----------------------------|------|----------|--------|----------|--------|----------|--------|----------|--------|----------------------|---------------------|
| Developed                  |      | 0.58     | 0.17   | 4.72     | 1.39   | 9.61     | 2.84   | 15.54    | 4.60   | 2569.55              | -10.39              |
| 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  | -16.03               | -13.42              |
| Shrub and Herbs            |      | 73.33    | 21.68  | 94.74    | 28.00  | 53.40    | 15.78  | 77.75    | 22.98  | -20.59               |                      |
| Native forest              |      | 12.96    | 3.83   | 15.11    | 4.47   | 11.29    | 3.34   | 7.77     | 2.30   | -5.22                | -40.03              |
| Paramo                     |      | 50.62    | 14.96  | 50.60    | 14.96  | 40.73    | 12.04  | 42.51    | 12.57  | -8.02                | -16.03              |
| Lake                       |      | 1.48     | 0.44   | 1.52     | 0.45   | 1.52     | 0.45   | 1.66     | 0.49   | -0.08                | 12.29               |
| River                      |      | 1.04     | 0.31   | 1.06     | 0.31   | 1.04     | 0.31   | 1.04     | 0.31   | 0.00                 |                      |
| Total                      |      | 338.29   | 100.00 | 338.33   | 100.00 | 338.29   | 100.00 | 338.29   | 100.00 | 0.00                 |                      |

Landscape dynamics through time was not homogenous along the study area, instead it shows a geographic pattern (Fig 2). Expansion of developed areas and floriculture crops occurred mainly in the southeastern part of the studied region (Fig 2). The greatest degree of loss in native forests and paramos occurred in the northeast (Figs 2 and 3), where there is almost no paramo left due to the expansion of agricultural land.

Land-change dynamics through time

Transitions of native ecosystems

In general, as expected the stability of native forests is decreasing through time in the entire territory (Fig 3), 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 (Fig 3). In contrast, areas located in the east tend to have lower values of stability through time and higher probabilities to change to paramo and agricultural land; this pattern was more evident in
the last period evaluated (2008-2014) (Fig 4). Additionally, this trend is more evident along
elevation bands; where native forests located above 3300 m showed a lower probability of
remaining as forest along the years (Fig 4) and in the 2800-3300 altitudinal belt there is a high
probability of converting native to planted forests, especially in the center of the territory (Fig 4).

Fig 4. Transition probability of native forests through time in Pedro Moncayo county, by altitudinal bands
at the parish level.

Furthermore, shrubs and herbs show variable change throughout the study period (Fig 3).
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 tend 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, where the landscape
seems to have a high probability of remaining as agricultural land (S1 Fig).

In contrast, paramo is the most stable among all 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) (Fig 3), 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 Fig).

Transitions to anthropic environments
Developed areas demonstrate a differential trend through time in the study area (Fig 5). In the
western areas of the territory (Fig 5) 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 the proximity of the larger towns (Fig 5). Since the territory studied is in general a rural area, there is a dynamic trend towards converting agricultural to urban areas, which follow a geographic pattern (Fig 5).

To the east and center of the study area, floriculture crops have not been fully established because it tends to change toward Agricultural land (Fig 5); in contrast this LULC type located in the eastern parishes is more stable with values around 0.75 throughout the period of study (Fig 5).

Agricultural land is a very stable land use class throughout the study period in the administrative zones located in the center and eastern part of the study area with values ranging above 0.77 (Fig 5); the stability of this land use class in the west followed a dynamic trend through time: in the first period of analysis (1990-2000) it was lower than in the second period of analysis and it increased again by the last period of analysis. In contrast, planted forests depict a very stable land use trend throughout the territory, their probability of remaining in the same land use class ranges from 0.6 to 0.90 (Fig 5).

Fig 5. Transition probability to anthropic environments through time in Pedro Moncayo county, at the parish level

Drivers of change

The drivers of change, which are mainly the result of a dimension reduction of distinct variables organized in grouping drivers by PCA analysis, displayed different spatial distribution within the study area (S3 and S4 Figs), depicting a territory with contrasting patterns. The details of the spatio-temporal distribution of the drivers of change are presented in S3 and S4 Figs.
Table 2 describes the results of the different LULC transitions studied and their main explanatory variable; the General Additive Models demonstrated different results when explaining each LULC transition (Table 2). The lowest total variance explained (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 LUCC in the region were the ecological context grouping driver (which incorporates elevation and slope), this grouping driver was highly significant for the majority of the transitions studied (p < 0.001, Table 2), with the exception of the Shrub and Herbs expansion. In contrast, the climate grouping driver PC1 (which depicts mostly the variation of precipitation and minimum temperature) was not significant in any model (p >0.05).

Table 2. Summary of the results of the General 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 |
| 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  |
| ecological context 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  |
| pressure drivers 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 |
| pressure drivers 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  |
| parrish gov              | 0.507   | 0.00   | <1  | 0.118   | 1.46   | <1  | 0.000   | 25.53  | 1.53 | 0.386   | 0.43   | <1  | 0.000   | 10.41  | 1.2 | 0.000   | 31.00  | 1.8 |

Deviance explained:
- 21.00% for native forest loss
- 20.80% for paramo loss
- 39.90% for shrub loss
- 36.50% for urbanization
- 35.00% for Floriculture expansion
- 41.80% for Agriculture expansion

R-sq(adj):
- 0.22 for native forest loss
- 0.15 for paramo loss
- 0.29 for shrub loss
- 0.30 for urbanization
- 0.21 for Floriculture expansion
- 0.33 for Agriculture expansion

For the native forest loss model, the most important grouping drivers (p < 0.001) were the socioeconomic and the ecological context grouping drivers (Fig 6, Table 2). For instance, paramo loss was only explained by the variation in elevation and slope (ecological context PC1) (Table 2, S5 Fig). Figure 6 shows the GAM PDPs 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 has higher values.

Fig 6. Generalized additive model partial dependence plots for forest native 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 grouping drivers such as: shrub loss and
agricultural expansion (Table 2), which also show a contrasting pattern in their response
variables, in such a way that when was prevalent an increase in agricultural areas it was a
decrease in shrub and herb extension (Fig 2); these models depicted the following grouping
drivers as significant parameters (p<0.001): pressure drivers (PC1) and a variable that describes
differences development of the distinct administrative areas within the study area (Table 2).
S7 and S8 Figs shows the GAM PDPs 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 (ecological context drivers), additionally as the main local cities are
further away increases the probability to convert natural areas to agricultural land, 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 ecological context grouping driver, the climate PC2, which includes water
irrigation and the development gradient across parishes. Floriculture crops increase as elevation
and slopes decrease. Complimentary, when more water is available through irrigation, the
probability of establishing floriculture crops increase (S9 Fig).
For instance, the urbanization transition model was explained by ecological context and pressure grouping drivers PC1 ($p<0.001$) (Table 2). Urban transition probabilities decrease significantly ($p<0.001$) with altitude and slope, it also significantly decrease ($p<0.001$) with the distance to the city centers (pressure PC1), and with higher values of total population change (pressure - PC2) (S10 Fig).

**Discussion**

Even though major milestones for landscape transformation occurred centuries ago in the Ecuadorian highlands [6,60–62], our study demonstrates that, at present, a combination of environmental variables and human induced factors still have an impact on an even LULC transformation as reported for other mountainous landscapes of Latin America [7,9,10,12]. The studied area depicts a rural Andean landscape dominated by an agricultural matrix which contains important areas of shrubland and paramo, accompanied by patches of remaining native forest, which is consistent with other current landscapes in the Tropical Andes [7,12,24,62].

We also found a geographic pattern of LULC transition across the study area; we report a clear deforestation pattern of native montane forests located below 3300 m.a.s.l, an unexpected high stability pattern of paramos for the majority of the studied territory and a dynamic transition between agricultural land and shrubland was found; in addition, 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 km$^2$ compared to other landscapes studied in Central Ecuador [62], in the Peruvian Puna [24] or in Colombia [12], where the land extent are 10, 120 and 800 times larger than our studied territory.
We estimated a paramo 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 [63]. Although most of the studied territory depicted a high stability pattern of paramo, as also described for a highland landscape of central Ecuador (Ross et al 2017), our results also demonstrated a hotspot of paramo conversion to agricultural land concentrated in the northeast. In contrast, our results are strikingly different with the land cover patterns observed in other paramos in the region, where a more widespread agricultural use of paramo was observed [64–66]. Although, another common transition reported for paramos in the Ecuadorian mountains is to exotic timber plantations [18], 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 [67]. We also found that the highest chances of loss occur in the altitudinal band of 2800 to 3300 (Fig 3); these findings are in accordance with the findings described for other representative highlands in central Ecuador [62]; however, LULC change studies carried out in more isolated landscapes of central and southern Ecuador reported deforestation hotspot for lowland montane forests and afforestation transition in upper altitudinal areas [10,68]; additionally, higher rates of deforestation was also observed in lowland forest of Colombia, in the Napo region along the Ecuadorean border [12].

Mountain forests are considered one of the most threatened forests in the tropics [69,70], which are also highlighted as a global priority for conservation due to their great biodiversity and high
level of endemism [71], and its vital role in the provisioning of different ecosystem services in
the region [72,73]. 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 [69] and limiting
the capacity of these ecosystems to provide services in the county, such as provisioning and
regulating of freshwater, "wild foods" and many other non-timber forest products [22,74], as
described for other latitudes [75–77].

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.a.s.l.
This pattern could demonstrate a gain of secondary vegetation, probably due to a temporal
abandonment of agricultural areas, follow by a net gain of agricultural land which has been
observed in other Andean systems of Colombia [12] and Central America [78].

We found that urban areas are dramatically increasing in the eastern part of the territory (Fig 1,
Table 1); we reported a 25-fold increase in urban cover from 1990 to 2014. This pattern is
following the global trend of urban expansion [79], but the rate of extension is even faster than
what has been reported for many cities around the world [80] and in small urban centers [81]
[79]. In our study, 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 [79], a zone characterized by areas of lower
altitude and slope, which in the Andean zones correspond 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, Fig 2). 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 [63]. This region, situated in Pichincha Province, 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) which make it possible to produce some of the highest quality flowers in the world [37,38].

Our analysis suggests that in addition to the ecological context variables, another driver that explain the floriculture expansion pattern is the water availability by irrigation, depicted by the geographic pattern of irrigation in the lower eastern part of the studied territory, creating a better environment for growing crops which would have been limited by natural precipitation as demonstrated by [82] 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), and reaches only to the center of the territory and distributes water to lower elevations, therefore only the area situated to south-east receives water for irrigation.

We found that ecological context variables (elevation and slope) are the most important drivers for all LULC transitions. For instance, native ecosystems transitions (including the models to explain loss of native forest and paramo) and agricultural expansion were both significantly related to changes in elevation and slope, in such a way that the probability of native ecosystems
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 paramo models) and even decrease
(shrubs and herbs loss and agricultural expansion models). These complementary trends suggest
that the major pressure for native ecosystems in this highland system of northern Ecuador is still
the expansion upwards of the agricultural-livestock frontier as also found in other Andean
landscapes [12,62]. 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 could
also make pressure for an 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 a nearby future due to the extreme events predicted in the
Tropical Andes [83], affecting the capacity of highland ecosystems to keep providing key goods
and services to people [84].

The trend of native ecosystem loss associated to higher elevation and slope observed in this
landscape of northern Ecuador could be attributed by its past patterns of land use as summarized
by [3,85]; since the most striking transformation and loss of native ecosystems in Andean
landscapes occurred centuries ago and it was even expanded in the mid-twenty century by the
agrarian reform, current native ecosystems are only the remnant patches, localized at higher
elevations and slopes [22]. However, the leveling off and the 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, like
establishing protected areas [3,22,62] or implementing national or local policies to limit
agricultural expansion [4] that have prevented the loss of high mountain ecosystems in other
Andean regions [7,19].
Paramos and other high-elevation ecosystems (pristine native forest patches), which are ecosystems situated above 3500m in the northern highlands of Ecuador, are currently more valued by its importance for provisioning critical ecosystem services and, thus, in Ecuador have received special protection measures at the national [86,87] and local level [88]. Although, other studies [7,12,24] have also found that environmental variables such as topography were better predictors of woody vegetation change, arguing that these variables place physical limits on the types of land-use practices that are feasible in a region, 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 [7,12,24]. However, 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 studies [7,68]. In our study, this pattern was also associated to variation in population change, which could be attributed to population migration dynamics within the territory; movements of farmers from higher mountainous zones to urban concentrated areas have been largely documented in different regions of Latin America and are the drivers associated to natural reforestation in higher elevations due to agricultural land abandonment [19]. This finding is consistent with the local demography dynamics, where urban population has tripled from 1990 to 2010 (from 3000 to 10000 inhabitants) while rural population has doubled (12000 to 23000 inhabitants) in the same period [26]. In many places where this landscape transition was reported it has facilitated ecosystem recovery in the highlands, likewise this has allowed maintaining the provision of ecosystem services for a growing urban population [19]. 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 [89], however in our study area the pattern is
uneven, for instance native forests are decreasing in some areas, while shrubland is expanding in
other areas, picturing a process of ecological succession before a fully recovered forest occurred.
Maintaining and increasing native ecosystems in higher elevations and expanding urban and
agriculture areas in the lowland and valleys raise new opportunities and challenges for
conservation; however, the consequences of these spatial transitions have not been studied in
depth [19].

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 by production support policies geared toward internal market and exports
[21,62], which were not included in our analysis. For instance, other studies suggest that the
greenhouse floriculture expansion initiated in the 1990s was partly in response to favorable trade
agreements but also due to diffusion of technologies from multiple sources and local
entrepreneurship [38]. Flower cultivation is a land- and labor-intensive activity with high land
productivity (that is, high market value of output per hectare) [37]. 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 [37].

All indications suggest that flower exports will continue to play a major and probably increasing
role in Ecuador’s economy [37]; in fact, it is steadily expanding and it 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 aptitude to agricultural production and
with access to irrigation systems have been transformed into green houses for flower cultivation, posing a the trade-offs between agricultural production and environmental concerns, including the asserted need for global land use expansion, and the issues of rural livelihoods and food security [30].

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. This characterization of landscape patterns through time and the analysis of their proximate drivers of landscape change enhance our understanding of how landscape pattern might influence ecosystem services [90] and point out that research and landscape management, zonation and ecological recovery/ restoration should become better integrated into land-use policy and conservation agendas at the local level to balance the multiple needs and benefits from Ecosystems of a growing population in a rural landscape of northern Ecuador [91].

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References

1. Körner C, Ohsawa M, Spehn E, Berge E, Bugmann H, Groombridge B, et al. Mountain systems. In: Hassan R, Scholes R, Ash N, editors. Ecosystems and human well-being: current state and trends,. volume 1. Washington DC,: Island Press; 2005. p. 683–716.
2. Payne D, Spehn EM, Snethlage M, Fischer M. Opportunities for research on mountain biodiversity under global change. Curr Opin Environ Sustain [Internet]. 2017;29:40–7. Available from: http://dx.doi.org/10.1016/j.cosust.2017.11.001
3. Young KR. Andean land use and biodiversity: Humanized landscapes in a time of change. Ann Missouri Bot Gard. 2009;96(3):492–507.
4. Peters MK, Hemp A, Appelhans T, Becker JN, Behler C, Classen A, et al. Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature. 2019;568(7750):88–92.
5. Gradstein SR, Homeier J, Gansert D. The Tropical Mountain Forest Patterns and Processes in a Biodiversity Hotspot. Biodiversi. Gradstein SR, Homeier J, Gansert D, editors. Vol. Biodiversi, Tropical Mountain Forest: Patterns and Processes in a Biodiversity Hotspot. Göttingen: Göttingen Centre for Biodiversity and Ecology; 2008. 35–50 p.
6. Sarmiento FO. Anthropogenic change in the landscapes of highland Ecuador. Geogr Rev. 2002;92(2):213–34.
7. Aide TM, Clark ML, Grau HR, López-Carr D, Levy MA, Redo D, et al. Deforestation and Reforestation of Latin America and the Caribbean (2001-2010). Biotropica. 2013;45(2):262–71.
8. Young KR. Ecology of land cover change in glaciated tropical mountains. Rev Peru Biol. 2014;21(3):259–70.
9. Madrigal-Martínez S, Miralles i García JL. Land-change dynamics and ecosystem service trends across the central high-Andean Puna. Sci Rep. 2019;9(1):1–12.
10. Gaglio M, Aschonitis VG, Mancuso MM, Puig JPR, Moscoso F, Castaldelli G, et al. Changes in land use and ecosystem services in tropical forest areas: A case study in Andes mountains of Ecuador. Int J Biodivers Sci Ecosyst Serv Manag [Internet]. 2017;13(1):264–79. Available from: https://doi.org/10.1080/21513732.2017.1345980
11. Young KR. Causality of Current Environmental Change in Tropical Landscapes. Geogr Compass. 2007;1(6):1299–314.
12. Rodríguez Eraso N, Armenteras-Pascual D, Alumbreros JR. Land use and land cover change in the Colombian Andes: Dynamics and future scenarios. J Land Use Sci. 2013;8(2):154–74.
13. Lambin EF, Geist HJ, Lepers E. Dynamics of land-use and land-cover change in tropical regions. Annu Rev Environ Resour. 2003;28:205–41.
14. Nelson GC, Bennett E, Berhe AA, Casman K, DeFries R, Dietz T, et al. Anthropogenic drivers of ecosystem change: An overview. Ecol Soc. 2006;11(2).
15. Wilson SI, Coomes OT, Dallaire CO. The ‘ecosystem service scarcity path’ to forest recovery: a local forest transition in the Ecuadorian Andes. Reg Environ Chang. 2019;19(8):2437–51.
16. Millennium Ecosystem Assessment. Ecosystems and Human Well Being [Internet]. Washington, DC.; 2005. Available from: http://www.who.int/entity/globalchange/ecosystems/ecosys.pdf
17. Lambin EF, Turner BL, Geist HJ, Agbola SB, Angelsen A, Bruce JW, et al. The causes of land-use and land-cover change: Moving beyond the myths. Glob Environ Chang. 2001;11(4):261–9.
18. Farley KA. Grasslands to Tree Plantations: Forest Transition in the Andes of Ecuador. Ann Assoc Am Geogr. 2007;97(4):755–71.
19. Grau HR, Aide M. Globalization and Land-Use Transitions in Latin America. Ecol Soc 13(2). 2008;113(2):16.
20. Rocha JM. Agricultural Intensification, Market Participation, and Household Demography in the Peruvian Andes. Hum Ecol. 2011;39(5):555–68.
21. Geist HJ, Lambin EF. Proximate causes and underlying driving forces of tropical deforestation. Bioscience. 2002;52(2):143–50.
22. Brandt JS, Townsend PA. Land use - Land cover conversion, regeneration and degradation in the high elevation Bolivian Andes. Landsc Ecol. 2006;21(4):607–23.
23. Hosonuma N, Herold M, De Sy V, De Fries RS, Brockhaus M, Verchot L, et al. An assessment of deforestation and forest degradation drivers in developing countries. Environ Res Lett. 2012;7(4).
24. Madrigal-Martínez S, Miralles i García JL. Land-change dynamics and ecosystem service trends across the central high-Andean Puna. Sci Rep. 2019;9(1):1–12.
25. Kristensen P. The DPSIR Framework. In: Workshop on a comprehensive / detailed assessment of the vulnerability of water resources to environmental change in Africa using river basin approach. Nairobi, Kenya: UNEP Headquarters; 2004.
26. GAD PM. Plan de Ordenamiento y Desarrollo Cantonal Pedro Moncayo [Internet]. 2015. p. 138. Available from: http://www.pedromoncayo.gob.ec/documentos/ord2015/PDOT.pdf
27. Ruiz S. Manejo Adaptativo de Riesgos y Vulnerabilidad en la Zona Lacustre de Mojanda. 2017.
28. De Noni G, Viennot M, Trujillo G. Chapter 13 Agricultural erosion in the Ecuadorian Andes. In: FAO Soils Bulletin. 1996.
29. Cáceres-Arteaga N, Ayala-Campaña O, Rosero-Vaca D, D. Lane KM. ¿Que nos depara el futuro? Análisis climático histórico y proyección de escenarios climáticos futuros para el cantón andino de Pedro Moncayo, Ecuador. Rev Geográfica América Cent. 2018;3(61E):297–318.
30. Gobierno Autonomo Descentralizado Pedro Moncayo. Plan De Ordenamiento Y Desarrollo Turistico. 2015.
31. MAE, MAGAP. Protocolo metodológico para la elaboración del mapa de cobertura y uso de la tierra del Ecuador Continental. Ministerio del Ambiente del Ecuador y Ministerio de Agricultura, Ganadería, Acuacultura y Pesca. 2015.
32. García-Llamas P, Geijzendorffer IR, García-Nieto AP, Calvo L, Suárez-Seoane S, Cramer W. Impact of land cover change on ecosystem service supply in mountain systems: a case study in the Cantabrian Mountains (NW of Spain). Reg Environ Chang. 2019;19(2):529–42.
33. Kroll F, Müller F, Haase D, Fohrer N. Rural-urban gradient analysis of ecosystem services supply and demand dynamics. Land use policy [Internet]. 2012;29(3):521–35. Available from: http://dx.doi.org/10.1016/j.landusepol.2011.07.008
34. Sreedhar Y, Nagaraju A, Murali Krishna G. An Appraisal of Land Use/Land Cover Change Scenario of Tummalapalle, Cuddapah Region, India—A Remote Sensing and GIS Perspective. Adv Remote Sens. 2016;05(04):232–45.
35. Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens Environ [Internet].
36. QGIS Development Team. QGIS (Version 3.1.2A-Coruna) [Internet]. Open Source Geospatial Foundation Project. [cited 2019 Dec 1]. Available from: https://qgis.org/en/site/.

37. Sawers L. Sustainable Floriculture in Ecuador. 2005.

38. Knapp G. Mountain Agriculture for Global Markets: The Case of Greenhouse Floriculture in Ecuador. Ann Am Assoc Geogr. 2017;107(2):511–9.

39. Guan D, Gao W, Watari K, Fukahori H. Land use change of Kitakyushu based on landscape ecology and Markov model. J Geogr Sci. 2008;18(4):455–68.

40. Zhang B, Li S, Jia X, Gao L, Peng M. Adaptive Markov random field approach for classification of hyperspectral imagery. IEEE Geosci Remote Sens Lett. 2011;8(3):973–7.

41. Kumar S, Radhakrishnan N, Mathew S. Land use change modelling using a Markov model and remote sensing. Geomatics, Nat Hazards Risk [Internet]. 2014;5(2):145–56. Available from: http://dx.doi.org/10.1080/19475705.2013.795502

42. Cheng L, Xia N, Jiang P, Zhong L, Pian Y, Duan Y, et al. Analysis of farmland fragmentation in China Modernization Demonstration Zone since “ Reform and Openness”: A case study of South Jiangsu Province. Sci Rep [Internet]. 2015;5(May):1–11. Available from: http://dx.doi.org/10.1038/srep11797

43. Spedicato G. Discrete Time Markov Chains with R. R package version 0.6.9.7 [Internet]. The R Journal. 2017 [cited 2019 Jan 5]. Available from: https://journal.r-project.org/archive/2017/RJ-2017-036/index.html.

44. INEC - Instituto Nacional de Estadísticas y Censos. Clasificador Geográfico Estadístico – DPA [Internet]. Available from: https://www.ecuadorencifras.gob.ec/clasificador-geografico-estadistico-dpa/

45. Rurales SN de I de tierras e infraestructura tecnológica. Centro Geomático Virtual [Internet]. Available from: http://www.sigtierras.gob.ec/descargas/

46. Meybeck M, Green P, Vörösmarty C. A new typology for mountains and other relief classes: An application to global continental water resources and population distribution. Mt Res Dev. 2001;21(1):34–45.

47. Clark M. General Additive Models [Internet]. 2019 [cited 2021 May 2]. Available from: https://m-clark.github.io/generalized-additive-models/

48. INEC (Instituto Nacional de Estadísticas y Censos). Base de Datos – Censo de Población y Vivienda [Internet]. 2020 [cited 2020 Jul 1]. Available from: https://www.ecuadorencifras.gob.ec/base-de-datos-censo-de-poblacion-y-vivienda/

49. Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, et al. Climatologies at high resolution for the Earth land surface areas. Sci Data. 2017;4 170122.

50. Valle C. Reseña Histórica de la Cartografía en el Instituto Nacional de Estadística y Censos [Internet]. 2015. Available from: https://www.ecuadorencifras.gob.ec/libros-metodologicos-inec/

51. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop). 2013;36(1):27–46.

52. Clark M. General Additive Models [Internet]. 2019 [cited 2021 May 2]. Available from: https://m-clark.github.io/generalized-additive-models/
environmental effects on pipe failure in clean water networks. npj Clean Water [Internet]. 2020;3(1):20–2. Available from: http://dx.doi.org/10.1038/s41545-020-0077-3

57. Wood S. Generalized Additive Models: An Introduction with R. 2nd ed. CRC Press; 2017.

58. Hastie T. Generalized Additive Models (gam). CRAN. 2020.

59. Ferrari S, Cribari-Neto F. Journal of Applied Statistics. J Appl Stat. 2004;31(7):799–815.

60. DELER JP, GOMEZ N, PORTAIS M. EL MANEJO DEL ESPACIO EN EL. ECUADOR. ETAPAS CLAVES. GEOGRAFÍA BÁSICA DEL ECUADOR. Tomo II. Quito: Centro Ecuatoriano De Investigación Geográfica; 1983. 239 p.

61. Halliday A, Glaser M. Management Perspective On Social Ecological Systems. Res Hum Ecol. 2011;18(1):1–18.

62. Ross C, Filedes S, Millington AC. Land-use and land-cover change in the páramo of South-Central Ecuador, 1979-2014. Land. 2017;6(3).

63. Wigmore O, Gao J. Spatiotemporal dynamics of a páramo ecosystem in the northern Ecuadorian Andes 1988-2007. J Mt Sci. 2014;11(3):708–16.

64. De S, Andes L, Del U, Charles E, Crissman C. La Agricultura En Los P Aramos: Estrategias Para El [Internet]. Lima; 2003. Available from: http://condesan.org/mtnforum/sites/default/files/publication/files/cds-01_agricultura_en_paramos_opt.pdf

65. Camacho M. Los Páramos Ecuatorianos : Caracterización Y Consideraciones Para Su Conservación Y. An la Univ Cent del Ecuador 372. 2013;76–92.

66. Garavito L. Los páramos en Colombia, un ecosistema en riesgo. Ingeniare, Univ Libr [Internet]. 2015(19):127–36. Available from: http://www.unilibrebaq.edu.co/ojsinvestigacion/index.php/ingeniare/article/view/704

67. Tejedor Garavito N, Álvarez E, Arango Caro S, Araujo Murakami A, Blundo C, Boza Espinoza TE, et al. Evaluación del estado de conservación de los bosques montanos en los Andes tropicales. Ecosistemas. 2012;21(1–2):148–66.

68. Tapia-Armijos MF, Homeier J, Espinosa CI, Leuschner C, De La Cruz M. Deforestation and forest fragmentation in south Ecuador since the 1970s - Losing a hotspot of biodiversity. PLoS One. 2015;10(9):1–18.

69. Ataroff M. Selvas y bosques de montaña. In: Aguilera M, Azócar A, González-Jiménez E, editors. Biodiversidad en Venezuela. Tomo II. Caracas,: FONACIT-Fundación Polar; 2003. p. 762–810.

70. Mosandl R, Günter S. Sustainable management of tropical mountain forests in Ecuador. In: Gradstein SR, Homeier J, Gansert D, editors. The Tropical Mountain Forest Patterns and Processes in a Biodiversity Hotspot. Biodiversi. Göttingen: Göttingen Centre for Biodiversity and Ecology; 2008. p. 177–94.

71. Penningtona RT, Lavin M, Sárkinen T, Lewis GP, Klitgaard BB, Hughes CE. Contrasting plant diversification histories within the Andean biodiversity hotspot. Proc Natl Acad Sci U S A. 2010;107(31):13783–7.

72. Anderson EP, Marengo J, Villalba R, Halloy S, Young B, Cordero D, et al. Consequences of climate change for ecosystems and ecosystem services in the tropical Andes. En: Clim. In: Herzog SK, Martínez R, Jørgensen PM, Tiessen H, editors. Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE); 2011. p. 1–18.

73. Balvanera P. Los servicios ecosistémicos que ofrecen los bosques tropicales. Ecosistemas.

74. Westphal C, Bommarco R, Carré G, Lamborn E, Morison M, Petanidou T, et al. Measuring bee diversity in different European habitats and biogeographic regions. Ecol Monogr. 2008;78(4):653–71.

75. Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, et al. Changes in the global value of ecosystem services. Glob Environ Chang [Internet]. 2014;26(1):152–8. Available from: http://dx.doi.org/10.1016/j.gloenvcha.2014.04.002
736 76. Lawler JJ, Lewis DJ, Nelson E, Plantinga AJ, Polasky S, Withey JC. Projected land-use change impacts on ecosystem services in the United States. Proc Natl Acad Sci U S A. 2014;111(20):7492–7497.

739 77. Millennium Ecosystem Assesment. Ecosystems and Human Well-being [Internet]. Vol. 5, Ecosystems. 2005. 1–155 p. Available from: http://www.who.int/entity/globalchange/ecosystems/ecosys.pdf%5Cnhttp://www.loc.gov/catdir/toc/ecip0512/2005013229.html

743 78. Wassenaar T, Gerber P, Verburg PH, Rosales M, Ibrahim M, Steinfeld H. Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. Glob Environ Chang. 2007;17(1):86–104.

746 79. Seto KC, Fragkias M, Güneralp B, Reilly MK. No TExpansion, A Meta-Analysis of Global Urban Landtide. PLoS One. 2011;6(8):e23777.

750 80. Angel S, Parent J, Civco DL, Blei A, Potere D. The dimensions of global urban expansion: Estimates and projections for all countries, 2000-2050. Prog Plann. 2011;75(2):53–107.

754 81. Moisés OA, Pablo DSJ. Urbanization in ecuador: An overview using the functional urban area definition. Region. 2018;5(3):39–48.

82. Singh D, Sharma R, Bhardwaj S. Micro-irrigation in floricultural crops. Agric Lett. 2020;(August).

83. Vanacker V, Molina A, Torres R, Calderon E, Cadilhac L. Challenges for research on global change in mainland Ecuador. Neotrop Biodivers [Internet]. 2018;4(1):114–8. Available from: https://doi.org/10.1080/23766808.2018.1491706

84. Buytaert W, Cuesta-Camacho F, Tobón C. Potential impacts of climate change on the environmental services of humid tropical alpine regions. Glob Ecol Biogeogr. 2011;20(1):19–33.

85. Hahs AK, McDonnell MJ, McCarthy MA, Vesk PA, Corlett RT, Norton BA, et al. A global synthesis of plant extinction rates in urban areas. Ecol Lett. 2009;12(11):1165–73.

86. Asamblea Nacional del Ecuador. Ley Forestal y de Conservación de áreas Naturales y Vida Silvestre. Ecuador: Registro Oficial - Órgano del Gobierno Nacional del Ecuador; 2004.

87. Asamblea Nacional de la República del Ecuador. Código Orgánico del Ambiente. Ecuador: Registro Oficial - Órgano del Gobierno Nacional del Ecuador; 2017.

88. Ministerio del Ambiente Agua Transición Ecológica. Ministerio del Ambiente, Agua y Transición Ecológica declara a Mojanda como Área de Protección Hídrica [Internet]. Boletín N° 233 MAAE. 2021 [cited 2021 Sep 22]. Available from: https://www.ambiente.gob.ec/ministerio-del-ambiente-agua-y-transicion-ecologico-declara-a-mojanda-como-area-de-proteccion-hidrica/

89. Mather AS, Needle CL. The forest transition: A theoretical basis. Area. 1998;30(2):117–24.

90. Jones KB, Zurlini G, Kienast F, Petrosillo I, Edwards T, Wade TG, et al. Informing landscape planning and design for sustaining ecosystem services from existing spatial patterns and knowledge. Landsc Ecol. 2013;28(6):1175–92.

91. Franco A, Sobral B, Silva A, Wall D. Amazonian deforestation and soil biodiversity. Conserv Biol. 2018;0(0):1–11.

Supporting information

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

S2 Fig. Transition probability of shrubs and herbs through time in Pedro Moncayo county, by altitudinal bands at the parish level.
S3 Fig. Spatial distribution of each grouping driver for the first period of analysis. Each map represents the PC1 from the Principal Component Analysis carried out for each grouping driver of change from the period 1 (1990 and 2000).

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

S5 Fig. Generalized additive model partial dependence plots for forest paramo 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.

S6 Fig. Generalized additive model partial dependence plots for shrubland 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.

S7 Fig. Generalized additive model partial dependence plots for agricultural transition. 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.

S8 Fig. Generalized additive model partial dependence plots for floriculture transition. 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.

S9 Fig. Generalized additive model partial dependence plots for urban transition. 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.

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

analysis [31]
