Topographic controls on the distribution of tree islands in the high Andes of south-western Ecuador

D. Coblentz and P. L. Keating

ABSTRACT

Aim To evaluate the hypothesis that geomorphometric parameters of upper montane Andean environments have an important influence on the regional fire ecology and consequently play a role in the spatial distribution of ‘remnant’ tree islands dominated by Polylepis.

Location A glacial landscape located between 3600 and 4400 m elevation in Cajas National Park, south-western Ecuador.

Methods The eigenvalue ratio method was used to evaluate the regional geomorphometric parameters of a 30-m digital elevation model for Cajas National Park. The landscape character was evaluated by quantifying the topographic roughness, organization, and gradient. This information was used to determine the spatial correlations between terrain characteristics and the distribution of tree islands in the region.

Results We demonstrate a strong spatial correlation between areas of high topographic roughness and gradient, and the locations of the major tree islands. We find that there is a distinctive relationship between the topographic roughness and organization in the vicinity of the tree islands (e.g. increased upslope roughness and decreased topographic grain strength) that substantiates the notion that the tree islands are located in relatively inaccessible topography.

Main conclusions In the northern and central Andes, the location of Polylepis-dominated ‘forest islands’ has been shown to be a function of climate, terrain characteristics, and anthropogenic disturbances. Although the relative importance of various ecological factors has been debated, it remains clear that fires have exerted a strong influence on these ecosystems. Other authors have noted that tree islands are more likely to occur at the base of cliffs, above moist areas, and in other areas where fires do not burn frequently. Our results corroborate these observations, and demonstrate that the occurrence of Polylepis patches is strongly correlated with specific combinations of terrain features. Although we do not discount the importance of other factors in determining the spatial position and areal extent of these forests, we demonstrate strong support for fire-related hypotheses.

Keywords Andes, Cajas National Park, fire ecology, geocology, geomorphometry, landscape ecology, Polylepis, remote sensing, topographic analysis, tropical montane forest.
plays a fundamental role in the distribution of vegetation and biodiversity (Coblentz & Riitters, 2004). Despite the important link between topography and geocology in montane regions, most studies of this relationship have been limited to a primarily qualitative framework (e.g. Brown & Gibson, 1983). Digital elevations models (DEMs), rectangular grids of elevation values, provide an unparalleled tool for the evaluation of geomorphometric parameters. The current availability of high-speed computing platforms, high-resolution DEMs now globally available at a 3-arc-second (about 90 m) resolution, and high-resolution land cover data sets (e.g. Riitters et al., 2000) make it possible to undertake a rigorous quantitative analysis that can be used to test the relationships discussed in previous qualitative investigations.

In the Andean highlands, the spatial distribution of tropical forests has been shown to be a function of both topographic features and anthropogenic disturbances (e.g. Troll, 1968, 1973; Young & Keating, 2001). Elevation establishes a complex set of environmental gradients, including temperature regimes and precipitation (Troll, 1968; Lauer, 1981). In addition, upper montane ecosystems are strongly influenced by topographic features such as slope, aspect, and shape (Troll, 1973; Young, 1998a; Keating, 1999). Given that humans have been present in the Andes for at least 7000 years (Bruhns, 1994), disturbances have also influenced the composition, structure and spatial position of forest communities. Agricultural practices, burning, grazing, road construction, and logging have continually modified many areas of the Andes (Ellenberg, 1979; Lægaard, 1992; Young, 1994, 1998b; Keating, 1998), leading to a land cover that is characterized by a complex mosaic of vegetation types (Gade, 1999). Understanding the timing and exact nature of landscape transformations is difficult, as each region has a different landscape history (Young & Zimmerer, 1998). Burning, however, continues to occur in conjunction with most land-use activities, especially grazing, and is probably the most significant disturbance in the Ecuadorian Andes above 3500 m elevation (Keating, 2007).

At elevations above 3000 m, the Ecuadorian Andes are covered with a spatially heterogeneous assemblage of agricultural lands, páramo (tropical alpine) and forest communities. Whereas continuous forest covers the outer flanks of both

Figure 1 Topographic map of south-western Ecuador with the study area indicated by the solid box. In the lower figure, the tree islands of Cajas National Park are designated by polygons with colours representing four area designations: red corresponds to tree islands covering an area < 1 ha; green to 1–5 ha; blue to 5–10 ha; and black to > 10 ha.
cordilleras up to 4300 m elevation, inter-Andean forest (*sensu* Sarmiento, 1995) tends to occur as remnant forest patches in remote locations (Valencia & Jørgensen, 1992; Stern, 1995; Young & Keating, 2001). Some continuous forest occurs in the southern tip of the country (Madsen & Øllgaard, 1994), but intensive, long-term land use has reduced most Andean forests to a series of strips and patches found in gullies, ravines, volcanic calderas, and remote high-elevation sites. Fragments of fire-sensitive vegetation are characteristic of many fire-prone landscapes (Bowman, 2000), and topographic protection of remnant vegetation communities is well documented in several tropical ecosystems (e.g. Fensham, 1995).

In many sections of the Andes, including south-western Ecuador, high-elevation patches of *Polylepis*-dominated forests occur above the timberline separating continuous, closed forest from páramo (Fig. 1). *Polylepis* is a taxonomically complex genus comprising c. 20 species whose centre of diversity occurs between central Peru and southern Bolivia (Kessler, 1995; Navarro et al., 2005). Often found at up to 5000 m elevation in Bolivia, these trees occur at the highest elevation of any angiosperm tree taxa (Navarro et al., 2005). Seven species of *Polylepis* are found in Ecuador, where they occur between 2700 and 4300 m a.s.l. (Romoleroux, 1994). Whereas *Polylepis incana* may occur as monospecific stands (Fehse et al., 2002), most ‘*Polylepis* forest islands’ in Ecuador contain other tree taxa, including *Columella, Escallonia* and *Gynoxys* (Fjeldså, 1992; Romoleroux, 1994).

Several thousand years ago, *Polylepis* forests probably covered a far more extensive area than they do at present. Palaeohistorical evidence suggests that the geographical distributions of these forests fluctuated widely, largely in response to climatic changes (Simpson, 1979). As a result of the dramatic landscape transformations described above, however, there has been a substantial reduction in the area covered. Fires, grazing and wood-cutting appear to be the principal factors explaining this change, and these activities continue to restrict the spatial extent of upper montane forests (e.g. Fjeldså, 1992; Hensen, 2002; Enrico et al., 2004; Renison et al., 2006). Given the frequency of these disturbances, these forests now occur primarily in ravines, on steep rocky terrain, near streams, and in other protected sites (Lægaard, 1992; Kessler, 1995). Recent studies indicate that only the upper limits of *Polylepis* patches are determined by harsh climatic conditions, which impede the growth and regeneration of trees (Lægaard, 1992; Cierjacks et al., 2007); under these conditions, certain sites afford the seedlings protection from the wind and cold (e.g. Simpson, 1986; Ibisch, 1993).

In this article we focus primarily on the notion that fires play a key role in maintaining the current spatial distribution of forest patches. Our study is motivated by the hypothesis that the tree islands in Cajas National Park are located in areas that experience lower fire frequencies owing to local topographic variations such as steep terrain. Other issues, such as climatic factors and disturbance history, are beyond the scope of this study. To test our hypothesis, we apply the eigenvalue ratio method (Woodcock, 1977) to quantify the character of the landscape and to evaluate the terrain where *Polylepis* patches occur in a section of south-western Ecuador, and discuss several salient trends in relation to the presence of fire. As discussed below, this technique extracts several types of information about the topographic fabric of the region, and provides a comprehensive topographic analysis.

**MATERIALS AND METHODS**

**Study area**

El Cajas National Park covers c. 29,000 hectares of upper montane ecosystems on the western cordillera of the Ecuadorian Andes (Ministerio de Ambiente, 2007). Located c. 35 km west of Cuenca, the middle of the park is found at 2°50’S, 79°15’W (Fig. 1). Elevations within the park range from c. 3180 to 4500 m. With the area having been glaciated during the Pleistocene (Hastenrath, 1981; Clapperton, 1993), the physiography includes more than 230 glacial lakes, interconnected ridges and peaks, and numerous broad hanging valleys. Glaciers were absent during the Holocene, and little tephra or pyroclastic materials from volcanoes have fallen on this region (Rodbell et al., 2002). Soils in El Cajas did not develop from underlying rocks, but instead are composed of organic and aeolian materials (Harden, 2007), and are often referred to as ‘black Andean soils’, histosols, or hydric andisols.

The dominant land cover is páramo, a form of tropical alpine vegetation. Much of the valley bottom is characterized by bogs or moist grasslands, whereas the slopes are better drained and covered with tussock grasses. Woody species occur infrequently in the grasslands, and shrubs are typically found in isolated patches on the valley floors. Plant community patterns are relatively uniform in the tussock-grass páramo but vary markedly along the valley bottoms (Keating et al., 2002). The species richness of this ecosystem is probably as high as in any páramo in the country, and its floristic composition differs significantly from that of páramos located to the north of this region (Sklenář & Jørgensen, 1999; Sklenář & Ramsay, 2001).

Three varieties of forest are found in the park. Continuous, relatively undisturbed forest occurs in the lower sections of the park; timberlines usually occur between 3330 and 3365 m a.s.l. Second, a diverse mixture of secondary forest and tall shrubs occurs near roads and along some valley bottoms. Finally, forest patches, which often occur at the base of cliffs or steep slopes (Fig. 2), are typically found above 3600 m a.s.l. These ‘forest islands’ are often dominated by 5–10 m tall *Polylepis* trees, although the interior portions may contain additional tree genera, including *Clethra, Gynoxys,* and *Myrsine.* Generally speaking, the relative importance of *Polylepis* increases above 3800 m (Hansen et al., 2003).

Climatic data have not been collected extensively for this section of El Cajas, but it has been suggested that the páramos in this region receive at least 2300 mm of precipitation annually (Morris, 1985). Most of this falls between January and June, and a relatively dry season occurs during the rest of the
The long-term environmental history of these highlands has been investigated only recently, and much of the disturbance history is a matter of speculation. After the late glacial period, which ended 11,000 yr bp, Polylepis increased in importance at higher elevations. Charcoal evidence suggests that fires also became more frequent at that time; however, it appears that this frequency decreased somewhat around 4000 years ago (Hansen et al., 2003). The role played by humans in modifying the landscape, however, is not clear; nor is there any documented spatial correlation between forest communities and the occurrence of fires.

Although the Ecuadorian highlands have been inhabited by various indigenous groups during the past several thousand years, past land-use practices and associated disturbance regimes in the Cuenca region have received little attention. Several anthropologists have examined pre-Conquest settlement patterns and material culture (e.g. Collier & Murra, 1943; Bruhns et al., 1990), and other authors have described more recent settlement patterns in the region (e.g. Borroto, 1989). To our knowledge, however, no one has provided detailed descriptions of human impacts within El Cajas for any period before the 20th century. It is worth noting, however, that early Spanish explorers described these mountains as lacking forests in the 1580s (Jiménez de Espada, 1965[1582]). We were unable to find photographs or other records that document forest cover change at any time during the past four centuries.

Between 1979 and 1996, this park was referred to as ‘Las Cajas Recreational Area’ (Fundación Natura, 1992). Because the designation of ‘recreational areas’ in Ecuador does not entail strict conservation protection, both burning and grazing by livestock have precluded the regeneration of woody species throughout the region. During the dry season, several fires could occur simultaneously during any given day (Keating et al., 2002). Many of the burns cover more than several hundred hectares, so that the páramo represents various states of recovery after these disturbances. Clearly, forest could not regenerate under such conditions, and shrub páramo (sensu Cuatrecasas, 1968), which often serves as a transition community between forests and grass páramo, rarely occurs. Given that this region has been under the influence of human activity for at least 3500 years (White & Maldonado, 1991), it is a reasonable assumption to treat the forest patches within El Cajas as relatively stable units. As we illustrate below, the position and areal extent of these forest islands have probably not changed during the past several decades. Only in rare cases did forest margins show any signs of recent burning.

**Analysis of vegetative cover**

The vegetative cover in the study area was quantified through an analysis of a $15 \times 15$ km subset of a Landsat Thematic Mapper (TM) image (30-m cell size) acquired on 26 March 1987. Although more recent imaging would be desirable, Landsat, SPOT and Aster images collected subsequent to this date have included substantially more cloud coverage and thus are of limited utility for mapping land cover. Atmospheric correction was performed with a technique described in Colby & Keating (1998). The subscene was rectified using 23 ground control points, and a root mean squared error (RMSE) of 0.230 was obtained. A nearest neighbour resampling algorithm was used, and the rectified image was subset to the coordinates given below. The normalized difference vegetation index (NDVI) was calculated to distinguish the forested areas from other land-cover types. Calculated as near infrared − red/near infrared + red, or TM bands 4 − 3/4 + 3, this index provides an indication of leafy green biomass (Sader et al., 1989; Mausel et al., 1993). Because the forested areas contained significantly more leafy biomass than the páramo vegetation, a density slice technique (Jensen, 2005) was utilized to map the forest islands and secondary forest. After the range of NDVI values was determined for each cover type, a threshold was established to separate trees from other land-cover types; aerial photographs acquired on 9 October 1976 were used to assist in this classification process.

To determine the characteristics and diversity of vegetation that occurs within Cajas National Park, extensive field reconnaissance was performed during June 1990 and October 1991. Initially, a $9 \times 12$ km$^2$ area was selected that included representative physiographic features, numerous forest patches, and several hundred hectares of secondary forest located near roads and in valleys; continuous, primary forest was not included in the study area. UTM coordinates (Zone 17 S) for the upper left corner of the study site are 695000 E, 9696000 N, and those for the lower right corner are 707000 E, 9687000 N. Further ground verification was performed during June and July 1995, and aerial photographs acquired on 12 December 1995 were also used to check the

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Figure 2 A typical tree island located in the south-west portion of the study area at c. 3900 m in Cajas National Park. Dominated by Polylepis, the forest patch covers c. 10 ha and is located in a boulder-strewn area at the base of a cliff. Note that the tussock-grass páramo surrounding this site has been burned within the past year.
accuracy of the mapping process. Comparison of photographs from both dates revealed that little, if any, change in forest cover has occurred during the past 20 years. Approximately 15% of the scene was covered with clouds or cloud shadows, and these areas were not included in the analysis.

**Evaluation of geomorphometric parameters**

Geomorphometry, the study of landscape geometry, provides a way to quantify the relationships between topographic variables and vegetative land cover. Within biogeography, there has been a growing recognition that topographic parameters exert a strong influence on patterns of vegetative cover (see discussion in Coblentz & Riitters, 2004), and are valuable in wildlife habitat modelling (Sappington et al., 2007). In the following analysis we employ a quantitative analysis of topography using the evaluation of geomorphometric parameters (see review in Mark, 1975). Specifically, we use the eigenvalue ratio method (see discussion in Appendix S1 and Fig. S1) to quantify topographic roughness, organization and gradient across the landscape (Chapman, 1952; Watson, 1966; Woodcock, 1977; Guth, 1999; McKean & Roering, 2003).

![Figure 3](image-url)

**Figure 3** The spatial relationship between the (a) topography, (b) topographic roughness, (c) topographic organization, and (d) topographic gradient for the study area shown in Fig. 1 computed using the eigenvalue ratio method. The white-filled polygons designate the spatial extent of the tree islands, which are generally located near regions of high topographic roughness, high gradient and low organization, suggesting a correlation between the location of the tree islands in Cajas National Park and the rough topographic features in the landscape.
discussed above, our study is motivated by the hypothesis that the tree islands in Cajas National Park are located in areas that experience lower fire frequencies owing to local topographic variations such as steep terrain. We test this hypothesis by determining spatial patterns of geomorphometric parameters and relating them to the locations of the tree islands. In addition, through the use of histograms and other graphical techniques, we demonstrate relationships among topographic variables, elevation, and size of forest patches. A summary of the topographic analysis methodology used to quantify various geomorphometric parameters is provided in Appendix S1.

Because the objectives of our topographic analysis require precise measurements, we constructed a 30-m DEM. Although this resolution gives a threefold improvement in the topographic resolution over commonly available DEMs (e.g. SRTM data), we acknowledge that it is still too coarse for a reliable evaluation of the metre-scale topographic details that would be required for a study of individual tree islands. The conclusions of our study are therefore limited to topographic features with a wavelength of about several tens of metres, and should be considered a first-order analysis of the broad-scale topographic characters that contribute to the existence and distribution of the tree islands in Cajas National Park. A more detailed geomorphometric analysis of individual tree island locales is left for future research efforts when higher-resolution DEMs (< 10 m) become available.

RESULTS

The study area, shown in Fig. 3a, covers an area of c. 90 km² and has considerable topographic relief, with elevations ranging from 3361 to 4406 m a.s.l., with a mean and standard deviation of 3892 and 115 m, respectively. In general, the tree islands (white polygons in Fig. 3) are located in close proximity to areas of high topographic roughness (red regions in Fig. 3b) and low topographic organization (Fig. 3c). Areas of high roughness generally correspond to high topographic gradients (Fig. 3d). The correlation between tree island locations and steep/rough topography is stronger for the larger tree island areas (> 10 ha), which also tend to be located at high elevations (at an average of 3900 m vs. about 3850 m for the smaller tree island patches). As shown in Fig. 4, the elevation distributions for the larger tree islands are also skewed towards higher elevations with a smaller standard deviation for the distribution (c. 95 m vs. a standard deviation of > 120 m for the tree island sites covering smaller areas).
Variations in the character of the topographic roughness and topographic organization between the tree island sites and a reference set of 481 sites (randomly selected within the study area) is shown in Fig. 5, with mean and standard deviation values listed in Table 1. Several generalizations can be made on the basis of these distributions. The low topographic organization for the highest tree island sites (blue) is indicative of a high degree of scatter in the topographic roughness distribution (quite similar to the case for a randomly oriented topographic distribution) – possibly reflecting the geomorphic processes of Pleistocene-era glaciation. Moreover, within the highest-elevation belt, grass height and coverage are typically lower, and other life forms such as cushion plants increase in importance. Fires not only are less likely to be ignited at high elevations, but are less likely to consume this relatively heterogeneous vegetation.

The topographic character of the smallest size class (< 1 ha) is closest to that of the random sites. This suggests that, given the spatial limitation of the DEM used in this analysis (cell size of 0.09 ha), we may not have detected terrain features that influence the locations of these islands. Tree islands at lower elevations (red distributions) have the most variable and highest organization, and consistently higher roughness values – which is expected given the mechanism by which glaciers ‘carve’ landscapes. We also note that the difference between the lower (red) and higher (blue) tree island sites increases with forest island area in both the roughness and organization distributions (Fig. 5). Sites with high values of both organization and roughness (e.g. lower-elevation tree islands with spatial extent greater than 10 ha) span regions with greater topographic variation, and the higher coherence in the surface-normal vectors (which define the surface orientation) in the flatter regions increases the organization values compared with those in the rougher regions. As expected, this effect is more pronounced for the larger tree island sites.

We applied the Kolmogorov–Smirnov test (KS-test) to determine if the tree island histograms for each elevation range and size subset differed significantly from the random sample distribution; this test has the advantage that it is not based on any underlying distribution of data. The \( D \)-statistic listed in Table 1 is a measure of the difference between the randomly selected distribution and the distribution at the listed elevation and size subset. The confidence level that the histograms are sampling different distributions is reflected in the significance level probability. For reference, identical distributions would return values of 0.0 and 0% confidence for \( D \) and the confidence probability, respectively. The null hypothesis that the histograms are sampling the same distribution can be
rejected at a > 99% confidence level for nearly all classes, with
the exception of the high-elevation subregion for 1–5 ha
patches and the lowest-elevation subregion for 5–10 ha tree
island patches – although we note that the KS-test confidence
level for these two regions is still in excess of 75%. These results
support our a priori assumption that the geomorphological
parameters of the tree island locations are significantly
different from those of the region (as measured by a random
sampling).

The trade-off between topographic roughness and topo-
graphic organization can be graphically illustrated given the
fact that only two of the three eigenvalues are independent.
The flatness $[\ln(S_1/S_2)]$ (the reciprocal of roughness) can be
plotted against organization $[\ln(S_2/S_3)]$ to eliminate one of the
dependent variables and to provide a way to describe the
pattern of vector orientations as clusters (unimodal distribution
of the vectors) or girdles (multimodal distribution of the
vectors) in $K$-space (cf. Fig. S2 and Woodcock, 1977). The
$K$-space distributions computed from the flatness and organ-
ization values for Cajas National Park are shown in Fig. 6, in
which much of the information present in the histogram
distributions is distilled graphically. In general, the lower tree
island sites (black symbols) have greater organization (reflect-
ing greater coherence in the surface-normal vector distribu-
tions) but lower flatness (higher roughness) values. In contrast,
the largest tree island sites (inverted triangles) are the least
organized, with significantly greater flatness values. Again, this
reflects the fact that the larger tree island sites include large
portions of the flatter down-slope landscape at the base of
high-relief topography. We also note that lower tree island sites
lie closer to the cluster-girdle threshold defined by $K = 1$,
whereas the higher tree island locations have distributions
more characteristic of clusters (see Fig. S2 for an explanation
of $K$-space).

**DISCUSSION**

Numerous authors have expressed concern about the ongoing
degradation of upper montane tropical ecosystems (e.g.
Millones, 1982; Hess, 1990). *Polylepis* forests are clearly
among South America’s most endangered ecosystems (Ro-
moleroix, 1994; Navarro et al., 2005); however, here we argue
that, in the case of Cajas National Park, most of the forest
removal probably occurred in the distant past. As a result of a
long history of several land-use practices, especially wood
gathering and grazing (Ellenberg, 1979; Lægaard, 1992), this
ecosystem is currently restricted to sites where burning is
strongly inhibited. Extensive field observations within our
study area suggest that burning rarely, if ever, occurs within
the boulder-strewn areas at the bases of cliffs, near road cuts,

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<th>Kolmogorov–Smirnov test (D-statistic, significance level probability [%])</th>
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<td>Organization</td>
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*The Kolmogorov–Smirnov test (KS-test) results for each elevation range and area subset are based on a comparison with the random distribution. The KS-test parameters listed are first the $D$-statistic (a measure of the difference between the two distributions) and second the confidence probability that the data sets are drawn from the different distributions. For reference, identical distributions would return values of 0.0 and 0% for $D$ and the confidence probability, respectively.
The tropical Andes are well known for their species diversity, endemism, and habitat diversity (Gentry, 1995; Jørgensen & León-Yánez, 1999; Luteyn, 1999; Young et al., 2002). Given both the high rates of land-cover conversion and the growing interest in conservation issues, the importance of mapping and analysing tropical montane ecosystems at the landscape scale is obvious. Most digital mapping projects for such areas have focused on either Central America or Mexico (e.g. Sader et al., 1989; Helmer et al., 2000; Nagendra et al., 2004; Aguilar, 2005). A growing number of mapping projects for the tropical Andes have been performed at the regional to subcontinental scale (e.g. Sierra et al., 1999), but thus far relatively few studies have involved mapping tropical Andean vegetation at the landscape scale (e.g. Colby & Keating, 1998; Echavarria, 1998). Even fewer have included GIS analyses or modelling to explain how vegetation is influenced by disturbance or terrain features (e.g. Keating, 1997; Vanacker et al., 2003; Kintz et al., 2006). In part this trend stems from the scarcity of cloud-free images for these regions, as well as from the difficulties associated with performing the necessary fieldwork. For a growing number of areas, however, digital data sets are becoming available, and we recommend that upper montane ecosystems be studied with geospatial techniques when possible.

Here we have taken advantage of DEMs to evaluate quantitatively the geomorphometric parameters of the landforms in Cajas National Park and to evaluate correlations between landforms and the occurrence of tree islands. We reiterate and readily acknowledge that it is an oversimplification to claim that the distribution of tree islands is controlled solely by the topographic character. Our working hypothesis, however, is that certain topographic features inhibit the movement of fire and therefore influence the current spatial distribution of tree islands in the Cajas region. The close proximity of the tree islands in Cajas National Park to areas of high topographic roughness, high gradient and low organization supports the notion that rough terrain encourages the persistence of tree islands in this area. Forest fragments are also highly threatened by burning in some lowland tropical ecosystems (Gascon et al., 2000; Cochrane, 2001), but, even in these environments, topographic features or rocky substrates may afford some protection (e.g. Fordyce et al., 1997).

Our twin goals were to demonstrate the utility of performing a quantitative topographic analysis and to evaluate to what degree topography controls the tree island distribution. Other influences are certainly important, but quantification of their role is beyond the scope of this study. These factors include grazing intensity, variance in precipitation, bedrock geology of the region, hydrology, and other topographic parameters. We also acknowledge that micro-climatic factors are very important in governing the position of treelines. Recent work demonstrates unequivocally that the relationships between microclimate and fire ecology are very complex (Bader, 2007). Regardless of the relative importance of other factors that we did not measure, this article...
demonstrates that the position of forest patches in El Cajas is indeed consistent with what is currently understood about fire behaviour. These results should motivate a more detailed study of the small-scale (< 10 m resolution) topography of individual tree islands as such data become available (most likely requiring 1-m resolution LiDAR data).

CONCLUSIONS

In this article we have tested the hypothesis that the spatial distribution of high-elevation tropical forest patches in Cajas National Park is controlled by the landscape-scale topographic character by evaluating the correlation between the tree island distribution and a number of geomorphometric parameters including organization, roughness and spectral power. Within the assumptions and resolution limitations of our study, we draw the following conclusions regarding the correlation between features in the topography and the location of the tree islands:

(1) A quantitative topographic analysis is a valuable tool for understanding the distribution of land cover, particularly in regions where insular mountain ranges dominate the topographic distribution.

(2) Whereas climatic factors may have determined the original distribution of Polylepis-dominated forests, it appears that fires exert a strong influence on the present distribution of these forests. Our quantitative analyses demonstrate that areas at the base of cliffs or above moist valleys are among the few places where these ecosystems persist in south-western Ecuador.

(3) The geomorphometric analysis of the topography indicates that the tree islands of Cajas National Park are found in close proximity to rough topography with strong topographic gradients. Overall, we find that the topographic roughness exerts the primary control on the topographic character of the landscape in the immediate area surrounding the tree islands.

(4) Climate, terrain, and disturbances all exert strong influences on the spatial position and areal extent of upper montane tropical forests. The interrelationships among these factors merit far more attention than they have previously been accorded. As technology improves, scientists’ ability to relate the position of plant communities to numerous variables will increase further. In the future, extensive field data could be coupled with model simulations to enhance the understanding of tropical forest dynamics.

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

Appendix S1 Topographic analysis and the eigenvalue ratio method.

Figure S1 Example surface-normal vectors illustrating topographic surface roughness.

Figure S2 Illustration of K-space (topographic flatness plotted vs. the topographic organization) and the location of several example topographic distributions.

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BIOSKETCHES

David Coblentz is a solid Earth geophysicist with a joint appointment at Los Alamos National Laboratory and the University of New Mexico who, through speculative geodynamics research, explores the common ground between geodynamics and geoecology.

Phil Keating has spent 17 years investigating the influences of anthropogenic disturbances on vegetation in the Ecuadorian Andes. He often combines field-based ecological studies with remote sensing and GIS to determine how different fire regimes modify floristic composition and landscape structure in both páramo and timberline forest communities. Dr Keating is currently a research associate at Indiana University.

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