

Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural *páramo*

Emily Matson · David Bart

Received: 28 March 2013 / Accepted: 30 July 2013 / Published online: 6 August 2013
© Springer Science+Business Media Dordrecht 2013

Abstract Woody encroachment in grasslands is a global phenomenon driven by complex interactions between climate, grazing and fire management. Alpine shrub encroachment is of particular concern for biological conservation because high-elevation grasslands harbor high levels of biodiversity and species endemism. *Páramo* grasslands of the high Andes are exceptionally high in floral diversity, but traditional agricultural practices have resulted in widespread livestock grazing and anthropogenic burning. Fire suppression has frequently been identified a driver of woody expansion in other grasslands, and conservation initiatives that aim to decrease burning and grazing in *páramos* may inadvertently lead to shrub encroachment. We tested whether interactions among fire and grazing legacies, topography and edaphic conditions predicted the patchy distribution of encroaching shrubs in an Ecuadorian *páramo* 10 years after release from burning and grazing. Interviews with land-users identified proximity to roads, footpaths and riparian areas as proxies for fire frequency and grazing pressure. A recursive partitioning model of shrub cover revealed

that woody abundance was generally lower at lower elevations, especially near the access road (where fire frequency and grazing pressure were high). Within the low-elevation areas, shrub cover was highest near streams (where grazing pressure was high). These results suggest that (1) the effects of fire and grazing legacies depend on the spatial patterns of grazing, and (2) legacy effects interact with topography to help explain patchy shrub encroachment.

Keywords Woody encroachment · Shrub invasion · Grasslands · Alpine · Land-use legacy · Ecuador · Andes

Introduction

Woody encroachment is a widespread phenomenon in grassland and savanna systems worldwide (Ratajczak et al. 2012; D’Odorico et al. 2013). Encroachment can occur gradually, with shrubs replacing grassland vegetation over the course of centuries, or as pulses of shrub recruitment driven by specific disturbance events (Roques et al. 2001). Woody encroachment generally reflects the transition of an ecosystem to an alternative stable state (Brock and Carpenter 2010; Brandt et al. 2013). Once this transition has occurred, it can be difficult to reverse because woody dominance is maintained by positive feedbacks related to changes in temperature, soil moisture or nutrient availability (e.g. Sturm et al. 2005; Ratajczak et al. 2011).

E. Matson
Gaylord Nelson Institute for Environmental Studies,
University of Wisconsin, Madison, Madison, WI, USA

D. Bart (✉)
Department of Landscape Architecture, Gaylord Nelson
Institute for Environmental Studies, University
of Wisconsin, Madison, Madison, WI, USA
e-mail: dbart@wisc.edu

The transformation of grassland vegetation to shrub- or woodlands is of concern to environmental managers because woody encroachment alters ecosystem structure and function (Zavaleta and Kettley 2006; Knapp et al. 2008) and can result in declines in biodiversity (Anthelme et al. 2007; Ratajczak et al. 2012). This problem is especially acute in alpine systems. Alpine environments have higher biodiversity than the global average (Korner 1999) and contain high levels of species endemism due to mountain orogeny and climate (Sklenar and Jorgenson 2004; Wu et al. 2007). Studies from alpine grasslands and meadows have found high alpha (Ramsay and Oxley 1996, 1997; Luteyn 1999) and beta (Salick et al. 2009) diversity in herbaceous communities. Due to the ability of shrubs to alter plant diversity and composition, understanding the drivers of shrub encroachment is therefore particularly important for the management of alpine biodiversity hotspots.

Fire and grazing are often important components of traditional land use in alpine grassland systems (e.g. Hofstede et al. 2002; Brandt et al. 2013) and changes in their regimes have long been associated with woody encroachment worldwide (Van Auken 2000). In alpine ecosystems, the spread of woody species has been associated with fire suppression (e.g. Janzen 1973; Laegaard 1992; Brandt et al. 2013) and pasture abandonment (Montane et al. 2007). However, spatial variation in shrub encroachment after agricultural abandonment suggests a complex relationship between land-use change and the spread of woody vegetation (Brandt et al. 2013). Some spatial variation in shrub encroachment may be due to the legacies of different grazing and burning practices across the landscape. The impact of fire on shrub vegetation often depends on fire frequency and intensity (Pendergrass et al. 1998; Archibald et al. 2013). In some cases, burning can lead to rapid shrub encroachment because some shrub species resprout vigorously following fire (Briggs et al. 2005). However, severe fire damage from frequent, high-intensity fires are expected to limit long-term woody recruitment and slow the rate of shrub encroachment, even where fire-tolerant shrubs survive (Roques et al. 2001). Livestock grazing, especially overgrazing, has been implicated in many woody encroachment scenarios because intensive grazing removes non-shrub vegetation, thereby reducing competition during shrub establishment (Eldridge et al. 2011). Higher grazing pressure may also influence

shrub encroachment through other mechanisms, including selective browsing (Podwojewski et al. 2002; Sarmiento et al. 2003; Hernandez and Monasterio 2006), propagule dispersal (Browning and Archer 2011), and persistent alteration of edaphic conditions (Hofstede et al. 2002; Podwojewski et al. 2002). Additionally, interactions between fire and grazing often help determine where shrubs invade (D'Odorico et al. 2012). In particular, high-intensity grazing reduces aboveground biomass and decreases fuel loads, thus decreasing the intensity and duration of fires in heavily grazed areas and allowing shrubs to establish (Roques et al. 2001; Van Wilgen et al. 2003).

The effects of fire and grazing management on alpine shrub encroachment are further complicated by the fact that alpine vegetation dynamics are strongly influenced by climate, especially along alpine treelines (Korner 1999). The interactions between climate and land use that drive woody invasion are not yet well understood (Fuhlendorf et al. 2008; Brock and Carpenter 2010). Near alpine treelines, climate may limit shrub expansion because low temperatures and high radiation are limiting factors for woody plant growth (Bader et al. 2007). On the other hand, increases in woody cover may cause warmer microclimates that favor shrub seedling establishment in an otherwise harsh environment (D'Odorico et al. 2013), thereby creating a feedback mechanism that results in further encroachment. A clearer understanding of how climate interacts with changes in fire and grazing to drive the spread of woody species would help predict future patterns of shrub encroachment.

Furthermore, edaphic conditions may influence encroachment across an alpine landscape after fire suppression. Highly-varied mountain topography can result in a variety of microenvironments determined by hydrology and soil type (Podwojewski et al. 2002; Buytaert et al. 2006). These conditions may also be altered by livestock use (e.g. Suarez and Medina 2001; Buytaert et al. 2005; Altesor et al. 2006). It is not well understood how variation in edaphic conditions interacts with climate and fire and grazing legacies to affect shrub encroachment in mountain environments.

Complicated responses to burning and grazing release are exemplified in *páramo* systems. *Páramo* grasslands are part of the Andean biodiversity hotspot (Myers et al. 2000) and contain exceptionally high levels of floral diversity and endemic species (Smith and Cleef 1988; Luteyn 1999). An estimated

3,000–4,000 woody and herbaceous plants are native to *páramos*, and approximately 60 % of these are endemic (Luteyn 1999). At its lower altitudinal boundary (2,500–3,000 m), the *páramo* ecosystem includes montane forest and shrub-lands, transitioning to open grasslands at higher elevations (3,400–4,100 m) and low-lying herbaceous cushion plants near the upper limits of vegetation ($\sim 4,900$ m) (Jørgensen and Ulloa 1994; Luteyn and Churchill 2000). Grassland vegetation, also called ‘true *páramo*’ or *pajonal*, is the most extensive vegetation type and is dominated by perennial tussock grasses with ground rosettes, scattered dwarf shrubs, cushion plants and in some areas, giant stemmed rosettes (Luteyn 1999).

Burning and grazing pressure increased greatly in the *páramo* during the twentieth century (Hofstede et al. 2002). Recent conservation initiatives aimed at protecting ecosystem services (e.g. Southgate and Wunder 2007; de Bievre and Calle 2011) have suggested reduction of grazing and burning pressure (Farley et al. 2011), which may in turn lead to a more shrubby community structure following (Janzen 1973; Laegaard 1992; cf Suarez and Medina 2001). Burning- and grazing-release of *páramo* grasslands can be followed by a non-uniform pattern of shrub expansion across the landscape (Matson 2012), with open herbaceous vegetation persisting alongside shrub patches for more than a decade after burning suppression (Fig. 1). What accounts for patchy encroachment is not well understood. Agricultural practices employed by Andean farmers (e.g. Luteyn 1992; Verweij 1995) can result in highly variable spatial patterns of grazing and burning (Hernandez and Monasterio 2006), and resulting long-term impacts (legacies) of variations in fire frequency and grazing intensity may contribute to patchy woody encroachment. However, it is likely that fire and grazing legacies also interact with environmental conditions to determine where shrubs persist and invade following fire suppression. Land-use legacies (Laegaard 1992; Wille et al. 2002) and altitudinal climatic gradients (Bader et al. 2007) have both been suggested as an explanation for the co-existence of patchy grasslands and woody vegetation near the lower altitudinal boundary of *páramos*. We expect that climate may act as a control on shrub expansion at high elevations of *páramos*, and that topography and climate interact with fire and grazing to determine patterns of woody encroachment following land-use change.

In this study, we present a model that describes the patchy distribution of shrub and grassland vegetation in a *páramo* grassland more than a decade after release from burning and grazing. Our objective was to determine whether interactions among topography, edaphic conditions, and indicators of burning and grazing legacy effects predict shrub cover in a shrub- and grassland mosaic.

Methods

Study site

The community of Zuleta in northern Ecuador (Fig. 2) owns and manages 2,178 ha of *páramo* grasslands ($0^{\circ}12'52''\text{N}$, $78^{\circ}03'16''\text{W}$) extending from 2,950 to 3,920 m in elevation (EcoCiencia 2009). The steep, highly varied topography (average slope of 19.6°) is blanketed by tussock-grass vegetation intermingled with patches of shrubs and bisected by forested stream incisions. Average annual temperature at the study site is 7.2°C with an annual precipitation of 1,190 mm. The Zuleta *páramo* was formerly owned by an adjacent *hacienda* and has a history of grazing extending back several decades. The most recent period of agricultural use was in the late 1970s to early 1990s. During that era, cattle grazing in the *páramo* intensified due to the formation of a farmers’ cooperative of approximately 30 Zuleta families who used parts of the *páramo* for crop cultivation and livestock activities. At its peak, up to 500 head of *ganado bravo* (fighting bulls) were grazed across more than 2,000 ha of *páramo* grasslands (Matson 2012). The farmers frequently ignited fires in the *páramo*, and in some areas the vegetation was burned as frequently as once a year or more.

In 1995, the community of Zuleta signed an agreement to protect the *páramo* from burning and grazing out of concern that livestock activities were negatively affecting headwater streams originating in the *páramo*. Under the agreement, permissible “conservation land use” in the *páramo* includes native *Polylepis* tree plantations (roughly 100 ha had been planted at the time of the study) and ~ 10 – 15 ha of pasture for an alpaca herd (~ 75 alpacas at the time of the study). Burning and grazing are prohibited in the protected *páramo*, which extends to the south and east of the areas of “conservation land use” (Fig. 2). Cattle



Fig. 1 Patchy shrub encroachment in Zuleta, Ecuador. *Dark gray* areas (background) are high shrub cover patches



Fig. 2 Zuleta (*star*) ($0^{\circ}12'52''\text{N}$, $78^{\circ}03'16''\text{W}$) in Imbabura province (*white*), Ecuador

grazing decreased substantially from 1995 to 2000, with only a few cattle remaining by 2000 (Matson 2012). The majority of the *páramo* has not burned in the last decade. Interpretation of aerial photography

and satellite imagery from 1993 to 2007 and interviews with community residents (Matson 2012) showed that shrub cover has increased in the *páramo* grasslands since 1995.

Data collection

Our study area was a 646-ha area of the protected *páramo* grasslands above 3,550 m in elevation. This area of the *páramo* was relatively easy for Zuleta residents to access for livestock use because of its proximity to the main access road (Fig. 3). We used a 2007 satellite image (ERSDAC 2007) to classify the vegetation in the study area as forest cover, shrub cover or herbaceous cover. Raster data derived from very near infrared wavelength reflectivity was classified by pixel value in ArcGIS 10 (ESRI 2011). Vegetation maps, aerial photography and satellite imagery were used to verify vegetation type. Areas with forest cover and slopes $>50\%$ were excluded from sampling. We used the Create Random Points tool in ArcGIS to generate 20 sampling locations in shrub cover and 20 locations in herbaceous cover, with all sampling locations spaced a minimum of 50 m apart (Fig. 3).

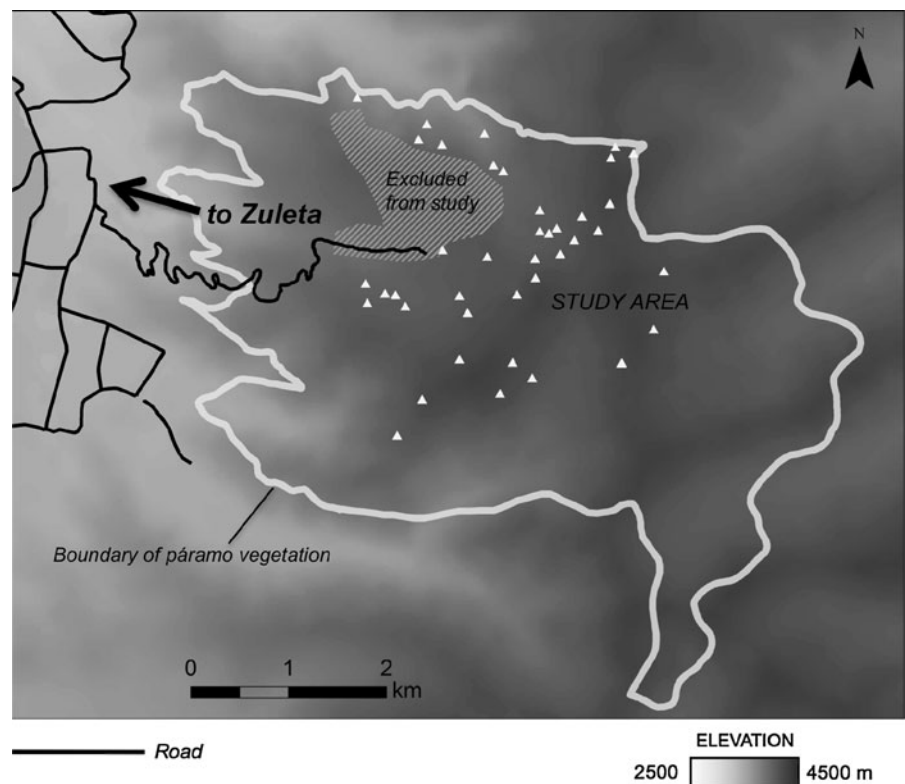
In the field, we used a hand-held GPS unit (Garmin GPSMap 60GS, Garmin, Kansas City, MO, USA) to locate each sampling location to within 50 m. Plots that were inaccessible due to steep slopes were replaced with additional locations randomly generated using the method described above. At each sampling location, shrub cover (%) was determined in a 5×5 m quadrat using a point-intercept method on a 0.5-m grid. Woody individuals <40 cm in height were not recorded.

At each plot, we sampled topographic characteristics [elevation, slope, hillslope position and slope-aspect (hereafter called aspect)]. Elevation was recorded with the GPS unit to 5-m accuracy. Aspect was measured using compass bearings on an 8-point scale (N, NE, E, SE, S, SW, W, NW). Slope was estimated in degrees using a compass and inclinometer. Hillslope position (top-of-slope, mid-slope convex, mid-slope concave, toe-slope) was assessed visually.

To sample soils, we excavated rectangular 50×70 cm soil pits at random locations adjacent to each plot. The pits were between 75 and 110 cm deep, exposing the lower A horizon or (rarely) the upper C

horizon at depth. In each pit, we recorded soil pedology and obtained two bulk samples, one from the maximum rooting zone (25–40 cm) in the upper A horizon and one at the base of the A1 or A2 horizon (55–80 cm). Each sample was retrieved from the soil profile in a 355-cm^3 aluminum cylinder (Blake and Hartge 2002). In one sampling plot, the soils were saturated and we were unable to retrieve the lower sample due to the pit filling with water. The samples were weighed (± 0.1 g) with a field balance following retrieval from the soil profile and stored in open ziplock plastic bags at ambient temperatures for the duration of fieldwork (~ 7 weeks). Volumetric water content, bulk density, organic matter content and soil pH were determined ex-situ at UW-Madison. Soil samples were oven dried at 105°C for 24 h and weighed (± 0.01 g). Bulk density (g cm^{-3}) was calculated by dividing the weight of the oven-dry soil mass (g) by the volume of the sample (cm^3). We used the field sample weights to determine water content gravimetrically (Black 1965), and volumetric soil moisture was calculated from gravimetric water content and bulk density. Organic matter content was determined for each sample by loss-on-ignition

Fig. 3 The study area with sampling locations (white triangles). The area excluded from the study is currently undergoing “conservation land use”



using 10 g of air-dry soil (Heiri et al. 2001). Soil pH was measured with a pH glass electrode (Fisher Scientific Accumet AR20 pH/conductivity meter, Thermo Fisher Scientific, Waltham, MA, USA) in a slurry of 5 g air-dry soil and 10 ml DI water.

Location-specific burning and grazing histories were not available at Zuleta, and no remote sensing data with <50 m resolution could be obtained. Therefore, we used semi-structured interviews with Zuleta farmers to develop proxies for past burning and grazing pressure. Summaries of the interview results are discussed here (see Matson 2012 for a complete discussion of the interviews). According to interview participants, cattle owners from the farmers' cooperative led their cattle to and from the *páramo* via the main access road from the community of Zuleta (Fig. 3). Cattle were released near the top of this road (hereafter referred to as "top-of-road") to graze. A livestock corral near the top of the road was used to corral and treat the cattle. The farmers periodically rounded up cattle from the *páramo* to herd them down the road to Zuleta. Interview participants confirmed that the vegetation near the top of the road was frequently burned (as frequently as once a year or more) to maintain fresh forage. According to the farmers, the cattle preferred to graze on fresh forage in recently burned areas. When good forage was not available, they were more likely to wander further from the road towards the higher-elevation slopes and ridges to the east (Fig. 3). Because of the frequent movement of cattle along the road, the *páramos* proximate to the top-of-road were likely subjected to higher grazing pressure than more distant *páramos*, a pattern seen in other *páramo* grazing studies (cf Hernandez and Monasterio 2006). In addition, the informants noted that the cattle frequently congregated along streams, where they sought water and cover daily. Finally, the informants indicated that cattle tended to move repeatedly along the same paths through the *páramos*. Likewise, farmers and hunters moving on foot and horseback tended to follow pre-existing paths, as they do today. Because choices about which areas to burn were based on *ad-hoc* visual assessment of forage conditions, it is possible that *páramos* in close proximity to paths were burned more frequently than areas where it was more difficult for people to travel. The repetitive movement of cattle along paths through the *páramo* vegetation also suggests that the vegetation in close proximity to

paths experienced higher grazing pressure than slopes that were not easily accessed via cattle trails.

Based on the historical patterns of movement of cattle and people described above, we selected three distance measures as proxies of burning and grazing pressure (Fig. 4). Distance from top-of-road was used as a proxy for burning and grazing frequency (with closer areas burned and grazed more frequently). Distance from streams was used primarily as a proxy for grazing pressure, with areas closer to streams being more frequently and intensely grazed. Distance from roads and paths was a third proxy for grazing pressure and fire frequency. To calculate proximity values, vector data for roads and streams in the study area were obtained courtesy of EcoCiencia, a non-governmental organization working in Zuleta. To map roads and paths, vector data for roads was supplemented with on-site mapping of current roads and paths using GPS (accuracy of ~50 m). A point along the access road at ~3,500 m was designated as "top-of-road." We used the Proximity:Near tool in ArcGIS 10 to calculate the distance from each sampling plot to the nearest stream, nearest road/path, and top-of-road. All distances were rounded to the nearest 50 m.

Data analysis

We used exploratory non-parametric recursive partitioning models (Regression Trees) (McCune and Grace 2002) to examine which interactions among edaphic conditions, topography and legacy proxies could be used to predict shrub encroachment. Recursive partitioning models are well-suited for predicting ecological outcomes because they allow for multiple pathways to predict the same outcome. These models allow for the simultaneous use of categorical and continuous predictor variables, and a single variable may be used more than once in different pathways (Therneau and Atkinson 1997; see also Rouget et al. 2004 and Vayssières et al. 2000). The algorithm selects independent variables in decreasing order of the proportion of variance they explain in the dependent variable. The process creates a series of splits from the "root" (top) of the tree. Each split partitions the dataset into subsets that are increasingly homogeneous with respect to the response variable (McCune and Grace 2002). Unlike the more familiar classification trees, regression trees

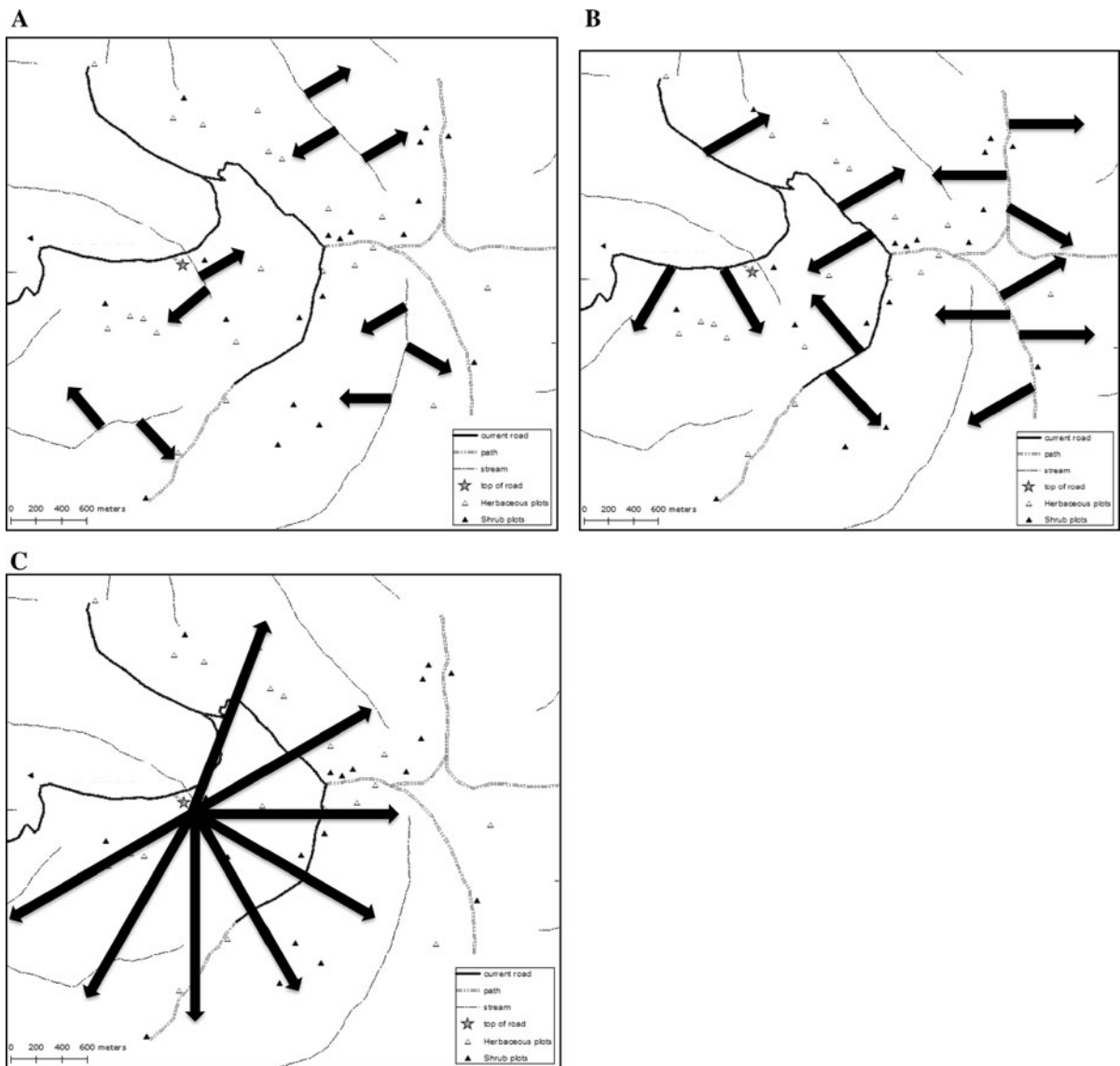


Fig. 4 Indicators of past grazing/burning pressure. **a** Proximity to streams (proxy for grazing pressure). **b** Proximity to roads and paths (proxy for burning frequency and grazing pressure). **c** Proximity to top-of-road (proxy for burning frequency and grazing pressure)

are used to model a continuous response (i.e. shrub cover) as opposed to categorical responses.

Ground truthing at the Zuleta site indicated that there was no clear cut-off for high and low shrub cover (i.e. ‘shrub patches’ vs. ‘grassland patches’) (Matson 2012), so shrub cover was treated as a continuous variable. We used the *rpart* package in R (R Development Core Team 2011) to build a regression tree with percent shrub cover as the outcome variable. Predictor variables (soil properties, topographic characteristics

and proxies for historical burning and grazing pressure) are shown in Table 1. For soil variables, we included the values from the upper A horizon (maximum rooting zone) in addition to the average value of the upper and lower soil samples. One plot was determined to be an outlier and was removed from the model based on its unusual topographic position on a rocky outcrop.

We used the standard *rpart* settings for regression trees (ANOVA method) but allowed splits to occur

Table 1 Predictor variables included in the regression model

Predictor variable	Units
Bulk density (average ^a)	g cm ⁻³
Bulk density (upper ^b)	g cm ⁻³
Volumetric water content (average)	% cm ³ H ₂ O cm ⁻³ soil
Volumetric water content (upper)	% cm ³ H ₂ O cm ⁻³ soil
Organic matter (average)	% g OM g ⁻¹ soil
Organic matter (upper)	% g OM g ⁻¹ soil
Elevation	m
Slope	Degrees
Aspect	N/NE-facing, S/SW-facing
Hillslope position	Mid-slope convex, mid-slope concave, top-of-slope, toe-slope
Proximity to roads and paths (proxy for burning frequency and grazing pressure)	m
Proximity to streams (proxy for grazing pressure)	m
Proximity to top-of-road (proxy for burning frequency and grazing pressure)	m

^a Average of the two sampling depths

^b Upper sampling depth (upper A horizon)

only at nodes containing 10 or more data points (minsplit = 10). The model was pruned to the number of splits that minimized the estimated 10-fold cross-validation error (xerror) (Therneau and Atkinson 1997). We reported R^2 and the mean squared prediction error (MSPE) for the fitted model. To validate the model, we used a ten-fold cross-validation procedure (rpart function) using the variables from the fitted model, and we reported the average MSPE across 500 iterations.

Results

The regression tree identifies four predictors of shrub cover: elevation, proximity to top-of-road, proximity to streams, and soil pH ($R^2 = 0.54$, MSPE = 19) (Fig. 5). Cross-validation yielded an average MSPE of 23. The model shows that high-elevation areas have high shrub cover, especially where soil pH is low. At low elevations, shrub cover is predicted to be highest either far from the top of road or close to streams.

Discussion

Interactions among elevation and past burning and grazing pressure best predict shrub cover

The regression tree identifies elevation, proximity to top-of-road, proximity to streams and soil pH as the most important predictors of shrub cover. According to the first split at the top of the tree, shrub cover is predicted to be 55 % at elevations above 3,743 m and 22 % at elevations below 3,743 m (Fig. 5). At each node in the tree, the recursive partitioning algorithm splits the data at the specific point that maximizes the within-group homogeneity. Thus, the cutoff of 3,743 m does not indicate a change in shrub cover precisely at that elevation. Rather, this split is indicative of overall differences in shrub cover between higher-elevation plots and lower-elevation plots. This finding is unexpected, considering that (1) the sources for propagules (forested stream incisions and montane forest along the lower grassland boundary) are generally at lower elevations and (2) higher elevations are expected to be higher-stress environments for woody plants (Korner 1999; Bader et al. 2007). However, our informants indicated that higher-elevation areas were less frequently grazed and burned. In addition, the most frequently burned areas near top-of-the-road were at relatively low elevations. Thus, we see a consistent pattern of higher shrub cover in less-frequently burned areas.

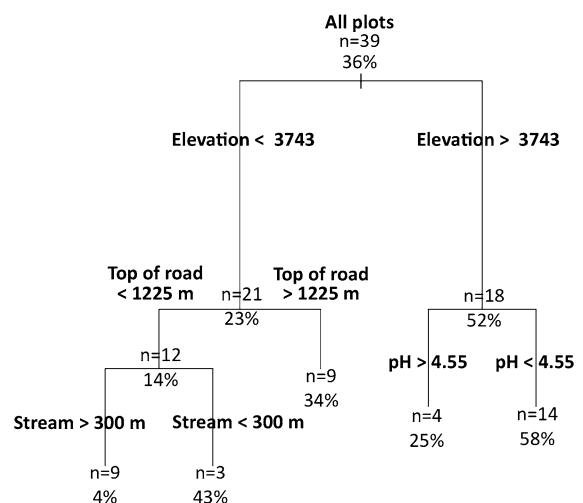


Fig. 5 Regression tree for shrub cover. Predicted shrub cover (%) is shown at each node and leaf. n = number of plots

The legacy of high fire frequency at the low elevations of the Zuleta *páramo* is also reflected in the second split on the tree. Within the low-elevation *páramos*, shrub cover is predicted to be relatively high (34 %) at distances >1,225 m away from the top of the road, and lower (23 %) on slopes surrounding the top of the road (Fig. 5). The mechanism that accounts for this legacy effect cannot be definitively stated, but it may be that remnant shrubs persisted in areas that were farther from the top-of-road because these areas burned less frequently. Other ways in which distance from the top-of-road would influence shrub cover (e.g. propagule dispersal or overgrazing) would produce the opposite association (i.e. more shrub cover closer to the top-of-the-road).

The role of edaphic conditions

At high elevations, the model predicts shrub cover to be especially high (54 %) on very acidic soils (pH < 4.55). This result requires further interpretation, however, because it is unlikely that high-acidity conditions facilitate shrub establishment or growth. High soil acidity is not favorable for plant growth because low-pH conditions reduce the ability of plants to uptake nutrients (Marschner 1991). A low-pH environment would likely favor the growth of lower-biomass species (such as herbs and grasses) over woody species. Therefore, we suggest that the split in the model at pH = 4.55 may reflect the influence of the overlying vegetation on soil pH. Inputs from overlying woody and herbaceous vegetation have been shown to influence soil chemistry and organic matter composition in *páramo* soils (e.g. Nierop et al. 2007), and shrub-derived organic matter has been shown to alter soil pH in other systems (Dahlgren et al. 1991; Pocknee and Sumner 1997). On volcanic ash soils, forest vegetation is reported to cause stronger acidification than herbaceous vegetation due to slower recycling of base cations and the production of organic acids in the forest floor (Dahlgren et al. 1991). The predicted relationship between shrub cover and soil pH in our model may reflect the influence of shrub litter decomposition on soil pH because shrub litter may release more organic acids than tussock grass litter. Apart from soil pH, no other edaphic conditions appear as important predictors in the model.

The legacy impacts of grazing and fire depend on location

According to the informants and published accounts, the cattle ingress point (top-of-road) and riparian areas were most frequently and intensely grazed. The results of the model therefore suggest that grazing pressure may have had different impacts on vegetation communities depending on where it occurred, i.e. by facilitating encroachment near streams and hindering encroachment farther from streams. We suggest two plausible explanations for these patterns. First, the removal of vegetation due to frequent and intense grazing near streams, coupled with generally wetter conditions, may have decreased the ability of fire to carry in these areas (cf Archer 1995; Roques et al. 2001; Browning and Archer 2011). Alternatively, the stream incisions at Zuleta harbor dense shrub vegetation and high-montane forests (EcoCiencia 2009), and previous studies at Zuleta have shown overlap in species composition between montane forest and *páramo* grassland shrub communities (Beltrán et al. 2009). Given that the cattle regularly sought shelter and water along the streams, the cattle may have increased the rate of propagule dispersal in the grasslands surrounding the streams by transporting plant propagules out of forested stream banks onto open slopes. Our data cannot answer whether the higher shrub cover within a few hundred meters of streams resulted from propagule dispersal or decreased capacity to carry fire. Nevertheless, it is possible that both of these factors contributed to higher shrub cover within 300 m of streams.

After more than 10 years of recovery from burning and grazing, the vegetation in the Zuleta *páramo* recovered to a patchwork mosaic of herbaceous vegetation and shrubs, reflecting interactions between past agricultural disturbance and processes of shrub regeneration and encroachment. In particular, our model suggests that subtle variations in historical fire frequency and propagule dispersal may help determine differential shrub recovery and establishment within a post-agricultural *páramo* landscape. The model indicates that the legacy effects of grazing and burning may depend on (1) the spatial distribution and frequency of these activities, and (2) the topographic and edaphic context where they occurred.

Grazing and fire management have been frequently implicated in woody encroachment scenarios, but it is

not yet clear how changes in grazing and burning regimes interact with climate and edaphic conditions to shape the pattern of shrub encroachment in alpine landscapes. Our results suggest that suppression of fire and grazing may act as a driver of shrub encroachment in *páramo* and that encroachment can occur in a non-uniform manner across the landscape, reflecting spatial variation in topography, fire frequency, and grazing and propagule dispersal. Contrary to our expectations, climatic and edaphic factors did not appear to limit shrub encroachment. Given that the process of woody encroachment can be difficult to reverse (Lett and Knapp 2003), predicting future patterns of shrub encroachment is critical for managing biodiversity and ecosystem services in mountain environments.

Acknowledgments We thank the community of Zuleta, CONDESAN and EcoCiencia for facilitating our research at the study site. Zuleta community members provided valuable assistance in the interviews and field survey. Funding was provided to Emily Matson by the Doris Duke Foundation, the Nave Foundation, and the Department of Agronomy and the Gaylord Nelson Institute for Environmental Studies at the University of Wisconsin—Madison.

References

- Altesor A, Pineiro G, Lezama F et al (2006) Ecosystem changes associated with grazing in subhumid South American grasslands. *J Veg Sci* 17:323–332
- Anthelme F, Villaret J, Brun J (2007) Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale. *J Veg Sci* 18:355–362
- Archer S (1995) Tree–grass dynamics in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2:83–99
- Archibald S, Lehman C, Gómez-Dans J, Bradstock R (2013) Defining pyromes and global syndromes of fire regimes. *PNAS* 110:6442–6447
- Bader M, Rietkerk M, Bregt A (2007) Vegetation structure and temperature regimes of tropical alpine treelines. *Arct Antarct Alp Res* 39:353–364
- Beltrán K, Salgado S, Cuesta F, León-Yáñez S, Romoleroux K, Ortiz E, Cárdenas A, Velástegui A (2009) Distribución Espacial, Sistemas Ecológicos y Caracterización Florística de los *Páramos* en el Ecuador. *EcoCiencia, Proyecto Páramo Andino y Herbario QCA*. Quito, Ecuador
- Black C (1965) Methods of soil analysis: part I physical and mineralogical properties. American Society of Agronomy, Madison
- Blake G, Hartge K (2002) Bulk Density. In: Klute A (ed) *Methods of soil analysis, Part 1. Physical and mineralogical methods*. Soil Science Society of America, Inc., Madison, pp 363–375
- Brandt J, Haynes M, Kuemmerle T, Waller D, Radeloff V (2013) Regime shift on the roof of the world: alpine meadows converting to shrublands in the southern Himalayas. *Biol Conserv* 158:116–127
- Briggs JM, Knapp AK, Blair JM, Heisler JL, Hoch GA, Lett MS, McCarron K (2005) An ecosystem in transition: woody plant expansion into mesic grassland. *BioScience* 55: 243–254
- Brock W, Carpenter S (2010) Interacting regime shifts in ecosystems: implications for early warnings. *Ecol Monogr* 80(3):353–367
- Browning D, Archer S (2011) Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. *Ecol Appl* 21:1629–1642
- Buytaert W, Wyseure G, De Bièvre B, Deckers J (2005) The effects of land-use changes on the hydrological behavior of histic andosols in south Ecuador. *Hydrol Process* 19:3985–3997
- Buytaert W, Cellieri R, De Bièvre B et al (2006) Human impact on the hydrology of the Andean *páramos*. *Earth-Sci Rev* 79:53–72
- D’Odorico P, Okin G, Bestelmeyer B (2012) A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecology* 93:520–530
- D’Odorico P, He Y, Collins S, DeWekker S, Engel V, Fuentes J (2013) Vegetation-microclimate feedbacks in woodland-grassland ecotones. *Glob Ecol Biogeogr* 22:364–379
- Dahlgren R, Vogt K, Ugolini F (1991) The influence of soil chemistry on fine root aluminum concentrations and root dynamics in subalpine Spodosol, Washington State, USA. *Plant Soil* 133:117–129
- De Bièvre B, Calle T (2011) The Andean *páramo* project: conserving biodiversity and hydrological services on the roof of the Andes. In: Mountain forum bulletin 2011: mountains and green economy, CONDESAN, Quito, Ecuador. <http://www.condesan.org/ppa>. Accessed Apr 2011
- EcoCiencia (2009) Plan de Manejo y Desarrollo de la Comuna Zuleta. Proyecto *Páramo* Andino. Conservación de la Diversidad en el Techo de los Andes, Quito, Ecuador
- Eldridge D, Bowker M, Maestre F, Roger E, Reynolds J, Whitford W (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol Lett* 14:709–722
- ERSDAC (Earth Remote Sensing Data Analysis Center) (2007) of Japan, ASTER scene ASTL1A_070205154349070 2090520, 1A, ASTER GDS IMS, http://imsweb.aster.ersdac.or.jp/ims/html/DPR/DPR_Menu.html. Accessed Apr 2011
- ESRI (2011) ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands
- Farley K, Anderson W, Bremer L, Harden C (2011) Compensation for ecosystem services: an evaluation of efforts to achieve conservation and development in Ecuadorian *páramo* grasslands. *Environ Conserv* 38:393–405
- Fuhlendorf S, Archer S, Smeins F, Engle D, Taylor Jr C (2008) From the Dust Bowl to the Green Glacier: human activity and environmental change in Great Plains grasslands. In: Van Auken O (ed) *Western North American Juniperus communities: a dynamic vegetation type*. Springer, New York, pp 219–238
- Heiri O, Lotter A, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in

- sediments: reproducibility and comparability of results. *J Paleolimnol* 25:101–110
- Hernandez Z, Monasterio M (2006) Functional diversity of wetland vegetation in the high-Andean páramo, Venezuela. In: Spehn E, Liberman M, Körner C (eds) Land use change and mountain biodiversity. CRC Press Group, Boca Raton, pp 187–197
- Hofstede R, Coppus R, Mena VP, Segarra P, Wolf J, Sevink J (2002) The conservation status of tussock grass páramo in Ecuador (El estado de conservación de los páramos de pajonal en el Ecuador). *Ecotropicos* 15:3–18
- Janzen D (1973) Rate of regeneration after a tropical high elevation fire. *Biotropica* 5:117–122
- Jørgensen P, Ulloa C (1994) Seed plants of the high Andes of Ecuador: a checklist. *AAU Rep* 34:1–443
- Knapp A, Briggs J, Collins S (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Glob Chang Biol* 14:615–623
- Körner C (1999) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin
- Laegaard S (1992) Influence of fire in the grass páramo vegetation of Ecuador. In: Balsev H, Luteyn J (eds) *Páramo: an Andean ecosystem under human influence*. Academic Press, London, pp 151–170
- Lett M, Knapp A (2003) Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. *J Veg Sci* 14(4):487–496
- Luteyn J (1992) *Páramos: Why study them?* In: Balslev H, Luteyn J (eds) *Páramo: an Andean ecosystem under human influence*. Academic Press Limited, U.K., pp 1–14
- Luteyn J (1999) *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature*. Memoirs of New York Botanical Garden 84. New York Botanical Garden Press, New York
- Luteyn J, Churchill S (2000) Vegetation of the tropical Andes: an overview. In: Lentz D (ed) *Imperfect balance: landscape transformations in the Precolombian Americas*. The Historical Ecology Series. University Press, New York, pp 281–310
- Marschner H (1991) Mechanisms of adaptations of plants to acid soils. *Plant Soil* 134:1–20
- Matson E (2012) Shrub cover, community composition and diversity in post-agricultural páramo grasslands of the high Andes. Dissertation, University of Wisconsin, Madison
- McCune B, Grace J (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach
- Montane F, Rovira P, Casals P (2007) Shrub encroachment into mesic mountain grasslands in the Iberian peninsula: effects of plant quality and temperature on soil C and N stocks. *Glob Biogeochem Cycles* 21: GB4016
- Myers N, Mittermeir R, Mittermeir C, da Fonseca G, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Pendergrass K, Miller P, Kaufmann J (1998) Prescribed fire and the response of woody species in Willamette Valley wetland prairies. *Restor Ecol* 6:303–311
- Pocknee S, Sumner M (1997) Cation and nitrogen contents of organic matter determine its soil liming potential. *Soil Sci Soc Am J* 61:86
- Podwojewski P, Poulouard J, Zambrana T, Hofstede R (2002) Overgrazing effects on vegetation cover and properties of volcanic ash soil in the páramo of Llangahua and La Esperanza (Tungurahua, Ecuador). *Soil Use Manage* 18:45–55
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>. Accessed Sept 2011
- Ramsay P, Oxley E (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetation* 124(2):129–144
- Ramsay P, Oxley E (1997) The growth form composition of plant communities in the Ecuadorian páramos. *Plant Ecol* 131(2):173–192
- Ratajczak Z, Nippert J, Hartman J, Ocheltree T (2011) Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairies. *Ecosphere* 2(11):121
- Ratajczak Z, Nippert J, Collins S (2012) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93(4):697–703
- Roques K, O'Connor T, Watkinson A (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall, and density dependence. *J App Ecol* 38:268–280
- Rouget M, Richardson D, Milton S, Polakow D (2004) Predicting invasion dynamics of four alien Pinus species in a highly fragmented semi-arid shrubland in South Africa. *Plant Ecol* 152:79–92
- Salick J, Zhendong F, Byg A (2009) Eastern Himalayan alpine plant ecology, Tibetan ethnobotany, and climate change. *Glob Environ Chang* 19:147–155
- Sarmiento L, Llambi L, Escalona A et al (2003) Vegetation patterns, regeneration rates and divergence in an old-field succession of the high tropical Andes. *Plant Ecol* 166:63–74
- Sklenar P, Jorgenson P (2004) Distribution patterns of páramo plants in Ecuador. *J Biogeo* 26:681–691
- Smith J, Cleef A (1988) Composition and origins of the world's tropic alpine floras. *J Biogeo* 15:631–645
- Southgate D, Wunder S (2007) Paying for watershed services in Latin America: a review of current initiatives (working paper no. 07-07). Sustainable Agriculture and Natural Resources Management Collaborative Research Support Program (SANREM CRSP) and Office of International Research, Education, and Development, Virginia Tech, USAID
- Sturm M, Schimel J, Michaelson G, Welker J, Obersauer S, Liston G, Fahnestock J, Romaovsky V (2005) Winter biological processes could help convert arctic tundra to shrubland. *Bioscience* 55:17–26
- Suarez E, Medina G (2001) Vegetation structure and soil properties in Ecuadorian páramo grasslands with different histories of burning and grazing. *Arct Antarct Alp Res* 33:158–164
- Therneau T, Atkinson, E (1997) An Introduction to recursive partitioning: using the RPART routines. Technical Report 61, Mayo Clinic, Section of Statistics
- Van Auken O (2000) Shrub invasions of North American semiarid grasslands. *Annu Rev Ecol Syst* 31:197–215
- Van Wilgen B, Trollope W, Biggs H, Potgeiter A, Brockett B (2003) Fire as a driver of ecosystem variability. In: Du Toit J, Rogers K, Biggs H (eds) *The Kruger experience: ecology and management of savanna heterogeneity*. Island Press, Washington, DC, pp 149–170

- Vayssières M, Plant R, Allen-Diaz B (2000) Classification trees: an alternative non-parametric approach for predicting species distributions. *J Veg Sci* 11:679–694
- Verweij P (1995) Spatial and temporal modeling of vegetation patterns: burning and grazing in the *páramo* of Los Nevados National Park, Colombia. Dissertation, International Institute for Aerospace Survey and Earth Sciences
- Wille M, Hooghiemstra H, Hofstede R, Fehse J, Sevink J (2002) Upper forest line reconstruction in a deforested area in northern Ecuador based on pollen and vegetation analysis. *J Trop Ecol* 18:409–440
- Wu Z, Sun H, Zhao Z, Peng H, Li D (2007) Origin and differentiation of endemism in the flora of China. *Front Biol China* 2:125–143
- Zavaleta E, Kettley L (2006) Ecosystem change along a woody invasion chronosequence in a California grassland. *J Arid Environ* 66:290–306