

## Accessibility predicts structural variation of Andean *Polylepis* forests

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**Abstract** High Andean mountain forests, formed almost purely by trees of the genus *Polylepis*, occur nowadays as scattered remnant patches of a more continuous past distribution. Apparently, the destruction of *Polylepis* forests has mainly been caused by millennia of human disturbance, although forest distribution may also have fluctuated according to prevailing climatic conditions. Nowadays, the remaining *Polylepis* forest stands are still threatened by anthropogenic disturbance, which gradually degrades the forests. The aim of our study was to test if the structural variation of *Polylepis* forest patches, as an indication of forest degradation, can be predicted by accessibility to humans. The study was carried out in the Cordilleras Vilcanota and Vilcabamba, Cuzco, Peru. We used indices of forest biomass and proportion of vegetative regeneration as forest structural variables. First we examined the dependence of these variables on elevation with linear regressions. We did this separately for different *Polylepis* species and combining the species within humid and dry areas. Thereafter, we used the residual forest structural variation to assess possible relationships with accessibility, quantified as geographical distance to the nearest village, road or market centre. We found several significant relationships between the structural variables and accessibility, which may reflect different landscape related preferences in forest use. The results suggest accessibility can be used for rapid spatial prediction of *Polylepis* forest degradation, which facilitates identifying *Polylepis* forests that are potentially the most degraded and therefore in the most urgent need of restoration or conservation activities.

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## Introduction

Trees of the genus *Polylepis* (Rosaceae) typically form monospecific stands in the Andean highlands above 3300 m. In the central Andes, *Polylepis* can reach up to 4800–5200 m, thereby forming the highest treelines in the world. *Polylepis* forests can be regarded as a key ecosystem in the high Andes and of outstanding importance for biodiversity, because they provide irreplaceable habitat for several endemic plant and animal species (Fjeldså 1993; Servat et al. 2002; Lloyd and Marsden 2008). Furthermore, they have an important role in water circulation and prevention of soil erosion (Fjeldså and Kessler 1996; Fjeldså 2002) and represent a potential carbon sink in the otherwise treeless landscape (Hoch and Körner 2005). *Polylepis* forests also provide an important source of timber and firewood for local people (Lazcano and Espinoza 2001; Aucca and Ramsay 2005; Hagaman 2006; Jameson et al. 2007).

The high Andes have been subject to intensive human land use for millennia (Chepstow-Lusty et al. 1996; Chepstow-Lusty and Winfield 2000), and as a consequence, *Polylepis* forests have been strongly decimated and fragmented through timber extraction, anthropogenic fires, and grazing by domestic animals (Ellenberg 1958; 1979; Laegaard 1992; Kessler 1995, 2000, 2002; Purcell and Brelsford 2004; Coblenz and Keating 2008). This human influence has been especially strong in the inner parts of the Andean mountain ranges that have been densely and permanently populated for thousands of years and are nowadays even more densely populated, in comparison to the sparsely populated Amazonian side of the Andes that is still partly inaccessible (Dobyns 1966; Kessler and Driesch 1993; Etter and Villa 2000). Human impact may not be the only cause for the current fragmented distribution of *Polylepis* forests. Palaeoecological studies have also shown that the extent of *Polylepis* forests has strongly fluctuated already before the arrival of humans in South America (>12,000 years ago), suggesting that *Polylepis* forests may partly be naturally fragmented due to climatic factors (Gosling et al. 2009). In any case, *Polylepis* forests are counted among the most endangered tropical and subtropical mountain forest ecosystems in the world (UNEP-WCMC 2004) and the majority of the ca. 30 species of the genus are classified as vulnerable (IUCN 2010).

Currently, one of the major threats for remaining *Polylepis* forest stands seems to be gradual habitat degradation (Renison et al. 2006, 2010, 2011; Jameson et al. 2007; Cingolani et al. 2008). Complete disappearance of the remaining forest patches also occurs, but it seems to be a smaller problem (Jameson et al. 2007). The degradation is caused especially by livestock grazing as well as wood harvesting for timber and fire wood (Renison and Cingolani 1998; Renison et al. 2004). Grazing animals affect *Polylepis* forest regeneration so that regeneration in general becomes more difficult and root suckers, being more resistant to physical damage than seedlings, become the dominant form of regeneration. Excessive grazing and wood harvesting inevitably lead to a decrease in forest biomass. This degradation has also been documented to manifest itself as a lack or diminution of certain more heavily used age and/or size cohorts (Renison et al. 2011) and overall decrease in canopy density (Jameson et al. 2007).

Our study is based on an assumption that forest degradation manifests itself as a decrease in above-ground biomass and changes in forest regeneration patterns. However,

these same changes can also be a consequence of natural factors, such as forest disturbance, diseases, herbivory or low temperature. Of these, temperature is a special case as it is by necessity closely linked with elevation above sea level. It is a general rule for mountain forests that above-ground biomass, and thereby canopy height and tree diameter decrease with elevation (e.g. Stadtmüller 1987; Young 1993; Rada et al. 1996; García-Núñez et al. 2004; Hoch and Körner 2005; Kessler et al. 2007; Hertel and Wesche 2008). There is also evidence of proportional increase in vegetative regeneration relative to sexual reproduction with elevation (Cuevas 2000; Germino and Smith 2002; Cierjacks et al. 2007a, b, c; Hertel and Wesche 2008).

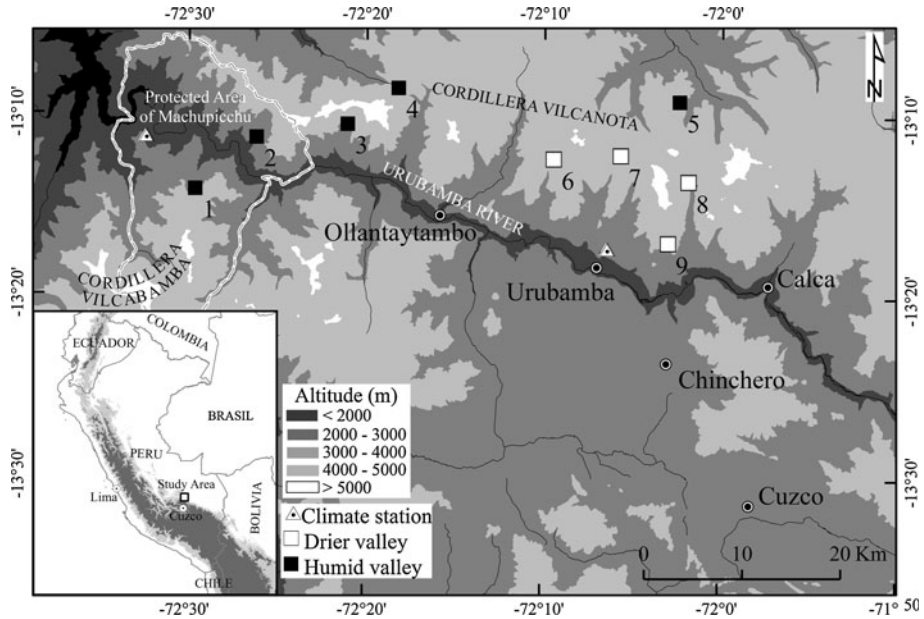
We assume that a statistical effect of elevation on above-ground biomass and relative abundance of vegetative regeneration can be taken as a biological necessity. Therefore, interesting variation in these features of *Polylepis* forests should be sought only in residuals after the effect of elevation has been taken into account. We are specifically interested in seeing if the residual variation can be explained by human disturbance. The amount of human disturbance in a forest patch is difficult to measure directly and therefore we use accessibility as its indicator. We hypothesize that accessibility is negatively related to above-ground biomass and positively related to the proportion of vegetative regeneration. We test this hypothesis by correlating indicators of *Polylepis* forest biomass and regeneration type with measures of geographical distance to road or human settlement. As human influence has historically been stronger in the central, drier parts of the Andes, where the centers of pre-Hispanic cultures were located and which are also nowadays the most densely populated areas, we hypothesize that structural variation of *Polylepis* forests is currently more strongly associated with human influence in dry areas than in more distant and inaccessible humid areas on the Amazonian side of the Andes.

The degradation of *Polylepis* forests can be counteracted by improving legislation and increasing public awareness. However, rapidly increasing forest degradation and fragmentation needs explicit spatial identification of potentially the most endangered and therefore critical areas for conservation. As resources for field inventories to identify the most critical *Polylepis* forest patches for conservation are necessarily limited, simple geographical measures would be useful for making spatial predictions of the degree of *Polylepis* forest degradation. Our study tests if indices of accessibility can provide such a measure.

## Methods

### Study area and species

We carried out our field work in the Cordilleras Vilcanota and Vilcabamba in Urubamba, Cuzco, south-eastern Peru ( $13^{\circ}07'–13^{\circ}17'$  S and  $72^{\circ}02'–72^{\circ}29'$  W) in 2006 (Fig. 1). The climate of the region varies from semi-humid to semi-dry with a clear wet season (October–March) and very strong diurnal temperature fluctuations especially in the dry season. The complex orography of the region directs clouds to the area from the north-west. When the clouds hit high Andean ridges, they discharge much of their water as rain. This process creates strong geographical gradients in precipitation so that areas behind the high ridges remain in the rain shadow. This situation is exemplified in our study area by the contrasting precipitation records at the climate stations of Urubamba (2863 m) with 454 mm mean annual precipitation and Wiñaywayna, protected area of Machupicchu (2800 m), with 1606 mm (records of former INRENA, National Institute of Natural



**Fig. 1** Map of the study area with nine studied valleys. Valleys 1–5 are in humid and 6–9 in dry climate

Resources of Peru and SENAMHI, National Service of Meteorology and Hydrology of Peru). Based on this gradient and the geographical variation in *Polylepis* species composition (Kessler 1995; Fjeldså and Kessler 1996), we separated the studied valleys as dry and humid ones as shown in Fig. 1. Drier valleys correspond to relatively densely inhabited inner parts of the Andes and humid valleys to less populous Amazonian side of the Andes.

Steep topography and remarkable elevational differences of the region have created diverse climatic conditions, which have enabled the evolution, diversification and specialization of many plant and animal groups, including *Polylepis* (Fjeldså 1992; Fjeldså and Kessler 1996). In our study area, at least five *Polylepis* species occur in close proximity to each other, representing the highest concentration of species of the genus found anywhere (Fjeldså and Kessler 1996). Species are segregated by elevation and humidity, and almost always form monospecific stands: *P. pauta*, *P. sericea* and *P. pepeii* in humid areas, and *P. racemosa* and *P. subsericans* in drier areas (Kessler 1995; Fjeldså and Kessler 1996).

#### Data collection

Our study area comprised nine different valleys at elevations between 3070 and 4550 m (Fig. 1). Five of the valleys were located in relatively humid and four in dry areas. In each valley we selected one to four forest patches for further study. The number of selected forest patches in each valley depended on the total area of the forest cover and the number of species in the valley. The forest patches were selected from different elevations to cover as well as possible the whole altitudinal range of each species in the study area. The altitudinal difference between two forest patches of the same species in the same valley was at least 100 m. Within each forest patch, we established one study plot of 10 m × 10 m. The plots were located in an accessible point in the middle of the

forest patch, at least 25 m from the edge so as to give—according to a subjective assessment—as representative sample as possible of the structure of the forest patch in general. In three valleys, we established two plots within the same forest patch with only small elevational difference between them, because of the problems to find accessible forest patches far enough from each other. In these cases, we used average values of measured forest characters of the two plots to avoid pseudo-replication. After the averaging, we had in total 13 forest patches in humid areas and 11 in dry areas of which four were formed by *P. pautta*, four by *P. sericea*, five by *P. pepeii*, six by *P. racemosa* and five by *P. subsericans*.

In each plot, we measured the circumference and visually estimated the height of all *Polylepis* trees ( $\geq 10$  cm of circumference at breast height). We also counted the number of all smaller individuals. Among them, we separated vegetatively generated root suckers from sexually produced individuals by inspecting if the individual sprouted from the roots or branches of a bigger tree. Root suckers were counted as separate individuals when clearly rooted fine roots were observed between the sprouts.

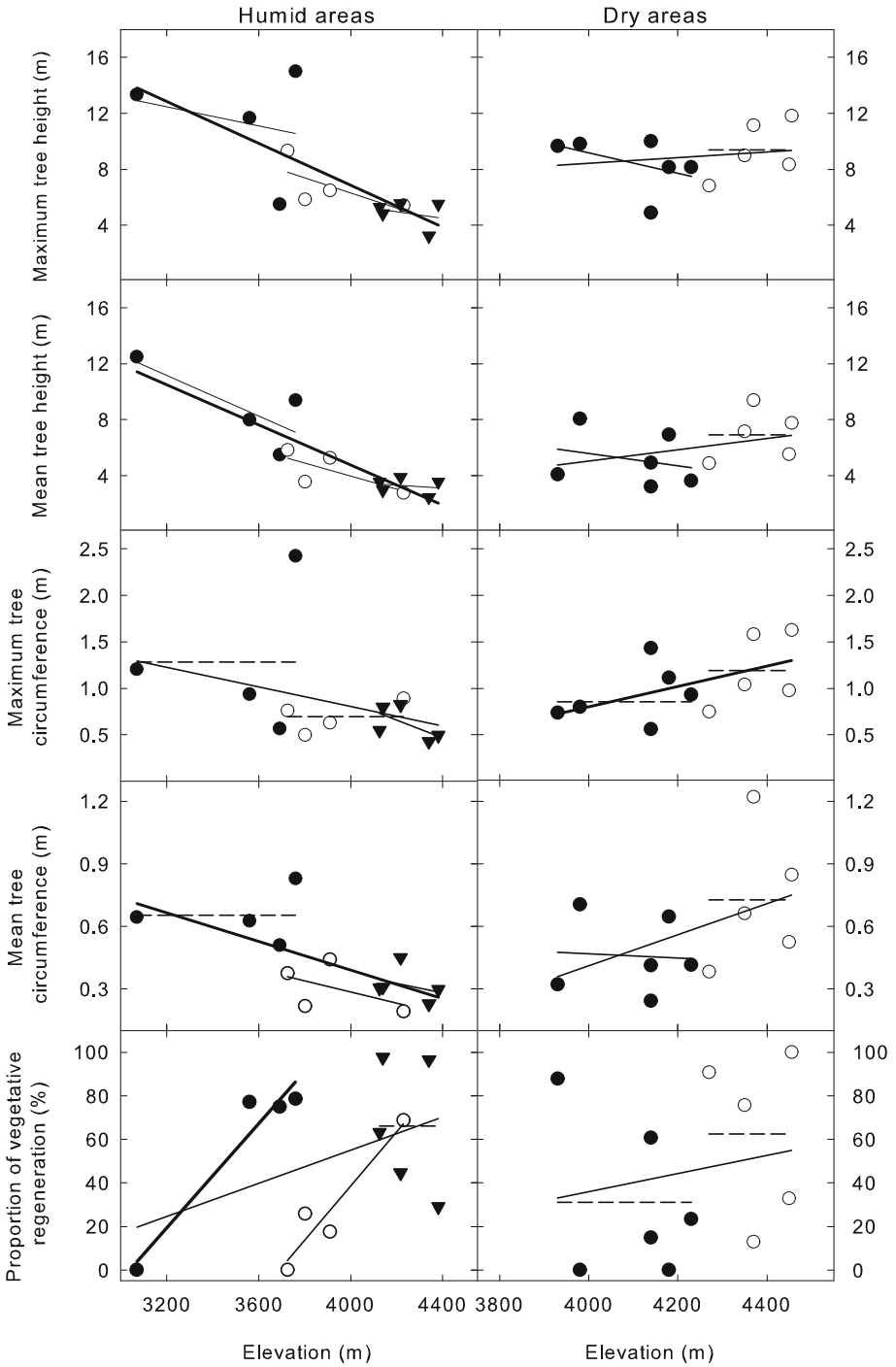
One forest patch always included just one *Polylepis* species and in 16 out of the 24 studied forest patches the given *Polylepis* species was the only observed tree species. In the mixed patches, *Polylepis* was always the most abundant tree species.

#### Forest structural variables

One of our aims in the field observations was to obtain measures that would give us information about the amount of *Polylepis* forest above-ground biomass, because a general effect of excessive forest use is reduction in biomass. For this end, we measured mean and maximum *Polylepis* tree height and circumference per plot. Maximum tree height and circumference were defined as average values of the three highest or thickest trees in a plot. Basal area per plot was not applicable as the given *Polylepis* species was not the only tree species in one third of the plots. Another forest feature that is often observed to be affected by human activities is the proportion of vegetative regeneration. As measures of this feature we used the percentage of root suckers of the combined number of seedlings, saplings and root suckers.

For very basic biological reasons, we take it for granted that forest above-ground biomass decreases and proportion of vegetative regeneration increases with elevation. In other words, we have a situation in which the variance of our variables of interest is associated with elevation. Therefore, before addressing our research question about forest degradation, we first removed the statistical dependence of these forest structural variables with elevation. We did this by calculating linear regressions in which elevation was the explanatory variable and each of the five forest structural variables separately the dependent variables. The residuals of each of the dependent variables were then taken as the new dependent variables to be explained by our indices of accessibility. We calculated the regressions both across all species taken together within dry and within humid area, and separately for each species.

Taking residuals from an overall regression in which all species are included can be justified if the decline in tree size in our study area is uniform over all species. However, if each species can have somewhat different mathematical function describing the decline and/or if different tree species have different sizes when growing at the same spot, then the residuals should be taken separately for each species. The available knowledge of natural size and its variation of the *Polylepis* species included in our study is not conclusive enough to define which way to deal with the residuals should be used.



◀ **Fig. 2** Forest structural characters in relation to elevation in *Polylepis* forest patches. Different symbols present different species. Humid areas: filled circle = *P. pauta*; open circle = *P. sericea*; filled inverted triangle = *P. pepel*. Dry areas: filled circle = *P. racemosa*; open circle = *P. subsericans*. Short solid lines are species-specific linear regressions. Short dashed lines indicate the cases when species-specific regression slope was opposite to the one expected and therefore the slope was set to zero and standardized values were used for further analysis. Long solid lines are overall regression across all species. When these lines were opposite to the expected elevational patterns, standardized values were also used for further analysis (four out of five cases in dry areas). Thicker lines indicate statistically significant regressions ( $P < 0.05$ )

Because of the strong biological justification, we took residuals only of regressions having the assumed sign of regression coefficient (i.e., positive or negative slope of the regression line, Fig. 2). In cases where the sign of the regression coefficient was actually observed to be opposite to the one expected, we took the original values (effectively the same as forcing the regression coefficient to be zero). In the case of calculating regressions for individual species, the residuals in each species-specific regression, or original values, were then separately standardised so as to keep each species' contribution to the final dependent variable directly proportional to the number of plots in which the species had been observed. Finally, the species-specific standardised residuals of each forest structural variable were put together for the dry and humid valleys separately.

#### Indices of accessibility

As indices of accessibility of forest patch, we used measures of geographical distance from the study plot (1) to the nearest village, (2) to the nearest paved road or railway station, and (3) to the nearest market centre (Table 1). Distances were measured along the easiest walking or driving routes deduced from topographic information extracted from the satellite images of Google Earth.

#### Data analysis

We tested the hypothesis that accessibility explains the degree of *Polylepis* forest degradation by calculating how well the indices of accessibility explain, in a linear regression, the residual variance of each of the measures of forest structure and regeneration.

Forest structure and regeneration can be affected by several naturally occurring biological factors, like herbivores, pathogens and symbiotic organisms. These factors are difficult to quantify in practice, but typical for them is a spatial structure in which sites that are nearby are more similar to each other in terms of the factor than sites that lie far apart (Dale et al. 2002). Such spatial structure can also complicate the interpretation of other statistical analyses. We tested this biologically justified spatial prediction separately in dry and humid valleys for each residual variable of forest structure and regeneration. We first constructed matrices of Euclidean distance separately on the basis of each residual variable. These distance matrices were then correlated in a standardised Mantel test (Smouse et al. 1986) with the corresponding horizontal geographical distance matrix of plots in either dry or humid valleys. The statistical significances of the Mantel tests were estimated through 999 permutations. We run regression and correlation analyses with the statistical software SPSS 19.0, and calculated the matrices and performed Mantel tests with the statistical software R-package (Legendre and Vaudor 1991).

**Table 1** Average values and standard errors of forest patch characteristics for each *Polylepis* species

Species: Number of plots:	Humid			Dry	
	<i>P. pauta</i> 4	<i>P. sericea</i> 4	<i>P. pepeii</i> 5	<i>P. racemosa</i> 6	<i>P. subsericans</i> 5
Forest patch character					
Elevation (m)	3520 ± 156	3916 ± 111	4240 ± 47	4100 ± 48	4379 ± 31
Max tree height (m)	11.4 ± 2.1	6.8 ± 0.9	4.9 ± 0.4	8.5 ± 0.8	9.4 ± 0.9
Mean tree height (m)	8.6 ± 1.5	4.5 ± 0.8	3.3 ± 0.3	5.1 ± 0.8	6.9 ± 0.8
Max tree circ (cm)	128.3 ± 40.1	69.6 ± 8.4	61.8 ± 8.1	85.3 ± 9.2	119.3 ± 17.4
Mean tree circ (cm)	65.3 ± 6.6	30.7 ± 6.1	31.7 ± 3.6	45.8 ± 7.4	72.7 ± 14.5
Tree density (ind./100 m <sup>2</sup> )	20.5 ± 10.4	46.3 ± 17.7	24.1 ± 3.9	25 ± 4.1	16.8 ± 4.8
Vegetative regeneration (%)	57.7 ± 19.3	28.0 ± 14.6	66.2 ± 13.7	31.2 ± 14.6	62.5 ± 16.9
Total regeneration	11.0 ± 4.7	81.5 ± 29.1	332.3 ± 192.0	382.7 ± 93.8	312.5 ± 56.6
Distance to village (km)	5.042 ± 0.82	3.914 ± 0.83	3.041 ± 1.00	4.374 ± 1.38	4.796 ± 1.06
Distance to road (km)	6.637 ± 2.16	3.939 ± 0.81	6.094 ± 2.39	8.503 ± 0.89	10.361 ± 0.97
Distance to market (km)	36.694 ± 4.49	25.878 ± 6.09	24.01 ± 3.52	15.694 ± 1.69	17.213 ± 1.96

All characteristics except tree density are calculated only on the basis of individuals of the given *Polylepis* species even if there were individuals of other species present in the study plots. Three plots of *P. pauta* were mixed with other tree species and in these plots on average 57% of the trees represented *P. pauta*. In the case of *P. sericea*, there were two mixed plots with on average 86% of the trees belonging to *P. sericea*. In one plot of *P. pepeii*, *P. racemosa* and *P. subsericans* there were also other tree species and the dominance of *Polylepis* was correspondingly 96, 82 and 94% of the individuals

## Results

### Elevational patterns of forest structure

The three *Polylepis* species (*P. pauta*, *P. sericea* and *P. pepeii*) of humid areas were observed in only slightly overlapping altitudinal ranges, and the two species (*P. racemosa* and *P. subsericans*) of dry areas had no overlap (Table 1; Fig. 2). All forests were rather low (tree height being roughly 10 m and below) and tree circumferences only rarely exceeded 100 cm.

In humid areas, when taking all species into one analysis, we observed the expected sign of regression coefficient in all forest structural features (Fig. 2). The regressions were statistically significant for features of mean and maximum tree height and mean tree circumference. In the similar regression analysis in dry areas, the expected sign was observed only for vegetative regeneration—in all other cases the sign was contrary to the biologically justified one, yet only in the case of maximum tree circumference the sign was statistically significantly different from zero.

Looking each species separately, the species in humid areas showed in most cases the expected sign of regression coefficient (Fig. 2). In dry areas, the expected relationships with elevation appeared in three out of five cases for *P. racemosa*, but *P. subsericans* consistently showed an opposite trend in relation with elevation. Due to the low number of



plots per species, it was not meaningful to estimate statistical significance of the species-specific regressions.

### Accessibility in relation to forest structure

Each of the three explanatory variables had a statistically significant relation to at least one of the dependent variables that describe residual forest structure or regeneration after removing the statistical effect of elevation (Table 2). The relationships between dependent and independent variables were somewhat different between dry and humid areas. Distance to the nearest village was related rather similarly with the dependent variables in both dry and humid areas. Distance to the nearest market centre explained remarkably well the residual maximum tree height and circumference in dry but not in humid areas. Distance to the nearest paved road or railway station was the explanatory variable that had most notably a different relationship with dependent variables between the dry and humid areas. In the dry areas, it had no statistically significant explanatory power over any of the dependent variables, whereas in humid areas it was statistically significantly related with most of the dependent variables. Because distance to the nearest village and nearest paved road or railway station were strongly intercorrelated in humid areas, they should be regarded as effectively a single independent explanatory variable. Consequently, it can be summarised that there were four independent significant or nearly significant relationships in both areas when the residuals of forest structural variation were extracted from species-specific regressions. When the residuals were extracted from the regression line across all the species within dry or humid areas there were four significant or nearly significant relationships in the humid and three in the dry areas. The explanatory variables were generally only weakly correlated with each other, but in humid areas distance to the nearest village and distance to the nearest paved road or railway station were strongly related (Pearson correlation coefficient  $r = 0.796$ ,  $P < 0.01$ ).

None of the forest structural variables produced a statistically significant correlation with geographical distances in the Mantel test (highest correlation was found for mean tree circumference in humid areas when the residuals were extracted from the overall regression line across all the species, Mantel  $r = 0.241$ ,  $P = 0.068$ ).

## Discussion

In both the climatically dry and humid areas, residual variation of the features on forest structure was explainable by at least one of the indices of accessibility. The fact that this statistical dependence was found in two independent data sets suggests that human activities are causing variation in the studied forest features. At least it is difficult to invoke other alternative explanatory variables that would covary with the indices of accessibility.

Our hypothesis was that the variation in *Polylepis* forest structure in the drier and more densely inhabited valleys would be more strongly controlled by human activities than in the relatively humid and more sparsely inhabited valleys. However, our results do not support this hypothesis. The variance in the dependent variables was explained quite as effectively by the indices of accessibility in both humid and dry valleys. This result is somewhat surprising given that dry valleys have been historically much more affected by humans (Binford et al. 1997; Etter and Villa 2000). The inner parts of the Andes have been densely populated for thousands of years (Dobyns 1966; Kessler and Driesch 1993). Also, it appears that the majority of centres of pre-Hispanic cultures were located in more

**Table 2** Results of linear regressions between dependent variables on forest structural characters, and independent variables describing accessibility (distance to the nearest village, paved road or railway and market centre) separately for dry and humid areas

Distance measure	Residuals of species-specific linear regression with elevation for forest structural characters					
	Max tree height	Mean tree height	Max tree circumf.	Mean tree circumf.	Veg. regener.	
Humid						
Village	(+0.15	(+0.27°	(+0.04	(+0.35*	(-0.26°	
Road	(+0.37*	(+0.50**	(+0.19	(+0.52**	(-0.43*	
Market	(+0.04	(+0.00	(+0.04	(+0.00	(-0.00	
Dry						
Village	(+0.13	(+0.30°	(+0.20	(+0.22	(-0.43*	
Road	(-0.00	(-0.20	(+0.02	(-0.13	(+0.03	
Market	(+0.54*	(+0.16	(+0.69**	(+0.19	(-0.06	
Distance measure	Residuals of overall linear regression with elevation across all species for forest structural characters					
	Max tree height	Mean tree height	Max tree circumf.	Mean tree circumf.	Veg. regener.	
Humid						
Village	(+0.16	(+0.15	(+0.11	(+0.20	(-0.16	
Road	(+0.39*	(+0.34*	(+0.30°	(+0.50**	(-0.08	
Market	(+0.03	(-0.04	(+0.00	(+0.03	(+0.02	
Dry						
Village	(+0.09	(+0.24	(+0.12	(+0.18	(-0.35°	
Road	(+0.00	(-0.07	(+0.12	(-0.00	(+0.06	
Market	(+0.33°	(+0.10	(+0.66**	(+0.26	(-0.05	

Numbers are proportion of variance explained in regression analysis, (+) or (-) symbols indicate positive or negative relationship of regression, \*\* indicate probability of error ( $P < 0.01$ , \*  $P < 0.05$  and ° nearly significant  $P$ -value ( $P = 0.051-0.082$ ))

accessible and climatically favourable inner part of the Andes rather than in inaccessible humid eastern side of the Andes, which is still nowadays sparsely inhabited (Etter and Villa 2000). However, one has to bear in mind that the statistical ability of accessibility to explain the residual variation in forest structure is not necessarily directly related to the degree of forest degradation. It may be that in one area forests are in general more degraded than in another, and yet, in both areas the variation one observes in forest features related to degradation can be equally strongly related to the level of human influence. In other words, forest degradation may have advanced more in one area than in the other, but the variance in it can be equally strongly associated to the degree of human influence in both areas. This may be exactly the situation between the studied dry and humid valleys. For this interpretation there is some evidence. The fact that only in dry areas there was a statistically significant tendency of trees getting thicker towards higher elevation—a pattern that is against ecological theory—and the statistically significant relation between this tendency and an index of human accessibility, suggests that forests in dry areas are more strongly degraded in absolute terms.

Even if the forests were equally degraded in climatically distinct areas, this is not to say that there would not have been any difference between the two data sets from distinct climatic conditions. In dry areas, the distance to nearest market centre was the only index of accessibility that explained significantly variance in the dependent structural variables. On the other hand, in the humid areas only distance to village or road were significant explanatory variables. This may indicate that in the dry areas, *Polylepis* forests are used more for providing products that can be sold, whereas in the humid areas the use of these forests is directed more at local subsistence. However, in this interpretation one has to realize that the sampled forest patches were not situated at equal distances from villages and other human installations in the two data sets. In the data from humid valleys, average distance to market centre was almost twice of that in the dry valleys. Therefore, it is possible that the difference in the explanatory power of the distance to market centre is just an indication of people having little interest to transport any products from *Polylepis* forests to a market centre beyond a distance of ca. 20 km.

In the case of distance to village and in distance to roads, there is relatively little difference between humid and dry areas in average distances as well as in their standard deviations. Therefore, the observed difference in the explanatory power of these variables appears to be indicative of a true regional difference in human socioeconomic behaviour. However, the role of distance to the nearest road or railway station as a significant predictor is not clearly evident as it is strongly correlated with distance to the nearest village. It is therefore quite risky to assume either one of these predictor variables more important than the other only on the basis of the data analyzed here. In theory, distance to the nearest village seems to be a more likely truly important variable explaining *Polylepis* forest degradation, as *Polylepis* stands are most often managed and utilized exclusively by the people who live in the village and own the forest (Hagaman 2006; Maxwell 2004). However, road building has been shown to increase deforestation, and forest fragmentation and exploitation in Amazonia and in highlands of Venezuela and Mexico (Fearnside 1980; Dirzo and García 1992; Young 1994; Allan et al. 2002), indicating a potential importance of this variable explaining forest degradation.

Our findings of easily measurable geographical indices of accessibility predicting *Polylepis* forest degradation are supported by earlier studies on *P. pepei* forests in northern Bolivia, where forest stands near the villages were shown to be more impacted by livestock grazing, in particular, than distant forest stands (Hagaman 2006). Indirect measures of human influence based on geographical distances have also been used by Cingolani et al.

(2008) and Renison et al. (2010) to explain variations in forest canopy cover and soil loss in forests of *P. australis* in central Argentina. We used a very simple linear model and our sample size was rather modest. Therefore, one would expect that it would be possible to build more powerful predictive models by increasing model flexibility if more data points were available. However, we do not think that building such better models would be particularly cost-effective if the purpose is to guide conservation and restoration efforts to the most critical areas. Improving the success of modelling would require considerable effort in increasing the number of field inventories. This effort would probably be better invested in looking for direct measures of disturbance such as fire scars, dung of domestic animals and cut trees or stumps, together with interviews of local people on their use of *Polylepis* forests. This kind of detailed field studies would most probably be necessary anyway before starting with conservation and management activities. However, one of the first steps in such activities would necessarily be the identification of the most vulnerable forest patches. Our results add to the increasing evidence (Hagaman 2006; Cingolani et al. 2008; Renison et al. 2010) that such first priority spots for active management and conservation efforts are to be found in the relative proximity of villages and other human infrastructure. Alternatively, if the aim of conservation action is to identify forest patches with least human impact and hence lowest potential conflicts with conservation action, then remote forest patches may be the best choice.

In conclusion, we found that purely geographical measures of accessibility of a *Polylepis* forest patch are related to indicators of forest biomass and proportion of vegetative regeneration in dry and humid areas in the cordilleras Vilcanota and Vilcabamba, in Cuzco, Peru. Use of these relatively easily obtainable variables can help to locate areas where *Polylepis* forests are most degraded and therefore in most urgent need of protection and sustainable management.

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