

CHAPTER 6

CONNECTIVITY DYNAMICS SINCE THE LAST GLACIAL MAXIMUM IN THE NORTHERN ANDES: A POLLEN-DRIVEN FRAMEWORK TO ASSESS POTENTIAL MIGRATION¹

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ABSTRACT

We provide an innovative pollen-driven connectivity framework of the dynamic altitudinal distribution of North Andean biomes since the Last Glacial Maximum (LGM). Altitudinally changing biome distributions reconstructed from a pollen record from Lake La Cocha (2780 m) are assessed in terms of their changing surface and connectivity within the study area. The upper forest line (UFL) ecotone lodged during much of the time around 2000 m (LGM), 2400 m (ca. 14–8 ka), 2800 m (ca. 8–3 ka), and 3550–3600 m (modern time). This resulted in a fourfold increase of the area covered by mountain forest (Andean and sub-Andean), a decrease of 96% of páramo, and a disappearance of permanent snow. Upslope migration of the UFL of 20 vertical m yr⁻¹ and more, as inferred from the pollen record, was spatially assessed: reduced surface area, dispersal limitation, reduced connectivity, and extirpation of the subpáramo biome during a few centuries is shown. The study area includes abundant higher mid-range altitudes (2600–3400 m), with a steep reduction of available surface area and increased dispersal distance in the high and low altitudes. In this range, each 100-m altitudinal rise of the UFL results in 20%–60% reduction of the surface area available for páramo and connectivity. The critical elevations where large biome surfaces start to disconnect depend on the elevation of lowest thresholds in the landscape and the elevation of summits. The 2500–3600 m elevation range is most dynamic in terms of geography and ecological species sorting; the 1000–1500 m interval is relatively stable and is permanently covered by Andean forest, making this interval less sensitive for monitoring climate change. When forests migrate to higher elevations, distribution nuclei of species are compressed, resulting temporarily in a higher species diversity. The species dissimilarity coefficient reflects rate of (ecological) change more adequately than the rate of palynological turnover, because the latter is much influenced by the lengths of the time steps between the pollen samples. Spatial analysis of site-specific dynamics provides exciting new insights into past vegetation dynamics, with potential for better understanding species-area distributions, distribution patterns of biodiversity, and conservation of mountain ecosystems.

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Landscape connectivity is considered a key issue for the maintenance of natural ecosystem stability and integrity (Saunders et al., 1991; Taylor et al., 1993; Collinge, 1998; With & King, 1999). The ability of species to survive is reduced by habitat loss, as well as by fragmentation of patches, since disconnections prevent recolonization (Fahrig, 2003; Foley et al., 2005). Therefore, the total available surface of a biome and its landscape connectivity are relevant to understanding the pressure on populations and species, i.e., survival of the gene pool.

Altitudinally shifting boundaries of montane biomes intrinsically mean changing degrees of connectivity (Ramírez-Barahona & Eguiarte, 2013). The present altitudinal distribution of biomes in the northern Andes is a “frozen” moment after a long series of Pleistocene changes, mainly driven by climate change (Bogotá-Angel et al., 2011; Torres et al., 2013). In the northern Andes biome responses to climate change have been captured in the dense network of palynologically studied sediment cores (e.g., Marchant et al., 2009; Grimm et al., 2013). In pollen-based studies of past vegetation change, pollen taxa are classified into ecologically meaningful groups, reflecting main biomes. Then, past altitudinally changing ranges of biomes are inferred from changing proportions of these ecological groups in the pollen spectra. Hooghiemstra and Van der Hammen (2004) compared altitudinal biome distributions of the last glacial maximum (LGM) in the Colombian Andes with the present day and provided first estimates of surface variability of the biomes through time. However, distributional dynamics of shifting biome boundaries in montane regions in terms of available habitat surface and landscape connectivity have not been addressed so far.

The landscape relief poses restrictions on habitat availability, connectivity, and dispersal patterns. Certain biomes and species are ecologically lim-

ited to the highest mountain ranges, such as the páramo vegetation in the northern Andes (Van der Hammen & Cleef, 1986; Lutteyn, 1999). The importance of understanding species dispersal in relation to landscape connectivity was recently stressed by several fine-resolution pollen records, showing very fast upslope shifts of ecotones, such as the upper forest line (UFL), for example, in the Colombian pollen records of Lake Fúquene at 2540 m (Groot et al., 2011, 2013), Lake La Cocha at 2780 m (González-Carranza et al., 2012), and in the pollen record of Llano Grande at 3460 m (Velásquez-Ruiz & Hooghiemstra, 2013). These records showed that forest may shift significantly faster upslope than subpáramo shrub, resulting in a temporary loss of the overruled biome. In such cases, a high connectivity, with areas where isolated populations were conserved, is crucial for a rapid return of the extirpated biome (Pearson, 2006). These dynamic patterns can be better understood by analysing biome and species distributions in a landscape perspective.

The objective of this study is to assess changes in connectivity of altitudinally distributed biomes in the northern Andes in terms of biome surface and migration potential. We make the step from a single-site view on the altitudinal distribution of biomes to a spatially integrated view of biome connectivity. Our analysis is driven by past environmental conditions inferred from pollen record La Cocha-1 (González-Carranza et al., 2012). We selected an area including the lake and showing the full elevational range from Amazonian lowland to the nearest mountaintops. Our connectivity assessment is focused in particular on the effect of the altitudinally shifting UFL on the habitat surface area and the connectivity of páramo biome patches. Results of this case study improve our understanding of how biomes in montane regions of the northern Andes respond to climate change in surface and connectivity. Implications

for scenarios of potential future developments are discussed.

SETTINGS OF THE STUDY AREA

CURRENT CONDITIONS AND LANDSCAPE

The selected study area is located in the Guamuez basin in the Eastern Cordillera of Colombia and covers a total area of 7559 km² (Fig. 1). The study area is found between 0°45'N and 1°30'N and between 76°44'W and 77°33'W, and elevations range from 300 to 4207 m.s.m. Toward the east the basin faces the Amazonian lowlands. Precipitation in the study area originates mainly from the Atlantic Ocean, and amounts are influenced by changes in the intensity of trans-Amazonian moisture transport (Gan et al., 2004). The typical wind patterns of this region are dominated by the trade winds blowing from the northeast, leading to enhanced precipitation on the eastern flank of the Andes. Mean annual precipitation (MAP) near Lake La Cocha is 1400 mm (Van Boxel et al., 2013), with values between 1300 and 2000 mm for most of the study area (Hernandez et al., 2004). Most precipitation falls between April and August, and it is lowest in December. Toward the west, dry inter-Andean high plains lie in the rain shadow and have a MAP

of 700 to 1400 mm. Lake La Cocha (1°05'N, 77°09'W) is located at an elevation of 2780 m.s.m. and is directly surrounded by steep slopes that reach up to 3600 m. At the elevation of the lake (2780 m), the mean annual temperature (MAT) is 11.6°C (Wetlands International, 2007), which is ca. 1.5°C less than expected in relation to its elevation (Van Boxel et al., 2013). With a surface of 41 km², Lake La Cocha is one of the largest lakes in the northern Andes.

MODERN VEGETATION

The altitudinal vegetation distribution of the northern Andes was studied by Van der Hammen (1974), Cleef and Hooghiemstra (1984), and Van der Hammen and Cleef (1986) (Table 1), among others. For the vegetation around Lake La Cocha we refer to González-Carranza et al. (2012), and here we present a general characterization appropriate to the aims of this study. The lake is surrounded by reed swamp. The lower parts of the slopes, once forested, are now covered by agricultural fields and pasture. Under natural conditions the slopes are covered up to 3550 m by Andean forest. Above this ecotone, reflecting the UFL, open páramo vegetation reaches to the summits. In the páramo small patches of forest dominated by *Polylepis* Ruiz & Pav. and *Gynoxis* Rchb. occur in protected areas (Van't Veer &

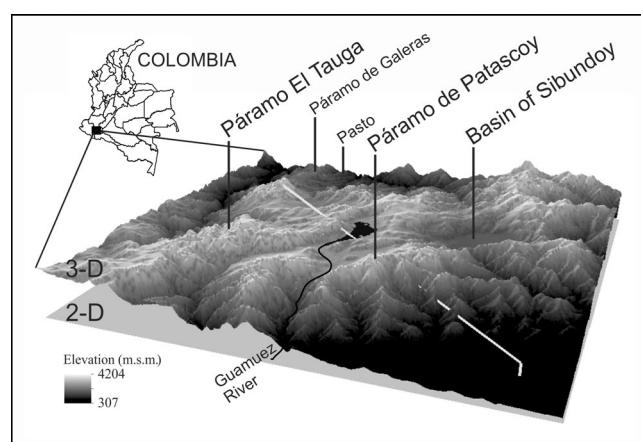


FIGURE 1. Relief map in 3-D of the study area in the south Colombian Andes, including Lake La Cocha at 2780 m elevation. The white line indicates the direction of the altitudinal profile shown as the background of Figure 7. Most important geographical references in the region are signposted, such as the páramos and the city of Pasto. A vertical exaggeration factor of 2.5 was applied to the digital elevation model.

TABLE I. Characterization of the present-day altitudinally organized biomes of the surroundings of Lake La Cocha.

Biome	Elevation (m.s.m.)	Characteristic taxa in pollen records	Mean Annual Temperature (mat)
Grasspáramo	~3700–4200	Graminaceous genera <i>Agrostis</i> L., <i>Calamagrostis</i> Adans., <i>Festuca</i> L., <i>Muehlenbergia</i> Schreb., and <i>Swallenochloa</i> McClure; stem rosettes of <i>Espeletia</i> Mutis ex Bonpl. (Asteraceae); and herbaceous genera <i>Gentiana</i> L., <i>Halenia</i> Borkh., <i>Valeriana</i> L., and <i>Aragoa</i> Kunth.	8°C–4°C
Subpáramo	~3600–3700	dwarf forest and shrub of Asteraceae, Ericaceae, <i>Polylepis</i> Ruiz & Pav., <i>Escallonia</i> Mutis ex L.f., Hypericum L.	10°C–8°C
	~3550–3600	UPPER FOREST LINE	
Andean forest	~2300–3600	<i>Weinmannia</i> L., <i>Alnus</i> Mill., <i>Myrica</i> L., <i>Styloceras</i> Kunth ex A. Juss., <i>Podocarpus</i> L'Hér. ex Pers., <i>Clusia</i> L., <i>Myrsine</i> L., <i>Juglans</i> L., <i>Ilex</i> L., <i>Hedyosmum</i> Sw.	16°C–10°C
Sub-Andean forest	~1000–2300	<i>Acalypha</i> L., <i>Alchornea</i> Sw., <i>Cecropia</i> Loefl., Arecaceae, <i>Hieronima</i> Allem., <i>Ficus</i> L., Malpighiaceae.	23°C–16°C

Hooghiemstra, 2000; Bakker et al., 2008). Human impact on the vegetation started at selected places in Colombia by the mid-Holocene time (Marchant et al., 2001). The pollen record of Lake La Cocha shows sudden and significant deforestation 1405 calibrated years before AD 1950 (cal yr BP).

UPPER FOREST LINE AND BIOME BOUNDARIES

In the present study, the altitudinal position of the UFL is pivotal. There is much debate on the natural (undisturbed) altitudinal position of the UFL (Wille et al., 2002; Bakker et al., 2008; Moscol-Olivera & Hooghiemstra, 2010; Jansen et al., 2013). Another relevant field of debate concerns the question of how plant associations shift altitudinally. Gleason (1926) observed that species are individualistically distributed along omnipresent environmental gradients and thus cannot form bounded communities. Gleason and many of his followers were of the opinion that plant species could not form integrated communities (plant associations and biomes) because of their individualistic behavior, and they criticized the community concept of Clements (1916) and

Braun-Blanquet (1921). This debate is well presented in Van der Maarel (1975), Fernández-Palacios and de Nicolás (1995), Vázquez and Givnish (1998), and Nicolson and McIntosh (2002), among others, and critically analysed by Shipley and Keddy (1987). Though Gleason and Clements held some contrasting views, they are not as incompatible as generally assumed (Nicolson & McIntosh, 2002; Jackson, 2006). In the present study we used the following assumptions: (1) the transition from continuous closed forest to open páramo vegetation reflects the natural UFL; (2) Andean forest and páramo are primarily climatologically constrained plant associations (biomes), but we do not exclude processes of interspecies competition. We support the working hypothesis that community structure depends on the local circumstances (Bader & Ruijten, 2008), the stage of the migration process (González-Carranza et al., 2012), and the degree of change (Van Nes & Scheffer, 2004; Jackson, 2006). We agree with the view that plant taxa respond individualistically to environmental and climatic change (Bush, 2002), but we observe that many plant taxa do respond in concert, thus allowing recognition of altitudinally constrained vegetation zones that, indeed,

may change floristic composition over time (Hooghiemstra et al., 2012). Such change is well illustrated in the Holocene pollen records of La Cocha (González-Carranza et al., 2012) and Llano Grande (Velásquez-Ruiz & Hooghiemstra, 2013).

The use of discrete biome boundaries in this study is considered useful because of the scale sensitivity of the definition of boundaries. Small-scale analysis restrains the identification of zones of transition between biomes, while at a larger scale, such as along local transects, limits of vegetation belts are normally diffuse. However in the latter case, discrete changes can occur where there are sudden shifts in abiotic conditions (Bach & Gradstein, 2011). For the scale of our analysis, and for the purpose of mapping changes in distribution and connectivity, biomes are first of all assessed as delimited vegetation associations (marked boundaries with limited transitions) along the altitudinal gradient. Subsequently, we discuss the implications of biome connectivity in the area of Lake La Cocha for the distributions of taxa based on current elevational occurrences. Hence, without disregarding the ongoing discussion on response mechanisms of plant associations to climate change (Feeley et al., 2011), we discuss connectivity implications for both levels of ecological responses to climate change, i.e., biome and species ecological responses.

METHODS

The pollen-driven connectivity framework was developed as follows: We summarized the main patterns of altitudinal biome distribution based on the La Cocha pollen record. We recognized four key distributions since the LGM. We characterized the landscape of the study area by its surface and relief variability along the elevation gradient. We then calculated the changes in surface of the different biomes as a two-dimensional, flat surface (2-D) to compare surface estimates when taking into account the three-dimensional

(3-D) relief. We estimated the degree of connectivity and surface loss of the páramo biome with an upslope-shifting UFL. Subsequently, we related rates of change in terms of spatial distribution of the different biomes to rates of change in terms of palynological taxa turnover, the latter reflecting the internal dynamics of forest. Finally, we discuss here the distribution patterns in relationship to the elevation ranges at both biome and species level.

BIOME DISTRIBUTIONS

We delimited an area of ca. 7600 km² around Lake La Cocha, defined to include the following four biomes types: lowland forest, sub-Andean forest, Andean forest, and páramo. Permanent snow was included as a separate class. Here, we follow the altitudinal vegetation distribution as elaborated for the northern Andes by Van der Hammen (1974) and further specified for the southern Colombian Andes by Wille et al. (2001). The latter study provided estimates on the altitudinal compression of biomes and the variation in lapse rates between the relatively dry LGM setting and the more humid atmospheric conditions of the Holocene (Hooghiemstra & Van der Hammen, 2004). The temporal variability in altitudinal biome distribution was inferred from the La Cocha pollen record. The position of the UFL is characterized by a proportion of 40% arboreal pollen (AP%) (Hooghiemstra, 1984; Van't Veer & Hooghiemstra, 2000; Groot et al., 2011; González-Carranza et al., 2012). The AP%-based estimate of the UFL elevation is fine-tuned by considering the proportions of specific pollen and spore taxa with clearly constrained altitudinal ranges (Groot et al., 2013). The La Cocha pollen record shows that the UFL occurred around four main altitudinal positions during specific periods of time: (A) UFL located around 3550–3600 m (modern); (B) UFL around 2800 m (in the study area prevailing during the period of 8060–2860 cal yr BP); (C) UFL around 2400 m (in the study area prevailing during

the period of 14,085–8060 cal yr BP); (D) Other pollen records (e.g., Van der Hammen, 1974; Hooghiemstra & Van der Hammen, 1993; Van't Veer & Hooghiemstra, 2000) showed that the UFL was around 2000 m during the LGM at ca. 21,000 cal yr BP. The lowland forest biome, at present below ca. 1000 m elevation and during the LGM below ca. 800 m (Wille et al., 2001), is not reflected in the pollen spectra because heavy orographic rains prevent pollen grains being transported from such low elevations to the lake.

SURFACE ESTIMATES OF THE BIOMES

In remote sensing studies, mapping ecosystem distribution at different time intervals is mostly based on the interpretation of satellite imagery of different years. Results are generally expressed as the area gained or lost by a certain type of land cover during the period of analysis. The resulting land cover maps do not take relief into account. This implies that the actual available surface area in montane regions is not fully explored. The most recent assessments of land cover change in the Andes overlooked landscape relief in surface estimates (Etter et al., 2006; Eva et al., 2012). To improve our understanding of connectivity dynamics, we integrated the relief into our surface estimates and the changing biome distributions. The 3-D landscape projection is considered both an approximation of available surface and dispersal distance. The surfaces are calculated in both 2-D and 3-D aspects (Fig. 1) with the Surface Volume tool of 3-D Analyst of ArcGIS, taking sea level as the horizontal reference plane (0 m.s.m.). Surface area estimates are analysed for four biomes (lowland forest, sub-Andean forest, Andean forest, and páramo), and permanent snow is treated as a separate class for the four different UFL settings. Although palynological studies differentiate between subpáramo (3550–3800 m), grasspáramo (3800–4200 m), and superpáramo (4200 m to the permanent snow line) vegetation, we consider the páramo biome as a single unit in our spatial

assessments. The method is further specified in Appendix 1. To model the UFL fluctuations and the corresponding biome surface areas we used a GIS-based algorithm developed by Rijssdijk et al. (2012; *in press*). Originally designed to derive quantitative metrics from changing oceanic island sizes and configurations due to sea level fluctuations, we applied this method to assess “islands in the sky” by implementing an index for biome “islands” that are formed at high elevations. We use a digital elevation model (DEM) to calculate biome surfaces.

CONNECTIVITY

Landscape connectivity can be defined as the degree to which the landscape allows the migration of species (individuals) between the present habitats, facilitating gene flow. Two basic groups of connectivity can be considered: structural connectivity refers to the degree to which some landscape elements are contiguous or physically linked to one another (With & King, 1999; Tischendorf & Fahrig, 2000); functional connectivity recognizes the behavioral responses of organisms to the physical structure of the landscape (Taylor et al., 1993; Bélisle, 2005). Thus, landscape connectivity depends not only on the amount and patterning of habitat, but also on the habitat affinities and dispersal abilities of species (Laita et al., 2010). In our study we assess the effect of a shifting UFL on the structural connectivity of the restricted range distribution of the páramo. Due to the shifting of the boundaries between the biomes, their ranges shrink or expand significantly, resulting in a dynamically changing number of patches and their surfaces. Patches may merge or fragment, opening or closing dispersal routes within or between patches. The degree of connectivity and surface change depend on the relief, such as the presence of high peaks. Hence, the effect of the rise of the UFL on páramo connectivity can be more or less profound, depending on the landscape relief.

We used the probability of connectivity (PC) index developed by Saura and Pascual-Hortal (2007), which is based on network graph structures, the habitat availability, and interpatch dispersal probabilities. A graph structure evaluates the network as a set of nodes (patches) and links (corridors) such that each link forms the connection between two nodes. The distance between nodes (interpatch distance) is considered the dispersal distance for species (Pascual-Hortal & Saura, 2006) and is commonly used as the probability of dispersal within a network (Saura & Pascual-Hortal, 2007). The integration of intra-patch and interpatch connectivity with patch area into a single index has been shown to produce improved connectivity measurements compared to other indexes (Saura & Pascual-Hortal, 2007). To overcome limitations due to study area size (when the habitat patches are small compared to the total area), Saura et al. (2011) suggested the equivalent connected area (ECA) as the alternative index directly derived from the PC. The ECA is defined as the size of a single habitat patch (maximally connected) that would provide the same value of the probability of connectivity as the actual habitat pattern in the landscape. The equations used are further specified in Appendix 2. The computations of the PC and ECA index have been implemented in the Conefor Sensnode 2.2 software (Saura & Torné, 2009).

We calculated the overall network connectivity for the páramo biome along the elevation gradient as the UFL moves upslope from 2000 to 4100 m (currently at 3550 m). The páramo biome includes the sparsely vegetated superpáramo, currently occurring between 4200 m and the snowline. The patch connections were estimated using Euclidean (straight line) edge-to-edge distances between patches. Patches were considered as of equal habitat quality, and colonization is equally likely to occur from each patch. Fragmentation of the landscape (e.g., introduction of 200 m distances) initially has a greater effect on plants with poor dispersal capacity, while for plants with good

dispersal capacity only increments of kilometers in distance will matter. For this reason, we included model outcomes with varying dispersal distances between 0.2 and 50 km.

RATES OF GEOGRAPHICAL AND PALYNOLOGICAL CHANGE

Based on the surface and connectivity estimates, three different geographical rates of change are obtained. The rate of elevation change (RoElev) of the UFL is calculated as the dissimilarity between reconstructed UFL positions in two adjacent pollen spectra, divided by the time interval between the spectra. The rate of surface change (RoSC) is obtained by calculating the dissimilarity between surface estimates in a 100 m elevation shift and at different altitudinal positions of the UFL. Additionally, changes in surface of the largest connected páramo patch (cp) are monitored along the altitudinal gradient. The rate of surface loss (RoSL_{cp}) is estimated for each 100 m elevation interval. High rates are considered indicative of where the patch undergoes a disconnection from an adjacent patch. Loss of connection is considered to occur when the patches are more than 1 km apart.

Estimates of changes in the species composition along environmental and climatic gradients provide information on the relationship between landscape features and the spatial patterns of biodiversity. Based on the pollen record of Lake La Cocha, rates of ecological change (RoEC) are estimated by calculating the palynological turnover rate (PTR) and the dissimilarity coefficient (DC) between adjacent pollen spectra. The PTR is defined here as the amount of taxonomic composition change per time unit. Pollen data were interpolated to produce intervals between samples equidistant in time. To account for the non-equivalent time intervals the DC is calculated as well. This coefficient is calculated as the distance between two samples in an N-dimensional space, with the coordinates defined by the pollen percentages of the pollen taxa in these samples (N

taxa) (Bennett & Humphry, 1995). Further explanation on rates of change implications is found in Appendix 3.

ALTITUDINAL DISTRIBUTION PATTERNS OF SPECIES

For pollen taxa well represented in the La Cocha pollen record, we downloaded all available herbarium records through the Global Biodiversity Information Facility (GBIF, 2013; Appendix 4). We followed the data filter method proposed by Feeley and Silman (2010) to reduce the potential influence of georeferencing errors and biased duplication of samples on the genus elevation distribution. This method includes screening the data to eliminate obvious georeferencing errors and duplicated records, resulting in a database of more than 67,000 unique records. We selected the records from Colombia and Ecuador as the most representative of the study area. For 49 genera represented by > 30 Global Biodiversity Information Facility (GBIF) records (collections), we estimated their altitudinal distributions. We only used elevation data recorded by the collections themselves, as elevations extracted on the basis of geographic coordinates are shown to present severe and problematic errors, especially in mountainous areas (Feeley & Silman, 2010).

RESULTS

BIOME AND UPPER FOREST LINE DISTRIBUTION IN THE LANDSCAPE

The landscape within the study area has been covered by a variety of spatial distribution patterns of the biomes through time (Fig. 2). The lake was surrounded by páramo up to 8060 cal yr BP (Fig. 2C, D), then by Andean forest after 8060 cal yr BP. During the LGM the large extension of permanent snow and páramo is evident, as is the fragmentation of the páramo into isolated patches at present time (Fig. 2A). These shifts of biomes along the slopes cause changes in surface area that show important differences between the

biomes at these four different periods (Fig. 3). Andean forest shows a relevant increase in surface from 17% during the LGM to 57% at present (Table 2). Sub-Andean forest increased with similar values but a higher factor (5 compared to 3.2 for Andean forest). During the LGM permanent snow covered more than 20% of the study area and is absent today. Páramo covered 47% of the study area during the LGM; this area was reduced to 2% over the last 8000 years. The páramo vegetation occurs within an altitudinal range of 600 m (3600–4200 m), but nonetheless this biome covers only 2% of the area today. The largest gains occurred for Andean forest and sub-Andean forest (1622 km² and 1268 km², respectively) during the period that the UFL shifted upslope from 2800 m to 3600 m, while during the same period of time the páramo lost 95% of its surface. Also during that period, the area with permanent snow lost 24 km², disappearing completely, while all forest biomes gained area.

CONNECTIVITY AND SURFACE

By projecting the reconstructed biome distributions to a more realistic 3-D model of the landscape (Fig. 1), approximations of variation in surface and distance can be better assessed. There are important differences in estimated surfaces as a flat area (2-D) versus as a 3-D projection (Table 3), especially in the mid-range altitudes between 900 and 2400 m. The total surface of the study area is 7559 km² as a 2-D flat surface but increases by 12% to 8467 km² when considered as a 3-D landscape. Surface estimates for the sub-Andean and Andean forest differ up to 15%–17%. The degree to which the 3-D model differs from a flat surface depends on the relief variability along the elevation gradient (Fig. 4A). The mountains around Lake La Cocha are characterized by abundant mid-range altitudes (2600–3400 m), with a steep reduction of available surface area in the adjacent higher and lower altitudes. The peaks in the 3-D/2-D line (Fig. 4A) point out where the relief deviates most from a flat surface, indicating

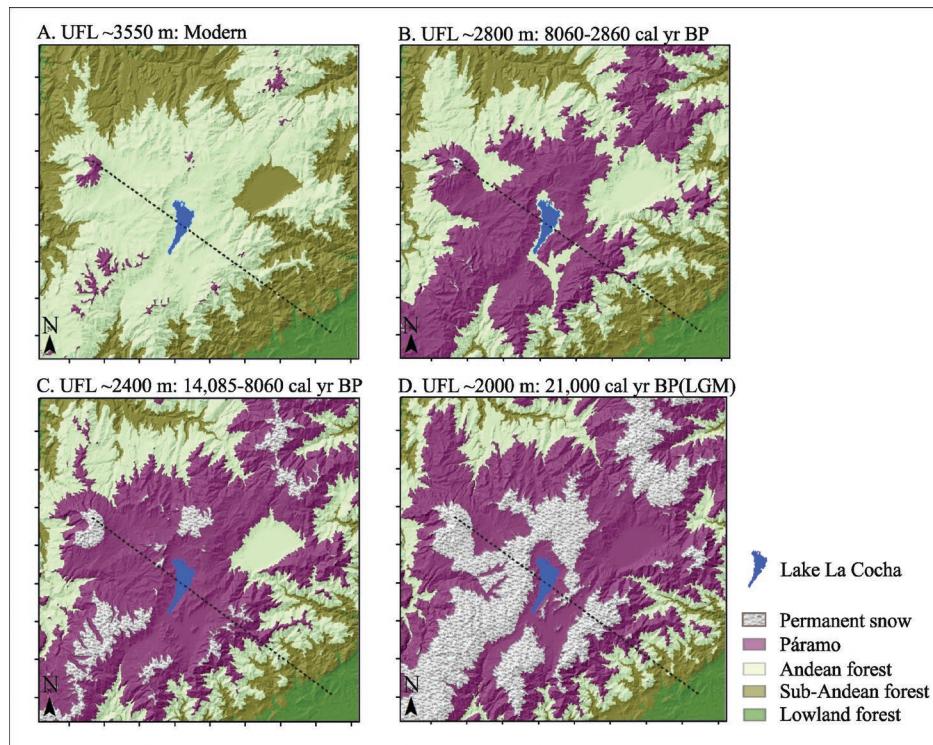


FIGURE 2. Distribution of lowland forest, sub-Andean forest (lower montane forest), Andean forest (upper montane forest), páramo (including subpáramo, grasspáramo, and superpáramo), and permanent snow during four different altitudinal positions of the upper forest line (UFL).—A. UFL at 3550 m, reflecting the present-day condition.—B. UFL at 2800 m, reflecting the period from 8060 to 2860 cal yr BP.—C. UFL at 2400 m, reflecting the period from 14,085 to 8060 cal yr BP.—D. UFL at 2000 m, reflecting the Last Glacial Maximum (LGM) at ca. 21,000 cal yr BP.

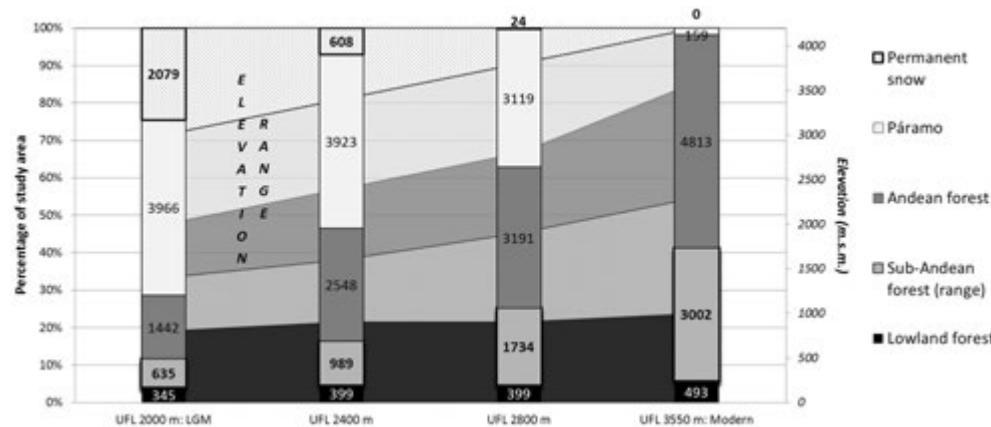


FIGURE 3. Estimated surface area and percentage cover of the four main vegetation associations and permanent snow for the following scenarios: upper forest line (UFL) located at 2000 m, 2400 m, 2800 m, and 3600 m elevation. The numbers within the bars indicate surface estimates (3-D, km²) of the biomes. The total area of the study site is 7600 km². The elevation ranges of the biomes along the elevation gradient are shown in the background (right vertical axis). The altitudinal intervals occupied by the various biomes during periods of the last 14,000 years follow the La Cocha pollen record as specified in Table 2.

TABLE 2. Calculated change in surface area (2-D and 3-D) of main biomes and permanent snow for different upper forest line positions. Maximum values are indicated in bold.

	Elevation range (m)	Vertical extent (m)	Surface area in 2-D (km ²)	Surface area in 3-D (km ²)	Difference 3-D/2-D	Surface area 3-D
UFL ~3550 m: Period A (Modern)						
Permanent snow	0	0	0	0		0
Páramo	3600–4200	600	146	159	9%	2%
Andean forest	2300–3600	1300	4357	4813	10%	57%
Sub-Andean forest	1000–2300	1300	2589	3002	16%	35%
Lowland forest	< 1000	1000	467	493	6%	6%
UFL ~2800 m: Period B						
Permanent snow	> 3800	600	22	24	9%	0%
Páramo	2800–3800	1000	2892	3119	8%	37%
Andean forest	1900–2800	900	2768	3191	15%	38%
Sub-Andean forest	900–1900	1000	1492	1734	16%	20%
Lowland forest	< 900	900	385	399	4%	5%
UFL ~2400 m: Period C						
Permanent snow	> 3400	900	563	608	8%	7%
Páramo	2400–3400	1000	3567	3923	10%	46%
Andean forest	1600–2400	800	2192	2548	16%	30%
Sub-Andean forest	900–1600	700	852	989	16%	12%
Lowland forest	< 900	900	385	399	4%	5%
UFL ~2000 m: Period D (LGM)						
Permanent snow	> 3000	1300	1919	2079	8%	25%
Páramo	2000–3000	1000	3524	3966	13%	47%
Andean forest	1400–2000	600	1236	1442	17%	17%
Sub-Andean forest	800–1400	600	549	635	16%	7%
Lowland forest	< 800	800	331	345	4%	4%
TOTAL	325–4200	3875	7559	8467	12%	

steeper slopes at lower altitudes between 1000 and 2000 m. A similar variable landscape geomorphology is found between 2000 and 2700 m, indicating an increase in surface and dispersal distance. There are several more plane intervals between 2800 and 3400 m, with steeper slopes gradually increasing to higher elevations. This means that biomes with a distribution restricted to 2700 m and higher constitute an important part of the available surface area in the region. Nevertheless, each 100 m altitudinal rise results in a substantial reduction of the surface area and connectivity (Fig. 4B). The size of the largest connected páramo patch shrinks when its lower

altitudinal boundary rises. At certain elevations, patches disconnect and dispersal routes between patches are lost. The first important decrease in connected surface occurs between 2700 and 2800 m, pointing to a first disconnection of a large area from the main patch. The result of this disconnection between the large páramo area in the northeast from the main páramo area surrounding the lake can be observed in Figure 2B. The next critical thresholds for connectivity loss occur between 3100 and 3300 m, and between 3400 and 3600 m (Fig. 4B). There, the topographical variation influences patch size and range shape of biomes. At the most profound fragmen-

TABLE 3. Calculated change in surface areas of main biomes and permanent snow as a 3-D landscape during the intervals between the four periods of characteristic UFL positions (Fig. 2A–D). Negative numbers indicate a decrease in surface area.

	Biome	Area change 3-D (km ²)	Change (%)
UFL 2800 to 3550 m.s.m. Period B to A (Modern)	Permanent snow	-24	-100
	Páramo	-2960	-95
	Andean forest	1622	51
	Sub-Andean forest	1268	73
	Lowland forest	94	24
UFL 2400 to 2800 m.s.m. Period C to B	Permanent snow	-584	-96
	Páramo	-804	-20
	Andean forest	643	25
	Sub-Andean forest	745	75
	Lowland forest	0	0
UFL 2000 to 2400 m.s.m. Period D (LGM) to C	Permanent snow	-1471	-71
	Páramo	-43	-1
	Andean forest	1106	77
	Sub-Andean forest	354	56
	Lowland forest	54	16

tation events, the rate of surface loss can decrease 40%–69%. Depending on the elevation interval, there is relatively more connectivity loss than surface area loss; each 100 m rise between 2000 and 3300 m affects the interpatch connectivity more than the intrapatch connectivity (Fig. 4C). As the lower páramo boundary further rises, more páramo patches disconnect, and intrapatch connectivity becomes more important. The degree of loss of the ECA also depends on potential dispersal distances, because initially species with a capacity for short distance dispersal would experience higher ECA loss, while at higher elevations long distance dispersal species become more affected.

GEOGRAPHICAL AND ECOLOGICAL RATES OF CHANGE

Geographical changes. The main pollen diagram of La Cocha (Fig. 5A) shows contributions of páramo, subpáramo, and Andean forest. The rec-

ord of UFL positions (Fig. 5B) shows a high variability of RoElev at a short time scale (Fig. 5C), indicating average migration velocities up to 20 vertical m yr⁻¹. Some peak values of upslope UFL shifts are based on single pollen samples and are considered meaningless outliers (indicated with asterisks in Fig. 5B). As the forest moves upslope a larger surface extension is occupied in the region (Fig. 5D). Both Andean and sub-Andean forests expand while páramo, in particular, is replaced by Andean forest (Fig. 5D).

Shifts of the UFL show several peaks (Fig. 5B) toward higher altitudes, causing sharp decreases in the representation of the subpáramo biome (Fig. 5A). During the period from 13,000 to 11,500 cal yr BP (Fig. 5A, zones 3 to 4) subpáramo nearly disappeared (González-Carranza et al., 2012). Significant peaks are also present between 8000 and 1000 cal yr BP; human presence is evidenced in the Andes during this period, yet we consider this part of the record to be reliable. However, during the last 1500 years (Fig. 5,

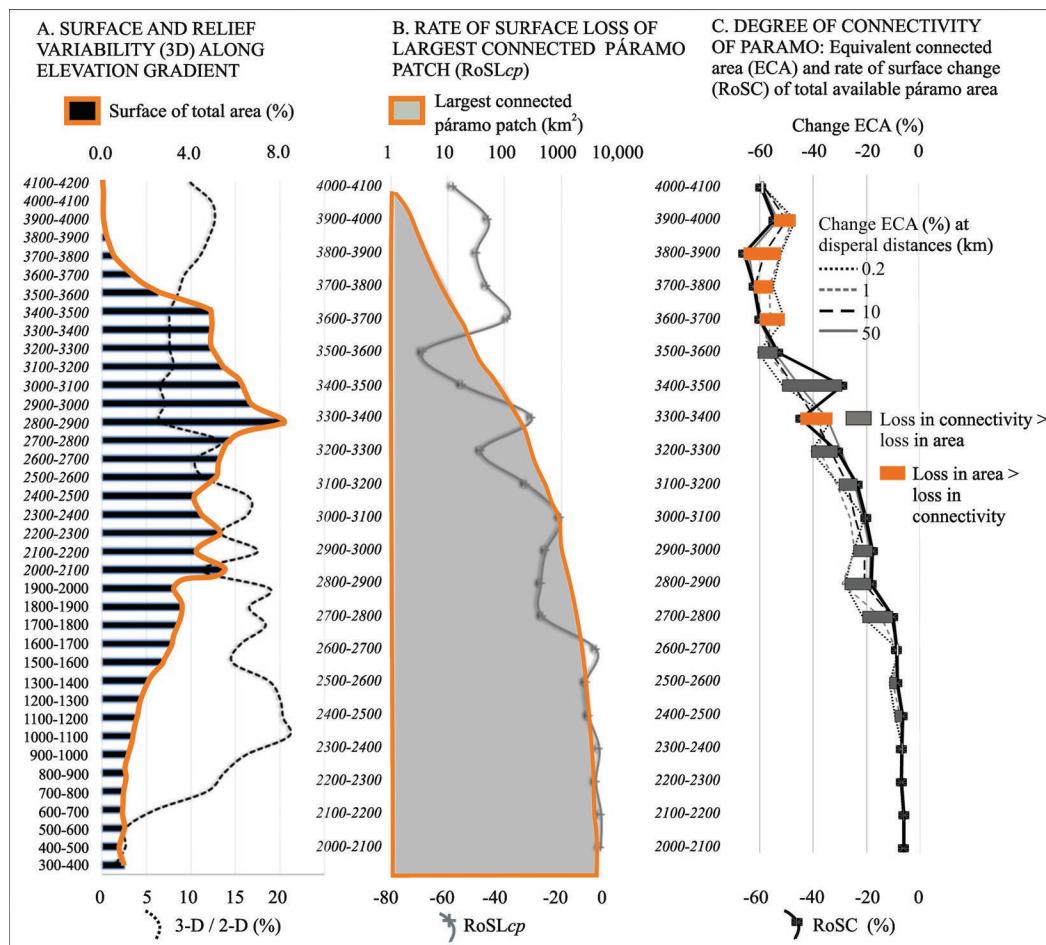


FIGURE 4.—A. Surface and relief variability along the elevation gradient expressed as the percentage cover as a function of the selected study area and the 3-D/2-D ratio (%).—B. Surface (2-D, km²) and upslope rate of surface loss of the largest connected páramo patch area (RoSLcp, %). Surface area is along a logarithmic scale and patch surface is estimated in absence of permanent snow.—C. Changes in equivalent connected area (ECA) along the elevation gradient as the indicator of páramo connectivity. The ECA values for varying dispersal distances (0.2–50 km) are plotted as lines, as is the rate of total surface area change (RoSC, %). Orange colored bars indicate where loss in area is larger than the relative loss in connectivity. Dark gray bars indicate where loss in connectivity is larger than the relative loss in area.

zones 20 to 23) there was significant anthropogenic impact (deforestation), and the record for this period was discarded as invalid. Periods in which the UFL reached high elevations (3100–3300 m) may not always show a profound effect on the total biome surface area (Fig. 5D), but they record a heavily reduced extension of the largest páramo patch (Fig. 5E), indicating reduced connectivity (Fig. 4).

The critical elevation limits for páramo patches to disconnect depend on the lowest elevation thresholds in the landscape and the elevation of the summits. When the UFL moves upslope, the number of patches increases and the distribution is increasingly confined to a group of patches (Fig. 6: C3) or isolated peaks (Fig. 6: C1, C2, C4, C5) in the landscape. For the region of La Cocha the first critical elevation trespass is between 3100

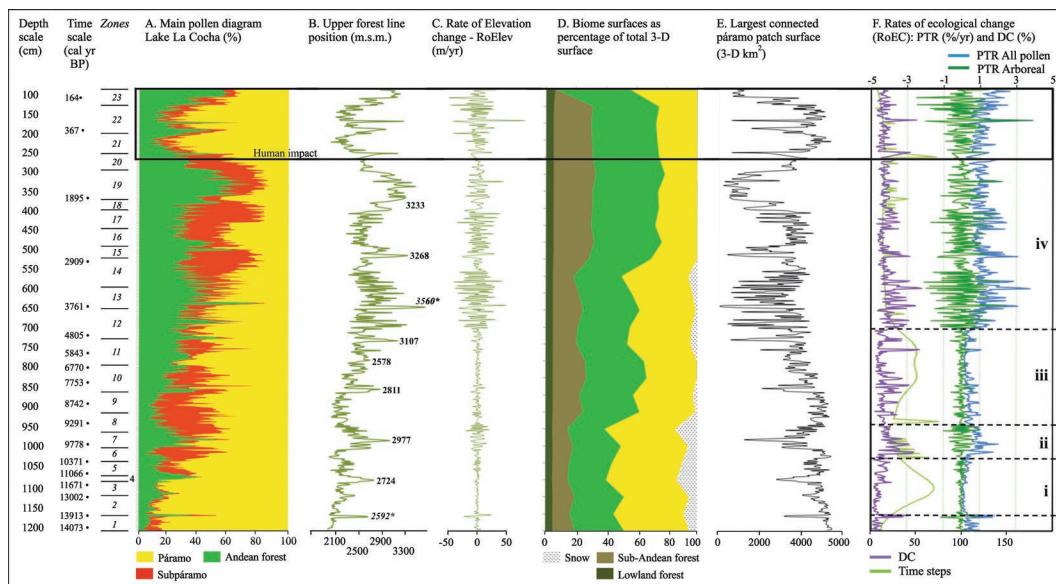


FIGURE 5. Records of vegetation dynamics and rates of change. The left vertical axis indicates, from left to right, the depth scale, time scale, and pollen zones.—A. Main pollen diagram of core La Cocha-I (after González-Carranza et al., 2012).—B. Upper forest line (UFL) position. The elevation peaks are indicated where the rapid increase of the UFL caused the disappearance of the subpáramo. Values with * are based on a single sample and therefore discarded.—C. Rate of elevation change (RoElev, $m \text{ yr}^{-1}$).—D. Biome surface areas of four vegetation associations and permanent snow as percentage of total 3-D surface.—E. Area (3-D, km^2) of largest páramo patch surface.—F. Rates of ecological change (RoEC): palynological turnover (PTR, %/yr) for the total and arboreal pollen sum, and dissimilarity coefficient (DC, %). Time steps of the age model are shown along the lower horizontal axes. Horizontal dashed lines indicate transitions between periods of higher (ii and iv) and lower (i and iii) species composition dynamics.

and 3200 m, when C1 disconnects from C6 and consequently, from the rest of the landscape. C2 disconnects at 3300 m, while important stepping stone patches previously present between C1 and C6 also disappear. These changes are more prominently affecting connectivity as seen in Figure 4. When the UFL moves further up to 3400 m, C6 practically disappears and loss in area is substantial in all components. C5 now becomes a group of separated patches. Connectivity is greatly affected when C3 disintegrates and C2 is nearly lost; this happens when the lower boundary migrates to 3600 m. Up to that limit páramo occurs relatively close to the lake on the surrounding ridges. Considering projections of a future up-slope shift of the UFL, the páramo biome will only remain on the Galeras volcano (C1) as a last refugium (but the volcano has had several eruptions in the last two decades potentially damaging the vegetation in the refugium).

Ecological changes. Transitions between periods of increased PTR (Fig. 5F: ii, iv) and decreased PTR (Fig. 5F: i, iii) are observed for both general and arboreal pollen composition. Intervals of increased PTR possibly indicate periods of variable climate conditions. The length of the time steps between pollen samples varies along the core from 20 to 70 years (Fig. 5, time step curve). The most striking observation to emerge from the PTR and time step comparison is the clear relation between PTR and the length of the time steps; long time steps weaken PTR dynamics. The DC also shows the same transitions between periods of increased and decreased variability, but to a lesser degree (Fig. 5F). Comparing the UFL position with the

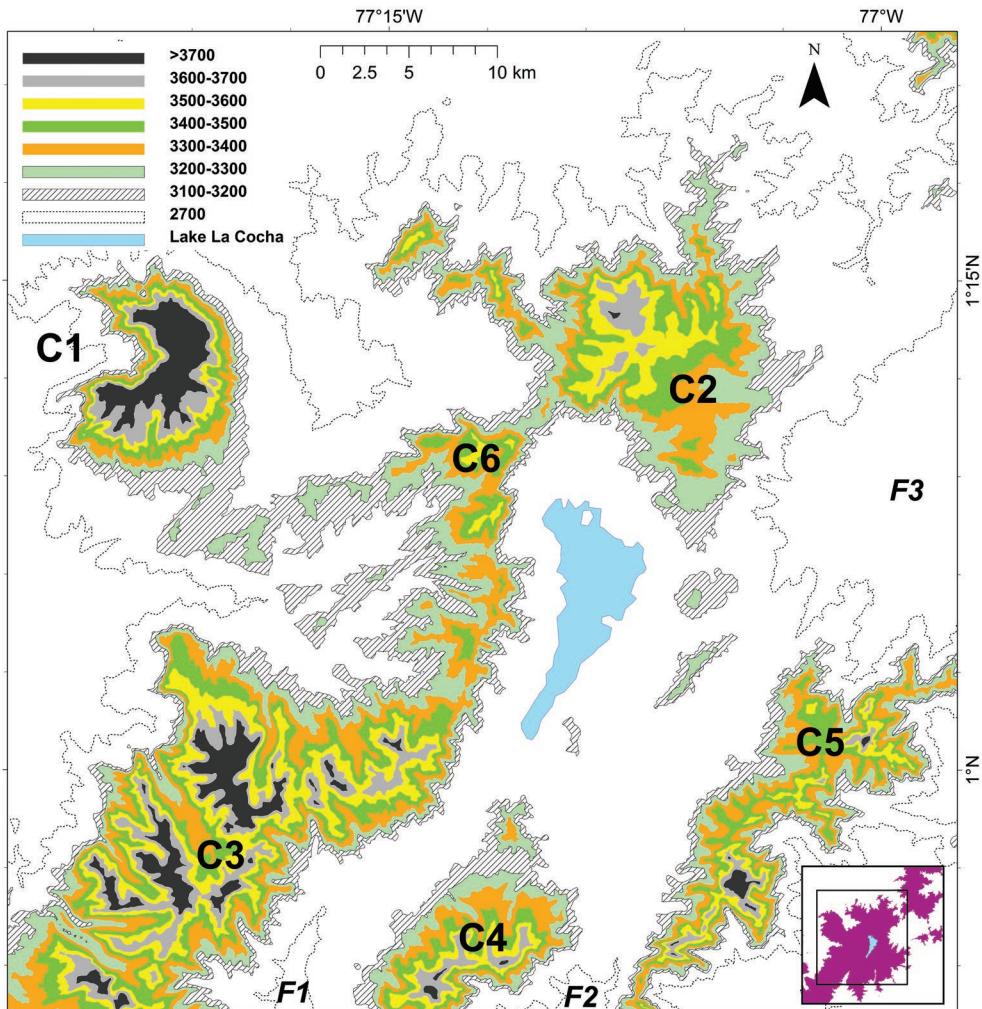


FIGURE 6. Geographical representation of the critical elevation thresholds of páramo connectivity and surface changes (Fig. 4) in a selected area in the region of Lake La Cocha. The small window in the lower right corner delimits the location of the selected area from within Figure 2B, showing the páramo extension. Shaded areas indicate elevation ranges of 100 m intervals (see legend), and the dashed line delimits the 2700 m elevation contour. Components (C) indicate groups of páramo patches. Forest areas toward lower elevations (< 2700 m) are indicated as F1, F2, and F3, the last one being the Basin of Sibundoy (Fig. 1).

DC values, there is tendency of increased DC when forest occurs at higher elevations (> 2600 m; Fig. 5B). Interestingly, the higher elevations are related to increased surface extensions (Fig. 5D), which indirectly points to a relationship between extended range of biomes and the DC.

The distribution of individual species along an elevation gradient is composed of a nucleus zone,

which represents the core of the species' range plus the trailing and leading edges of biogeographical boundaries of the species' distribution. Shifts in the geographic ranges of individual plant species, as well as whole plant associations, occur by expansion of the population at the leading edge of the distribution area and retraction at the trailing edge (Jump et al., 2009). Species may show a re-

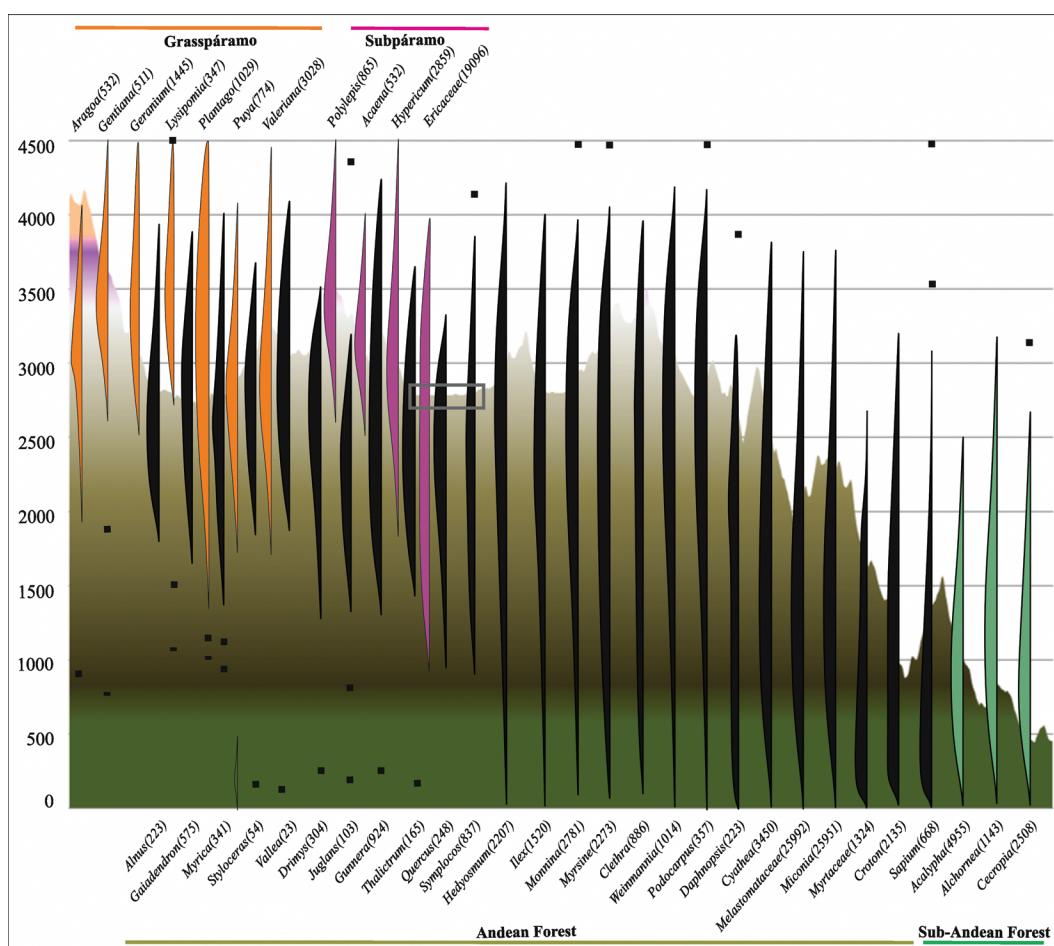


FIGURE 7. Altitudinal ranges of modern plant species present in pollen records from the northern Andes. The sequence of taxa follows the grouping of pollen taxa reflecting specific biomes. The curves follow the shape of the frequency distributions: the thickest part of the curve indicates the highest frequencies of the observed distribution. Outliers are indicated as dots. The number of herbarium collections included per taxon is specified in parentheses. The background shows the landscape profile of the region as drawn in Figure 1. The location of Lake La Cocha is indicated by a box. Distribution data were obtained from the Global Biodiversity Information Facility (GBIF, 2013).

stricted nucleus range, while others show a relatively broad core range and distribution along a wide elevation gradient (Fig. 7). Several arboreal genera are distributed over the entire range of altitude, such as *Podocarpus* L'Hér. ex Pers., *Weinmannia* L., and *Hedyosmum* Sw. The trailing and leading edges of species distributions are relatively widely spread along the elevation gradient, for both high montane as well as for lowland species. The distribution of subpáramo species does not

differ from the grasspáramo species; both the nuclei and edges show similar patterns. This justifies the strategy chosen for this analysis, to assess páramo dynamics as a single biome. The leading edges of the Andean forest biome overlap the core ranges of the páramo biome, although the nuclei of the arboreal species are all below 3000 m. This reflects the difference between all GBIF-loaded data from Colombia and Ecuador leading to an average position of the UFL ecotone, and the region-

specific positions of the UFL ecotone as used in the various pollen studies: UFL in Llano Grande at 3450 m (Velásquez-Ruiz & Hooghiemstra, 2013); in Fúquene at 3200 m (Groot et al., 2011, 2013); in La Cocha at 3550 m (González-Carranza et al., 2012); and in Guandera at 3600 m (Bakker et al., 2008). Depending on MAT, MAP, cloudiness, and night frost (Hooghiemstra et al., 2012), the altitudinal ranges of some species can differ significantly between the forest and páramo biomes, while many others occur in the mid-ranges.

DISCUSSION

GEOGRAPHICAL AND ECOLOGICAL CHANGES

Spatial analysis of the landscape provides the geographical context to better understand climate-driven biome dynamics. The ratio between the elevation range and the associated available biome surface area depends on the relief only. In the study area, biomes at mid-range altitudes have higher surface area available compared to biomes prevailing at high and low altitudinal ranges (Fig. 4). Although biomes may not show substantial surface change along the elevation gradient, certain 100 m shifts have profound effects on their connectivity. The degree of fragmentation depends on the altitudinal range. The projected loss of biome surface due to global warming is disproportionately large compared to the reduction in elevation range which is typical of a mountain setting (Bush, 2002). As a consequence, the most important surface reductions are processes of isolation between patches of biomes.

Fast UFL shifts, indicative of rapid climate change, cause critical consequences for the connectivity of the páramo biome (Fig. 5). Trees with pioneer qualities and a short life cycle allow a fast response to climate change and may expand into new areas and produce fertile individuals within less than two decades. A high variability in UFL positions at short time scales indicates average migration velocities up to ca. 20 vertical m yr⁻¹, with

peaks up to 40 vertical m yr⁻¹. Estimates of migration in deep ecological time based on fossil pollen records are known to be significantly higher than observed rates from dispersal studies based on plots in the field (Pearson & Dawson, 2005). Estimates based on fossil records from temperate lakes mention rates of horizontal spread exceeding 1000 m yr⁻¹ (Davis, 1981; Huntley & Birks, 1983), but these velocities have not been observed from ecological studies (Clark, 1998). Ecologists suggest that rare long-distance dispersal of pollen grains may explain the higher migration rates inferred from pollen records (Clark et al., 2001; Pearson & Dawson, 2005; Nathan, 2006). This is substantiated by Jansen et al. (2013), who showed in a case study from northern Ecuador that when grass-rich biomes prevail, their pollen signal may lead real forest change by about a thousand years. Willis et al. (2010) argued that although the underlying mechanisms responsible for past changes in climate were very different, the rates and magnitude of climate change were similar to those predicted for the future and therefore relevant to understanding future biotic response. What emerges from records of deep ecological time is evidence for rapid community turnover, migrations, development of novel ecosystems, and thresholds from one stable ecosystem to another. In Figure 5B, the arboreal pollen peaks based on single pollen samples and peaks that start to grow from below 40% (Fig. 5A) (thus reflecting páramo conditions at the coring site) are considered unreliable (i.e., peaks labeled 2592* and 3560*).

Patches of forest within the páramo are thought to contribute to fast expansions when conditions become favorable (Ammann et al., 2000; Bush, 2002; Sarmiento & Frolich, 2002; Pearson, 2006). When the UFL passes the level of the lake at 2800 m the surrounding ridges still host páramo vegetation at a very close distance. Even at the highest peak of the UFL at 3268 m (Fig. 5B), páramo is still present directly around the lake. This makes a local extirpation of the subpáramo as an ecotone plausible when the leading edge of

forest is overpassing the slower-migrating lower edge of the subpáramo biome (Breshears et al., 2008).

Replacement of forest by páramo vegetation is considered a slower process. When climate conditions become unfavorable for trees in the current ecotone, individual trees may die, leaving abundant dead wood prone to fire. After opening the landscape by fire, subpáramo is able to become reestablished as a transition zone between grasspáramo and the retreating forest. A lag greater than 100 years between the climate deterioration and the downslope retraction of the forest seems feasible. The pollen record of La Cocha indeed shows horizons with abundant charcoal at events of forest retraction (González-Carranza et al., 2012). Rapid ecosystem reconfigurations between alternative states are known as ecological regime shifts (Andersen et al., 2008; De Boer et al., 2013). The trigger may be an external perturbation, such as climatic fluctuations, or a change in the system's internal dynamics. The longest period of relative stability is 600 years at Lake La Cocha, while a period of 400 to 1500 years was observed at Lake Fúquene (Bogotá-Angel et al., 2011).

Mountain slopes between ca. 1000 and ca. 1500 m were permanently covered by the Andean forest, following the hypothesis of Wille et al. (2001) that this particular interval is unique because the biome cover has remained unchanged since the LGM. This implies that pollen records from the ca. 1000–1500 m interval are less sensitive to minor climate change. Although the PTR is proposed as a useful indicator for the speed of past vegetation change (Jacobsen et al., 1987; Williams et al., 2001; Urrego et al., 2009), care should be taken in extracting easy conclusions from the RoEC estimates, since variation in time intervals has significant impact. In the La Cocha pollen record, temporal steps vary between 5 and 70 years, respectively enforcing and weakening the PTR values. Without the corresponding data on time step variability and absolute pollen change values, rates of change estimates could lead to

misinterpretation of the degree of biome change. Therefore, we suggest standardizing the notion of time step variability for PTR and RoEC estimates as a common denominator in future studies.

NO-ANALOGUE VEGETATION COMPOSITION

The most dynamic altitudinal range for species in the region of Lake La Cocha is between 2500 and 3500 m. Here several biological and geographical processes converge: the characteristic geomorphology of the region (Fig. 4); the isolated habitat patches at distinct elevation levels (Fig. 6); and the distribution nuclei of species within this range (Fig. 7). At the same time this is an important elevation range for surface availability (Fig. 4). The relief plays an important role in species sorting and their potential versus realized distribution. The species with greatest amplitude, arboreal species in this study, are distributed over the entire range of altitude (Fig. 7). This offers opportunities for rapid expansion when conditions improve toward higher altitudes or from isolated patches that remained in the landscape. Altitudinal range width of ecosystems and species influence the observed patterns of species richness and the homogeneity along the elevation gradient (Bach et al., 2007). The tendency to observe higher turnover rate at mid and higher elevations is explained by the convergence of upper and lower elevation distribution limits and the density of distribution nuclei of the different biomes along this elevation range (Bach et al., 2007). Nevertheless, the UFL and the transitions from the foothills to the flat lowland terrain are well-known zonations (Kessler, 2000; Richter et al., 2008).

FUTURE IMPLICATIONS

The timing, magnitude, and direction of biotic responses to projected future climate change is thought to vary greatly among species and geographical conditions, allowing novel plant assemblages as well as different types of distribution

patterns to develop (Williams & Jackson, 2007; Breshears et al., 2008; Willis et al., 2010; Chen et al., 2011). Since the last interglacial period, biotic communities have been resorted, leading to the formation of new species assemblages linked to new climatic conditions (Jackson & Williams, 2004; Willis et al., 2010; Bertrand et al., 2011). Assuming that Andean montane species distributions are significantly influenced by temperature (as well as precipitation, atmospheric $p\text{CO}_2$, clouds, night frost frequency, and UV-radiation; Hooghiemstra et al., 2012), the projected future climate warming (IPCC, 2007) will probably cause an upward migration of species in montane arboreal communities, since temperature decreases predictably with increasing elevation. The effect on páramo connectivity and available habitat area is projected to be substantial (Fig. 4). Currently, the pressure on ecosystems has reached a dangerous level due to the combination of rapid climate change and extended land use (Travis, 2003). The greatly reduced range sizes of natural systems due to grazing and other activities can pose barriers for upslope shifts of the leading edges of forests, if the surrounding forests and natural habitats are not maintained (Chen et al., 2009). The key is to understand the ecological network across elevation gradients and, thus, the reason to focus local conservation efforts on guaranteeing habitat availability and connectivity in the montane landscape. The improved insight on the ecological complexities obtained through the framework developed in this paper should be applicable to studies in a wide range of disciplines, such as evolutionary and genetic studies, biogeography, landscape ecology, and landscape conservation.

CONCLUSIONS

Some exciting insights were developed by assessing palynological reconstructions in a landscape perspective. Biome and species distribution patterns, their responses to climate change, and critical landscape thresholds for connectivity in

montane areas have been integrated. The assessments concerning connectivity directly inform our understanding of montane biome dynamics through time and space. The applicability of this innovative approach is shown for the pollen record of Lake La Cocha. The region offers a very diverse migratory environment as available habitat surface, dispersal distances, and connectivity differ along the elevation gradient. These characteristic landscape features clarify the observed differences between the biomes in terms of rates of surface, and altitudinal, and palynological change. We showed that care must be taken in the interpretation of palynological change as an indicator of dynamics, because trends are related to the lengths of the time steps in the record. Since the LGM, forest biomes have increased while páramo is being pushed to a narrower altitudinal range due to the rising UFL along the slope. These shifts of the UFL can be swift (20 vertical m yr^{-1} and more), causing the local extirpation of the ecotone biome (subpáramo) between páramo and forest and important losses in connectivity of páramo. Although the present-day páramo biome reflects only 4% of its LGM extension, its level of diversity seems untouched. During Pleistocene times the gene pools of these species must have passed such bottlenecks multiple times. This has interesting implications for future dynamics in gene pools; keeping connectivity available is a crucial prerequisite for long-term conservation of the gene pools.

The prime elevation zone where biological and geographical dynamics converge in the region of Lake La Cocha is between 2500 and 3600 m. Within this range, different biomes have dominated through time, there is a higher surface availability, and there are shorter dispersal distances compared to higher and lower elevations. Here, species from different biomes overlap in their potential distribution, and loss of interpatch and intrapatch connectivity of the páramo biome is most profound. Furthermore, when the forest expands to these higher elevations, there is a tendency

for diversification of species assemblages (as estimated by the PTR and DC), indicating the temporal overlapping of altitudinal distribution of biomes within the same altitudinal range. The concurring potential altitudinal ranges of species observed in current distribution records confirm that finding. Spatial assessments of the landscape need to be incorporated into palynological thinking to improve the interpretation of biome and species responses to climate change. The application of palynological research for conservation strategies is urged to expand its potential. Its integration with other disciplines will have far-reaching implications.

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APPENDIX 1. Three-dimensional calculations of surface in ArcGIS.

The landscape of a study area can be analyzed as if it were a flat 2-D area (Fig. 1; custom surface) or as a dynamic diverse feature (Fig. 1; floating on a custom surface), in this study showing the relief around Lake La Cocha. To estimate the available surface of the different biomes at different moments in time, the digital elevation model (DEM) (Jarvis et al., 2008) is projected from 2-D into a 3-D representation. Therefore, the DEM is converted into a so-called triangular irregular network (TIN), which is a continuous, non-overlapping triangular network representing the surface topography of an area. The boundaries of each triangle define the position of linear features that play an important role in a surface, such as ridgelines or stream course. Each corner of a triangle has a z-value, which is the value of the altitude. To create a TIN within ESRI ArcGIS 10 (Redlands, California, U.S.A.), a contour map of the available 90 m DEM is created with soft isolines between every 25 m, which is then converted into the final TIN. For surface modeling, TINs should be constructed using projected coordinate systems, as geographic coordinate sys-

tems are not recommended because their angular units of degrees can produce incorrect results in slope, volume, and area calculations. Consequently, the surface of the created TINs is calculated in both 2-D and 3-D aspects with the Surface Volume tool of 3-D Analyst of ArcGIS, taking sea level as the horizontal reference plane (0 m.s.m.). Surface area estimates are analyzed for all biomes during the four different UFL settings and also for the altitudinal range of the total study area.

APPENDIX 2. Connectivity index.

The connections between habitat patches are best characterized by a probabilistic model in which there is a certain probability of dispersal among patches typically modeled as a decreasing function of interpatch Euclidean or effective distance (Saura & Pascual-Hortal, 2007). These probabilities are defined as the chance that two species randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the connections (p_{ij}) between them. The probability of connectivity index (PC) is given by the following expression (Saura & Pascual-Hortal, 2007):

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p^{*ij}}{A_L^2}$$

where a_i and a_j are the areas of the habitat patches i and j , and A_L is the total landscape area (area of the study region, comprising both habitat and non-habitat patches). PC increases with improved connectivity and has a bounded range of variation between 0 and 1. PC equals 0 when no habitat patches are present in the study area, and equals 1 when all the landscape is occupied by habitat. The strength of each link is characterized by p_{ij} , which is the probability of direct dispersal between patches i and j . The value for p^{*ij} is the maximum product probability of all the possible links between patches i and j (including the direct patch between i and j).

It is calculated as follows:

$$ECA = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p *_{ij}}$$

The equivalent connected area (ECA) value will not be smaller than the area of the largest patch in the landscape. The value of the ECA will coincide with the surface area of the single habitat patch (no fragmentation) or when the habitat is fragmented into different patches but there is a maximal interpatch connectivity such as that $p*_{ij} = 1$ for each pair of patches (Saura et al., 2011).

APPENDIX 3. Rate of change estimates.

Greenland ice cores revealed the first hint at how fast climate can change. Based on $\delta^{18}\text{O}$ records, the Dye3 record showed a 7°C temperature increase in ~50 years (Dansgaard et al., 1989) and the North Greenland Ice Core Project (NGRIP) record documents 11.2°C in 21 years (Dahl-Jensen et al., 2002; NGRIP Members, 2004). Understanding of rates of change in terrestrial ecosystems is poorly developed, but first studies report results that have significant implications. Millennial-scale variability in precipitation was reported by Cruz et al. (2009) for Brazil and Baker et al. (2009) for Peru. Vimeux (2009) studied similarities and discrepancies between records from tropical Andean ice cores and high-latitude ice sheets and discussed mechanisms to propagate drivers from high to low latitude. Urrego et al. (2009) studied rates of change (RoC) from 13 Neotropical pollen records and identified periods of fastest change since the last glacial maximum (LGM). They state that RoC analysis showed that the speed of these climate changes never exceeded the species response capabilities. However, the RoC values were not specified nor directly compared to species response indicators. The robust age model of the new Fúquene-9Composite (Fq-9C) record (Groot et al., 2011) allowed inference of first estimates of RoC in the upper part of the

montane forest in Colombia and showed that the fastest change of $10^\circ\text{C} \pm 2^\circ\text{C}$ occurred at terminations and during marine isotope stage (MIS) 3. All this evidence is indicative of teleconnections between the high latitudes and Neotropical low latitudes, and Grimm and Ambrizzi (2009) and Khodri et al. (2009) discuss several mechanisms.

APPENDIX 4. Full reference for the GBIF Data Portal.

Global Biodiversity Information Facility—GBIF Data Portal. 2013. Biodiversity occurrence data published by: Administración de Parques Nacionales, Argentina; Arizona State University, Global Institute for Sustainability; Asociación de Becarios del Casanare—ABC; Australian National Herbarium (CANB); Berkeley Natural History Museums; Bernice Pauahi Bishop Museum; Biologiezentrum Linz Oberösterreich; Bioversity International; Botanic Garden and Botanical Museum Berlin-Dahlem; Botanical Research Institute of Texas; British Antarctic Survey; California Academy of Sciences; Canadian Biodiversity Information Facility; Centro Nacional Patagonico—CONICET; Comisión nacional para el conocimiento y uso de la biodiversidad; Conservation International; Corantioquia; Facultad de Ciencias Naturales y Museo—U.N.L.P.; Fairchild Tropical Botanic Garden; Federación Nacional de Cafeteros de Colombia; Field Museum; Fundación Alma; Fundación Miguel Lillo Provider; GBIF New Zealand; GBIF-Spain; GBIF-Sweden; Georg-August-Universität Göttingen, Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik; Harvard University Herbaria; Herbaria of the University and ETH Zürich (Z+ZT); Herbario SANT, Universidade de Santiago de Compostela; Herbarium Hamburgense; Herbarium of the University of Aarhus; Herbarium of Université de Montpellier 2, Institut de Botanique; iNaturalist.org; INRA Antilles-Guyane; Institute of Botany, University of Hohenheim; Instituto de Botánica Darwinion—CONICET; Instituto

de Ciencias Naturales; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt; Instituto Nacional de Biodiversidad (INBio), Costa Rica; Instituto Nacional de Tecnología Agropecuaria—Instituto de Recursos Biológicos; Karl Franzens University of Graz, Institute for Botany—Herbarium GZU; Ministerio de Ciencia, Tecnología e Innovación Productiva; Missouri Botanical Garden; MNHN—Museum national d'Histoire naturelle; Mountain Invasion Research Network—MIREN_ETH; Museo Argentino de Ciencias Naturales; Museo Nacional de Costa Rica; National Herbarium of New South Wales; National Museum of Natural History, Smithsonian Institution; National Museum of Nature and Science, Japan; Natural History Museum, Vienna—Herbarium W; Netherlands Centre for Biodiversity Naturalis, section National Herbarium of the Netherlands; Organization for Tropical Studies; Royal Botanic Garden Edinburgh; Royal Botanic Gardens, Kew; Royal Ontario Museum; Senckenberg; Staatliche Naturwissenschaftliche Sammlungen Bayerns; SysTax; the New York Botanical Garden; UNIBIO, IBUNAM; Universidad de La Salle; Université de Montréal Biodiversity Centre; University of Alabama Biodiversity and Systematics; University of Arizona Herbarium; University of British Columbia; University of California, Davis; University of Connecticut; University of Malaga; University of Vienna, Institute for Botany—Herbarium WU; US National Plant Germplasm System; Utah Valley State College (UVSC); Wrocław University, Museum of Natural History; Yale University Peabody Museum (accessed through data.gbif.org; 28 April 2013 and 4 May 2013).

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