

Article

Elevational Shifts in the Topographic Position of *Polylepis* Forest Stands in the Andes of Southern Peru

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Abstract: The patchy distribution of high-Andean treeline forests has provoked discussion about the relative importance of anthropogenic and climatic causes of this pattern, both of which vary with topography. We aimed to understand the topographic controls on the distribution of *Polylepis subsericans* treeline forests in the Andes of southern Peru, and the changes in these controls along an elevational gradient. We mapped *Polylepis* forests in the Cordillera Urubamba, Cusco, using high-resolution aerial images and related forest cover to topographic variables extracted from a digital terrain model (30-m resolution). The variables were selected based on their expected biological relevance for tree growth at high elevations. We constructed logistic regression models of forest cover, separately for each of five 100-m elevational belts. To deal with spatial autocorrelation, models were based on randomized 10% subsampling of the data with 1000 repetitions. The results suggest a consistent shift in topographic preference with elevation, with forests at lower elevations showing a preference for topographically protected sites near rivers and forests at higher elevations being increasingly restricted to north-facing and well-drained sites. Our study offers the first indication of the ability of Andean treeline forests to benefit from the topographic heterogeneity of the high-Andes. Providing that dispersal and establishment are possible, local relocation between microsites could help these forests to persist regionally in spite of changing climatic conditions.

Keywords: topography; *Polylepis*; Andes; treeline; Peru; digital terrain model; topographic wetness index; morphometric protection index; exposure; exposition

1. Introduction

Andean *Polylepis* forests, like other high mountain forests across the globe and especially in tropical regions, show patchy distributions. *Polylepis* (Rosaceae) is an endemic tree genus in the high Andes, forming upper high-elevation treelines often disconnected from the lower-elevation cloud-forest treelines by puna grasslands [1,2]. These high-elevation forests are an essential element of the Andean landscape, harboring a significant part of high-mountain biodiversity [3]. Their patchy distribution, though probably of anthropogenic origin, may also reflect the habitat suitability of topographic positions varying in, e.g., moisture or thermal regimes, as well as in land-use intensity. However, the relationship of *Polylepis* forest cover with topography has not been quantified so far. With the predicted increase of drought in the Andes, caused by the current anthropogenic climate warming, *Polylepis* forests may be increasingly restricted to moist microsites. On the other hand,

warming may allow future growth outside thermally favored positions. Whether *Polylepis* forests are currently restricted to wet or warm sites or whether their current distribution is predominantly anthropogenically determined remains a disputed question, e.g., [2,4]. Better understanding of the environmental niche preferences of *Polylepis* species is crucial, however, for identifying potential climatic resilience areas for these forests and forest-based biodiversity.

It has been shown that environmental factors strongly constrain tree growth at high elevations, with growing-season warmth being the main limitation at the global scale [5]. A lack of warmth likely also limits *Polylepis*, although this genus has been found at somewhat lower mean growing-season temperatures than the global average [6]. Also, other abiotic factors such as annual precipitation, soil texture, and hydrological conditions have been shown to play a role in determining *Polylepis* forest distributions in the Andean landscape [7–9].

Pollen records indicate that *Polylepis* forest cover has strongly fluctuated in the past, with the highest forest cover in warm and wet periods and almost no high-elevation forest cover in cold and dry periods [10,11]. Additionally, humans have inhabited the Andes for millennia, collecting firewood and using fire to turn natural grasslands into man-made pastures suitable for domestic animals [1,12]. Therefore, the more recent pollen records are more difficult to interpret in terms of climatic conditions. Animal husbandry in particular may have strongly contributed to the current patchy distribution of *Polylepis* forests by direct negative fire and grazing effects on regenerating trees and by modifying the structure of the grass vegetation. The short grazed pastures possibly have lower facilitative effects on seedling establishment outside of forest edges than natural tall tussocks [13], thus preventing tree colonization.

In mountain areas, topography strongly affects the distribution of solar energy and drainage patterns and consequently air and soil temperatures, soil water availability, and soil texture [14,15]. Therefore, terrain features derived from digital terrain models (DTMs) can be used as a proxy for biologically relevant environmental variables like local temperature and humidity. Several studies have been carried out modelling mountain vegetation as a function of DTM-derived environmental indicators [16–18]. However, only few have focused on tropical mountains [7,19,20]. One of the advantages of using DTM-based terrain features and indices is the easy and free access to data covering the whole world. The disadvantage has been the limited resolution of these data (Shuttle Radar Topography Mission, SRTM of 90-m resolution), but this limitation is reduced with the release of new products like the Aster Global Digital Elevation Model (30-m resolution) and TanDEM-X (evaluation status, 8-m resolution). Previous attempts to apply DTM-based approaches to relate high-Andean forest distribution to topography have shown that forests avoid eastern slopes probably due to a strong morning solar radiation, which is particularly detrimental for seedlings [13,20,21]. On the other hand, *Polylepis* forests have been observed to grow taller on eastern slopes because the increased solar radiation may increase overall temperatures [9]. There is also evidence for forests avoiding sites with topography-related water logging and/or cold-air ponding [20], and occurring preferentially at sites of inaccessible topography, where fires are not frequent [7,22]. Abiotic factors constraining *Polylepis* tree growth seem to vary between the species and geographical regions, with solar radiation being an important factor in humid and cloudy regions whereas water availability becomes more relevant in dry regions [9].

With the aim of better understanding the topographic controls on *Polylepis* forest distribution in a semi-arid mountain range in the high Andes of southern Peru, we studied how the distribution of forest patches of *P. subsericans* depend on topographic position. Our specific aims were to find out (1) the best topographic predictors of *P. subsericans* forest cover; and (2) since abiotic conditions strongly change with elevation, whether the importance of different predictors also changes with elevation. We hypothesized that (1) the best predictors would be moisture and temperature-related topographic variables; (2) topographic controls would generally become stronger with elevation due to stronger land-use influences at lower elevations; and (3) forest cover would be associated with high-moisture sites at low elevations while thermal benefits should become increasingly important at high elevations.

Better understanding the environmental niche preferences of this species is particularly important to assess its potential for regional persistence under a changing future climate.

2. Materials and Methods

2.1. Study Area

The study area was located on the south-facing side of the Cordillera Urubamba (part of the Vilcanota mountain chain in southeast Peru) from the Ollanta Valley to the Cancha Cancha Valley between 4300 m and 4800 m elevation ($13^{\circ}08'–13^{\circ}18' S$, $71^{\circ}59'–72^{\circ}16' W$) (Figure 1). The study area was selected based on the availability of high-resolution and cloud-free remote sensing data and extensive field surveys for ground truthing carried out in the area since 2006 [23]. The climate in the study area is a semi-arid tropical alpine climate, with mean annual growing season air and soil temperatures at 4450 m of $3.9^{\circ}C$ and $4.6^{\circ}C$, respectively [6], and with low annual but high diurnal variations in temperature [15]. There is a pronounced wet season from October to March. The study area is topographically complex, with several steep north-south directed U-shaped glacial valleys and smaller ravines connected to them. The highest snow peak of the Cordillera, Nevado Chicon, reaches 5400 m in elevation. Soil erosion and landslides are frequent at high elevations.

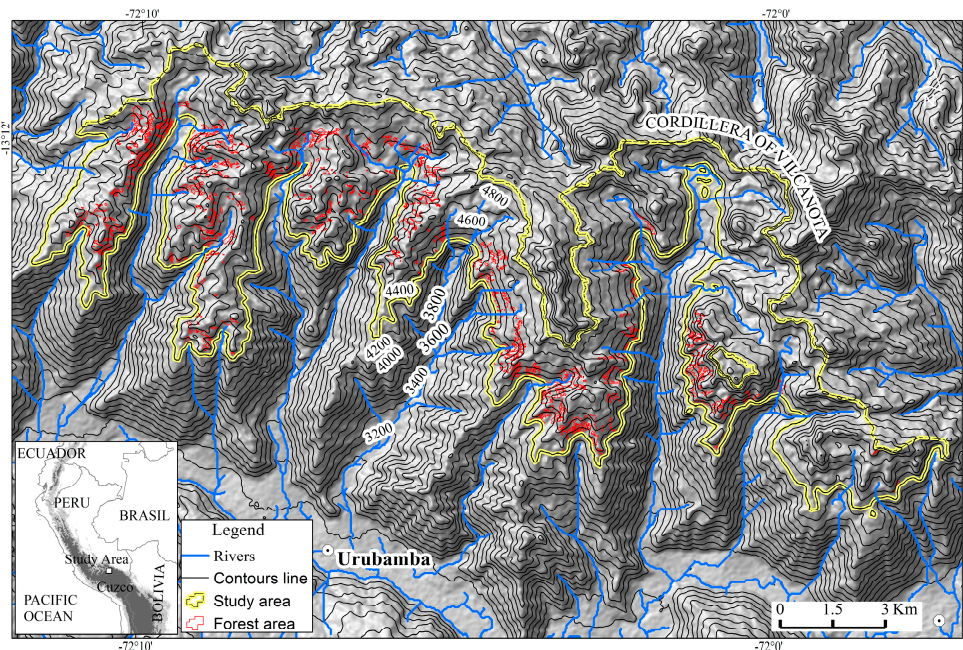


Figure 1. Map of the study area (yellow outline) between 4300 and 4800 m a.s.l. on the southern flanks of the Cordillera Urubamba, Cusco. The location of *Polylepis subsericans* forest stands is shown by red outlines. Rivers are shown by blue lines.

The vegetation of the study area consists of alpine humid puna vegetation dominated by tussock grasses (*Deyeuxia* spp., *Festuca* spp.) and various shrub and herb species [22]. Forests of *Polylepis racemosa* R. & P. are found between 3800 m and 4200 m, and of *P. subsericans* J.F. Macbr from 4200 m up to 4950 m. These two species do not grow intermixed, but are found in separated stands located only a few tens of meters apart from each other. To ensure that we included only pure *P. subsericans* stands to our study, we set the lower elevational limit of the study area to 4300 m. The upper limit was set to 4800 m, because above that only few small patches or single trees can be found (covering an area of 0.03 km^2 , corresponding to 0.27% of the landscape at that elevation).

The area has been influenced by humans for millennia due to its proximity to the ancient centers of human settlements in the Urubamba Valley [24,25]. During the last decades, human population has

strongly increased at low elevations (<3800 m), especially in the valley bottom of the Urubamba River, but the rural areas at high elevations have remained sparsely populated. Only few villages are found at elevations above 3800 m.

2.2. Data Acquisition and Processing

We mapped *Polylepis* forest patches in the study region using an aerial image with a pixel size of 2 m × 2 m (Bing Maps web mapping service, image of the year 2010). The image was in general largely cloud free. Parts that were covered by clouds were mapped using a Quickbird satellite image with a pixel size of 2.4 m × 2.4 m (Google Earth, image of August 2012, accessed on September 2013). An extensive ground truthing was carried out during several field excursions between 2006 and 2012. The images allowed an accurate digitization of *Polylepis* forest stands in a GIS platform, resulting in much higher resolution data than in previous studies examining associations between topography and high-Andean forest distribution [7,19,20]. The digitized *Polylepis* forest polygons were overlaid with Aster Global DTM (version 2, with 8 m vertical resolution and 30 m × 30 m pixel size), and each 30 × 30 m pixel that was crossed by a *Polylepis* polygon was classified as forest (presence) and the rest as non-forest (absence) (Figure 1).

We selected eleven topographic features and indices based on their expected importance for tree growth and seedling establishment at tropical high elevations, of which we used six weakly correlated ones (Spearman's rank correlation coefficient <0.5) for the analyses. These indices expressed, for example, average and extreme temperature conditions, soil hydrological condition, solar radiation, and the risk of landslides (Table 1). Topographic features and indices were calculated with algorithms available in SAGA GIS 4.1 (General Public License) and ArcGIS 10.4 (Environmental Systems Research Institute, CA, USA). Mathematical formulae of the terrain indices are given in Hengl and Reuter (2008) [26].

Table 1. The selected topographic features and indices derived from the digital terrain model (DTM) of spatial resolution 30 m × 30 m, their descriptions, and ecological importance. The weakly correlated variables (Spearman's rank correlation coefficient <0.5) included in the GLMs are marked with a hash (#).

Acronym	Variable	Description	Ecological Importance
# North	Northern exposure	Relation to north (1 to −1)	Summer vs. winter solar radiation
# East	Eastern exposure	Relation to east (1 to −1)	Morning vs. afternoon solar radiation
Sl	Slope	Slope angle in degrees	Solar radiation, terrain stability, soil moisture
Pro	Profile curvature	Terrain surface curvature described parallel to slope steepness (convex, linear or concave)	Soil moisture and erosion
Pla	Planar curvature	Terrain surface curvature described perpendicularly to the slope steepness (convex, linear or concave).	Solar radiation, wind exposure, soil erosion
Convg	Convergenceindex	Overland flow convergence and divergence	Soil hydrological condition and soil erosion
# Twi	Topographic wetness index	Soil moisture and surface saturation index, calculation based on the control of local topography on hydrological processes, $(\ln(A_s/\tan\beta))^*$	Soil moisture, water logging, cold air accumulation
# Srd	Annual solar radiation hours	Duration of potential annual direct incoming solar radiation	Solar radiation, annual temperature sum
# Ofd	Overland flow distance	Overland distance to the nearest river measured using the DTM-based potential river network	Soil hydrological conditions, topographic protection
Vfd	Vertical flow distance	Vertical distance to the nearest river measured using the DTM-based potential river network	Soil hydrological conditions
# Mpi	Morphometric protection index	Topographic sheltering, calculation based on pixel values within 300 m radius	Sheltering, solar radiation, temperature extremes

* A_s = contributing area, derived with $D\infty$ algorithm (Tarboton 1997), β = local slope angle.

2.3. Analyses

To study the effects of topographic variables on forest occurrence and the changes in these effects with elevation, we applied generalized linear models (GLMs) for the logistic response of forest occurrence (presence/absence) separately in five 100-m elevational belts (Table 2). Species distribution data typically contain spatial dependence or spatial autocorrelation. This is particularly true with intensively sampled data such as continuous spatial grids [27,28]. A common method to deal with autocorrelation is to determine the distance beyond which autocorrelation becomes minimal and to use a subsample of the data respecting this distance [29]. In our case, due to the patchy distribution of the forest cover, this distance was about 1000 m, i.e., 33 pixels. Respecting this distance would imply that lot of potentially valuable information is not used, which is especially problematic if, as in our case, many forest patches are small and might be missed completely by a subsampling scheme. Therefore, to reduce, though not eliminate, autocorrelation without losing any information and without running the risk of missing the small forest patches, we carried out a repeated stratified subsampling of the data, randomly selecting 10% of presence data and 10% of absence data. Results are based on means of the estimates, z -values (slope estimate divided by standard error) and p -values of 1000 model runs. Because some autocorrelation remained after subsampling, we interpret the results based on the z -values, with statistical significance being an indication of the relative strength of the effects rather than a valid test statistic.

3. Results

Polylepis subsericans forests covered a total of 12.4% (11.8 km²) of the landscape in the study area. This corresponds to 13,150 out of 106,028 30 × 30-m pixels. Forest cover was highest at 4400–4500 m (17.1%) and decreased to 2.5% at 4700–4800 m (Table 2).

Table 2. *Polylepis subsericans* forest cover in five elevational belts in the study area of a 95-km² in the Andes of Southern Peru. The area is calculated based on 30 m × 30 m pixels assigned as ‘forest’.

Elevation (m)	<i>Polylepis</i> Forest Cover (km ²)	Total Landscape (km ²)	<i>Polylepis</i> Forest Cover (%)
4300–4400	2.79	18.16	15.34
4400–4500	3.57	20.91	17.08
4500–4600	3.26	21.42	15.22
4600–4700	1.84	19.86	9.29
4700–4800	0.37	15.07	2.47
Total	11.84	95.43	12.40

At low elevations, forests were located near the rivers and in topographically protected sites (Table 3, Figure 2). The importance of topographic protection was indicated by the strong positive contribution of morphometric protection index (Mpi) to the models at the three lowest elevations (Table 3). The change with elevation from sites near rivers to sites further from rivers or independent of rivers was reflected in the negative effect of overland flow distance (Ofd) at the two lowest elevations and positive or no effect at higher elevations. There was a shift from west-facing slopes at middle elevations to north-facing slopes at the highest two elevations (Figure 2, Table 3). The increased preference for north-facing slopes was reflected in the changed sign of the effect of northern exposure from negative at the two lowest to positive at the two highest elevations. There was also a shift with elevation to well-drained sites, which was reflected in the negative effect of topographic wetness index (Twi) at the two highest elevations (Table 3).

Table 3. Statistics of the logistic regression models by elevation belts divided in 100-m intervals. The analyses were carried out with a randomized subsampling of the data with 1000 repetitions, including 10% of presence and 10% of absence data in each model run. Mean estimates and their standard errors, mean standard errors, mean z-values and their standard errors, and mean *p*-values are reported. North = northern exposure, East = eastern exposure, Twi = topographic wetness index, Srd = annual solar radiation hours, Ofd = overland flow distance, Mpi = morphometric protection index.

4300–4400 m	Mean Estimate ± S.E.	Mean Std Error	Mean z-Value ± S.E.	Mean Probability
(Intercept)	−1.88 ± 0.001	0.07	−26.35 ± 0.008	0.000
East	−0.01 ± 0.002	0.07	−0.20 ± 0.028	0.526
North	−0.19 ± 0.002	0.07	−2.78 ± 0.029	0.041
Twi	−0.02 ± 0.002	0.07	−0.37 ± 0.028	0.512
Ofd	−0.30 ± 0.003	0.09	−3.44 ± 0.028	0.010
Srd	−0.10 ± 0.003	0.10	−0.99 ± 0.030	0.366
Mpi	0.46 ± 0.003	0.09	4.94 ± 0.027	0.000
4400–4500 m	Mean Estimate ± S.E.	Mean Std Error	Mean z-Value ± S.E.	Mean Probability
(Intercept)	−1.71 ± 0.001	0.06	−27.90 ± 0.004	0.000
East	−0.12 ± 0.002	0.06	−1.98 ± 0.028	0.130
North	−0.31 ± 0.002	0.06	−5.09 ± 0.028	0.000
Twi	−0.14 ± 0.002	0.06	−2.30 ± 0.027	0.081
Ofd	−0.31 ± 0.002	0.07	−4.37 ± 0.026	0.001
Srd	0.23 ± 0.003	0.08	2.77 ± 0.031	0.046
Mpi	0.57 ± 0.002	0.08	6.94 ± 0.027	0.000
4500–4600 m	Mean Estimate ± S.E.	Mean Std Error	Mean z-Value ± S.E.	Mean Probability
(Intercept)	−1.82 ± 0.001	0.06	−29.27 ± 0.005	0.000
East	−0.29 ± 0.002	0.06	−4.64 ± 0.029	0.001
North	−0.07 ± 0.002	0.06	−1.24 ± 0.028	0.310
Twi	−0.10 ± 0.002	0.06	−1.61 ± 0.029	0.216
Ofd	0.08 ± 0.002	0.06	1.45 ± 0.030	0.252
Srd	0.15 ± 0.003	0.09	1.76 ± 0.031	0.189
Mpi	0.49 ± 0.003	0.09	5.56 ± 0.029	0.000
4600–4700 m	Mean Estimate ± S.E.	Mean Std Error	Mean z-Value ± S.E.	Mean Probability
(Intercept)	−2.61 ± 0.002	0.10	−27.26 ± 0.017	0.000
East	−0.47 ± 0.003	0.09	−5.44 ± 0.029	0.001
North	0.38 ± 0.002	0.08	4.85 ± 0.025	0.000
Twi	−0.55 ± 0.003	0.10	−5.23 ± 0.024	0.000
Ofd	0.25 ± 0.002	0.07	3.33 ± 0.030	0.015
Srd	0.29 ± 0.004	0.12	2.38 ± 0.028	0.073
Mpi	0.20 ± 0.003	0.12	1.63 ± 0.029	0.211
4700–4800 m	Mean Estimate ± S.E.	Mean Std Error	Mean z-Value ± S.E.	Mean Probability
(Intercept)	−4.84 ± 0.008	0.33	−14.64 ± 0.032	0.000
East	−0.43 ± 0.008	0.21	−1.92 ± 0.031	0.155
North	0.89 ± 0.005	0.21	4.22 ± 0.012	0.000
Twi	−1.32 ± 0.009	0.31	−4.18 ± 0.016	0.000
Ofd	0.10 ± 0.005	0.18	0.62 ± 0.027	0.471
Srd	0.36 ± 0.008	0.29	1.21 ± 0.026	0.320
Mpi	0.16 ± 0.008	0.28	0.57 ± 0.028	0.470

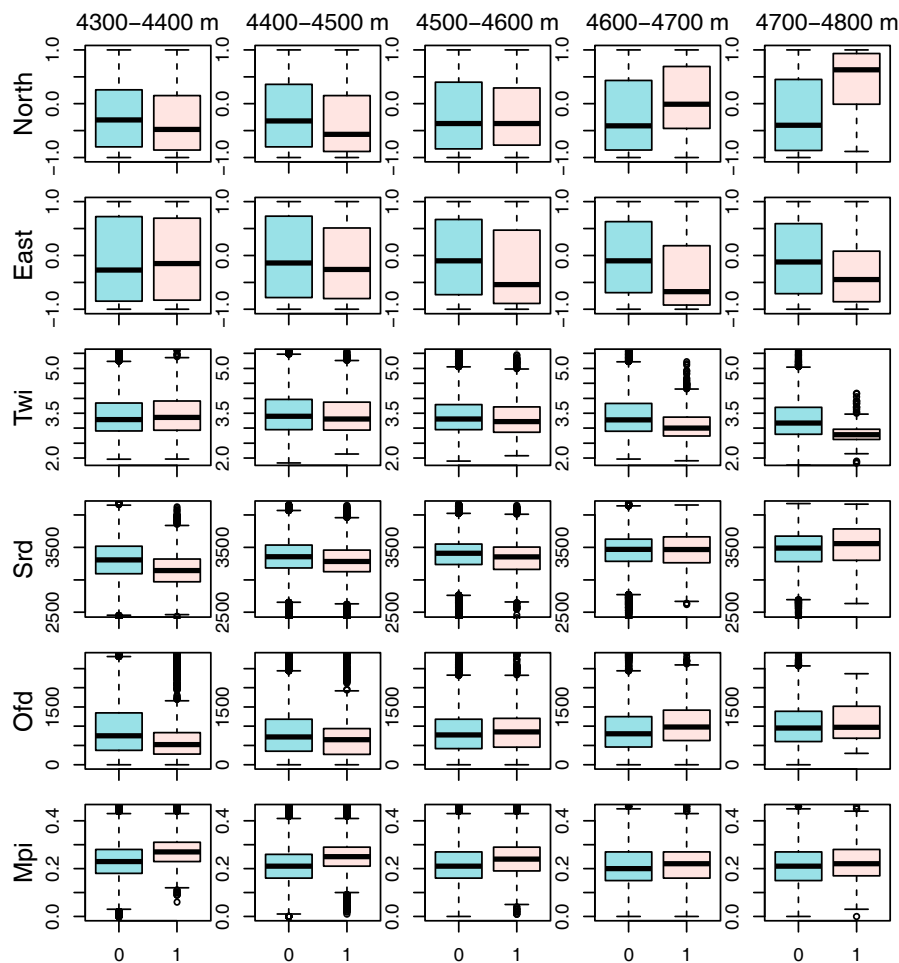


Figure 2. Boxplots of topographic variables explaining *Polylepis subsericans* forest stand distribution in the high Andes of southern Peru in five 100-m elevational bands. Light blue boxes: non-*Polylepis* (0), pink boxes: *Polylepis* (1). North = northern exposure, East = eastern exposure, Twi = topographic wetness index, Srd = annual solar radiation hours, Ofd = overland flow distance, Mpi = morphometric protection index.

4. Discussion

The current *Polylepis* forest distribution in the Andes is highly fragmented, with both natural and anthropogenic causes [1,2,4,6]. The aim of this study was to find out whether the forest stands of the treeline-forming species *Polylepis subsericans* are found at specific topographic positions, and whether their potential associations with topography change with elevation. Environmental constraints on the growth of high-elevation trees are generally thought to increase with elevation as a result of increasing environmental harshness [30]. We therefore expected shifts in the topographic niche space of *P. subsericans* with elevation. The results of our study suggest topographic constraints on the distribution of *Polylepis* forests and a consistent shift in the preference with elevation.

4.1. Topographic Preferences

At the macro scale, *Polylepis* forests have been found to prefer south-facing slopes in the central and southern Andes, probably because these sites are usually more humid [9]. In this study, we explored the variation within a south-facing slope in more detail. In the lower elevation belts, *Polylepis* was more often found on south-facing slopes and in topographically protected positions, which reflects a preference for moister sites. However, we found an increasing preference for north-facing slopes with increasing elevation. This suggests that near the upper treeline, forest distribution becomes restricted

to warmer sites. This is line with global observations that low temperatures set critical limits to tree growth at high-elevation treelines [5,30].

Morphometric protection was an important predictor especially at the lower elevations. The positive effects of sheltering can involve many factors, including wind and sky exposure. The latter determines the likeliness of night-time freezing and exposure to solar radiation. In spite of being located within the tropics, our study area has a colder season coinciding with the southern hemisphere winter, when night temperatures frequently fall below 0 °C in this part of the high Andes [6,15,31]. *Polylepis* trees can tolerate or avoid freezing for short periods with different physiological adjustments [32,33], but long-term freezing is critical to tree growth. Additionally, seedlings are particularly vulnerable to dehydration and photoinhibition caused by strong radiation especially in the mornings, when soil temperatures are still low after cold nights and root water uptake is hindered, and photosynthesis not yet fully functional [34,35]. At the upper elevations, the positive effects of morphometric protection may be overridden by the positive effect of high insolation, which may explain why there was little to no effect of protection at the two highest elevations.

Positions of forest stands shifted towards drier soils than the landscape in general (negative relationship with topographic wetness index) with increasing elevation. This may indicate the avoidance of water-logged soils located in wide valley bottoms, which are more frequent at high than lower elevations due to the specific topography of the area (steep glacial U-valleys at lower elevations and more gentle slopes and wide valley bottoms at higher elevations). *Polylepis* and other high-Andean forests are generally observed to avoid wide valley bottoms, which is probably due also to the night-time accumulation of cold air masses in such valleys [15,20,36].

4.2. Factors other than Topography Determining *Polylepis* Forest Distribution

Humans have modified the Andean landscape for millennia and have strongly affected vegetation distribution patterns and structure [1,24,25]. This is particularly true for *Polylepis* forests and poses a challenge for detecting natural environmental preferences of the forests and for modelling forest distribution. The current forest locations can be biased towards sites that are the most inaccessible to humans, human-induced fires, and animal grazing, or they may have the highest capacity for recovery after human disturbance [2,7,22]. Both accessibility and recovery capacity are topography dependent, but only the latter is related to the ecology of the trees, whereas the former is more related to the ecology of humans and livestock. The mentioned bias is likely strongest at lower elevation due to higher anthropogenic influence [23]. However, these highly impacted areas were excluded from this study, as we focused only on treeline-forming *P. subsericans* stands, which are mostly of difficult access. Nevertheless, even these sites have suffered from some degree of human impact, which has affected the naturalness of the current forest stand distribution [22].

Generally weak, albeit notable relationships between topography and *Polylepis* forest distribution may also be due to the data resolution relative to the scale of the studied forest patches. The current freely available terrain data at 30 × 30-m resolution cannot yet capture the finest micro-topographic variations, but higher-resolution DTMs are being evaluated and should soon become available globally (e.g., TanDEM-X, at 8-m resolution, from the German Space Agency). As forest cover can already be mapped at the 2-m resolution, these new DTMs will allow a more detailed analysis of high-Andean forests, including small forest patches that may be associated with topographical features smaller than 30 m. This will be an important further advance, as landscape patterns are very heterogeneous in the Andes and small-scale topographic features can be crucially important for local forest establishment and persistence.

5. Conclusions

Our data show that the relationship between *Polylepis* forest distribution and topography changes with elevation. The shift to north-exposed sites agrees with our hypothesis that the preference of forests for warm sites should be stronger at higher elevations. Evidence for the expected preference

for humid sites was weaker and was only shown indirectly through a preference for south-facing and topographically protected sites at low elevations. Weak relationships with topography may be due to the confounding effects of human land use and to the coarse scale of the digital elevation model relative to the fine patterns observed in forest distributions in this rough mountain terrain. Nevertheless, the results of this study are the first indications of the ability of an Andean treeline forest species to benefit from the topoclimatic heterogeneity of the high Andes in order to maintain forests across varying climatic conditions. This can be an advantage in a changing future climate, if forests are able to establish in nearby new suitable sites. On the other hand, currently suitable sites may not be suitable any more in the future, which will challenge forest persistence. Information on the overlap between the current and future suitable sites and the dispersal and establishment abilities of the species are required to be able to predict the future of these forests and to locate potential climatic resilience areas for these forests and the unique biodiversity associated to them.

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