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Snowlines and Treelines in the Tropical Andes

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Examination of the dynamism of snowlines and treelines could provide insights into environmental change processes affecting land cover in the tropical Andes Mountains. Further, land cover at these ecotones represents a powerful lens through which to monitor and understand ecological processes across biophysical gradients while acknowledging their socioenvironmental dimensions. To illustrate this approach, we draw on recent research from two sites in the high tropical Andes where, at the regional scale, land cover assessments document retreating glaciers and changing amounts of forest cover, even though steep topographic gradients impose spatial shifts at much finer scales. Our results show that heterogeneous patterns of glacier recession open up new ecological spaces for plant colonization, potentially forming new grasslands, shrublands, and wetlands. In addition, treeline shifts are tied to changes in woody plant dominance, which can vary in rate and pattern as a result of aspect, past land use, and current livelihoods. We suggest that the telecoupling of regional and global biophysical and socioeconomic drivers of land use and land cover change to specific landscape combinations of elevation, aspect, and slope position might explain much of the spatial heterogeneity that characterizes landscape stasis and flux in mountains. *Key Words: Andes Mountains, climate change, ecological succession, glacier recession, land use/land cover change.*

检视雪线和树线的动态, 能够为影响热带安第斯山脉的土地覆盖之环境变迁过程提供洞见。此外, 这些交错群落的土地覆盖, 呈现一个有力的视角, 藉此监控并理解生物物理梯度中的生态过程, 同时认识其社会环境之面向。为了阐述此一方法, 我们运用在高山热带安第斯山中的两地进行的晚近研究, 在区域尺度上, 这两个地方中的土地覆盖评估, 记录了后退的冰川以及森林覆盖的改变量, 尽管陡峭的地形梯度是在更细微的尺度上加诸空间变迁。我们的研究显示, 冰川倒退的异质模式, 开展了植物定殖的崭新生态空间, 并有可能构成新的草原、灌丛带和溼地。此外, 树线变迁与木本植物优势的改变有关, 并可能因坡向、过往的土地使用和当前的生计, 而在速率和模式上有所不同。我们主张, 驱动海拔、坡向和坡位的特定地景组合的土地使用和土地覆盖变迁之区域及全球生物物理及社会经济驱力的远程耦合, 或能大幅解释以山区地景静止和流动为特徵的空间异质性。*关键词: 安地斯山脉, 气候变迁, 生态演替, 冰川倒退, 土地使用/土地覆盖变迁。*

El examen de la dinámica en las líneas de nieve y las líneas arbóreas podría suministrarnos una mayor comprensión de los procesos de cambio ambiental que afectan la cubierta de la tierra en las montañas andinas tropicales. Más todavía, esa cobertura en estos ecotones representa una lente poderosa a través de la cual monitorear y entender los procesos ecológicos a través de gradientes biofísicos, al tiempo que se reconocen sus dimensiones socioambientales. Para ilustrar este enfoque, nos apoyamos en investigación reciente conducida en dos sitios de los altos Andes tropicales donde, a escala regional, las evaluaciones de la cubierta de la tierra documentan el retroceso de los glaciares y las cantidades cambiantes de cobertura forestal, incluso si los fuertes gradientes topográficos imponen cambios espaciales a escalas mucho más finas. Nuestros resultados muestran que los patrones heterogéneos de la recesión glaciaria abren nuevos espacios ecológicos de colonización por las plantas, formando potencialmente nuevos pastizales, matorrales y humedales. Además, los cambios de la línea arbórea están ligados a cambios en el dominio de plantas leñosas, las cuales pueden variar en rata y patrón como resultado del aspecto, uso del suelo anterior y actuales medios de subsistencia. Sugerimos que el acoplamiento a distancia de los controles biofísicos y socioeconómicos regionales y globales del uso del suelo y del cambio de la cubierta de la tierra, por combinaciones específicas de paisajes de elevación, aspecto y posición de las laderas, podrían explicar gran parte de la heterogeneidad espacial que caracterizan la movilidad y el flujo del paisaje en las montañas. *Palabras clave: montañas de los Andes, cambio climático, sucesión ecológica, recesión de glaciares, cambio del uso del suelo/cubierta de la tierra.*

Shifting climate regimes and socioeconomic processes are altering perceptions and decisions by people in the Andes Mountains, thus affecting their land uses, while concurrent changes in ecological processes alter land cover types, ecosystem responses and functions, and environmental services used by people (Young 2009; Ponette-González et al. 2014). Such global-to-local connectivity has been referred to as *telecoupling* (Liu et al. 2013). For example, glacier recession in the Andes is driven by climate change

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(Rabatel et al. 2013), with many implications for livelihoods (Postigo, Young, and Crews 2008) and watersheds (Bradley et al. 2006; Carey et al. 2014), whereas other studies report increased woody plant cover, especially in drier areas (Aide et al. 2013). Demographic shifts to urban areas (Álvarez-Berríos, Parés-Ramos, and Aide 2013) and massive investments in irrigation and energy infrastructure have pulled people and their environmental influences to lower elevations (e.g., Bury et al. 2013).

Evaluation of shifting ecological transition zones, or ecotones, might provide an important means of monitoring these global as well as localized influences on land cover dynamics in the Andes and in similar places worldwide. Snowlines separate the cryosphere, including places with permanent or seasonal snow or ice cover, from other landscapes, and treelines distinguish places along biophysical gradients where land cover switches from dominance by woody plants to herbaceous vegetation or nonvegetated cover types. At a small cartographic scale, such lines can be used to indicate locations of important biophysical changes that control, for example, the mass balance of glaciers and the altitudinal limit of closed forest (Gerrard 1990). These ecotones also might be highly sensitive to global- and local-scale changes.

Tropical glacier snowlines are located near the 0° isotherm, so any shift in temperature or precipitation can trigger shifts in mass balance. Thus, tropical glaciers fluctuate over yearly and decadal time periods (Rodbell 1993; Thompson et al. 2006; Stansell et al. 2013). During the Little Ice Age, tropical Andean glaciers reached maximum extensions, but then later—beginning in 1880—they experienced significant and accelerated recession that continues today (Vuille et al. 2008). Additionally, steep elevation gradients and tropical seasonality influence glacier fluctuations. Drivers of contemporary tropical glacier retreat are thought to include combinations of shifts in air temperature, humidity, precipitation, cloudiness, incoming shortwave radiation, and related anthropogenic climate change (Kaser 1999; Vuille et al. 2003; Thompson et al. 2006; Vuille et al. 2008).

Tropical Andean treelines are affected by multiple ecological processes (e.g., seed dispersal, seedling growth) in a grassland–forest ecotone that can experience cool (6–10°C) and humid (500–2,000 mm per year) conditions, frequent fogs, and episodic frost events (Young and León 2007). Since 1939, surface temperatures in the tropical Andes have increased ~0.10°C per decade (Vuille et al. 2008). Sediment records show that treeline is responsive to such climatic fluctuations on millennial timescales, shifting up- and downslope in response to warm–wet and cool–dry periods, respectively (Bush et al. 2005). Human-set fires and grazing, however, play a decisive role in shaping treeline structure and distribution as well (White 2013). Where grasslands are grazed and burned, altitudinal treeline is often depressed by several hundred meters (Young 1993a); woodlands might be absent or switch abruptly into grasslands (Ponette-González et al. 2016). Future dynamics of tropical forest–grassland ecotones are thus likely to be far more complex than the upslope shift predicted with simple climate models.

In this research, we examined the landscape-scale consequences of three decades of change in both glacier extent and representation of woody and nonwoody vegetation in Peru. A case study in Huascarán National Park, in the Cordillera Blanca, documents and interprets recent land cover change using satellite imagery. Another case study evaluates treeline response to past land use in Río Abiseo National Park, on the Eastern Andean Cordillera. We posit that such examinations reveal additional complexity in spatial patterns, which in turn might lead to insights into processes of change associated with the cryosphere, the biosphere, and interactions with human land use. Regional trends of receding glaciers and shifting vegetation mosaics, although indicative of coupling to global processes, do not necessarily provide useful parameters for predicting future change in particular montane landscapes, given high place-to-place variation. This article attempts to elucidate some of the implications of spatial heterogeneity, both for improving knowledge of mountain environments and for better assessing results of land use/land cover change studies.

Glacier Recession in the Cordillera Blanca of Peru

Study Site and Methods

The effects of glacier recession on downslope ecosystems were studied in the Cordillera Blanca range in northern Peru (8.5° to 10° S), where glacier retreat is widespread (Kaser and Osmaston 2002; Mark and Seltzer 2005; Burns and Nolin 2014). According to the Peruvian government's first detailed countrywide glacier inventory in 1970, glacier area in the Cordillera

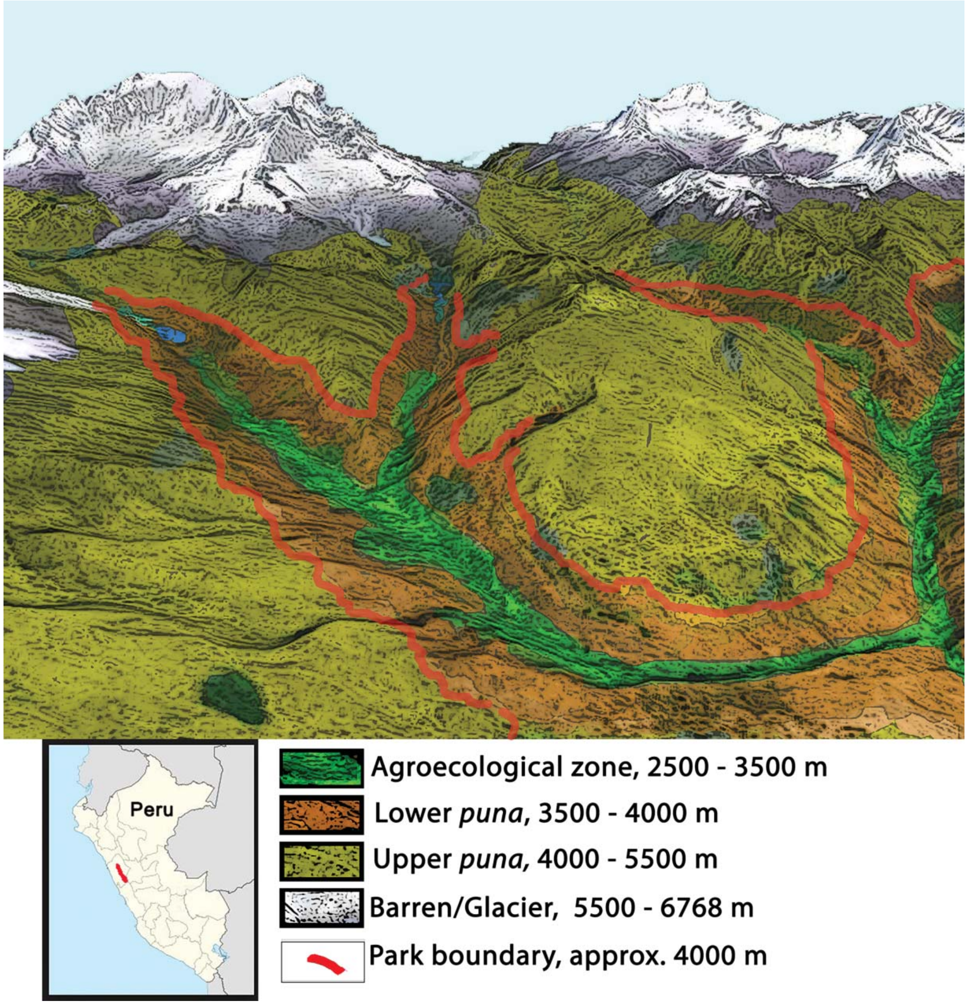

Figure 1. Ecological zonation near and inside Huascarán National Park. The agroecological zone (green) has a mixed tenure regime of private land, sectorial fallow, and park buffer zone; the lower puna (orange) has private and communal land, sectorial fallow, and park buffer zone; the upper puna (yellow) includes communal land and the core area of the park; and the barren rock and glacial ice area (gray/white) is under the tenure of Huascarán National Park. (Color figure available online.)

Blanca was 723 km^2. By 2003, glacier area had decreased about 30 percent to 527 km^2. The remaining glaciers have also become more fragmented: In 1970 there were 722 glaciers compared to 755 in 2003 (Autoridad Nacional del Agua, Unidad de Glaciologia 2013). With increased surface-to-area (or mass) ratios, these small glaciers are likely to disappear. Yet, relatively little is known about effects of recession on lower elevation ecosystems, including grasslands, shrublands, forests, and wetlands (Young 2015).

The Cordillera Blanca is oriented on a northwest–southeast axis and is composed of a series of parallel valleys separated by high ridges. Much of the Cordillera Blanca is inside Huascarán National Park (3,400 km^2). The precipitation regime is defined by a dry season from June to September and a wet season from October to May (Kaser and Osmaston 2002). Land cover in the park is heterogeneous, with patches of wetlands, shrubs, *Polylepis* forests, and rock outcroppings embedded in a grassland matrix (i.e., "*puna*" ecological zone); scree, bare rock, and snow and ice cover dominate landscapes above 5,000 m. In addition to rising temperatures (Vuille et al. 2003), topography is an important variable affecting biophysical gradients and land use (Figure 1).

Roughly 270,000 people inhabit the Santa River basin (Bury et al. 2011). Livelihoods are predominately based on subsistence agriculture, livestock production, mining, and tourism (Lipton 2014). Semistructured interviews were conducted with 117 informants (89 men, 28 women); interviews were conducted in Spanish and Quechua with the aid of field assistants in the buffer zone and core of Huascarán National Park to identify land use and tenure arrangements and to make land cover observations. Multiple elevation and ecological gradients are simultaneously used for agropastoral and community land use systems (Figure 1) and operate under distinct tenure regimes (private lands, sectorial fallow lands, communal lands), modified by national park regulations since 1975. Households typically maintain croplands from 2,500 to 3,500 m, whereas fields in middle elevations (3,500–4,000 m) are seasonally planted for household or community use. Throughout the region, the upper *puna* (4,000–5,500 m) is used for transhumance of cattle, sheep, and other stock. Cattle and horses typically graze freely in upland valleys, often on wetland or riparian sites. Land use intensity has lessened in recent years given increased migration to the coast; availability of jobs in other sectors including mining, tourism, and corporate farms; and decreased returns on crops.

Land use/land cover in the Cordillera Blanca was mapped by classifying Landsat TM images acquired on 15 May 1987, 20 August 1999, and 18 August 2010 (downloaded from http://glovis.usgs.gov). For each date, two Level 1T images (path-rows 8–66, 8–67) from the dry season were mosaicked together. Level 1T processing provides systematic, radiometric, and geometric accuracy by using a digital elevation model; image coregistration is consistent and spatial errors are less than one-half pixel (Hansen and Loveland 2012). A hybrid supervised–unsupervised classification was performed (using ERDAS Imagine 2014), a technique that uses all seven bands in 30-m spatial resolution (Walsh et al. 2003). Band 6, the Landsat TM thermal band, was resampled from 120-m to 30-m spatial resolution. This technique was selected due to previous good performance (Kintz, Young, and Crews-Meyer 2006). First, an unsupervised classification technique (ISODATA) clustered the spectral information into 255 signatures. Signatures were then evaluated using the transform divergence method, a test that measures the statistical distance between signatures on a scale of 0 to 2,000. We removed signatures with poor spectral separability (defined as <1,950). Next, the remaining signatures were classified using a supervised classification, resulting in thirty-five to forty-five classes. Using expert knowledge of the study area, 360 ground control points, and photographs, these classes were individually identified as one of seven land cover classes: barren, puna (nonwetland tropical alpine vegetation), wetland, snow and ice, lake, shadow, and cloud. Classes were selected based on previous remote sensing analyses in the study area (Lipton 2008; Silverio and Jaquet 2009). Following Ozesmi and Bauer (2002), we

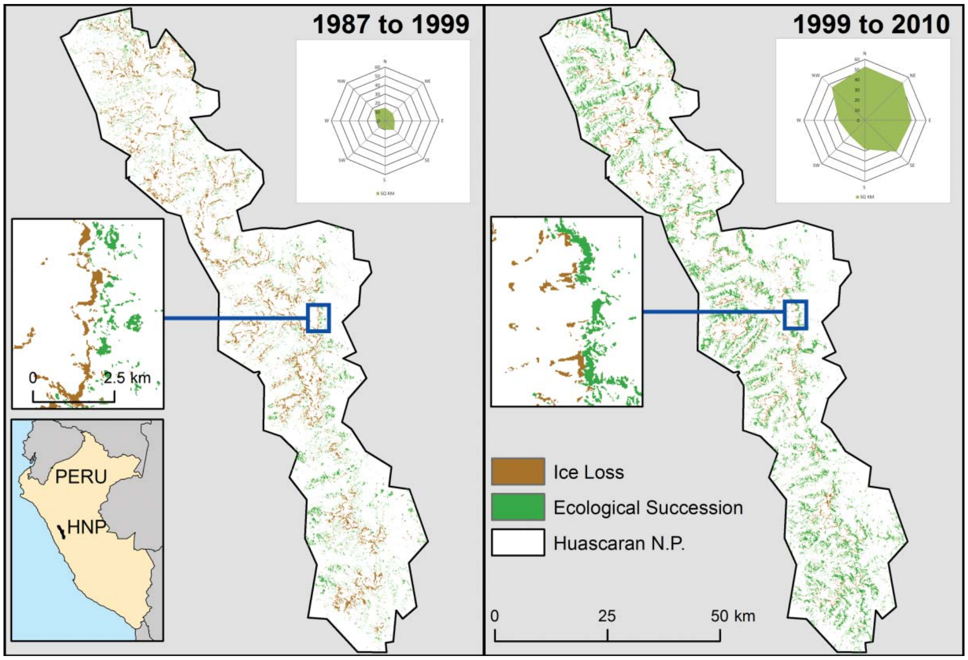

Figure 2. Land cover change in Huascarán National Park, northern Peru, for 1987 to 1999 (left) and 1999 to 2010 (right). Glacier recession (brown) could be followed by primary succession on barren spaces exposed by glacier retreat and by woody plant establishment on scree slopes and other expansions of shrublands and grasslands (shown in green). Inset shows aspect differences in ecological succession for the two time periods. HNP = Huascarán National Park. (Color figure available online.)

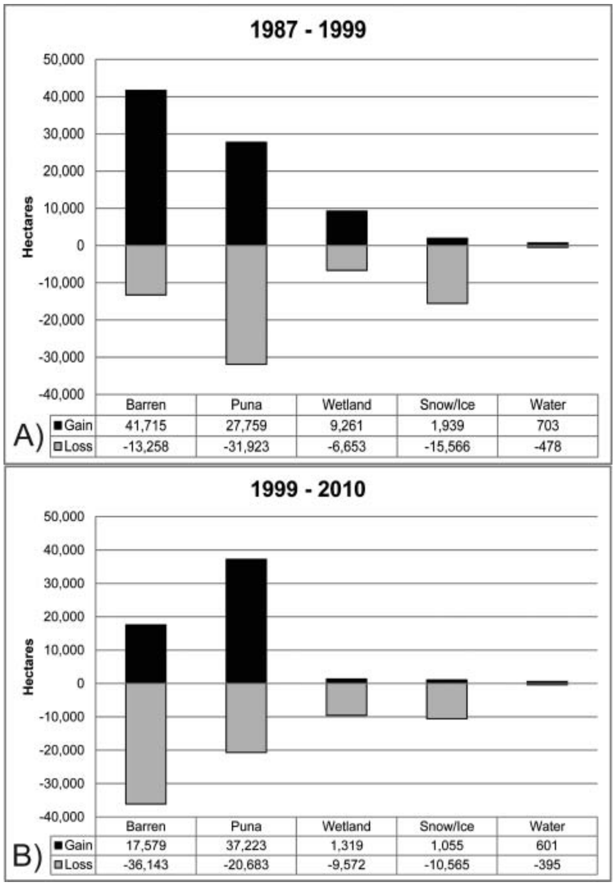

Figure 3. Land cover gains (black) and losses (gray) for barren, puna, wetland, snow and ice, and water in Huascarán National Park, northern Peru, from 1987 to 1999 (top) and 1999 to 2010 (bottom).

added a near infrared–red band ratio (Landsat TM Band 4/Band 3) to the classified image to improve the accuracy of difficult-to-classify wetlands. Lake colors vary widely due to suspended glacial flour in the study area, giving poor classifications. Therefore, lakes were digitized manually using the GLIMS data set and added to the classified image (http://www.glims.org/; Kargel et al. 2014).

The final product was a categorical map for each date. Accuracy assessments for image classification were within standard norms of >85 percent with the exception of 2010. For 1987, overall accuracy was 89.4 percent and overall kappa was 87.5 percent; for 1999, the respective values were 91.5 percent and 89.8 percent. For 2010, overall accuracy was 78.5 percent and overall kappa was 74.2 percent; lower accuracy values in 2010 were due to confusion between shadow and puna classes. In the final step, a geographic information system (GIS; Land Change Modeler 2.0, Clark Labs, Clark University, Worcester, MA, USA) was used to evaluate the extent of changes from snow and ice to barren (interpreted as glacier recession) and from barren to puna (interpreted as ecological succession, including primary succession) for 1987 to 1999 and 1999 to 2010 (Figure 2). Aspect is an important spatial organizing feature (see Figure 1) and for this analysis was derived from an ASTER GDEM v.2 product and categorized into eight bins representing the cardinal and intercardinal directions. Using a GIS (ArcGIS, Version 10.2, Esri, Redlands, CA, USA), the area of change from barren to puna was calculated for each of the bins.

Principal Findings: Glacial Recession Affects Downslope Ecosystems

Land cover assessments showed that glacier loss resulted in opportunities for ecological succession (Figure 3), as barren lands were exposed and plants colonized open areas. The area subject to plant colonization was, however, much larger in extent than the area affected directly by recession (Figure 2). Field observations suggest that much of this increase was due to forbs and graminoids appearing on newly exposed substrates, in addition to increasing shrub presence on rocky slopes. From 1987 to 1999, there were no differences in ecological succession by aspect, whereas from 1999 to 2010 barren-to-puna change was concentrated on north- and northeast-facing slopes (Figure 2, insets).

The land change analysis revealed additional complexities, including cover changes that were not consistent over time (Figure 3) and from–to class changes that were interconnected with other class changes: (1) from 1987 to 1999, there was a slight net loss of puna, suggesting that some tropical alpine vegetation areas contracted to expose additional barren sites; (2) from 1999 to 2010, there was a large increase in puna due to barren lands converted as succession occurred and grasses and shrubs increased in extent, mostly on north- and northeast-facing slopes previously lacking dense vegetation (Figure 2; we note that confusion in classifying shadows makes some dynamics associated with the puna class ambiguous); and (3) from 1987 to 1999, wetlands experienced a net increase in area but then decreased in area from 1999 to 2010 (Figure 3). The effects of glacier recession (and other concurrent changes) thus extend downslope, directly affecting ecosystems that expand with new sites available for colonization and those affected by changing amounts of glacier meltwater. Gains and losses in land cover varied by aspect, however, and the direction and type of change were not consistent over time.

Woody Plant Encroachment at Treeline in the Eastern Andean Cordillera, Peru

Study Site and Methods

Spatial patterns of woody plant encroachment into grasslands were examined at treeline in the Eastern Andean Cordillera after nearly three decades of grazing reduction and fire exclusion. In the glacially sculpted landscapes of northern Peru (Rodbell 1993), treeline is found in a relatively narrow transition zone (3,200–3,600 m) that extends from the upper limit of closed-canopy montane forest (i.e., timberline) to humid alpine grassland (i.e., *puna* or *páramo*). Above the closed forest limit, woody plants encroach into grasslands, decreasing in stature, area, and contiguity with increasing elevation (Kintz, Young, and Crews-Meyer 2006). These high-elevation woodlands or shrublands are frequently located in topographically sheltered sites, such as ravines or atop small boulder fields, and are considered a characteristic and enigmatic feature of high Andean sites (Kessler 2002). The elevation, patterning, and abruptness of this Andean forest–grassland ecotone vary spatially as a result of differences in climate, land use, and terrain (Young 1993b, 1993c). Timberline and woodlands are found higher on valley sides than on parts of valley bottoms, where cold air drainage, waterlogged soils, and occasional fires prevent tree establishment, creating an inverted treeline (Young 1993b).

This study was conducted in a U-shaped valley above the closed forest limit in Río Abiseo National Park (7°56.88′ S, 77°21.35′ W). The site is characterized by a wet (ca. 1,000–2,000 mm per year) and foggy climate, with extreme topographic complexity (Fry, Ponette-González, and Young 2015). Prior to the park's creation in 1983, herders maintained grasslands with fire, resulting in the creation of a mosaic landscape composed of closed forest, different-aged (and different-sized) woodlands, and grassland. Small-statured C_4 grasses exist at the study site (e.g., *Paspalum*, *Muhlenbergia*, and *Bothriochloa*) alongside the dominant grass genera *Calamagrostis* and *Festuca*. After 1983, fire was prohibited and the number of cattle in the park's alpine zone decreased by about 70 percent. Although limited grazing by local people is still permitted, in 2007 an estimated dozen cattle remained in the valley, a stocking rate of 0.017 cattle ha^{-1} (Ponette-González et al. 2016).

Vegetation and soil sampling were conducted across the valley in 2010 and 2011. All forested woodlands larger than 250 m^2 were mapped and stratified by valley position (low, mid, upper) and aspect (east, west). Seventeen (3,400–3,900 m) were randomly selected from these strata. To assess patterns of woody plant encroachment into alpine grasslands, fifty transects were laid perpendicular to forest-grassland boundaries on the upper, lower, windward, and leeward sides of the woodlands, except where steep topography prevented access. Along these transects, three 2×1 m^2 plots were established in each habitat: at the forest–grassland edge (0 m) and 5 m on either side of the edge (edge habitat); between 10 and 40 m into forest (forest habitat); and between 10 and 40 m into grassland (grassland habitat). Within these plots, all seedlings and ramets (<1 m tall) were counted; those counts were pooled for analysis and are hereafter referred to as *regeneration*. Soil sampling was conducted along seventeen of these transects parallel to slope contours and perpendicular to north-facing woodland edges. Composite soil samples were collected in the regeneration plots ($n = 3$ plots per habitat). In each plot, three soil cores were collected to 20 cm depth, combined, and air-dried in the field. Bulk soil samples were homogenized and passed

Table 1. Stable carbon isotopic composition of soils and fine roots, proportion of plots with regeneration, observations of shrubs and cattle dung, and sodium concentrations in soils on east- and west-facing slopes in a U-shaped valley at treeline in northern Peru

	East	West
Forest fine root δ13C (‰)	−28.3	−28.0
Forest soil δ13C (‰)	−26.1	−26.2
Edge fine root δ13C (‰)	−26.6	−26.5
Edge soil δ13C (‰)	−24.1	−25.1*
Grassland fine root δ13C (‰)	−24.6	−25.7
Grassland soil δ13C (‰)	−23.7	−24.6*
Regeneration in edge habitat (% of plots)	84	91
Regeneration in grassland habitat (% of plots)	59	74*
Shrub presence in grassland (no. of transects)[a]	3/9	8/8*
Cattle dung presence in grassland (no. of transects)[a]	7/9*	0/8
Na concentration (ppm ± SE)[a]	110 ± 9.7*	68 ± 5.9

Note: [a]Data from Ponette-González et al. (2016).

*Significant difference between east- and west-facing slopes ($p < 0.1$).

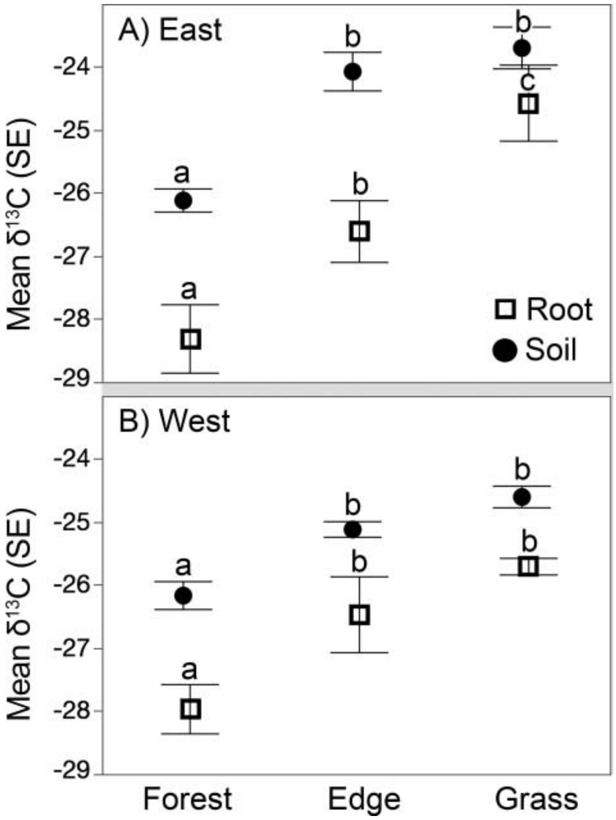

Figure 4. Mean δ13C (SE) of soils and fine roots for forest, edge, and grassland habitat ($n = 17$ transects) on east- and west-facing slopes sampled at treeline in northern Peru. Different letters represent significant differences among habitats (one-way analysis of variance, $p < 0.1$).

through a 2-mm sieve, and live fine roots (<2 mm) were separated. A subsample of soil and fine root material was dried, ground to a fine powder, and analyzed for total carbon and δ13C on a mass spectrometer. Stable carbon isotope natural abundance is expressed as $\delta(‰) = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1,000$, where R is the ratio of 13C/12C. Further details are in Ponette-González et al. (2016).

The proportion of plots with regeneration in forest, edge, and grassland habitat was calculated for the study valley; Fisher's exact test was used to test for aspect-related differences in the proportion of plots with regeneration for each habitat. Natural abundance of δ13C in soil and fine roots was used to detect vegetation shifts along the forest–grassland ecotone. Given the presence of C4 grasses or species-specific differences in the δ13C of Andean C3 trees and grasses (Szpak et al. 2013), we hypothesized that edge and grassland soils would be enriched in δ13C compared to forest soils. Further, we hypothesized that soil and fine root δ13C would have similar values unless vegetation change had occurred. Differences in the stable isotopic composition of soil and fine roots among habitat types were assessed for the entire valley, and by aspect, using one-way analysis of variance (ANOVA) with Tukey's honestly significant difference post hoc comparisons, and Kruskal–Wallis with Steel Dwass pairwise comparisons where data were nonnormally distributed. Significance was set at $p < 0.1$.

Principal Findings: Woody Plant Encroachment Varies by Aspect

Previous analysis of soil and fine root δ13C at this site revealed that the mean δ13C values of edge and grassland soils at treeline were similar but enriched compared to forest soils (Ponette-González et al. 2016). Yet, the δ13C of roots displayed a different pattern, with edge fine roots intermediate between forest and grassland. These results suggest that forest roots are extending into the grasslands and that this treeline ecotone might be advancing.

The new analyses presented here indicate that patterns of woody plant encroachment additionally differ by aspect (Table 1). The stable carbon isotopic composition of soil and fine roots was nearly identical in forest habitat irrespective of aspect. This was not the case at forest–grassland edges, where mean soil and fine root δ13C differed more on east-facing compared to west-facing slopes (Figure 4). The smaller difference between soil and fine root δ13C observed at west-facing edges was due to the depletion of soil δ13C (Table 1). Compared to east-facing edges, soils at west-facing edges were depleted in δ13C ($p = 0.0096$) and thus isotopically more similar to fine roots. Grassland soils were also more depleted in δ13C on west-facing than on east-facing grasslands ($p = 0.032$). Seedling and ramet counts showed that regeneration was present in 93 percent of forest, 87 percent of edge, and 66 percent of grassland plots across the valley. Aspect differences for the forest and edge plots were not statistically significant (for forest, east = 91 percent, west = 96 percent; for edge, east = 84 percent, west = 91 percent). There was, however, a significantly greater proportion of plots with regeneration on west-facing (74 percent) than on east-facing (59 percent) grasslands ($p = 0.056$). Taken together, the soil and fine root δ13C data and the large proportion of plots in edge and grassland habitat with regeneration indicate that woody plants are encroaching into grasslands above the closed forest limit. Yet, our findings also highlight the influence of aspect on patterns of woody plant encroachment and, by extension, treeline migration.

Discussion

Land cover at snowline and treeline showed much dynamism in our tropical Andean sites. From 1999 to 2010, about a quarter of the area inside Huascarán National Park underwent some form of change (i.e., gains or losses) in land cover (Figure 3). We documented glacier loss in the Cordillera Blanca as well as gains in shrublands and grasslands in both national parks. These changes conform to observations of glacier retreat across the Andes (e.g., Burns and Nolin 2014) and some indications of treeline migration on tropical mountains (Kintz, Young, and Crews-Meyer 2006; Morueta-Holme et al. 2015). For example, our landscape-scale evidence of woody plant encroachment at treeline in Río Abiseo National Park supports the findings of a park-wide remote sensing analysis by Kintz, Young, and Crews-Meyer (2006). That study detected an upward shift in the treeline ecotone between 1987 and 2001, revealing a significant increase in shrubland area (34 percent) as well as in the number, size, and connectivity of forest patches. Our case studies nevertheless show that although there might be a tendency for ecological zones to shift upward, there are also many exceptions and time lags obscured by regional-scale assessments.

Exceptions and Time Lags

In the high mountains of the Cordillera Blanca, ecological succession is occurring on surfaces exposed by glacier recession. Plant colonization is heterogeneous, though, under different biophysical constraints than glacier loss. Spatial patterns of plant colonization did not always mirror those of glacier loss as we had expected: We found that ecological succession was not necessarily restricted by aspect (1987–1999) or was concentrated on north- and northeast-facing slopes (1999–2010; Figure 2, inset). Succession is perhaps also affected by distance to sources of colonizing plants from nearby vegetation types, in addition to aspect, which would affect duration of solar radiation and photosynthetic capacity.

Wetlands occupy a relatively small part of the landscapes studied (Figure 3), but their change during glacier recession was also complex. Similar to findings from this case study, Polk (2016) found that wetland area showed an overall decrease from 1987 to 2010 (losing approximately 5,581 ha or 45 percent), but that loss was not consistent, with some five-year intervals showing increases. The effects of reduced discharge from melting glaciers presumably could be observable in the spatial distributions of wetlands and other water-controlled ecosystems (Young 2015; Polk 2016). These fluctuations are expected to be associated with hydrologic connectivity, including groundwater interconnections. It is possible that area changes approximate the humpback curve showed by stream discharge as controlled by glacier retreat (Baraer et al. 2012). With decreased future hydrological input into wetlands, desiccation is likely to occur and these ecosystems might transition to increased dominance by seasonal wetlands and precipitation-dependent bogs.

Along the Eastern Andean Cordillera, forest edges at treeline are expanding in some areas, but there is considerable heterogeneity associated both with aspect and with current and past land use. We found that woody plant regeneration was more abundant on west-facing slopes, where differences in soil and fine root $\delta 13C$ were also less pronounced, possibly suggesting a longer history of plant establishment. Working in the same study valley, Ponette-González et al. (2016) observed that recent cattle dung in alpine grasslands was concentrated on east-facing slopes, where soil concentrations of sodium, an animal-limiting nutrient, were also twofold higher compared to west-facing slopes (Table 1). They attributed the lower apparent grazing on west-facing slopes to the lower proportion of grazable area (Fry, Ponette-González, and Young 2015).

Recent studies at tropical Andean treelines, including ours, show considerable variation in the direction, rate, and pattern of treeline migration (Kintz, Young, and Crews-Meyer 2006; Harsch et al. 2009; Lutz, Powell, and Silman 2013). For example, Morueta-Holme et al. (2015) redid observations first carried out by Alexander von Humboldt in Ecuador and showed that native plant distributions have shifted upward, accompanied by both upslope and downslope expansions of humanized landscapes affected by agriculture and burning. That study, however, was restricted to the same southeast-facing slope studied originally by von Humboldt, so there might be additional aspect-related changes not considered in their research. Other studies document little to no change in treeline position (Lutz, Powell, and Silman 2013), suggesting that Andean treelines might exhibit a lagged response to climate change as a result of multiple and often interacting factors (Rehm and Feeley 2015): biophysical controls (e.g., solar radiation; Bader, van Geloof, and Rietkerk 2007); barriers to reproduction (Rehm and Feeley 2013); topography (Coblentz and Keating 2008); and land use. Our findings indicate that the effects of herbivory and topography, and their interactions, on tropical treeline ecotones warrant further study. More broadly, both case studies suggest that accounting for topographic controls on plant colonization and growth at snowlines, treelines, and other transition zones could help improve predictability of future landscape change.

Socioenvironmental Dimensions

Protected areas, such as the national parks studied here, have a mandate to allow natural processes to regulate land cover but in reality often must serve additional land use needs for local people (Zimmerer 2011; Lipton 2014). In addition, they are exposed to global biophysical changes and are under increasing demands to provide ecosystem services downstream; for example, for water used for irrigation, domestic needs, and hydroelectric facilities. As species shift their locations with future climate change, protected area systems could provide needed habitat connectivity to permit movement (e.g., Dullinger et al. 2012). For example, Figure 1 suggests that wild plant species moving upslope would find ~3-km high habitat corridors within Huascarán National Park. Such habitat connectivity might not exist outside that park or among the different protected areas in the region, requiring conservation corridors (Young and Lipton 2006) or assisted migration (Richardson et al. 2009). Rates of soil development or slope instability might limit upward expansion in cases of primary succession, and we would also expect interactions and feedbacks with land use to affect ecological succession, as livestock and other herbivores can potentially graze near the highest peaks.

What people do with and to a particular landscape might be explainable by reference to their land uses, environmental governance, tenure rights, and economic goals (Huber et al. 2013; Liu et al. 2013). Predicting such landscape outcomes through time, however, might also require, in addition to downscaling from global climate models, information on the social telecoupling that provides additional or new information through the media or Internet that could alter the decision making of local land users. Considering such dynamics in the context of the landscapes of the tropical Andes suggests that aspect and other topographically controlled features such as soil depth and type could be important local controls. They would direct vegetation dynamics and constrain human land use in ways that might provide a useful framework in which to assess the resulting landscape change.

In conclusion, at the regional scale in the tropical Andes, our land cover assessments, and those of other researchers, continue to elucidate the downslope processes associated with retreating glaciers (Aubry-Wake et al. 2015) and changing amounts of forest cover (Holtmeier 2009; Toivonen et al. 2011; Balthazar et al. 2015). Steep spatial gradients impose land cover shifts at fine scales, though. As seen in our data from northern Peru (Figures 1–4, Table 1), places a few kilometers apart might have distinct climates, natural disturbance regimes, responses to glacier recession, soil and vegetation types, land use patterns, and land tenure. Topography is specific to a particular place given its history of bedrock formation, orogeny, and interactions with other Earth surface processes. The discipline of geomorphology evaluates specific landscape controls but attempts also to make generalizations that permit its development as a science (e.g., Murray et al. 2009). Equally, ecology tries to create generalizations that provide predictions useful for species and climate other than those studied directly (e.g., Billick and Price 2010). Nevertheless, these investigative approaches could tend to downgrade the significance of understanding the place-specific consequences of interacting geospatial, ecological, and social contingencies (cf. Crews and Young 2013). Global changes could be expressed locally in variable ways as seen in effects on changing species distributions (García et al. 2014; Pardikes et al. 2015), altered vegetation structure (Malanson et al. 2011; Higgins and Scheiter 2012), and the effects of fire–climate–human interactions (Butsic, Kelly, and Moritz 2015; Tepley and Veblen 2015). Here, we explored those topics in relationship to land cover in the Andes, which telecouples to distant biophysical and social processes but is expressed in landscapes through local combinations of soil, slope, and exposure. We suggest that change (or stasis) in land cover could offer insights into relevant processes and potentially provide a general tool for evaluating the multiple contingencies acting to create place-to-place uniqueness.

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