Recent Changes in Patch Characteristics and Plant Communities in the Jalca Grasslands of the Peruvian Andes

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ABSTRACT

Habitat loss and fragmentation are considered major threats to biodiversity, especially in tropical mountain ecosystems. Most studies focus on the relationships between biodiversity and patch characteristics such as patch size, connectivity or degree of contrast with the surrounding matrix, but leave the rate of change within these variables little explored. We analyzed the importance of changes in patch characteristics over time on species diversity and species composition in the paramo of northern Peru, a tropical grassland ecosystem, locally known as jalca. We obtained land use/cover maps for 1987 and 2007 spanning an area of 6300 km^2, and quantified land use change, jalca patch characteristics and their proportional changes over 20 yr. In 2009, 371 vascular plant species were recorded in 92 plots, each plot representative of single patches. Between 1987 and 2007, jalca cover decreased from 47 to 35 percent due to encroaching agriculture. This activity showed an upward shift probably favored by climate change. The number of jalca patches increased, mean patch size decreased, and the patches showed a higher contrast with the surrounding matrix. Multiple linear regression failed to show that species diversity relates to changes in patch characteristics. Canonical correspondence analysis indicated that species composition relates to the degree of contrast between the patch and its surrounding matrix and its changes through time. We concluded that changes in patch characteristics are important only for species composition. This study highlights the importance of considering matrix management with a long term perspective for conservation efforts.

Abstract in Spanish is available in the online version of this article.

HABITAT FRAGMENTATION DUE TO THE EXPANSION OF AGRICULTURE (Andrén 1994, Ewers & Didham 2006) and climate change (Peterson *et al.* 1997, Dirnböck *et al.* 2003) is one of the major threats to biodiversity (Tilman *et al.* 1994, Fahrig 2003), especially in high-mountain ecosystems. Fragmentation may produce a reduction of patch size, an increase of isolation between patches, the creation of boundaries with edge effects and an increase in the number of patches (Andrén 1994, McGarigal & Marks 1995, Gustafson 1998, Fahrig 2003, Turner 2005, Ewers & Didham 2006). Within single landscapes, patch size and connectivity have been associated with species richness (Bruun 2000, Helm *et al.* 2006), habitat occupancy (Hodgson *et al.* 2009) and species abundances (Eriksson *et al.* 1995). Also, the structure and quality of the matrix that surrounds patches have been correlated to biodiversity patterns (Ricketts 2001, Jules & Shahani 2003, Williams *et al.* 2006, Prugh *et al.* 2008).

The spatial setting of current patches in a matrix only represents the present-day result of fragmentation. It does not reveal any information about the rate and intensity of the changes to which a particular patch or matrix and the associated biodiversity have been subjected (McGarigal & Cushman 2002). Fragmentation studies, which included manipulation of the landscape to

compare pre- and post-treatment effects on biodiversity generally, require complicated logistics, especially in tropical ecosystems (McGarigal & Cushman 2002). Intermediate approaches which link current biodiversity patterns with metrics of patches at some time in the past (Helm *et al.* 2006) or with dynamically changing patch metrics in time, remain little explored.

In the equatorial Andes above 3000 m altitude, the paramo is a tropical alpine grassland bordered by the snowline at its upper limit and by cloud forests and shrublands at its lower limit (Luteyn 1999). Paramo systems are naturally fragmented because of the steep terrain. At century and millennium scales patches of paramo vegetation have experienced continuous changes in isolation and connectivity, because of the alternate expansion and contraction of the paramo zone driven by climate change (van der Hammen 1979, Hooghiemstra & van der Hammen 2004). Adaptations of paramo plants to high levels of natural fragmentation include short regeneration times (Janzen 1973), a prevalence of anemochory and zoochory dispersal (Melcher *et al.* 2000) and effective short-range migration (Weigend 2002). In the past decades paramo vegetation has become increasingly threatened by fragmentation due to encroaching agriculture.

The aim of our study was to assess how paramo patches (locally known as jalca) changed through time and how such changes affected patterns of biodiversity in northern Peru. Our

two main research questions were: (1) which changes have occurred in the jalca patches over the last 20 yr? (2) How did changes in patch characteristics affect plant diversity and species composition? To answer these questions we analyzed land use change and patch metrics of jalca vegetation on the basis of land use/cover maps derived from Landsat TM5 imagery of 1987 and 2007. We studied the diversity (Shannon diversity index) and composition of vascular plant species in 92 small plots stratified over patches of natural jalca vegetation, as function of the current patch metrics and their changes over the period of 20 yr. We specifically tested if jalca patches, which were small, isolated and surrounded by a more contrasting matrix in 2007, or that changed in that direction between 1987 and 2007 showed a lower diversity and a different composition of vascular plants compared to patches which were less affected by fragmentation.

METHODS

STUDY AREA.—The study was conducted in an area spanning 6300 km^2, situated in the Andean region of south Cajamarca, north Peru (6°30′ S–7°30′ S; Fig. S1). The natural paramo (locally known as jalca) vegetation in this area is found between 3000 and 4200 m asl and typically consists of bunch grasses (Weberbauer 1945, Luteyn 1992). The total annual precipitation in the area ranges from 650 mm in the west to 1370 mm in the east (Hijmans et al. 2005). Mean annual temperature ranges from 5.7°C in the upper areas to 16.3°C in the lower areas (Hijmans et al. 2005). Paramo vegetation is well known for its high endemism and diversity (Luteyn 1992), and its capacity to regulate the water supply to the lowlands nearby (Buytaert et al. 2006). Despite these important environmental services, agriculture has largely replaced the natural jalca vegetation during the last years (Sánchez-Vega et al. 2005). The presence of two important dairy factories in Cajamarca has intensified overgrazing (Sanchez 2003). Mining has developed intensively since the beginning of 1990 (Sanchez 2003), and tree plantations (Pinus sp.) have increasingly replaced jalca vegetation.

LAND USE/COVER MAPS AND FRAGMENTATION.—Two orthorectified LANDSAT images were analyzed. To reduce problems related to seasonality, we selected the available images from the dry season, which is known to minimize differences in reflectance of vegetation (Martinuzzi et al. 2007) and applied object-based classification, which is less dependent on weather conditions (Walter 2004) compared to a pixel-based approach and which leads to better classification results (Dingle Robertson & King 2011). The images were taken on 23 June 1987 and 24 August 2007 and downloaded from the Global Land Cover Facility site (http://www.landcover.org/index.shtml) and re-projected to UTM zone 17S, datum WGS84. The images were first segmented into image objects and then classified using the Definiens Developer 7 (Definiens 2007) software. First we applied a multi-resolution segmentation algorithm (Baatz & Schäpe 2000) that clusters individual pixels into image objects based on three criteria: reflectance values (color), shape, and compactness (Benz et al. 2004). For

land use applications the reflectance values are most influential when classifying satellite images. In this part of the Andes, land cover categories occur as units with highly irregular shapes. Therefore, a low weight was given to the parameters of shape and compactness. We used a weight of 0.5 for color, 0.3 for shape and 0.2 for compactness. The nearest neighbor classifier was subsequently used in an object-based supervised classification of the image objects. The classification step was repeated to correct initially misclassified image objects by visual inspection of the satellite images. In this procedure the following land cover/use classes were identified: jalca, shrublands, cloud forest, lakes, agriculture, mining, and tree plantations. The map was again visually inspected for small patches (< 0.5 ha) incorrectly classified as jalca. These were merged with the desired adjacent class. The classification accuracy assessment for the 1987 image was performed following the method described by Congalton (1991) by comparing the classification results with a reference dataset and presented as a confusion matrix with the User's, the Producer's and the Overall accuracy and KHAT statistics. We used 198 randomly placed points in the image in the accuracy assessment of the land use/cover classes. For the accuracy assessment of the 2007 image we used the same 198 points and 40 additional GPS points taken during the fieldwork campaign. The overall accuracy for both years was 78 percent (Table 1).

Patches of jalca were extracted from these land use/cover maps using FRAGSTATS 3.3 (McGarigal & Marks 1995). We used the eight pixels rule to mark out a patch. Both orthogonal and diagonal adjacencies defined continuous patches. Metrics at patch and at class level were calculated for the jalca from the 2007 land use/cover map (Table 2) following McGarigal and Marks (1995). Patch core areas were defined using an inside buffer of 100 m (McGarigal & McComb 1995, Laurance et al. 1998). The search radius for the PROX variable was set at 300 m (Gustafson & Parker 1992). The weighted values of the contrast variable ECON were assigned considering similarity with the jalca vegetation as follows: a weight value of one was used for lakes, bare soils, and mining areas, an intermediate contrast level was used for agricultural (0.7) and plantation areas (0.6), and a low contrast level was taken for natural vegetation types (0.1 for shrublands and 0.3 for cloud forest). Class level metrics were only calculated for the jalca. Finally, the proportional change of each patch metric in two decades was calculated according to equation 1:

$$(p_{2007} - p_{1987})/(p_{1987}) \times 100, \tag{1}$$

where p_{2007} represents the value of the patch metric derived from the 2007 image, and p_{1987} the value derived from the 1987 image (Table 2).

FIELDWORK.—In 2009, field sampling was done in 92 jalca patches (Fig. S1), which were selected from the 2007 land use/cover map. This selection was stratified according to the range of patch sizes and the range of distances to the nearest patch. Within the limits of terrain accessibility, the vegetation plots were located as close as possible to the centroid of each patch, using a

TABLE 1. *Accuracy assessment of the classification for LANDSAT 5TM of 1987 (a) and 2007 (b).*

Reference data	Classification								Total	User's accuracy (%)	Producer's accuracy (%)	Overall accuracy (%)	KHAT
	Clouds	Jalca	Shrublands	Cloud forest	Agriculture	Mining	Tree plantations						
(a) 1987													
Clouds	2	0	0	0	0	0	0		2	100	100	78	0.65
Jalca	0	68	1	0	10	0	0		79	76	86		
Shrublands	0	9	8	0	8	0	0		25	67	32		
Cloud forest	0	0	2	1	0	0	0		3	100	33		
Agriculture	0	12	1	0	72	0	0		85	80	85		
Mining	0	0	0	0	0	2	0		2	100	100		
Tree plantations	0	0	0	0	0	0	2		2	100	100		
Total	2	89	12	1	90	2	2		198				
(b) 2007													
Clouds	1	0	0	0	0	0	0		1	50	100	78	0.62
Jalca	0	58	1	0	15	2	1		77	77	75		
Shrublands	0	2	2	0	9	0	0		13	40	15		
Cloud forest	0	0	1	1	0	0	0		2	100	50		
Agriculture	1	15	1	0	111	0	0		128	80	87		
Mining	0	0	0	0	0	3	0		3	60	100		
Tree plantations	0	0	0	0	4	0	10		14	91	71		
Total	2	75	5	1	139	5	11		238				

TABLE 2. *Patch and class metrics following McGarigal and Marks (1995). The metrics representing the percentual differences of patch characteristics between the 1987 and the 2007 Landsat imagery were labeled with a capital D at the start of the label (D_AREA, D_GYRATE, D_FRAC, D_CONTIG, D_CORE, D_NCORE, D_ENN, D_PROX, D_ECON).*

Label	Description
Patch metrics	
AREA[*]	Area of patch (ha)
GYRATE[*]	Mean distance between each cell in the patch and the patch centroid (m)
FRAC	Shape complexity. FRAC approaches 1 for very simple perimeters (i.e., *squares*) and approaches 2 for highly convoluted perimeters
CONTIG	Connectedness between the pixels of the same patch. CONTIG equals 0 for a one-pixel patch and increases to 1 as patch contiguity increases
CORE[*]	Remaining area of a patch after removing a depth-of-edge distance from the patch perimeter (ha). We used a distance of 100 m
NCORE[*]	Number of disjoint core areas in one patch after removing the depth of edge distance
ENN	Euclidean nearest distance to the closest patch (edge to edge) (m)
PROX[*]	Proximity index measures the proportion between the total area of a patch and its neighboring patches (within a specified radius) and the sum of edge to edge distances from the focal patch to the other patches. We used a search radius of 300. PROX = 0 if a patch has no neighbors and it increases as the neighborhood is increasingly occupied by patches of the same type and as those patches become closer in distribution
ECON	Edge contrast index (%). ECON equals the sum of the patch perimeter segment lengths (m) multiplied by their corresponding contrast weights, divided by total patch perimeter (m). ECON = 100 when the entire patch perimeter is maximum-contrast edge. Values of weights for each land use/land cover are described in methods
Class metrics	
NP	Number of total patches
CPLAND	Total core area of jalca patches divided by total study area (%)
LPI	Largest patch index: largest patch area divided by total study area (%)

[*]Variables were log-transformed in further analyses.

handheld GPS device. In each selected patch one plot of 2 × 2 m was sampled. In all plots the abundance and cover percentage were recorded for each vascular plant species. Specimens from all species were collected to allow species identification. Position (UTM zone 17S coordinates), percentage of exposed rocks and altitude were also registered for each plot. We took one soil sample at 0–5 cm depth in the centre of each plot, after removing litter. Soil analyses regarding texture (Hydrometer), total N (micro Kjeldahl), available P (modified Olsen), available K (sulfuric acid), pH (water), C (modified Walkley-Black) and exchangeable Al (extracted with 1 N KCl) were conducted at the Instituto Nacional de Investigación y Extensión Agraria (INIA) in Cajamarca (Table 3).

STATISTICAL ANALYSIS.—Means of patch metrics of 1987 and 2007 were compared by means of Mann–Whitney U-tests using R v.2.11.1 (R Development Core Team 2008). We considered all patches identified on the 1987 and 2007 land use/cover maps. Species diversity was calculated for each 4-m^2 plot using the Shannon Index (Shannon 1948). Applying multiple linear regression analyses in R v.2.11.1 this species diversity was related to four sets of explanatory variables: (1) current patch metrics (from the 2007 land use/cover map); (2) changes in metrics of patch characteristics; (3) soil and terrain properties; and (4) spatial variables (location of the plot). Following Borcard *et al.* (1992) and Legendre and Legendre (1998) we modeled our spatial informa-

TABLE 3. *Vegetation measures, soil properties and terrain characteristics obtained in 92 plot (4 m^2) samples of jalca patches.*

Name	Mean	SD	Range
Plant density (number per 4-m^2 plot)	176	74	42–433
Species richness (number per 4-m^2 plot)	18	5	7–30
Shannon Index	2.3	0.4	0.7–3
Vegetation cover (%)	90	25	25–161
N (%)	0.6	0.3	0.09–2.04
P[*] (ppm)	9.7	10.0	1.91–53.9
K (ppm)	221.3	63.4	149–380
pH	4.4	1.2	3–7
C_org (%)	8.0	4.5	1.11–26.29
Al[*] (Meq/100 g)	2.2	2.5	0–8.26
Clay (%)	28.7	12.2	7–73
Sand (%)	48.3	15.6	17–87
Rock cover (%)	14	17	0–60
Elevation asl (m)	3480	270	3030–4130

[*]Variables were log-transformed in further analyses.

tion by adding all terms for a cubic trend surface regression, allowing to extract information in the response related to linear spatial patterns but also to non-linear patterns. Thus, the spatial variables were created by calculating the nine terms of the polynomial to the third degree (X, Y, X^2, Y^2, X^3, Y^3, $X*Y$, $X*Y^2$,

$Y*X^2$) of the centered and standardized UTM (zone 17S) easting (X) and northing (Y). Some explanatory variables were log-transformed (Tables 2 and 3). Redundancy among the explanatory variables was examined by means of bivariate correlation coefficients (Table S1). Model simplification was done by backward stepwise regression analysis for each of the explanatory sets separately, using the step function in R. Models were evaluated using the corrected Akaike's information criterion (AIC_c), which is especially appropriate in situations of a low number of samples relative to the number of parameters (Burnham & Anderson 2002). In this process, the probability of each model was evaluated using so-called Akaike weights (w_i) (Burnham & Anderson 2002, Whittingham *et al.* 2006). These values are based on the difference between the AIC_c value of each model and the AIC_c value of the best model (Δi) (Burnham & Anderson 2002). The importance of each variable was evaluated using the selection probability which is calculated by summing the w_i values of all models in which the variable appears (Burnham & Anderson 2002, Whittingham *et al.* 2005). We included all variables with selection probabilities above 0.95 to build a final suite of regression models. The final parameter of each variable (β) was estimated by model averaging of that final suite (Burnham & Anderson 2002). This estimate was calculated as the sum, over all models of the final suite, of the product of a parameter found in a model and the Akaike's weight of that model. The model selection bias represented the difference between the averaged parameter and the parameter of the regression model including all variables, divided by the averaged parameter (Whittingham *et al.* 2005). Normality of residuals was checked for all the models. We calculated Moran's I of the residuals to check for spatial autocorrelation using the function Moran.$I()$ in R.

With canonical correspondence analysis (CCA) in CANOCO for Windows 4.5 (ter Braak & Smilauer 2002), metrics of current patches (2007) and those of changes in patch characteristics were related to the species composition in the plots. CCA analyses were carried out using a biplot-scaling focused on inter-species distances. Preliminary CCA analyses were performed using each of the four above mentioned sets of explanatory variables separately. In each of these analyses, the most relevant variables were selected by means of a forward selection procedure (at $P < 0.05$) using Monte Carlo permutation test with 999 permutations. Subsequently, all relevant explanatory variables were used in the final CCA. Introduced species (Appendix S1) were excluded from all analyses.

RESULTS

HABITAT FRAGMENTATION.—In 1987 jalca covered 47 percent of the study area, only slightly more than agriculture (43%). After two decades, agriculture had expanded to 55 percent and the jalca cover had diminished to 35 percent. A substantial part of this agricultural expansion took place at a relatively high elevation: 29 percent of the new agricultural patches were located at 3600–3800 m asl whereas only 12 percent were found at the lower limits of the jalca (3000–3200 m asl). Mining and tree plantations

expanded as well (from 0.2% to 1.2% and 0.2% to 1.9%, respectively). Most important changes are shown in Figure 1. Most jalca patch metrics decreased significantly in this time lapse (Table 4). Also, patches showed a stronger contrast (ECON) with the surrounding matrix, implying that a higher proportion of the patch perimeters were exposed to more contrasting land use/cover classes. Shape complexity (FRAC) and number of core areas (NCORE) did not show a significant change. Between 1987 and 2007 the number of jalca patches (NP) increased from 744 to 1196. The total proportion of jalca core areas (CPLAND) decreased from 32.4 percent in 1987 to 19.3 percent in 2007, which is another indication that most jalca patches became smaller in this time lapse. In 1987 the largest jalca patch (LPI) still occupied almost a quarter of the study area (22.8%). In 2007 this class metric had reduced to 4.3 percent.

FLORISTIC DIVERSITY.—The 92 plots were located between 3000 and 4200 m (Table 3). In total 371 vascular species were observed (Appendix S1). Seven of these species were introduced and 55 were endemic to Peru. Asteraceae was the most species-rich family (97 species of which 19 endemic), followed by Poaceae (54; 6 endemic), Scrophulariaceae (27; 15 endemic) and Fabaceae (16; 3 endemic). On average, a plot contained about 18 species and 176 plants, which represented a Shannon Index of 2.3 (Table 3). Frequent species were *Calamagrostis* sp. (present in 62% of the plots), *Bidens triplinervia* (44%), *Rumex acetosella* (42%), *Stevia puberula* (37%), *Paspalum tuberosum* (32%), *Hieracium peruanum* (29%), *Werneria nubigena* (28%) and *Paranephelius uniflorus* (27%).

REGRESSION MODELS OF DIVERSITY AND COMPOSITION.—The preliminary regression analyses of species diversity against each of the four sets of explanatory variables, considering a variable selection probability of 95 percent or more, led to the selection of

TABLE 4. *Patch metrics of jalca vegetation in 1987 (744 patches) and 2007 (1196 patches). For the patch metrics the results of the Mann–Whitney U-test of the differences between 1987 and 2007 are given.*

Metrics	1987		2007		Mann–Whitney test
	Mean	SD	Mean	SD	
AREA	400	5550	180	1340	*
GYRATE	400	1070	340	660	*
FRAC	1.1	0.06	1.1	0.06	ns
CONTIG	0.72	0.27	0.68	0.29	***
CORE	280	4250	100	850	*
NCORE	2	14	2	10	ns
ENN	260	380	200	300	***
PROX	15,300	60,700	3000	10,600	*
ECON	46	23	49	22	**

ns = P $\geq$ 0.05.

*0.01 $\leq$ P < 0.05.

**0.001 $\leq$ P < 0.01.

***P < 0.001.

TABLE 5. *Stepwise regression results evaluated using the corrected AIC (AIC_c), the difference between the AIC_c of each model and the best model (ΔAIC) and the Akaike weights (w_i). For each variable the selection probability (s. prob.) was calculated by summing the weights of the models where they are present. Finally, the parameter for each variable was calculated by averaging all models (β) by using the weights as well and the bias of these averaged parameters from those of a model considering all variables.*

Step	D_CONTIG	D_PROX	FRAG	CONTIG	AREA	ENN	N	Al	Elevation	Y^3	Y^2	X	Y	X*Y	AIC_c	ΔAIC	w_i
1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	−120.48	15.74	0.00
2	x	x	x	x	x	x	x	x	x	x	x		x	x	−122.47	13.75	0.00
3	x	x	x	x	x	x	x	x	x	x			x	x	−124.45	11.77	0.00
4	x	x	x	x	x	x		x	x	x			x	x	−126.33	9.89	0.00
5	x	x	x		x	x		x	x	x			x	x	−127.91	8.31	0.01
6	x	x	x			x		x	x	x			x	x	−129.62	6.60	0.01
7	x	x				x		x	x	x			x	x	−131.56	4.66	0.03
8	x	x				x		x	x				x	x	−132.90	3.32	0.07
9	x					x		x	x				x	x	−134.45	1.77	0.13
10						x		x	x				x	x	−135.84	0.38	0.25
11						x			x				x	x	−136.22	0.00	0.50
s. prob.	0.25	0.13	0.02	0.00	0.01	1.00	0.00	0.50	1.00	0.06	0.00	0.00	1.00	1.00			
β	0.0017	0.000	0.0177	0.0075	−0.0006	0.0002	0.0003	−0.0358	−0.0003	0.000	0.000	0.0000	0.0039	0.0002			
Bias	−3.4	−8.0	−125.0	−232.5	−159.5	−0.8	−196.0	−0.7	−0.0	−12.5	−2119.5	−7350.1	−0.4	−0.0			

D_CONTIG, D_PROX, FRAG, CONTIG, AREA, ENN (distance to closest patch), N, Al, elevation, Y^3 and X*Y (Table S2). In the final regression (Table 5) the lower polynomial terms (Y^2, X, and Y) were included as well (Venables 1998) and steps 7–11 represent the so-called confidence set of models (Burnham & Anderson 2002, Whittingham *et al.* 2006), which best approximates the true model (summed weights > 95%). None of these models showed spatial autocorrelation in their residuals ($P = 0.61$, $P = 0.72$, $P = 0.78$, $P = 0.85$, $P = 0.77$ for step 7 to 11, respectively). In these final models ENN, elevation, Y and X*Y showed selection probabilities at or above 95%. Only elevation showed a negative partial regression coefficient while the others showed a positive partial regression coefficient. This implied that a higher diversity was found in patches, which occurred at longer distances from other patches, at locations represented by a higher product of UTM northing and UTM easting, further north areas (Y) and in low elevation areas. Bias was higher for those variables with low selection probabilities.

In the CCA analyses of species composition, the stepwise procedures for each set of descriptor variables led to the selection of two metrics of changes in patch characteristics (D_GYRATE and D_ECON), five metrics of current patch characteristics (ENN, ECON, PROX, FRAG, NCORE), three soil and terrain variables (pH, altitude and percent of sand) and three spatial variables (X, X^3, X^2*Y). The final CCA considered all these variables and also the lower polynomial terms (X^2, Y, and X*Y). The stepwise selection procedure in the overall CCA led to the elimination of PROX, FRAG and percent of sand. The first axis of this CCA accounted for 3.2 percent of the species composition, and the second axis 2.4 percent. Soil pH and altitude explained most of the species composition along these two axes (Table 6). The patch metrics ECON (edge contrast

TABLE 6. *Canonical coefficients for standardized variables and intra-set correlation coefficients of the overall CCA considering only variables selected from the sub models.*

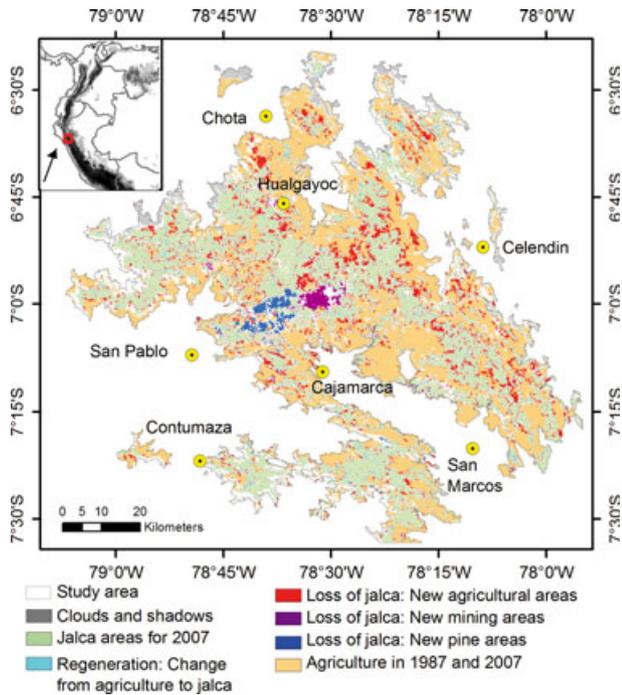| Variables	Canonical coefficients		Intra-set correlation coefficients	
	AXIS1	AXIS2	AXIS1	AXIS2
D_GYRATE	0.11	−0.01	0.47	−0.01
D_ECON	−0.04	−0.11	0.00	0.16
ENN	0.12	0.08	0.39	0.11
ECON	−0.21	−0.36	−0.33	−0.45
NCORE	−0.10	−0.69	−0.03	−0.51
pH	0.57	−0.71	0.79	−0.43
Elevation	−0.42	−0.60	−0.72	−0.31
X	0.33	0.11	0.13	0.15
X^2	−0.17	−0.27	−0.10	0.45
X^3	−0.12	0.19	−0.02	0.37
Y	−0.08	0.41	−0.09	−0.25
X*Y	0.00	−0.47	0.11	−0.30
X^2*Y	−0.10	−0.69	−0.03	−0.51

FIGURE 1. Areas of major land use/land cover change between 1987 and 2007.

index) and NCORE (number of core areas), and the spatial variable X^2*Y were strongly related to the second axis. When the effects of the soil, terrain and spatial variables were filtered out (by entering them as co-variables in the CCA), four patch metrics (ECON, ENN, D_ECON, and D_GYRATE) continued to show a significant effect on species composition (Fig. S2). Edge contrasts with the surrounding matrix, both in the current patch metric (ECON) and in the way these contrasts changed between 1987 and 2007 (D_ECON) explained most the species patterns. Species mostly related to strong edge contrasts and strong changes in this metric over the past two decades (showing optima along the negative side of the first CCA axis; Fig. 1) were *Hesperomeles lanuginose*, *Pteridium aquilinum*, *Brachyotum naudinii* and *Stipa rosea*. On the other hand, *Dalea exilis*, *Tagetes filifolia*, *Setaria parviflora*, *Coreopsis townsendii* and *Luzula racemosa* showed optima when patches had developed low edge contrast values.

DISCUSSION

CHANGES IN HABITAT CONFIGURATION: FRAGMENTATION.—The land use/cover change analysis between 1987 and 2007 clearly showed that the natural vegetation of the jalca system is fragmenting mainly by encroaching agriculture. As a consequence the number of jalca patches increased by the breaking up of larger patches. These patches became smaller and more different in physiognomy with the surrounding matrix, implying that the natural ecotones of forest-jalca or shrubland-jalca degraded. More patches became surrounded by arable fields and other human activities. The decrease of the edge-to-edge Euclidean distance between 1987 and 2007 is

probably due to the new patches formed after a large one was broken up. Since such patches remain close to each other, fragmentation easily contributes to a decreasing mean edge-to-edge distance between patches. The patch proximity index was distinctly higher in 1987 than in 2007 indicating less proximity between patches in 2007. This index is weighted, however, by the size of the neighboring patches (larger patches nearby yield a higher index than smaller patches). Therefore, given the reduction in the mean distance between patches (shown by the decreasing edge-to-edge Euclidean distance between patches), the decreasing proximity index likely showed that neighboring patches have become smaller in the past 20 yr. The only patch metrics, which did not change in the fragmenting jalca landscape, were the shape complexity, representing by fractal value of the patches, and the number of core areas. The constancy through time in the fractal values of the jalca patches probably reflects the low degree of mechanization of the agricultural activities. Most arable field created in the past 20 yr were still coerced to follow the natural boundaries between the jalca patches (as these are imposed by slope, altitude, soil rock cover and exposed bedrock).

The conclusions regarding the differences in time of the CORE (and NCORE) and PROX metrics are potentially biased by our arbitrary choice of the depth-to-depth distance (100 m) and search radius (300 m) for these metrics, respectively. Also our conclusions about the effects of these metrics on species diversity and composition as discussed below suffer from these restrictions. To our knowledge, there is no information how to define the most useful or informative values of these distances in a region with a complex topography such as the Andes. This issue certainly deserves more attention in the future, but is beyond the scope of the present study.

NO LINK BETWEEN CHANGES IN PATCH CHARACTERISTICS AND PLANT DIVERSITY.—With the exception of the edge-to-edge distance between patches, our regression analyses did not detect evidence that current patch properties or the rate of change within patch characteristics affected the vascular plant species diversity of the jalca vegetation. This is in accordance with the pattern found for periurban forests (Guirado et al. 2007), where changes in patch characteristics were assessed in a quantitative way. Possibly the degradation of the jalca patches was not strong enough to effectively influence species diversity. Some authors suggested that only strong habitat disturbances or severe loss of habitats lead to detectable relations between patch area and species diversity (Andrén 1994, Arroyo-Rodríguez et al. 2009). Recently fragmented patches may still function as a refuge for animals, which contributes to increasing seed dispersal into these patches (Jules & Shahani 2003). Such patches may also experience an increased influx of plant species because of the larger edge boundary with the matrix (Laurance et al. 2001). Higher species diversity was found in patches, which occurred at longer distances from other patches. As argued above, recent fragmentation presumably creates numerous patches, which are at close distance to each other. In turn, this would imply that more distant patches tend to be less affected by recent fragmentation, which might explain their

relatively high species diversity. Finally the spatial effect on species diversity showed that the species diversity in the jalca increases toward the northeast and the north in general. This suggests that jalca areas with higher humidity tend to contain more species on an area basis.

EFFECTS OF CHANGES IN PATCH CHARACTERISTICS ON PLANT SPECIES COMPOSITION.—Soil acidity and altitude mostly explained patterns in jalca species composition. The strong pH effect, which was consistent with Cooper *et al.* (2010), reflects the impact of the outcropping calcareous formations. The shallow soils in those areas show a high pH (potentially invoking P limitation) and low water retention capacity but a high warmth capacity. Deeper soils are more acidic and show a high level of soil organic matter, which induces a favorable environment regarding water storage and rooting. The impact of altitude reflects the general tendency for temperature in tropical alpine environments to strongly limit growth and nutrient availability (Janzen 1973, Ramsay & Oxley 2001).

Even after cancelling the effects of soil, terrain, and spatial variables, the current patch metrics and those of changes in patch characteristics significantly explained the variation in species composition, especially the contrast of patch edges with the surrounding matrix and the way this contrast changed through time. The jalca patches, which were surrounded by agriculture, mining and bare soils in 2007 or which became more surrounded by these land use/cover types over the past two decades, showed different species assemblages than jalca patches surrounded by cloud forest or shrublands.

The surrounding matrix is important because it affects resource availability, movements of pollinators, seed dispersers, and herbivores (Jules & Shahani 2003). If the edge contrast is low, the similarity in cover type and physiognomy between patch and matrix increases which enhances species exchange. Most likely, low edge contrast situations represent conditions of low disturbance by agriculture or mining in the surroundings of the jalca patches. We therefore assume that the plant composition in such patches best reflects the wide variation found in natural jalca patches. Contrary, in view of the encroaching agriculture, the jalca patches which show a high contrast with the surrounding matrix most likely represent jalca plant communities under threat by isolation, human disturbance and invasion by arable taxa. In such patches we would expect higher frequencies of species adapted to maintain viable populations under stress conditions (*i.e.*, ferns like *P. aquilinum* or woody taxa like *H. lanuginosa* or *B. naudinii*). We would also expect a peak of fire resistant or species resistant to grazing activities (*i.e.*, grass species like *S. rosea*). Our exploratory study suggests that potentially predictive information about the response of jalca communities to human stress can be obtained by measuring these plant traits in jalca patches as function of human disturbance, especially if conditions of soil pH, soil depth, substrate and altitude are controlled for.

CONSIDERATIONS FOR CONSERVATION MEASURES.—Our results show an increasing fragmentation process where a clear upward shift of agricultural practices has occurred over the last decades and similar tendencies have been reported for the Ecuadorian paramos (Hess 1990, López Sandoval 2004). The main drivers for this encroachment are most likely socio-economic in nature, such as an increasing population pressure, changes in land tenure, and economic resources stimulated by migration (López Sandoval 2004). Between 1950 and 1998, however, temperatures have increased throughout the tropical Andes (Vuille *et al.* 2003). It is therefore likely that this upward migration is favored by more suitable crop conditions. Future climate change will further increase temperatures, and is therefore expected to lead to higher fragmentation of the Andes in general (Young 2009), perhaps, reaching the threshold at which diversity index is affected by the fragmentation process. In addition, shifting cultivation in the jalca system, leading to the regeneration of jalca patches after agriculture, imposes a further hazard. The interaction of succession with fragmentation may influence extinction dynamics (Collins *et al.* 2009), and negatively affect the diversity and composition of species in the long run.

Our results also showed that not only the matrix surrounding each patch correlated with the abundance and persistence of some species (Ricketts 2001, Williams *et al.* 2006) but its temporal changes as well. Therefore, conservation efforts should consider matrix management with a long term perspective in this tropical alpine ecosystem. Despite the naturally fragmented condition of the jalca, human induced fragmentation in the last 20 yr showed an effect on species assemblages. Here, the history of the landscape may be even more important than the current landscape structure (Burel 1992).

Our approach might be replicable in other alpine areas and contribute to understand how landscape changes affect biodiversity. The methodology might be improved, however, by considering a longer period of time or more temporal resolution allowing for more detailed insights how jalca vegetation is affected by recent changes in the jalca landscape. In these, further evaluations how to apply CORE and PROX metrics are needed. More essentially, information about dynamic changes in the species composition and diversity of the jalca vegetation should be included, measured in permanent plots and analyzed through manipulative experiments. For this, initiatives like those of the GLORIA network (http://www.gloria.ac.at/?a=7) to set-up and maintain permanent sites of paramo vegetation and other high-mountain ecosystems worldwide, should be encouraged.

CONCLUSIONS

Comparative land use/cover maps indicate that the natural jalca vegetation has become increasingly more fragmented mainly by encroaching agriculture in the period from 1987 to 2007. In two decades jalca patches became smaller and more contrasting with the surrounding matrix. Vascular plant species diversity did not relate to metrics of changes in patch characteristics, neither to patch size or edge contrast, possibly because the degradation of the jalca patches was not strong enough or because species invaded patches out of the surrounding matrix. Metrics of changes in patch characteristics were associated to vascular plant species composition of the natural jalca vegetation, mainly through patch contrast change

with the surrounding matrix, after controlling by soil and terrain characteristics. Conservation efforts should consider matrix management with a long term perspective as a strategy to protect the jalca vegetation. While our methods might be applicable to other alpine areas to improve management, more long term analysis would be important to fully understand the ecological processes creating the patterns observed.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Spearman correlation between variables.*

TABLE S2. *Stepwise regression results for each of the four sets of variables defined to explain diversity.*

FIGURE S1. Study area in the northern Andes of Peru.

FIGURE S2. CCA ordination diagram showing how the four patch metrics relate to the species composition in the plots after controlling for soil pH, spatial variables and elevation.

APPENDIX S1. Species list and species scores of the canonical correspondence analysis.

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