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AGROECOSYSTEMS

Agroecosystem patterns and land management co-develop through environment, management, and land-use interactions

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Citation: Caulfield, M. E., S. J. Fonte, J. C. J. Groot, S. J. Vanek, S. Sherwood, P. Oyarzun, R. M. Borja, S. Dumble, and P. Tittonell. 2020. Agroecosystem patterns and land management co-develop through environment, management, and land-use interactions. Ecosphere 11(4):e03113. 10.1002/ecs2.3113

Abstract. A poor understanding of the interactions between biophysical and social elements within rural mountainous landscapes can lead to suboptimal management and recommendations. The objective of this study was to contribute to more contextualized natural resource management in a rural landscape in the Ecuadorian Andes by (1) identifying biophysical patterns in soil properties, biodiversity, and C stocks that emerge from natural landscape pedogenic processes, resulting from elevation-induced climate gradients, erosion and soil textural patterns, and (2) assessing farm management and land-use effects on and their interactions with these biophysical patterns. Our findings revealed that the climate and soil texture gradients within the landscape led to an exponential increase in SOC with elevation moderated by slope gradient, indicating significant erosion processes. Farmers adapted their farm management according to the observed environmental patterns creating three distinct management zones. Differentiated agricultural management in these zones and asymmetrical distribution of land-uses in turn were observed to significantly influence soil and agroecosystem properties. For example, available P was found to be significantly higher in the upper and middle agricultural management zones (24.0 and 28.7 mg/kg, respectively), where agricultural inputs were higher compared to the lower agricultural management zone (8.9 mg/kg, $P < 0.001$). Mixed hedgerows, on the other hand, displayed significantly higher Shannon index scores for ground vegetation (1.8) and soil macrofauna (2.0) compared to agricultural land-uses (1.0 and 1.7). Our results provide important insights into how agroecosystem patterns and land management co-developed through complex environment, management, and land-use interactions.

Key words: co-development; Ecuador; elevation; environmental gradients; farm management; socio-ecological systems; soil organic carbon.

Received 19 August 2019; revised 21 January 2020; accepted 28 January 2020; final version received 12 March 2020. Corresponding Editor: Debra P. C. Peters.

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Introduction

Mountainous rural landscapes in the Andes exhibit biological, physical, and social components that interact within multiple dimensions (spatial, temporal, and organizational) and result in complex coupled human–natural systems (Pickett et al. 2005, Cadenasso et al. 2006). While such socio-ecological relationships have long been recognized, the nature and complexity of their interactions remain poorly characterized (Liu et al. 2007). Insufficient understanding of these interactions can result in suboptimal management, unsound policies, and poor decision-making frameworks (Ascher 2001).

In rural Andean landscapes, families often manage fields dispersed throughout a large geographical area that is comprised of diverse topography and micro-climates (Zehetner and Miller 2006, Buytaert et al. 2007, Fonte et al. 2012). These biophysical contexts are shaped by dynamic pedogenic processes that drive the emergence of patterns in soil properties and soil-based agroecosystem functions. This perspective reinforces the idea that soils should be studied as dynamic entities within a landscape, in recognition of the role of landscape processes in shaping and changing soils (Pennock and Veldkamp 2006).

One important natural driver of soil properties within mountainous landscapes is elevation and associated climatic gradients in temperature and precipitation. For example, soil organic matter (SOM) generally increases with elevation in mountainous regions (Leifeld et al. 2009, Nottingham et al. 2015). Underlying these landscape-level patterns are local pedogenic processes. For example, the accrual of SOM is often associated with cooler, moister areas that slow organic matter decay (Lavoie and Bradley 2003, Zehetner and Miller 2006) and/or higher clay content that supports both the physical and chemical stabilization of SOM (Chivenge et al. 2007). These patterns of soil physical and chemical properties across the landscape, in turn, drive multiple aspects of soil health and biological function. For example, in providing energy resources for soil food webs, SOM supports a range of soil biological activity and diversity (Moore et al. 2004), including soil macrofauna communities.

These biophysical contexts shape farmers' agricultural practices and often result in different agricultural management zones across the landscape, where farmers' fields located in each zone are managed distinctly in terms of crops grown, resource allocation, soil preparation, among other factors (Mayer 2002, Li et al. 2013). Farming practices then interact with the biophysical context of the landscape generating complex patterns, often with non-linear responses to landscape gradients. For example, research in the highlands of East Africa has revealed significant socio-ecological interactions, where existing soil fertility gradients determined farmer resource allocation within the farm (Kamanga et al. 2010, Tittonell et al. 2010). As such, farmers would tend to allocate more resources to fields perceived to be more fertile creating a feedback loop where the increased inputs would improve soil fertility, which would consequently increase (perceived) fertility.

While this growing body of work aims to tease apart the complexity in a variety of coupled human–natural systems, much remains to be learned (Ellis and Ramankutty 2008). In this study, we sought to understand different environmental (elevation, geomorphology, and soil texture), farm management (agricultural inputs and cropping patterns) and land-use effects on, and interactions with, key agroecosystem components related to soil fertility and ecosystem functions that are commonly impacted by management and land degradation processes in rural mountain landscapes (soil chemical and physical properties, soil macrofauna communities, ground vegetation and C storage). Specifically, the objective of this research was to contribute to more contextualized and nuanced natural resource management in the region of study by (1) identifying the biophysical patterns in soil quality, biodiversity, and C stocks that emerge from elevation-induced climate and topographic gradients, and (2) assessing how farm management (agricultural inputs and cropping patterns) and land-use interact with these biophysical patterns. We hypothesized that the biophysical patterns of the landscape identified are neither natural or anthropogenic, but a historically dependent outcome of human–environment interactions complexly linked via feedbacks.

Materials and Methods

Site description

The study was carried out between April and May 2015 in an indigenous Kichwa community (Naubug) located in the parish of Flores, Chimborazo Province in the Central Ecuadorian Andes (1°51′24.0″ S, 78°39′15.6″ W). The community is located on a steep topographic gradient facing south to southeast with a maximum elevation of around 3600 m running down to around 2850 m at Cebadas River, part of the Chambo River basin (Fig. 1). Annual precipitation at the highest point in the community was measured to be around 640 mm between 2015 and 2016 by a private weather station, with an average temperature of 9.0°C. A public weather station (Guaslan M0133) ran by INAMHI (the National Institute for Meteorology and Hydrology) located at a similar elevation to the lowest part in the community (2850 m asl) a couple of km away, indicated an important climate gradient within the landscape, recording a lower average annual precipitation rate of 592 mm, but a higher average annual temperature of 14.2°C. Rain in the parish of Flores mostly falls between January and June with a drier, windier period from July to December (GAD de Flores 2015). The long-term pedogenic processes of the region are dominated by volcanic activity with pyroclastic deposits which gave rise to the formation of relatively uniform and thick layers of hardened volcanic ash upon which lie volcanic (Andisol) soils. The A horizon of the soils in this area is usually stone free and relatively rich in organic matter having developed under cool, moist conditions and natural dense vegetation (either grass páramo at the higher elevations; sub-páramo between 3000 and 3500 m asl or Andean forest below 3000 m asl; De Noni et al. 2001, Zehetner et al. 2003, Zehetner and Miller 2006). Most of the households of Naubug are located in the middle to upper elevations of the landscape (between 3200 and 3500 m asl). However, in this intensively farmed rural landscape, nearly all remnants of páramo, sub-páramo, and Andean forest vegetation types have been removed resulting in erosion and exposure of low organic matter sub-soils composed of hardened volcanic ash, known locally as cangahua (Podwojewski and Germain 2005). In these areas where significant erosion has occurred, soils can be classified as either inceptisols or entisols. Subsistence farming dominates the landscape with only small quantities of crops and livestock being sold at the local market of Cebadas. Potato (*Solanum tuberosum L.*) comprises the most important crop in the community and the largest investment in terms of area and agronomic inputs (e.g., manure, fertilizer, pesticides). Potato and cut forages dominate the middle and upper elevations of the landscape, but quinoa (*Chenopodium quinoa*) has become an increasingly popular crop in these zones as well. The lower elevations are mainly dedicated to the production of maize (*Zea mays*) and barley (*Hordeum vulgare L.*). Weather conditions enable nearly year-long production in the upper and middle elevations, and therefore, these areas can be cultivated twice a year. Agricultural fields in the lower slopes are up to an 1.5-h walk from homesteads, are generally considered to have poorer soils, a lower precipitation to evapotranspiration ratio, and are only cultivated once per year.

Participatory mapping and determination of land-uses

In order to develop a land-use map of the community, a user-consultative participatory mapping process was developed and applied based on the International Fund for Agricultural Development's (IFAD) Review of Good Practices in Participatory Mapping (2009). This process involved three main steps: (1) presentation of the research project to the community in order to raise awareness, inform, and encourage participation; (2) identification and mapping of the dominant land-uses via three workshops with key local stakeholders to identify important land-uses on a printed orthophoto (1.8 × 1.5 m; 0.3 m resolution; taken in 2012) of the community (resulting land-uses and polygons were then digitized using QGIS Desktop 2.4.0); and (3) ground-truthing (via transect walks) and presentations of the map to key stakeholders to verify the location of the polygons and make any necessary adjustments.

Sampling methodology

Randomly generated sampling points within the landscape were stratified by land-use and elevation (agricultural management zone).

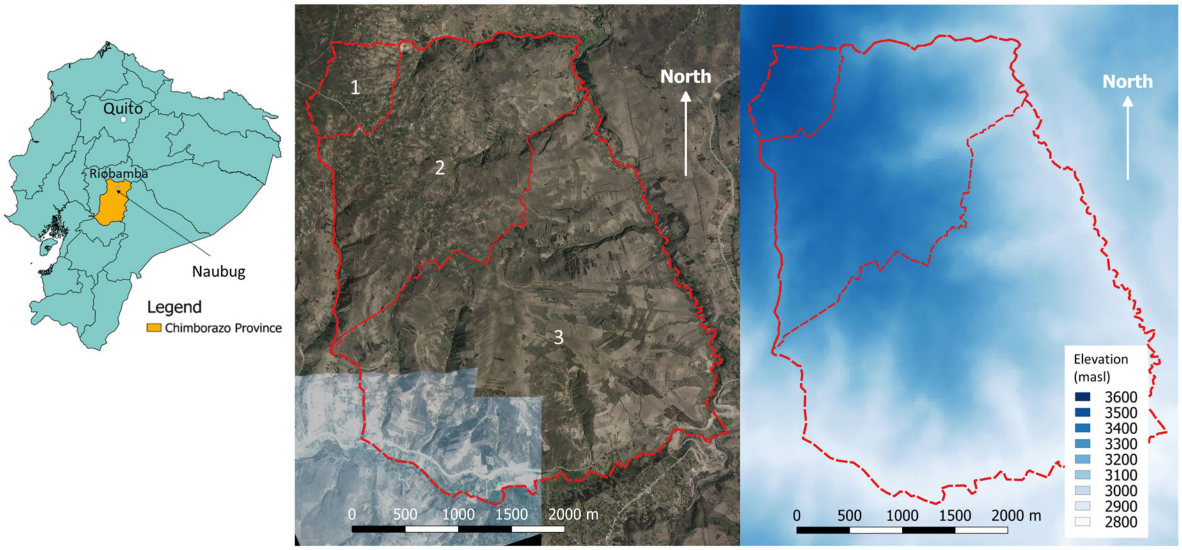

Fig. 1. Left: Map of Ecuador with the province of Chimborazo highlighted and the study site indicated (Community of Naubug, Flores Parish); center: outline of Naubug community boundaries with the three agricultural management zones delineated (1. Upper Agricultural Management Zone; 2. Middle Agricultural Zone; 3. Lower Agricultural Management Zone); right: outline of Naubug community boundaries with the elevation gradient displayed.

While agricultural land-use and mixed hedgerows were found throughout the landscape, other land-uses were restricted to either a small range within the upper and top end of the middle agricultural management zones (in the case native tree hedgerows and grass strips) or the middle and lower agricultural management zones (in the case of abandoned agricultural land and forested land). Sampling occurred at 91 points across the landscape (Table 1). At each point, a 10 × 20 m sampling area was delineated for a suite of soil and vegetation measurements. Slope and elevation were also noted at the center of this area.

At each sampling point, three equally spaced sub-sampling points were located along a 20-m transect running through the center of each sampling area. For each sub-sample point, a soil monolith (25 × 25 cm and 20 cm deep) was excavated for evaluation of soil macrofauna communities and other soil parameters. Soil from the three monoliths was combined into a composite sample used for characterization of soil chemical fertility. Soils were air-dried and transported to the laboratory of the Ecuadorian National Institute for Agricultural Research (INIAP) for analysis of texture (Bouyoucos 1962), soil organic carbon (SOC; Walkley and Black 1934), and available P (Olsen method; Olsen et al. 1954). Bulk density was assessed by inserting a cylinder (~7 cm diameter × 6 cm long) into the side wall of each soil monolith at two depths, 1–8 cm and at 11–18 cm. The extracted soil was then dried before calculating bulk density.

Soil macrofauna were assessed by excavation and hand-sorting of all macro-invertebrates (>2 mm) from the soil based on methods outlined by Anderson and Ingram (1993). Specimens were collected in 70% ethanol (or 4% formalin for earthworms) and then brought to the laboratory for identification, generally to the order level.

Ground vegetation (vegetation excluding trees and larges bushes) was also evaluated at three points adjacent to the monoliths using a 0.64-m^2 square frame. Each species (or morphospecies) was noted, and the area of each was visually estimated within the frame. In agricultural land-uses, the dimensions of the area evaluated were slightly modified to conform with the width of the planting rows, such that ground cover was measured in an area of 1 m× the width between two rows. For both macrofauna and vegetation,

Table 1. Description of the different land-uses identified in Naubug, Ecuador, using a participatory mapping process and characterization according to dominant vegetation and management types.

Land-use	Description	Surface area by zone† (ha)	Total surface area (ha)	No. samples
Agricultural land (Ag)	Agricultural fields that have been cultivated within the last two years. Three sub-categories of this land-use were also identified: the upper agricultural management zone, the middle management agricultural zone, and the lower agricultural management zone			
	Upper Ag Zone: Intensive year-round cultivation with maximum 1–2 months between harvest and planting. Crop rotation typically characterized by potatoes followed by two cycles of forage crops. OM and fertilizer inputs and pesticide use are usually restricted to the potato crop. Typical OM inputs vary between around 2–7 Mg/ha (fresh weight), although some farmers reported even higher levels of inputs.	...	56.1	10
	Middle Ag Zone: Intensive year-round cultivation with maximum 1–2 months between harvest and planting. Crop rotation typically characterized by potatoes followed by cereals for human consumption and then either a forage crop or another cereal crop for human consumption. OM and fertilizer inputs and pesticide use are usually restricted to the potato crop. Typical OM inputs vary between around 2–7 Mg/ha (fresh weight), although some farmers reported even higher levels of inputs.	...	294.76	16
	Lower Ag Zone: Less intensive cropping cycles with 4–6 months between harvest and planting (one crop per year). The main crops are maize and barley. Little, if any, OM and fertilizer inputs are used.	...	200.56	10
Abandoned agricultural land (Ab)	Agricultural fields that have not been cultivated in the recent past and which the owners no longer intend to cultivate in the foreseeable future (this is usually a result of either emigration or declining yields). This land-use is present in lower and middle agricultural management zones.	0.07; 76.12; 195.18	271.37	10
Eucalyptus and/or Pine Forests (For)	Areas of land that have been planted with eucalyptus and/or pine trees for the purpose of either providing a source of firewood or for sale as timber. This land-use is present in lower and middle agricultural management zones.	0.00; 11.41; 22.83	34.24	10
Native tree hedgerows (TH)	Hedgerows that have been planted by farmers surrounding fields composed of local native trees such as Yagual (Polylepis incana and Polylepis reticulata), Andean Alder (*Alnus acuminata*), Lime (*Tilia*), Kishuar (*Buddleia incana*), and Andean lupin (*Lupinus mutabilis*). This land-use is present in middle and upper agricultural management zones.	0.24; 0.47; 0.00	0.71	10
Grass strips (GS)	Hedgerows that have been planted comprising primarily of bulbous canary-grass (*Phalaris tuberosa*). This land-use is present in middle and upper agricultural management zones.	0.49; 0.99; 0.00	1.48	10
Mixed hedgerows (MH)	Hedgerows comprising of a variety of different types of vegetation: trees, bushes, and grasses. This land-use is present in all of the agricultural management zones.	2.38; 4.77; 7.15	14.30	15
Inaccessible land	Land that is inaccessible, usually comprising of very steep canyons. No sampling was conducted in these areas due to its inaccessibility.	...	349.19	NA

Notes: The number of sampling points for each land-use is also indicated. These points were stratified by the elevation with between 10 and 16 sampling points per land-use. See Appendix S1 for photographs of the landscape and examples of the different land-uses.

† Values are presented in the order upper, middle, and lower agricultural management zones.

diversity was estimated using the Shannon index based on the number of taxonomic groups encountered and their relative abundance (Shannon 1948).

Upon evaluating the cover of all plant species in each 0.64-m^2 frame, vegetation was cut at a 1–2 cm height and weighed in the field. A representative sub-sample of this material was taken to the laboratory and dried in an oven at 60°C to determine the biomass of ground vegetation on a Mg/ha basis (excluding shrubs or trees). All agricultural land-use sampling points were measured when the crops were at or nearing physiological maturity.

For land-use other than agriculture (hedgerows, grass strips, forests, and abandoned land), vegetation in the four quadrants of the 200-m^2 sampling area was categorized into three types: shrubs, small trees, and large trees. Measurements included the volume (height, width, and length) of all the shrubs (Conti et al. 2013) and diameter at breast height (1.3 m; DBH) of all small trees (<10 cm DBH) found in 2 of the 4 quadrants of each sampling area. For large trees (>10 cm DBH), DBH was measured in the entire 200-m^2 sampling area (Van Breugel et al. 2011). Allometric equations from (Kearney et al. 2019) and from the GlobAllomeTree database (www.globallometree.org) were then used to calculate the biomass. Aboveground biomass components were then summed to determine total aboveground biomass. This was converted into aboveground C stocks by assuming a 50% C content (Giese et al. 2003).

Belowground biomass of the vegetation was estimated by assuming a shoot-to-root ratio of 1:0.205 according to Knoke et al. (2014) and Mokany et al. (2006). Belowground C stocks were estimated assuming 45% C content in roots (Gayoso and Schlegel 2001). SOC was multiplied by bulk density data to estimate C stored within the surface 20 cm of each sampling area. Total C stocks in above- and belowground biomass as well as in soils were reported on a Mg/ha basis.

Statistical analyses

All analyses were conducted using the average of the sub-samples within each sampling location. To identify interactions between management and environmental factors within the landscape, multiple linear regression was applied to a set of predictor and response variables. The main predictor variables tested were elevation (as a continuous variable) and land-use, treated as a categorical predictor variable. Response variables analyzed include the following: clay and sand content, SOC, available P, macrofauna diversity, vegetative diversity, and C stocks. The linear regression models were built using a forward step-wise approach, first testing for associations between the response variable and elevation with land-use as an additive variable, and then testing for interactions between elevation and land-use. Predictor variables and interactions with a $P > 0.15$ were removed from the final linear regression models. Post hoc Tukey's honestly significant difference test were applied to explore differences between land-uses, when significant.

A further linear regression model was built to test the effect of topography (slope) on the relationship between SOC and elevation, thereby assessing the potential influence of erosion processes on soils in this landscape. Furthermore, ANOVA with a post hoc Tukey's honestly significant difference test was applied to explore the effects of different agricultural management (between the agricultural management zones) on SOC and available P given their differentiated sensitivity to environmental and management factors (van Apeldoorn et al. 2014). All analyses were carried out within the RStudio environment Version 1.1.453 for R (Version 3.5.1, R Foundation for Statistical Computing, Vienna, Austria) using the packages agricolae, emmeans, and ggplot2. Assumptions of homoscedasticity and normality were tested and data transformed as needed using either the log or exponential function.

RESULTS

Participatory land-use mapping

The participatory mapping identified six dominant land-uses located across the landscape (in addition to inaccessible land); these included agricultural land (in three separate agricultural management zones), abandoned agricultural land, eucalyptus and/or pine forest, and three types of hedgerows (native trees, grass strips, and mixed vegetation). Land-uses were asymmetrically distributed such that a greater proportion of forest and abandoned agricultural land were found in the lower elevations of the landscape. In the upper elevations, agricultural land dominated and was interspersed with hedgerows. The three agricultural management zones varied in elevation and management regime (farming intensity, cropping patterns, and inputs, see Table 1 and Fig. 1). Farmers reported that the differences in agricultural management between zones were a result of varying biophysical conditions (climate, soil fertility, and productivity) and distance from homestead. Specifically, farmers reported that cultivation focus differed between the upper and middle zone due to climatic conditions, while inputs were much lower in the lower zone due to poor productivity and distance from homestead.

Soil texture and soil chemical properties

The regression model for soil sand and clay content displayed significant effects of elevation in that clay content increased by 2.5 percentage points per 100 m increase in elevation (Fig. 2), while the soil sand content decreased by 3.2 percentage points for every 100 m increase in elevation (Table 2; Appendix S2: Table S1).

SOC increased exponentially with elevation (Fig. 3A, Table 2). Land-use also had a significant influence on SOC. However, a significant interaction between elevation and land-use suggested that the response of SOC to elevation differed significantly with land-use such that agricultural land-uses displayed the strongest effect (SOC increasing 1.5 times per 100 m increase in elevation) and forest the weakest effect (increasing just 1.05 times per 100 m increase in elevation; Fig. 3A, Table 2; Appendix S2: Table S2). While hedgerows tended to have higher SOC overall (Appendix S2: Table S2), the strength of effect of elevation on SOC under agricultural land-use meant that at the lowest elevations SOC displayed the lowest levels (minimum 0.21%), while in the upper elevations of the landscape it surpassed the other land-uses, exhibiting the highest levels (maximum 4.70%; Fig 3A, Appendix S2: Table S2). Significant interactions between elevation and slope on SOC were also evident, with the effect of elevation decreasing at sites with steeper slopes (Fig. 4).

Available P displayed significant effects and interactions for elevation and land-use. Abandoned land, forest, and tree hedgerows land-uses decreased in available P with elevation, while agricultural land-uses, grass strips and mixed hedgerows increased with increasing elevation (Table 2). The three types of hedgerows displayed higher levels of available P compared to the other land-uses. It is noteworthy that agricultural land exhibited the largest range of available P (4.2–96.0 mg/kg), indicating large variability (Table 2; Appendix S2: Table S2).

When exploring the effect of the agricultural zones on soil chemical properties, SOC levels increased from lower to higher zones, while available P showed no significant difference between the upper and the middle agricultural management zones, but presented significantly lower levels in the lower agricultural management zone (Fig. 5).

Biodiversity and carbon stocks

Vegetative diversity displayed a significant relationship with land-use. Mixed hedgerows displayed significantly more diversity (measured on the Shannon index) of ground vegetation (1.8) than forested (1.3), agricultural (1.0) and grass-strips (1.0) land-uses (Fig. 6A; Appendix S2: Table S2). For macrofauna diversity, significant differences were found among land-uses, with the highest levels of macrofauna diversity observed in mixed hedgerows (1.9) and the lowest under forest land-uses (1.1; Fig. 6B, Table 2).

Total C stocks (above- and belowground) increased exponentially with elevation (Fig. 3B, Table 2). Total C stocks also displayed significant differences between land-uses, exhibiting highest levels in land-uses with perennial components, such as eucalyptus/pine forests, mixed hedgerows, and tree hedgerows. A significant interaction between elevation and land-use was also observed for C stocks, such that agricultural land-use displayed a stronger effect of elevation (C stocks increasing by 1.45 times per 100 m increase in elevation) than other land-uses (Fig. 3B, Table 2; Appendix S2: Table S2).

DISCUSSION

Our findings highlight the biocomplexity of rural Andean landscapes and provide strong evidence that both natural and anthropogenic factors contribute to the emergence of distinct biophysical patterns. Pedogenic factors such as climate and geomorphology are clearly responsible for landscape-scale processes that contribute to biophysical patterns, which subsequently influence, and are influenced by, farm management and land-use (Fig. 7A). This finding supports our hypothesis that the biophysical patterns of the landscape are dependent on human–environment interactions complexly linked by feedback loops.

Environmental drivers of agroecosystem patterns

In this study, important patterns in the landscape were observed for soil chemical properties, such that SOC displayed an exponential, positive association with elevation (Figs. 3A, Table 2). This finding corroborates past research (e.g., Chatterjee and Jenerette 2015, Badía et al. 2016) that reported significant effects of elevation on soil properties. Part of the explanation for the SOC gradient observed in the landscape is linked to the parallel pattern in soil texture which saw soil clay content also increase with increasing elevation (Fig. 2). Clayey soils are known to better stabilize SOM than sandy soils, which has important implications for nutrient management and availability, and subsequent impacts on productivity (Chivenge et al. 2007). However, given the large elevation range, climatic conditions (i.e., temperature and precipitation) are also important pedogenic factors across the studied landscape. Such gradients in temperature (an annual average of 9°C in the upper agricultural management zone vs. 14°C in the lower zone) are also likely to contribute to greater SOC accrual in the upper parts of the landscape due to slower organic matter decomposition in cooler climates (Lavoie and Bradley 2003, Zehetner and Miller 2006), thus creating a synergistic (exponential) driver with the soil textural properties.

Furthermore, the influence of topography on SOC is also evident, such that the effect of elevation on SOC decreased with increasing slope (Fig. 4). This suggests that erosion processes may be significant in the landscape, and is supported by two studies in the Ecuadorian Andes reporting average erosion rates of 25 $\mathrm{Mg{\cdot}ha^{-1}{\cdot}yr^{-1}}$ in the study region (Molina et al. 2008, Henry et al. 2013).

Total C stocks also increased with elevation (Fig. 3B, Table 2) suggesting an important role for the climatic gradients with regard to this agroecosystem function. While aboveground biomass variation accounts for some of this relationship, the increase in SOC with elevation also played an important role as a reservoir of C. Takimoto et al. (2008) found that in non-forested areas, such as croplands and abandoned land, soil C accounts for up to 95% of C stocks, while in forested parkland this figure was still between 38% and 55%.

Biophysical context drives farm management and land-use

Given the strong environmental gradients across this landscape, our findings highlight the need for context-specific management to address the relative benefits and limitations of different fields. Delineation of the landscape into three agricultural management zones (broadly along elevation lines) by farmers during the community mapping process provided clear evidence that this is already occurring. For example, the relatively fertile, organic matter rich top soils of the upper and middle agricultural management zones differ in terms of cultivation focus, with a greater proportion of the upper zone crop rotations dedicated to forage crops compared to the middle zone (Table 1). As reported by farmers in the participatory community mapping, the temperature gradient within the landscape is likely an important determinant of the variation in cultivation focus between zones, as lower average temperatures in the upper elevations lead to slower crop development and this may be balanced by a greater focus on forage crops, which take comparatively less time to reach harvest. On the other hand, the lower fertility status of the soils, greater distance from homesteads, and lower precipitation in the lower agricultural management zone likely explain why farmers use this area less intensively than the upper and middle zones, planting a maximum of one crop per year. Differences in productivity were also reasons why farmers reported they were less willing to invest resources (e.g., manure inputs) into the lower agricultural management zone compared to the other two zones (Table 1). This analysis reflects the work of Mayer (2002) who described how farming households in the Andes tended to manage land distinctly based on local knowledge with regard to environmental variation in mountain ecosystems.

As observed during the participatory landscape mapping, land-uses were distributed asymmetrically throughout the landscape (Table 1). No patches of eucalyptus or pine forest and very little (0.07 ha) abandoned land were recorded in the upper zone, while the lower zone displayed the greatest proportion of these types of land-use, with forest and abandoned land accounting for 3% (22.83 ha) and 26% (195.18 ha) of the total land area of the lower zone, respectively.

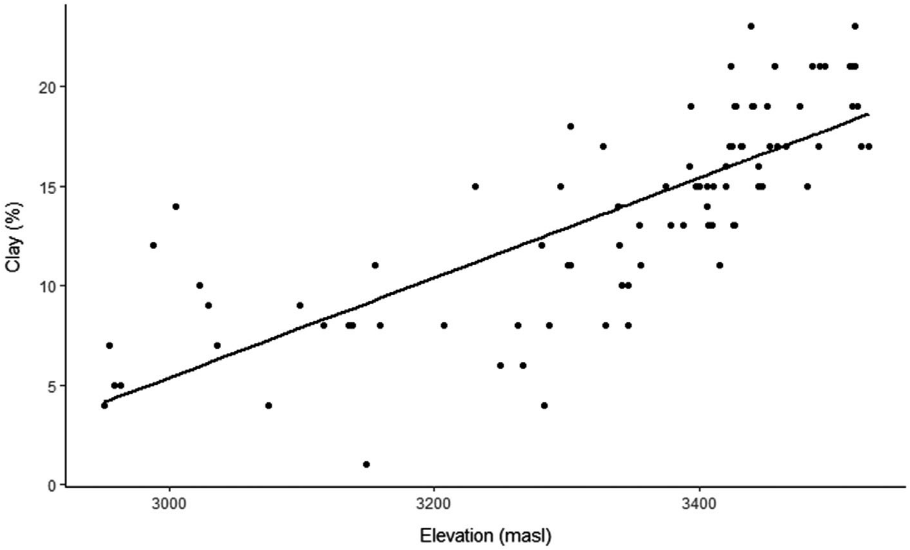

Fig. 2. Relationship between elevation (m asl) and clay content (%) within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador.

Table 2. Summary of the multiple linear regression analyses applied to the biophysical response variables within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador.

Response variable	Elevation	Land-use	Interaction *p*-value	R^2
Clay	**<0.001**	0.322	. . .	0.60
Sand	**<0.001**	0.585	. . .	0.44
SOC	**<0.001**	**0.019**	**<0.001**	0.75
Available P	**<0.001**	**<0.001**	**0.010**	0.54
Macrofauna diversity	0.095	**0.007**	. . .	0.13
Vegetative diversity	0.305	**<0.001**	. . .	0.38
C stocks	**<0.001**	**<0.001**	**<0.001**	0.70

Note: More detailed summary of the data analyses can be found in the supplementary tables in Appendix S2. Bold values indicate $P \leq 0.05$.

According to the explanations provided by farmers, the main reason why more land had been converted into forest or abandoned in the lower zone was due to lower productivity in the this zone, again suggesting an important relationship between the biophysical context and land and farm management (Benayas et al. 2007).

Socio-ecological feedback loops

While biophysical factors are clearly important drivers of soil properties and land and farm management in this landscape, differential farm management and land-uses distribution across agricultural zones result in feedbacks that further accentuate landscape trends, thus forming a (bio)complex socio-ecological system. The development of distinct management regimes in the three agricultural management zones appears to result in important feedbacks into the biophysical patterns of the landscape by reinforcing the existing soil fertility gradient created by the underlying natural context. For example, the asymmetrical distribution of organic inputs by farmers, whereby fields in the upper and middle zones typically received more inputs than those in the lower zone (Table 1, Fig. 1), likely explains at least part of the observed soil fertility gradients.

Evidence for this is observed in the comparison of available P levels under agricultural land-use between the agricultural management zones. Mirroring the nutrient inputs reported by farmers, available P displayed no significant difference between the upper and middle agricultural management zones, but was significantly reduced in the lower agricultural management zone (Fig. 5). The reduced investment in soil fertility in the lower agricultural management zone may therefore be regarded as an important farm-agroecosystem feedback loop, where reduced

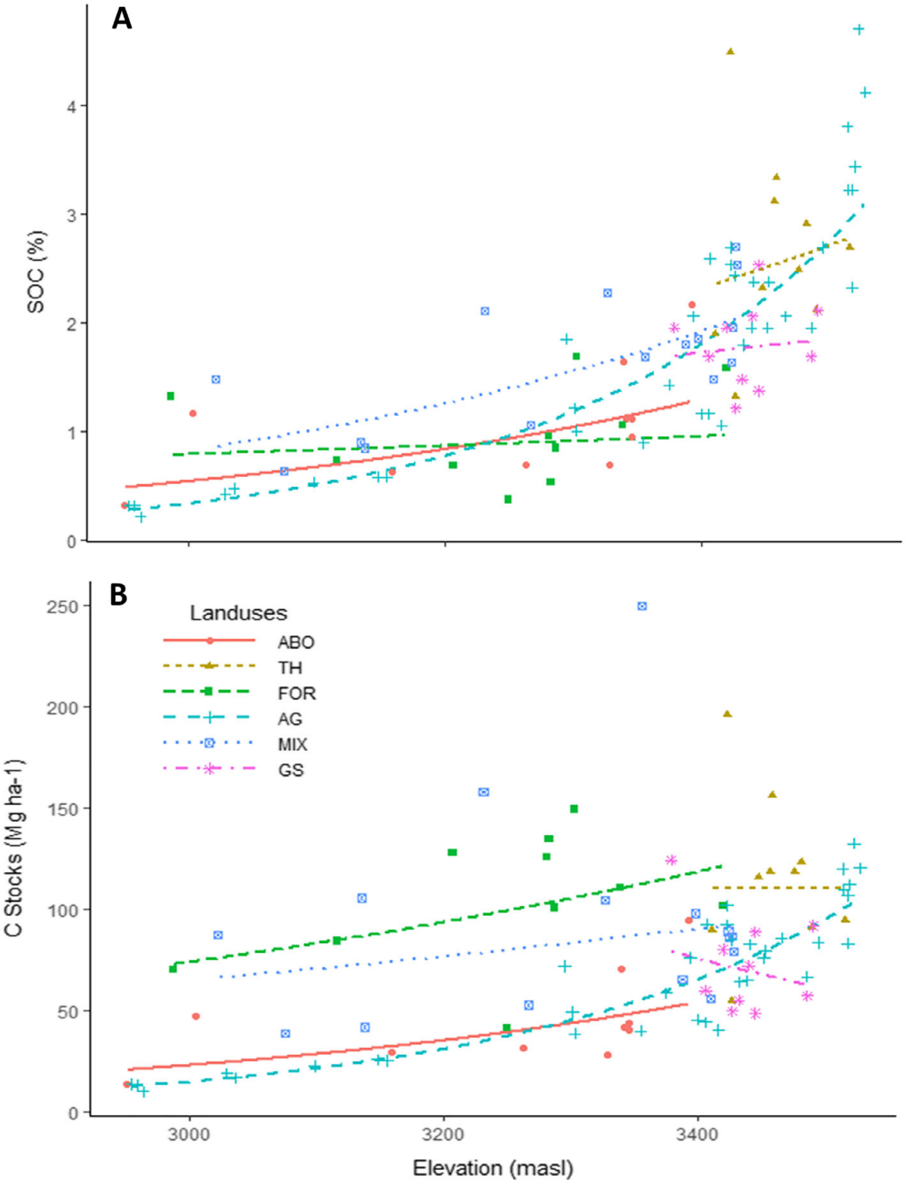

Fig. 3. (A) Relationship between elevation (m asl) and soil organic carbon (%) of the six different land-uses identified using a participatory mapping process. (B) Relationship between elevation (masl) and C stocks (MG/ha) of the six different land-uses within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador. The land-uses identified include ABO, abandoned land; TH, tree hedgerows; FOR, Eucalyptus and/or pine forest; AG, agricultural land; MH, mixed hedgerows; GS, grass strips.

productivity further reduces the incentives for farmers to invest in soil fertility inputs, further reducing productivity (see Fig. 7B for a graphical representation of this potential socio-ecological feedback loop within the broader landscape).

Another noteworthy pattern that may suggest the presence of a cross-scale socio-ecological feedback loop is that while the available P levels closely reflect the asymmetric organic matter inputs in the landscape, SOC levels do not follow the same pattern. Instead, SOC patterns under agricultural land-use see even greater accumulation of SOC in the upper agricultural management zone when compared to the middle zone and

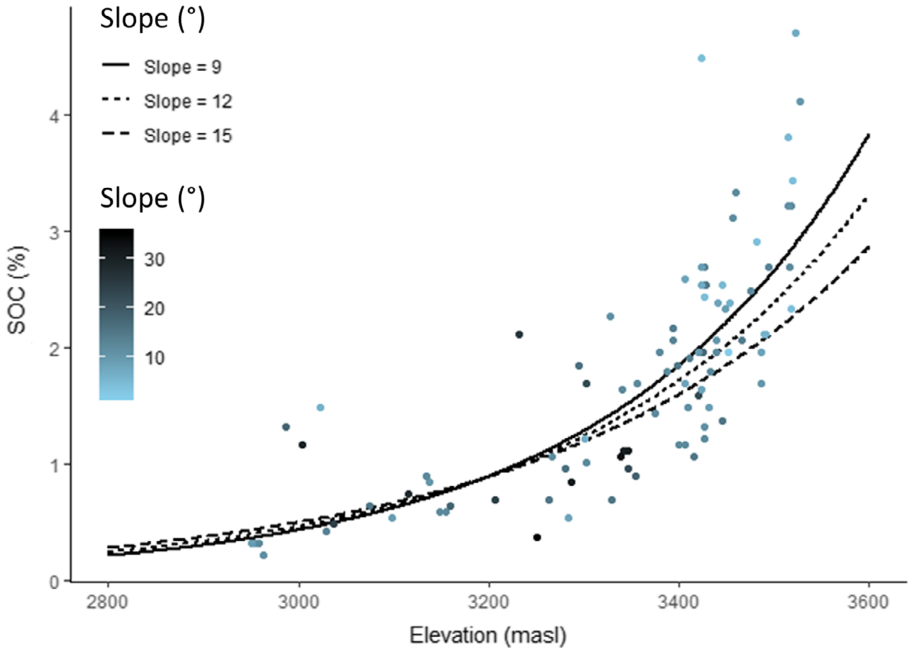

Fig. 4. The relationship between elevation (masl) and soil organic carbon (SOC; %) at different slope gradients (9°, 12°, and 15°) within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador. The fitted linear regression lines of the three slope gradients are indicated by different line-types (unbroken line, 9°; short dashed line, 12°; long dashed line, 15°). Slope displayed a significant interaction with the association between SOC and elevation ($P < 0.004$).

other land-uses, while it displays lower levels compared to other land-uses in the lower elevations of the landscape (Figs. 3A and 5). This pattern of greater SOC variability under agricultural land-use within the landscape could be the result of feedbacks between the socio-ecological processes driving SOC accumulation. Specifically, the cooler climatic conditions and greater soil clay content in the upper elevations of the landscape could be combining with greater farm organic inputs to increase SOC levels above that of other land-uses in that portion of the landscape. Meanwhile, the lower level of organic inputs in the lower zone may not compensate for normal SOC losses resulting from farming activities (e.g., tillage). This combined with a warmer climate and lower soil clay content may be an important reason why SOC under agricultural land-use is lowest among all land-uses in the lowest elevations of the landscape. These observations support our hypothesis that important feedbacks exist between environmental variables, farm management, and agroecosystem patterns leading to the interdependent development of biophysical and farming patterns in rural landscapes as also concluded by Van Apeldoorn et al. (2013).

When examining the effect of land-use more broadly, it is not surprising that vegetative parameters (vegetative diversity and C stocks) displayed significantly different values between land-uses (Figs. 3B and 6A, Table 2), given that land-uses are inherently associated with distinct management of crops and trees. However, significant differences were also observed for key soil properties and macrofauna diversity (Table 2). Mixed hedgerows were especially associated with increased levels of different agroecosystem components (Figs. 3 and 6), confirming previous studies investigating the benefits of hedgerows/agroforestry for C sequestration (Albrecht and Kandji 2003, Palma et al. 2007, Takimoto et al. 2008), vegetative diversity (Deckers et al. 2004, Smukler et al. 2010, Kearney et al. 2019), and macrofauna diversity (Pauli et al. 2011, Rousseau et al. 2013).

Eucalyptus/Pine forests performed poorly compared to mixed hedgerows for SOC,

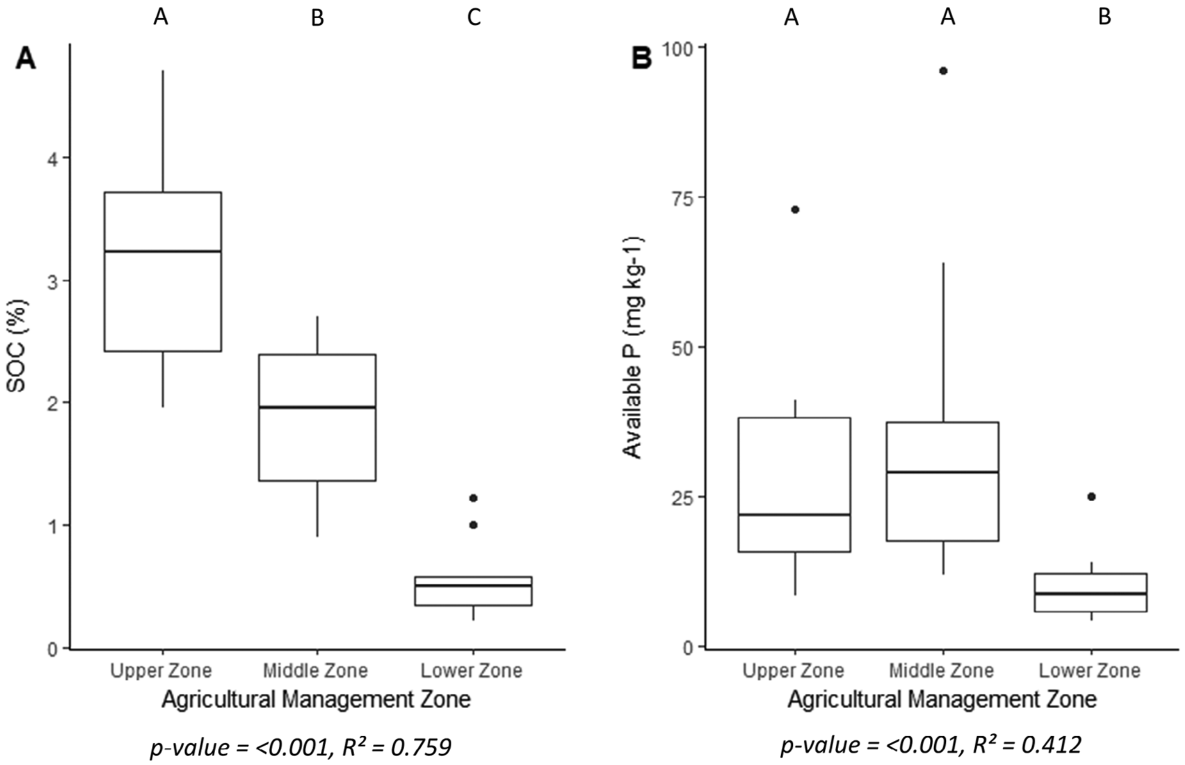

Fig. 5. Boxplots displaying interquartile ranges of (A) SOC (%), and (B) available P (mg/kg) levels by agricultural management zone within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador. Points located outside the whiskers of the boxplots are considered outliers (>1.5 interquartile range). Post hoc Tukey's honestly significant difference test results are presented above each box at the top of the plots, with management zones having different letters significantly different at the $P < 0.05$ level. P and R^2 values are presented underneath the plots.

vegetative diversity, and macrofauna diversity (Figs. 3A and 6). As reported by farmers in the participatory community mapping, these patches of forest are often planted on already degraded land. Nevertheless, the fact that most of these patches of forest are still performing poorly after 20 or more years since establishment indicates that their potential to restore degraded land may be limited and that attention is needed to explore how best to encourage alternative mixed forestry for purposes of biomass production as suggested by de Valença et al. (2017) and Hall et al. (2012), rather than the planting of monoculture pine or eucalyptus patches of forest.

As hypothesized, the notable differences observed between land-uses suggest that land-use choices are contributing to greater spatial heterogeneity across the landscape (Hall et al. 2012). Moreover, this greater spatial heterogeneity in the agroecosystems of the landscape is unlikely to be a random phenomenon, but a result of the historical socio-ecological interactions and feedback loops outlined above that have led to an asymmetrical distribution of land-uses across the landscape. This observation reflects the findings of other studies, even those conducted in drastically different biophysical contexts. For example, Duvall (2011) similarly concluded that land-uses in the Western African Savanna created a complex mosaic on top of the natural biophysical patterns of the landscape.

Understanding this biocomplexity is important from a practical level, as it can inform more context-specific and effective intervention strategies to enhance the sustainability of landscapes and the livelihoods of those who manage it. By better understanding the inherent biophysical heterogeneity of landscapes and key natural and

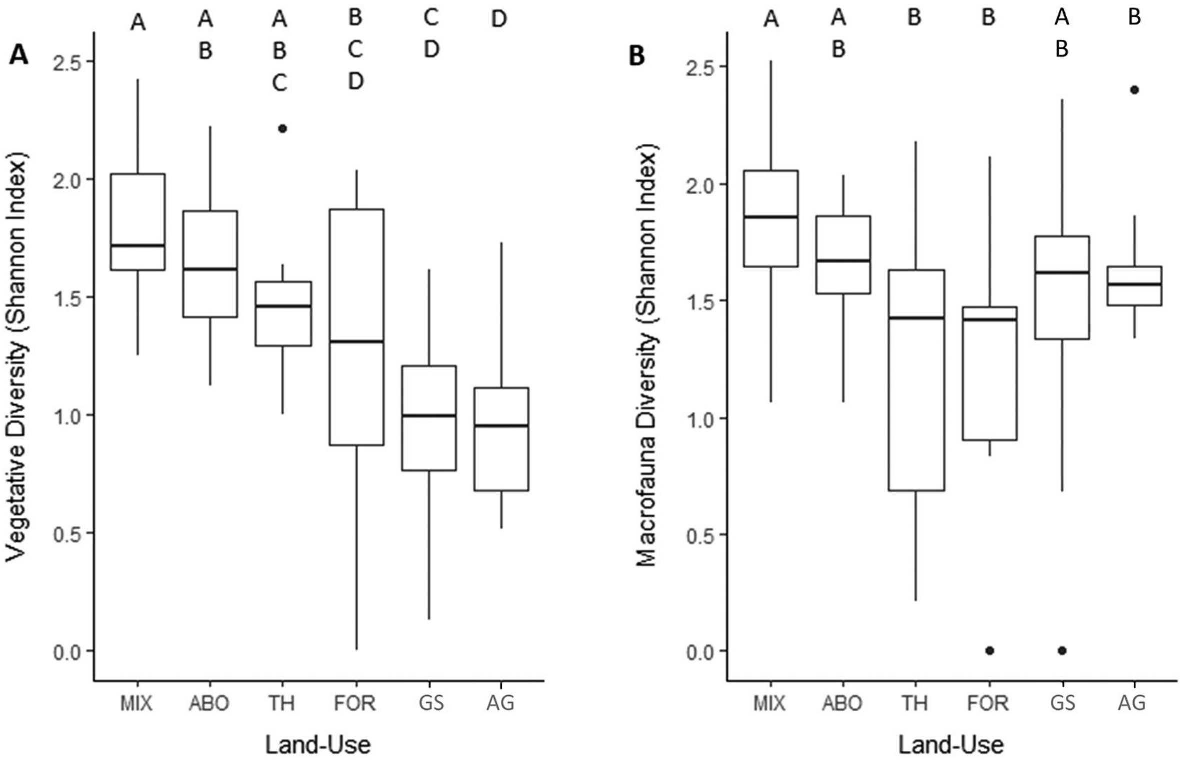

Fig. 6. Boxplots displaying interquartile ranges of (Plot A) vegetative diversity (Shannon index); and (Plot B) macrofauna diversity (Shannon index) levels by agricultural management zone within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador. Points located outside the whiskers of the boxplots are considered outliers (>1.5 interquartile range). Post hoc Tukey's honestly significant difference test results are presented above each box at the top of the plots, with management zones having different letters significantly different at the $P < 0.05$ level. The land-use acronyms are MIX, mixed hedgerows; ABO, abandoned land; TH, tree hedgerows; FOR, Eucalyptus and/or pine forest; GS, grass strips; AG, agricultural land.

anthropogenic drivers, decision-makers may be able to develop more nuanced and efficient approaches to increasing both the productivity and overall sustainability of the landscape (Rushemuka et al. 2014).

CONCLUSION

Our findings provide evidence that both environmental and human factors contribute to the emergence of distinct agroecosystem patterns in the rural landscape. Pedogenic influences such as climate, soil textural gradients, and geomorphology are clearly responsible for landscape-scale processes that contribute to biophysical patterns along elevational niches, which has given rise the development of context-specific management by the local farmers. Asymmetric organic matter inputs within the landscape coupled with environmental interactions appear to have accentuated the underlying biophysical attributes, creating important socio-ecological feedbacks as exemplified in SOC and available P patterns under agricultural land-use. In addition, land-uses, which are distributed across the landscape asymmetrically due to the underlying biophysical conditions, further influence soil and agroecosystem properties (e.g., SOC, available P, macrofauna diversity, vegetative diversity, total C storage). These findings support our original hypotheses that natural landscape-level processes drive biophysical patterns in landscapes, which then influence, and, in turn, are influenced by soil management and land-use decisions. These findings support our hypothesis that the biophysical patterns of the landscape result from

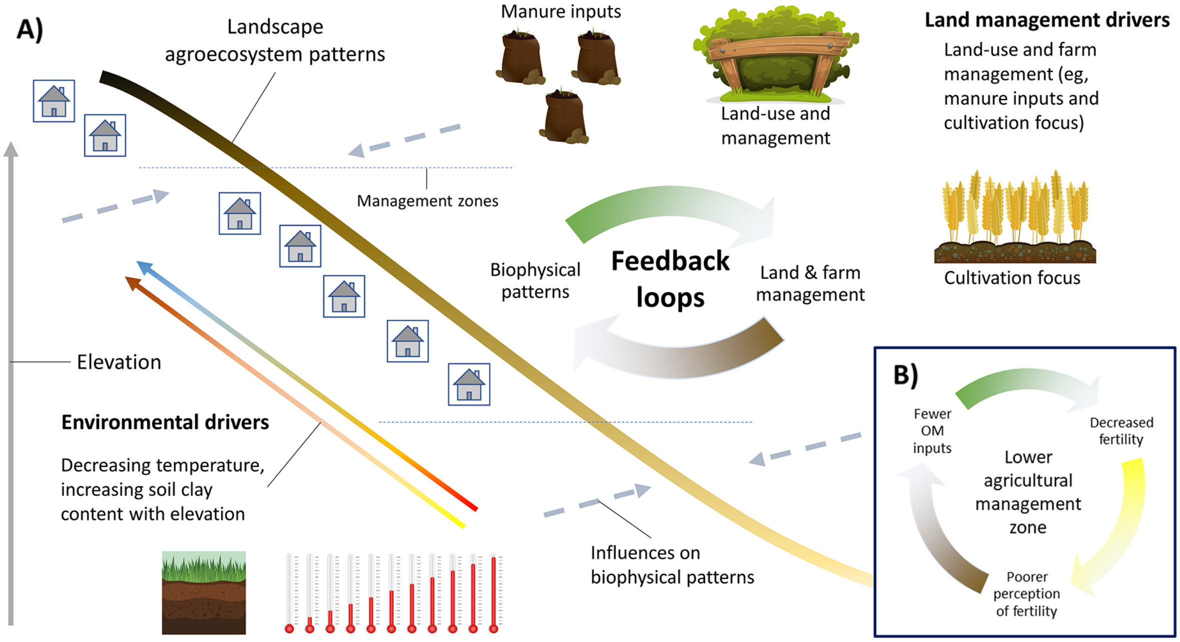

Fig. 7. (A) Visualized conceptualization of the socio-ecological interactions within a rural landscape (Community of Naubug) in the Parish of Flores, Chimborazo Province, Ecuador. (B) Feedback loop located in the lower agricultural management zone.

both natural and anthropogenic influences as well as complex interactions driven by feedbacks between these two factors. Improved understanding of such socio-ecological systems in these landscapes can provide more nuanced entry points for improving resource use and conservation strategies, in particular when developed through thoughtful engagement between farmers and local development agencies. For example, by better understanding the inherent environmental and biophysical heterogeneity of this landscape, farmers and other stakeholders may be able to co-develop more nuanced land management practices that target specific areas of the landscape for agricultural intensification and other parts for land conservation while taking into account current management practices within the three management zones.

ACKNOWLEDGMENTS

The research was funded by the McKnight Foundation's Collaborative Crop Research Program, USA, and executed under the auspices of Fundación EkoRural, Ecuador. The authors wish to thank the generous participation of all local stakeholders involved in the research, in particular Xavier Mera and Franklin Arcos at the Natural Resources Department of the Escuela Superior Politecnica de Chimborazo (ESPOCH) and the involved departments from the Provincial Government of Chimborazo. The local orthophotos used in the study were kindly provided by SIGTierras, the GIS department from the Ecuadorian Ministry of Agriculture and Livestock. The community members of Naubug deserve special recognition, in particular Cesar "Julio" Guambo, who led a group of farmer-experimenters and the project field assistant, Silvia Guambo.

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