

Tree species distribution in Andean forests: influence of regional and local factors

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Abstract: We identified and quantified regional and local environmental factors and spatial variation associated with tree-species composition across a 2000-m altitudinal gradient of Andean forest in north-western Argentina. A network of 47 1-ha plots was established along the altitudinal gradient within an area of about 25 000 km²; all trees ≥ 10 cm dbh were identified and measured. Constrained ordinations and variance-partitioning analyses were performed to investigate the determinants of tree-species distribution at the regional scale, across and within forest types (i.e. dry and cloud forests). We marked and measured a total of 22 240 trees belonging to 160 species. Significant environmental factors and spatial location combined accounted for 35% of total variation explained. A high proportion of variation was explained by climatic factors that were spatially structured; after removing the spatial effect, climate explained more variation in species composition across the complete gradient than did local factors. Relative importance of regional and local factors varied with geographic extent. Local factors explained more variation in tree-species composition at the within-forest scale than at the scale of the complete gradient. Our findings support the conceptual model of multi-scale controls on vegetation distribution, where local community composition and abundance result from processes at both regional and local scales.

Key Words: canonical ordination, climate, cloud forest, disturbance, dry forest, permanent plots, space, topography

INTRODUCTION

The structure of ecological communities is thought to respond to interrelated factors acting at different spatial scales. Climate, historical processes and geology interact to determine plant community composition at the regional scale, whereas microclimate, edaphic conditions and species interactions play a major role in structuring plant communities at the local scale (Ricklefs 1987, 2004; Ricklefs & Schluter 1993). Particularly interesting are studies that link explanatory variables obtained at one or more spatial scales with one or several aspects of species diversity (Ohmann & Spies 1998, Oliveira-Filho & Fontes 2000, Svenning & Skov 2005, Tuomisto *et al.* 2003).

The importance of many factors in determining species composition and distribution may vary greatly with scale and locality (Condit *et al.* 2002). In temperate forests,

species turnover has been associated with environmental change at both landscape (Gilbert & Lechowicz 2004, Peterson & McCune 2001) and regional scales (Lobo *et al.* 2001, Ohmann & Spies 1998, Ricklefs *et al.* 2004, Svenning & Skov 2005). In tropical forests, structure and diversity of plant communities have been associated mainly with soil conditions at a local scale (Clark *et al.* 1999, Phillips *et al.* 2003, Tuomisto *et al.* 2003) and climate at a regional scale (Duivenvoorden *et al.* 2002, Oliveira-Filho & Fontes 2000, Pyke *et al.* 2001, Toledo *et al.* 2010). In wet montane forests, vegetation dynamics and structure are heavily conditioned by climate, mediated by temperature and rainfall (Ashton 2003, Bhattarai & Vetaas 2003, Lieberman *et al.* 1996, Vazquez & Givnish 1998). Within a climatic region, vegetation is influenced by several other factors, including substrate, topography, soil composition (Ashton 2003, Givnish 1999) and disturbance (Baruch 1984, Martin *et al.* 2007).

Andean forests are particularly diverse and climatically and geomorphologically complex (Kappelle & Brown

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2001). At the southernmost extension of Andean forests (southern Bolivia and north-western Argentina) and elsewhere (Gentry 1988, Kessler 2002), several studies have evaluated regional gradients in forest composition and structure (Brown & Ramadori 1989, Brown *et al.* 1985, Grau 2002, Grau *et al.* 1997, Morales *et al.* 1995), but few have considered explicit links to potential explanatory factors (Aragón & Morales 2003, Lopez & Duque 2010).

In this study, we assess the relative importance of local and regional environmental factors as determinants of changes in species composition across and within forests. Specifically, we studied: (1) the association of environmental factors with tree species composition along an Andean forest gradient; and (2) the relative importance of regional factors (i.e. climate), local factors (i.e. topography and disturbance) and spatial location for structuring tree communities at decreasing geographical extents from the complete gradient to specific forest types. We predict that climate (i.e. temperature and moisture) will best explain patterns of community composition at the regional scale. Then, as spatial extent decreases from the complete gradient to a particular forest type (i.e. dry and cloud forest), we predict that local factors will gain importance for explaining species composition. To evaluate these predictions, we undertook a quantitative analysis of tree species composition across 47 1-ha permanent plots within an area of about 25 000 km² in north-western Argentina.

METHODS

Study area

Fieldwork was carried out in north-western Argentina within Andean forest (i.e. selva tucumano-boliviana; Cabrera 1976) and its transition to chaco forest, which represent the southernmost extension of Neotropical montane forests located on the eastern Andean slope (Cabrera & Willink 1980). Based on floristic composition, four vegetation units are differentiated along the altitudinal gradient; (1) chaco forest from *c.* 300–400 m asl; (2) lowland forest from *c.* 400–900 m asl; (3) lower montane forest from *c.* 900–1600 m asl; and (4) upper montane forest from *c.* 1600–2300 m asl (Cabrera 1976). The tree flora of the area is relatively well known (Demaio *et al.* 2002, Digilio & Legname 1966, Killeen *et al.* 1993, Legname 1982).

The study area covers a 250-km latitudinal transect from 22° S (border between Bolivia and Argentina) to 24° S (Salta and Jujuy Provinces, Argentina) and a 2000-m altitudinal gradient that can be divided into two main forest types: dry forest, from 300–400 m asl to *c.* 800–900 m asl; and cloud forest, from 800–900 m asl

to tree line (*c.* 2300 m asl). Chaco and lowland forest are seasonally dry forests with >79% deciduous tree species (Sarmiento 1972). Lower and upper montane forests are cloud forests with a high proportion of evergreen and semi-deciduous tree species (Brown *et al.* 2001).

Climate is defined as subtropical with a marked dry season (April–October) and occasional frost during cold months (Brown *et al.* 2001). Annual rainfall averages 625 mm (450–700 mm) in chaco forest, 820 mm (550–1400 mm) in lowland forest, 1800 mm (1100–2300 mm) in lower montane forests and 1100 mm (800–1400 mm) in upper montane forests (Bianchi & Yáñez 1992). In cloud forests, water input through fog interception can equal direct rainfall (Hunzinger 1997). Mean annual temperature is 21.5°C (mean maximum = 27.6°C, mean minimum = 15.4°C) in the lowlands and 11.7°C (mean maximum = 21.8°C, mean minimum = 8.8°C) in montane forest (Arias & Bianchi 1996).

Data collection

We established a network of 47 1-ha plots (45 permanent and two non-permanent plots) between 2003 and 2009, with plots distributed along the altitudinal gradient (Figure 1). All plots were established in relatively well-conserved forests (13 out of 47 plots were established in protected areas) undisturbed by human activities; e.g. selective logging, cattle transhumance. These activities have been practiced in the study area for at least the past 100 y (Brown *et al.* 2001). For this reason, we included disturbance indicators such as cattle presence and stumps. Three plots were established in chaco forest (CF), 20 plots in lowland forest (LF), 10 plots in lower montane forest (1000–1200 m, LMF), seven plots in the transition between lower and upper montane forests (1500–1700 m, L-UMF), and seven plots in upper montane forest (2000–2300 m, UMF). In summary, 23 plots were established in dry forests and 24 plots in cloud forests.

All plots were 20 × 500 m corrected for slope to cover 1 ha (Condit 1998); orientation with respect to the main slope was random. A full inventory was made of all trees ≥10 cm dbh in every plot. Trees were marked with numbered aluminium tags, measured for dbh (1.30 m, avoiding trunk irregularities) and identified to species or morphospecies if field identification was not possible. We collected voucher specimens of all species and morphospecies sampled in the plots. Voucher specimens were distributed to taxonomic specialists or matched to specialist-identified material. One hundred individuals (0.4% of total) remained unidentified (e.g. trees with no leaves, database errors) and were excluded from all analyses.

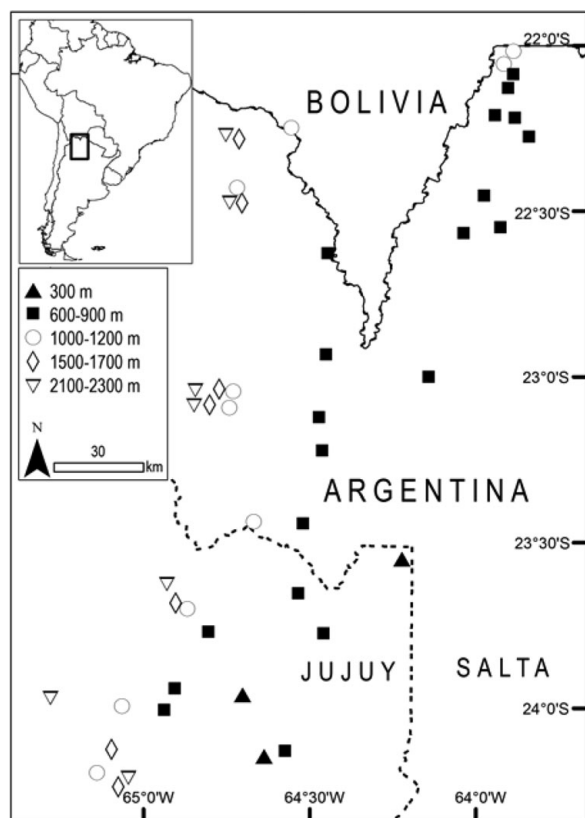


Figure 1. Extent of study area and spatial location of 47 1-ha plots in Andean forests of north-western Argentina. Black symbols correspond to plots in dry forest and white symbols correspond to plots in cloud forest. Symbols indicate approximate plot elevation.

Response and explanatory variables

Our response variable was number of individuals per species. Twenty-two species (involving only 41 individuals) were eliminated from the species data matrix because their poor representation introduced a large number of zeroes in the data matrix (Borcard *et al.* 1992) and to avoid an unduly large influence on the analysis (ter Braak & Šmilauer 2002). The remaining 139 species (22 099 individuals) were included in the analyses.

We compiled data on 10 explanatory variables pertaining to three subsets: spatial location, regional environmental factors and local environmental factors in each 1-ha plot (Appendix 1). We used a GPS unit to measure altitude at the extremes of each plot and used the average. We recorded latitude and longitude at the beginning of each plot. To account for complex non-linear spatial trends in species composition, we considered quadratic and cubic combinations of latitude and longitude (Borcard *et al.* 1992). These derived spatial variables did not explain more species variation than raw latitude and longitude in a forward stepwise procedure and, therefore, only raw latitude and longitude measures

were used in subsequent analyses. Altitude, latitude and longitude were considered as spatial variables.

We considered regional factors as those that can potentially vary across plots; i.e. climate. We derived climatic data from a local precipitation model and local mean monthly temperature from a map surface (<http://www.inta.gov.ar/prorenea/info/clima>) developed by Bianchi *et al.* (2008) for north-western Argentina. Both models were generated from 450 stations with weather data from 1934 to 1990. We used total annual rainfall and mean annual temperature as climatic variables. We log-transformed precipitation, following Ohmann & Spies (1998), because vegetation does not respond linearly to precipitation; i.e. a 1-cm difference in precipitation is more important at low than at high levels. In addition, we included a derived climate index, moisture stress (MS, °C mm⁻¹), which is a ratio between temperature and rainfall. Pronounced MS reflects higher temperatures coupled with lower rainfall.

We measured slope, per cent canopy cover (with a densitometer) and stump diameter in 25 quadrats of 20 × 20 m inside each plot. We considered these variables as local factors because they can potentially vary within each 1-ha plot. We used mean slope as a measure of topographic variation between plots, and canopy cover coefficient of variation and stump basal area as disturbance indicators. Additionally, we considered cattle presence-absence in each 1-ha plot from direct and indirect evidence (Appendix 1).

Data analyses

We analysed the entire dataset (47 1-ha plots) and each forest type separately (i.e. dry and cloud forests). Although the two forest subsets were not independent of the complete gradient, we analysed them separately because we wanted to stratify the gradient to examine within forest-type ecological variation and effects of geographic extent on ecological patterns.

To select the appropriate ordination techniques, species matrices for the entire gradient (47 plots, 139 species), dry forest (23 plots, 99 species) and cloud forest (24 plots, 113 species) were analysed using Detrended Correspondence Analysis (DCA; ter Braak 1988), with detrending by segments and untransformed species data. Since the length of the extracted gradient was more than 4.0 SD units in all data-sets, we subsequently conducted Canonical Correspondence Analysis (CCA; Lepš & Šmilauer 2003).

We performed CCAs with all explanatory variables to determine relationships between species and explanatory variables (H_0 : There are no relationships between species and explanatory variables matrices). We logarithmically transformed species relative abundance (i.e. $\log(x+1)$)

to dampen the influence of dominant species (Lepš & Šmilauer 2003) and we down-weighted the influence of rare species (option available in CANOCO). We used Hill's scaling method on inter-sample distances, appropriate for data with large species turnover across samples. The fraction of species variation explained by the explanatory variables (total variation explained, TVE) was calculated as the sum of all canonical eigenvalues (or trace) divided by the total variation (TV) in the species data (total inertia *sensu* ter Braak & Šmilauer 2002). A Monte Carlo permutation test was performed to determine the accuracy of the relationship (999 randomizations) between species and explanatory variables. The trace was used to build the F -ratio statistic (ter Braak 1990) and, when $P < 0.05$, the relationship between the two data-sets was considered significant. Then, a forward stepwise procedure was carried out to retain only significant variables for each set of explanatory data (i.e. spatial location, regional environmental factors and local environmental factors). We added explanatory variables in order of greatest additional contribution to TVE but only if they were significant ($P < 0.05$), where significance was determined by a Monte Carlo permutation test with 999 randomizations (H_0 : Additional influence of variables on vegetation is not significantly different from random), and if adding the variable did not cause any variance inflation factors (VIF) to exceed 3 (following Zuur *et al.* 2010). Variables with large inflation factors are strongly multicollinear with others and contribute little unique information to the model (Lepš & Šmilauer 2003). We performed all analyses using CANOCO 4.5.

Variance partitioning with CCA was performed to evaluate the relative importance of spatial location, regional factors and local factors. First, we found the pure fraction of variation explained by each set of explanatory variables; i.e. the independent effects of space (S), regional environmental factors (R) and local environmental factors (L), using a set of variables as constraining variables and the others two sets as covariables (i.e. S|R+L, R|L+S, and L|R+S). Then, we found the mixed fractions of variation explained by all possible combinations of each sets of explanatory variables (i.e. R+S, L+S, R+L and R+L+S), following recommendations of Anderson & Gribble (1998).

RESULTS

We marked and measured a total of 22 240 trees and 204 stumps in the 47 1-ha plots. We recorded 160 species (including three morphospecies), 124 genera and 60 families (Appendix 2). All species datasets exhibited large compositional gradients as estimated using DCA. Lengths of the extracted gradients in species-turnover SD units were: 7.4 and 4.0 for the complete gradient; 4.7 and 3.0

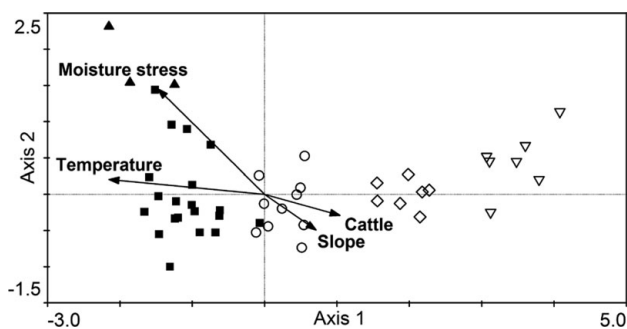


Figure 2. Biplot of sample plots and significant environmental variables from stepwise CCA for the altitudinal gradient in Andean forests of north-western Argentina. Symbols indicate approximate plot altitude: (▲) c. 300 m, (■) c. 600–900 m, (○) c. 1000–1200 m, (◇) c. 1500–1700 m, (▽) c. 2100–2300 m.

for dry forest; and 5.7 and 2.6 for cloud forest, for axes 1 and 2, respectively.

Environmental and spatial factors along an Andean forest gradient

Considering the complete gradient, species composition and all explanatory variables were significantly correlated, as indicated by CCA with Monte Carlo permutation tests ($P < 0.001$ for the sum of all canonical axes). Species turnover was relatively high along the altitudinal gradient (eigenvalues 0.69, 0.28 and 0.14 for axes 1–3, respectively). The first canonical axis in the species ordination was correlated with altitude and temperature, followed by moisture stress (Table 1). Altitude was negatively correlated with temperature and moisture stress, indicating that the data structure summarized by the first axis primarily reflected a geographic gradient from a warmer and drier climate in the lowlands to a colder and wetter climate in the highlands (Figure 2).

Plots with the lowest scores on axis 1 were located at lower altitudes and experienced higher temperatures and more pronounced moisture stress. These plots were located in CF and LF (dry forests). Species such as *Achatocarpus praecox* and *Ruprechtia triflora* were the most abundant in CF, whereas *Anadenanthera colubrina*, *Phyllostylon rhamnoides* and *Ocotea puberula* were the most abundant in LF (Appendix 2). Plots with intermediate scores were mainly located at 1000–1200 m in LMF and were characterized by steeper slopes. *Miconia molibdaea*, *Croton piluliferus* and *Chrysophyllum gonocarpum* were the most abundant tree species in LMF. Finally, plots with highest scores were located roughly above 1500 m and corresponded to L-UMF and UMF. These plots were characterized by low temperatures and presence of cattle (Figure 2). The most common tree species at this

Table 1. Results of canonical correspondence analysis (CCA) for 47 1-ha plots in Andean forests of north-western Argentina considering 10 explanatory variables (spatial location, regional and local environmental factors). Intra-set correlations for the first three axes and weighted correlation matrix for the explanatory variables are shown. Latitude (Lat, °), longitude (Lon, °), altitude (Alt, m asl), mean annual temperature (MAT, °C), total annual rainfall (Rain, mm), moisture stress (MS, °C mm⁻¹), mean slope (°), canopy cover coefficient of variation (CC), basal area of stumps (BAS, m² ha⁻¹) and cattle (presence = 1, absence = 0).

	Intra-set correlations			Weighted correlation matrix								
	Axis 1	Axis 2	Axis 3	Lat	Lon	Alt	MAT	Rain	MS	Slope	CC	BAS
Lat	0.03	0.47	-0.46									
Lon	0.48	0.29	-0.44	0.75								
Alt	0.97	-0.04	0.02	0.00	0.45							
MAT	-0.95	0.09	-0.01	-0.02	-0.52	-0.98						
Rain	0.41	-0.57	0.11	-0.44	0.05	0.43	-0.54					
MS	-0.65	0.57	-0.03	0.33	-0.19	-0.68	0.76	-0.93				
Slope	0.31	-0.21	-0.34	0.06	0.34	0.38	-0.41	0.31	-0.42			
CC	0.30	0.01	-0.27	0.19	0.20	0.31	-0.25	-0.02	-0.12	0.09		
BAS	-0.22	0.12	0.01	0.17	-0.12	-0.26	0.28	0.29	0.30	-0.32	0.01	
Cattle	0.46	-0.12	0.53	-0.34	-0.16	0.53	-0.48	0.23	-0.36	0.08	0.15	0.02

altitude were *Podocarpus parlatorei*, *Viburnum seemenii* and *Blepharocalyx salicifolius* (Appendix 2).

The second CCA axis partially showed a gradient of humidity from drier to wetter forests (highest to lowest scores on axis 2). The compositional gradient reflected by the second axis was negatively correlated with rainfall and positively correlated with moisture stress (Table 1). When a stepwise procedure was performed, only moisture stress was included in the simple model to avoid collinearity, because this variable explained a higher proportion of total variation. Finally, the third CCA axis (not shown) tended to segregate plots within altitudes (mainly at LF and LMF), based on cattle presence and slope (Table 1).

Simpler models, with all significant environmental (regional and local) and spatial variables obtained by stepwise forward selection, explained 35.4% of the variation in tree-species composition and abundance along the complete gradient. Spatial factors (altitude and latitude) explained 4.8% of total variation (TV), regional factors (temperature and moisture stress) explained 6.7% of TV, and local factors (slope and cattle presence) explained 4.2% of TV. Regional environmental factors spatially structured (R+S) explained 13.4% of TV and environmental (both regional and local) factors spatially structured (R+L+S) explained 5% of TV. Based on these results, altitude was correlated with temperature and moisture stress (regional factors) and with cattle presence (local factors; Table 1) and accounted for a large proportion of the spatial structure in environmental variation.

Relative importance of regional, local and spatial factors within forest types

Species composition and all explanatory variables were significantly correlated within dry forest ($P < 0.004$)

Table 2. Results of canonical correspondence analyses (CCAs) for 23 1-ha plots in dry forest and 24 1-ha plots in cloud forest in Andean forests of north-western Argentina. Intra-set correlations for the first two axes in CCAs with 10 explanatory variables (spatial location, regional and local environmental factors) are shown.

Explanatory variables	Dry forest		Cloud forest	
	Axis 1	Axis 2	Axis 1	Axis 2
Latitude	0.59	-0.59	0.20	0.34
Longitude	0.44	-0.70	0.44	0.31
Altitude	-0.57	0.33	0.97	-0.12
Temperature	0.67	-0.21	-0.95	0.01
Rainfall	-0.76	0.12	0.03	-0.03
Moisture stress	0.85	-0.08	-0.46	0.06
Slope	-0.35	-0.38	0.17	0.08
Canopy cover	-0.20	0.01	0.42	-0.16
Basal area stumps	0.06	0.01	-0.03	0.64
Cattle	-0.29	0.64	0.44	0.36

and within cloud forest ($P < 0.002$), as indicated by CCA results with Monte Carlo permutation tests. Dry forest showed more than one environmental gradient, as reflected by percentage of variation explained by axes 1 and 2 (eigenvalues 0.36, 0.23 and 0.18 for axes 1–3, respectively). The first canonical axis in species ordination was correlated with moisture stress, rainfall and temperature but only moisture stress was included in the simple model in stepwise procedure. The second canonical axis was correlated with longitude and cattle presence (Table 2). Cloud forest showed a main environmental gradient along axis 1 (eigenvalues 0.64, 0.22 and 0.17 for axes 1–3, respectively). The first canonical axis in the species ordination was correlated with altitude and temperature, reflecting the spatial structure in regional factors. The second canonical axis was correlated with stump basal area and cattle presence (Table 2).

Variance partitioning results varied between dry and cloud forests (Table 3). Reduced models with all

Table 3. Variance decomposition by partial CCA (following Anderson & Gribble 1998) of species abundance data into pure regional (R not shared with L and S), pure local (L not shared with R and S), pure spatial (S not shared with R and L), and all possible mixed components for all datasets. R = regional variables, L = local variables and S = spatial variables.

Variance components	Total variance explained (%)		
	Complete gradient	Dry forest	Cloud forest
Regional (R L+S)	6.7	10.7	2.4
Local (L R+S)	4.2	8.7	10
Spatial (S R+L)	4.8	5.6	9.4
R+S	13.4	2.8	13.7
L+S	0.6	4.8	1.2
R+L	0.7	3.3	1.3
R+L+S	5	1.1	4.1
Total	35.4	37	42.1
Undetermined	64.6	63	57.9

significant environmental (regional and local) and spatial variables explained 37% and 42.1% of TV in tree-species composition in dry and cloud forests, respectively. Considered separately, spatial factors explained more TV in cloud forest, whereas climate explained more TV in dry forest. Local factors alone explained about 10% of TV in both forest types. In dry forest, local environmental factors spatially structured (L+S) explained 4.8% of TV. In cloud forest, regional environmental factors spatially structured (R+S) explained 13.7% of TV and environmental (both regional and local) factors spatially structured (R+L+S) explained 4.1% of TV, similar to the results observed at the complete gradient.

DISCUSSION

This study is the first systematic quantification of tree-community composition and abundance and its association with environmental variables for subtropical Andean forest at the regional scale. Our modest performance in explaining variation in tree species composition (~35%) is common in floristic gradient analyses, where some overlooked factors or large amounts of stochastic variation remain unclear (Borcard *et al.* 1992). Still, low explained variances do not impair the significance of species-environmental relations (ter Braak 1988).

The issue of scale in defining the relative importance of explanatory variables in ecological communities has received increased recognition in recent decades (Ashton 2003, Ricklefs 2004). In regional studies of plant distribution or diversity, a primary control of regional factors over local factors is common, but the identity of the main factors usually changes among studies (e.g. climate: Ohmann & Spies 1998; geology and spatial variables: Lobo *et al.* 2001; history: Svenning & Skov 2005). In our study, the relative contribution of the explanatory variables was influenced by geographic

extent and location (i.e. from the complete gradient to within forest type), and varied with the scale of the explanatory factor (i.e. regional vs. local environmental factors).

Factors influencing tree species distribution along an Andean forest gradient

Tree community composition along the Andean forest gradient was predominantly controlled by regional environmental factors that were spatially structured (i.e. R+S explained 13% TV). The altitudinal gradient varied from a warm and dry climate in the lowlands to a cold and wet climate higher in the mountains. The strong spatial structure of the climatic variables is partially due to spatial autocorrelation (Borcard *et al.* 1992), since altitude and temperature were highly correlated. We found a strong association between altitude and species composition, as observed in other vegetation studies (Bhattarai & Vetaas 2003, Carpenter 2005, Ohmann & Spies 1998, Vazquez & Givnish 1998). In our study, altitude explained more variation in species composition than any other variable both along the complete gradient and within cloud forest. In contrast to temperature, precipitation is commonly found to have a relatively complex pattern (Lomolino 2001), statistically independent of a linear change in altitude. Rainfall in subtropical Andean forest has a unimodal trend, which peaks at LMF (1000–1200 m asl). Therefore, altitude is a complex gradient where several biotic and abiotic factors correlate (Grubb 1977, Kitayama 1992, Whittaker 1967). The interaction between a variable with a linear response (temperature) and a variable with a unimodal response (rainfall) may partially explain the patterns in species composition reported here.

After removing the spatial structure from the species composition data, the fraction explained by regional factors alone (R|L+S) was higher than the fraction explained by local factors (L|R+S). Our results support the prediction that climate is the primary control of community composition along the complete altitudinal gradient. Brown *et al.* (2001) suggest that climatic variables play an important role in determining tree-species distribution across and within Andean forest. Our findings support the conceptual model of multi-scale controls on vegetation distribution, where local community structure results from a combination of both regional and local-scale processes (Ricklefs 2004).

Relative importance of regional and local environmental factors within forest types

Species composition was structured by two main sets of variables within dry forest, where independent

effects of local and regional factors contributed in quite similar proportions (~9–10% each). We predicted that local environmental factors would increase their relative importance in explaining species composition as geographic extent of analysis decreased from the complete gradient to a particular forest type. Although the relative importance of local environmental factors increased within dry forest, we found that climate also explained a high proportion of variation in community composition. Moisture stress best explained tree-species composition, followed by cattle presence and slope. Elevated levels of moisture stress reflect high temperatures coupled with low rainfall. These extreme conditions occur prior to the beginning of the wet season, when temperatures may reach 40°C (October–November). Additionally, there is a decreasing rainfall gradient within dry forest of about 150 mm of total annual rainfall from the north-eastern side towards the south-western side of the study area (Appendix 1), which produces dramatic changes in species abundance. For example, *Diatenopteryx sorbifolia*, *Ocotea puberula*, *Cordia americana* and *Eugenia uniflora* showed the highest relative abundance on the more humid north-eastern side, but were poorly represented on the south-western side. Similarly, *Calycophyllum multiflorum*, *Phyllostylon rhamnoides*, *Astronium urundeuva* and *Anadenanthera colubrina* were the most abundant species on the south-western side, but showed low relative abundance on the north-eastern side.

The pattern within cloud forest was similar to that for the complete gradient; i.e. altitude and temperature best explained variation in tree-species composition. Low temperatures are well known to affect tree distribution and diversity towards the tree line (Givnish 1999, Stevens & Fox 1991) by allowing only a subset of high-montane forest trees to reach high altitudes (39 out of 160 species sampled were present at *c.* 2100 m). After removing the spatial structure from the species composition data, the fraction explained only by regional factors was lower than the fraction explained by local factors alone (2.4% and 9.4%, respectively). This result supports our second prediction, stating that when the spatial scale of analysis is reduced from the complete gradient to a particular forest type (i.e. cloud forest), local environmental factors would increase in relative importance.

A disturbance gradient, mainly represented by cattle presence, also explained a high proportion of variation in species composition in Andean forests at both geographic extents (the complete gradient and within forest types). Baruch (1984) has reported that vegetation changes along an altitudinal gradient in Venezuela appear to be related primarily to environmental changes occurring with altitude, and secondarily to disturbances caused mainly by grazing. Livestock is a long-standing disturbance factor in Andean forest

of north-western Argentina. Local people have been practising cattle transhumance for centuries, alternating grazing at grasslands above the tree-line during the warm season with grazing within the forest during the cold season (Ramadori & Brown 1997). Effects of livestock transhumance on seedling establishment and mortality of *Cedrela angustifolia* (a timber tree species) were reported for Andean forest in southern Bolivia (Zamora Petri 2006). However, no studies have evaluated the effect of cattle on species composition and forest structure at the community level. Whereas livestock is an historical anthropogenic disturbance in Andean forest (Brown *et al.* 2001, Reboratti 1995), this practice could influence species composition by promoting different environmental conditions for tree establishment and growth. Finally, our results support the notion that where regional climate is more stressful for plant life (e.g. dry and hot in lowlands and cold in mountains), species respond to smaller-scale variation in local factors such as topography, soil conditions and biotic interactions (Neilson *et al.* 1992).

In this study, we found that a small set of explanatory variables account for about 35–40% of the variation in tree-species composition and abundance in the spatially and environmentally heterogeneous Andean forests of north-western Argentina. Considerations of smaller spatial extent (e.g. local scale) and plots (e.g. 0.1 ha) might have increased the match between species composition and local factors, enhancing in turn the relative importance of local factors and the total amount of floristic variation explained. It seems clear from this study, however, that consideration of both local and regional environmental factors may be a useful approach to understand tree community composition and variation across and within forests.

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Appendix 1. Summary of 10 explanatory variables by subset (spatial, regional environmental factors and local environmental variables) for 47 1-ha plots along the altitudinal gradient in Andean forests of north-western Argentina. Latitude (Lat, °), longitude (Lon, °), altitude (Alt, m asl), mean annual temperature (MAT, °C), total annual rainfall (Rain, mm), moisture stress (MS, °C mm⁻¹), mean slope (°), canopy cover coefficient of variation (CC), basal area stumps (BAS, m² ha⁻¹) and cattle (presence = 1, absence = 0).

Plot ID	Spatial location			Regional factors			Local factors			
	Lat	Lon	Alt	MAT	Rain	MS	Slope	CC	BAS	Cattle
FP	23.960	64.784	320	20.7	700	3.0	0.2	4.6	0	0
ET	23.549	64.222	325	21.4	579	3.7	0	4.3	0.9	1
Sau	23.653	64.535	396	20.3	986	2.1	0	1.6	0.4	0
AG	23.121	64.472	465	19.8	1058	1.8	16.6	11.9	0.6	0
LQ	23.774	64.459	473	20.5	694	3.0	7.8	7.4	1.3	0
Yu	23.941	64.905	500	19.2	804	2.4	3.7	4.6	0.7	0
He	24.146	64.636	509	20.3	691	2.9	0	5.1	4.5	0
TI	23.222	64.462	521	19.9	1002	2.0	15.3	4.8	1.1	0
Te	22.932	64.451	524	19.7	1212	1.6	15.8	7.7	0.3	0
CC	22.627	64.445	572	18.5	1401	1.1	18.7	4.4	0	0
SM	23.770	64.804	595	19.6	1000	1.9	3.4	3.7	0.3	0
RSI	22.452	63.975	596	19.6	1185	1.8	0.9	18.9	2.6	1
SA	22.566	64.036	609	19.7	1097	1.8	0.7	7.6	2.9	1
CN	22.924	64.141	619	19.7	1002	1.9	4.5	3.0	8.5	1
AB	24.129	64.574	654	19.2	800	2.2	0.7	8.8	4.0	0
VM	23.442	64.520	677	19.3	1118	1.7	16.4	14.9	1.9	0
RSII	22.549	63.926	711	19.3	1000	1.9	8.8	19.4	0.3	1
Ai	24.006	64.937	735	19.1	796	2.5	18.7	3.4	0.6	1
BMI	22.105	63.900	778	18.9	1211	1.6	14.9	1.0	0.8	1
Km34	22.218	63.881	827	18.2	1172	1.6	10.0	0.4	0.4	1
BMI	22.127	63.902	829	18.5	1212	1.5	12.7	1.0	0.6	1
Km25	22.274	63.839	845	18.6	1010	1.7	11.8	13.6	1.6	1
VM_a	23.437	64.667	934	17.5	1400	1.2	9.2	11.5	0	0
Ma	23.093	64.741	982	17.2	1405	1.2	12.9	6.0	0	1
MS	22.209	63.942	996	18.0	1210	1.5	8.9	8.9	0.4	1
AcII	22.045	63.915	1014	18.0	1207	1.7	8.3	4.9	1.2	1
Si	22.247	64.556	1051	17.6	1270	1.5	16.6	4.8	0.7	0
Me	23.699	64.868	1082	16.4	1241	1.3	15.9	1.7	1.1	0
Fo	23.994	65.065	1084	17.4	974	1.8	28.7	16.1	0.6	1
CB	23.085	64.747	1136	16.7	1406	1.2	4.0	10.7	0	1
Ho	24.195	65.140	1159	16.9	995	1.8	7.9	18.2	4.3	1
Li	22.435	64.732	1175	16.2	1707	0.9	12.9	5.6	0.4	1
AcI	22.016	63.905	1181	17.6	1067	1.8	10.0	4.5	0	1
LC	23.084	64.800	1486	15.4	1253	1.2	11.2	8.2	0.6	1
Es	24.124	65.096	1548	14.6	1179	1.2	25.8	6.8	3.1	1
Za	24.237	65.075	1610	14.4	1231	1.2	13.0	5.4	0.5	1
TO	23.071	64.785	1616	14.5	1400	1.0	18.6	8.1	0.3	1
No	22.279	64.724	1650	14.4	1232	1.1	6.3	7.4	0.4	1
Ba	22.461	64.742	1684	13.9	1619	0.8	15.8	7.4	0.5	1
Mo	23.682	64.903	1747	15.0	1201	1.3	18.4	6.2	0.2	1
Oc	23.970	65.280	1961	13.2	1144	1.2	16.2	15.4	0	1
Ba_a	22.463	64.738	1973	13.2	1758	0.8	13.3	12.0	0	1
Ap	23.060	64.851	1984	14.1	1013	1.4	14.1	14.2	0	1
Za_a	24.235	65.062	2059	13.0	1234	1.1	11.1	26.9	0.5	1
Ta	23.087	64.848	2134	13.2	1000	1.3	14.7	12.5	0	1
No_a	22.271	64.752	2200	13.2	1200	1.1	14.7	18.1	0.5	1
PH	23.626	64.930	2304	12.9	800	1.6	18.9	26.0	0	1

Appendix 2. Species and absolute abundance recorded in 47 1-ha plots along the altitudinal gradient in Andean forests of north-western Argentina. Chaco forest (CF), lowland forest (LF), lower montane forest (LMF), transition between lower and upper montane forests (L-UMF), and upper montane forest (UMF). Nomenclature follows <http://www2.darwin.edu.ar/Proyectos/FloraArgentina/FA.asp>.

Family	Species name	CF	LF	LMF	L-UMF	UMF
Achatocarpaceae	<i>Achatocarpus praecox</i>	200	96	4		
Adoxaceae	<i>Sambucus nigra</i>		1	18	42	82
	<i>Viburnum seemenii</i>			5	153	394
Anacardiaceae	<i>Astronium urundeuva</i>	5	271	10		
	<i>Loxopterygium grisebachii</i>		10			
	<i>Schinopsis lorentzii</i>	7				
	<i>Schinopsis marginata</i>		40	6		
	<i>Schinus gracilipes</i>				7	41
	<i>Schinus meyeri</i>				1	9
Annonaceae	<i>Rollinia emarginata</i>		1			
Apocynaceae	<i>Aspidosperma quebracho-blanco</i>	3	6			
Aquifoliaceae	<i>Ilex argentina</i>			6	160	270
Araliaceae	<i>Aralia soratensis</i>		72	10		
	<i>Oreopanax kuntzei</i>				45	3
Asteraceae	<i>Nicotianthus lorentzii</i>		1	1		
	<i>Eupatorium arachnoideum</i>			21	2	
	<i>Eupatorium lasiophthalmum</i>			22	2	
	<i>Eupatorium saltense</i>		1	3	6	13
	<i>Tessaria integrifolia</i>		2			
Berberidaceae	<i>Berberis jobii</i>					24
Betulaceae	<i>Alnus acuminata</i>				106	96
Bignoniaceae	<i>Handroanthus impetiginosus</i>		175	6		
	<i>Handroanthus lapacho</i>		30	64	144	
	<i>Handroanthus ochraceus</i>		26	13		
	<i>Tecoma stans</i>			45		
Bombacaceae	<i>Ceiba chodatii</i>	5	105	3		
	<i>Pseudobombax argentinum</i>		33			
	<i>Tartagalia roseorum</i>		2			
Boraginaceae	<i>Cordia americana</i>		310	34		
	<i>Cordia saccellia</i>	1	163	2		
	<i>Cordia trichotoma</i>		226	59		
Cactaceae	<i>Cereus forbesii</i>		4			
Capparidaceae	<i>Capparis prisca</i>		72			
	<i>Capparis retusa</i>		1			
Cardiopteridaceae	<i>Citronella apogon</i>			11	32	7
Caricaceae	<i>Carica quercifolia</i>		1	4		
Cervantesiaceae	<i>Acanthosyris falcata</i>	3	6			
Clethraceae	<i>Clethra scabra</i>			1		10
Combretaceae	<i>Terminalia triflora</i>	8	88	101	75	1
Cunoniaceae	<i>Weinmannia boliviensis</i>		19			2
Cyatheaceae	<i>Alsophila odonelliana</i>			39	1	
Elaeocarpaceae	<i>Crinodendron tucumanum</i>			4	15	184
	<i>Vallea stipularis</i>					23
Erythroxylaceae	<i>Erythroxylum argentinum</i>		27			
Escalloniaceae	<i>Escallonia millegrana</i>				5	2
Euphorbiaceae	<i>Cnidoscolus vitifolius</i>		30			
	<i>Croton piluliferus</i>		54	234	19	
	<i>Jatropha hieronymi</i>		1			
	<i>Sapium haematospermum</i>	27		22		
	<i>Sebastiania brasiliensis</i>		44	30	1	
	<i>Acacia praecox</i>	21	3			
Fabaceae	<i>Acacia visco</i>			17		
	<i>Amburana cearensis</i>		7			
	<i>Anadenanthera colubrina</i>	4	893	111		
	<i>Caesalpinia paraguariensis</i>	54	11			
	<i>Caesalpinia pluviosa</i>		10			
	<i>Enterolobium contortisiliquum</i>		11	10		
	<i>Erythrina falcata</i>			3	29	
	<i>Geoffraea decorticans</i>	102				
	<i>Gleditsia amorphoides</i>	38	216			

Appendix 2. Continued.

Family	Species name	CF	LF	LMF	L-UMF	UMF
	<i>Inga edulis</i>		16	48		
	<i>Inga marginata</i>		41	143		
	<i>Inga saltensis</i>		9	22		
	<i>Jacaranda mimosifolia</i>		18	1		
	<i>Lonchocarpus lilloi</i>		57	69		
	<i>Myroxylon peruiferum</i>		98	44	1	
	<i>Parapiptadenia excelsa</i>	33	303	111	241	1
	<i>Piptadenia viridiflora</i>		1			
	<i>Prosopis alba</i>	31				
	<i>Prosopis nigra</i>	23				
	<i>Pterogyne nitens</i>		4			
	<i>Senna spectabilis</i>		18	8		
	<i>Tipuana tipu</i>		49	12		
Juglandaceae	<i>Juglans australis</i>			28	167	15
Lamiaceae	<i>Aegiphila saltensis</i>			7	11	
Lauraceae	<i>Cinnamomum porphyrium</i>		25	125	80	1
	<i>Nectandra cuspidata</i>		41	98		
	<i>Ocotea puberula</i>		414	175	2	
Malpighiaceae	<i>Ptilochaeta nudipes</i>		2			
Melastomataceae	<i>Miconia molybdaea</i>		2	591		
Meliaceae	<i>Cedrela angustifolia</i>			29	108	110
	<i>Cedrela balansae</i>	14	169	21		
	<i>Trichilia clausenii</i>		328	74		
Moraceae	<i>Ficus maroma</i>		10	17		
	<i>Maclura tinctoria</i>		48			
	<i>Morus insignis</i>			2	2	
Muntingiaceae	<i>Muntingia calabura</i>		5			
Myrsinaceae	<i>Myrsine coriacea</i>				2	
	<i>Myrsine laetevirens</i>	20	3	69	61	
Myrtaceae	<i>Blepharocalyx salicifolius</i>		35	181	464	29
	<i>Eugenia hyemalis</i>				7	
	<i>Eugenia moraviana</i>		5			
	<i>Eugenia repanda</i>		1			
	<i>Eugenia uniflora</i>		255	46		
	<i>Gomidesia barituensis</i>			36	77	
	<i>Myrcianthes callicoma</i>				12	1
	<i>Myrcianthes mato</i>				99	58
	<i>Myrcianthes pseudomato</i>			1	223	26
	<i>Myrcianthes pungens</i>		357	84		
	<i>Paramyrciaria ciliolata</i>			32	1	
	<i>Siphoneugena occidentalis</i>			164	95	
Nyctaginaceae	<i>Bougainvillea stipitata</i>	67	12	28	2	
	<i>Pisonia zapallo</i>		113	91	13	
Opiliaceae	<i>Agonandra excelsa</i>		97	28		
Phyllanthaceae	<i>Phyllanthus acuminatus</i>			1		
Picrodendraceae	<i>Parodiodendron marginivillosum</i>		1			
Piperaceae	<i>Piper tucumanum</i>		61	78		
Podocarpaceae	<i>Podocarpus parlatorei</i>				529	1524
Polygonaceae	<i>Coccoloba cordata</i>		5	1		
	<i>Coccoloba tiliacea</i>		24	22		
	<i>Ruprechtia apetala</i>	108	270	61		
	<i>Ruprechtia laxiflora</i>	3	49	39	8	
	<i>Ruprechtia triflora</i>	242				
Proteaceae	<i>Roupala montana</i>			64	58	4
Rhamnaceae	<i>Condalia buxifolia</i>	12	2			
	<i>Rhamnus sphaerosperma</i>				1	8
	<i>Scutia buxifolia</i>		1	12	25	
	<i>Ziziphus mistol</i>	107				
Rosaceae	<i>Prunus tucumanensis</i>			45	95	466
Rubiaceae	<i>Calycophyllum multiflorum</i>	1	348			
	<i>Coutarea hexandra</i>		29	5		

Appendix 2. Continued.

Family	Species name	CF	LF	LMF	L-UMF	UMF
	<i>Pogonopus tubulosus</i>		188	5		
Ruscaceae	<i>Randia armata</i>			2	5	41
	<i>Cordyline spectabilis</i>				1	
Rutaceae	<i>Citrus aurantium</i>			2	1	
	<i>Zanthoxylum coco</i>				19	
	<i>Zanthoxylum fagara</i>		69	36		
	<i>Zanthoxylum petiolare</i>	7	18	2		
	<i>Zanthoxylum rhoifolium</i>		8	10		
Salicaceae	<i>Azara salicifolia</i>				4	1
	<i>Casearia sylvestris</i>		10	1		
	<i>Salix humboldtiana</i>	1				
	<i>Xylosma longipetiolata</i>		20		18	6
	<i>Xylosma pubescens</i>		1	9		
Sapindaceae	<i>Allophylus edulis</i>		68	108	542	2
	<i>Athyana weinmannifolia</i>		31			
	<i>Cupania vernalis</i>		142	71	21	
	<i>Diatenopteryx sorbifolia</i>		310	147	6	
Sapotaceae	<i>Chrysophyllum gonocarpum</i>		164	220	1	
	<i>Chrysophyllum marginatum</i>		48	6	14	
	<i>Sideroxylon obtusifolium</i>	6				
Solanaceae	<i>Solanum riparium</i>		79	69		
	<i>Solanum trichoneuron</i>		2	10	5	26
	<i>Vassobia breviflora</i>		18	30	18	2
Styracaceae	<i>Styrax subargenteus</i>			32	35	
Tiliaceae	<i>Heliocarpus popayanensis</i>		16	38		
	<i>Luehea grandiflora</i>			12		
Ulmaceae	<i>Celtis ehrenbergiana</i>	3				
	<i>Celtis iguanea</i>		20	2	2	
	<i>Phyllostylon rhamnoides</i>	12	636	1		
Urticaceae	<i>Boehmeria caudata</i>			1		
	<i>Myriocarpa stipitata</i>		109	15		
	<i>Urera baccifera</i>		224	56		
	<i>Urera caracasana</i>		218	111		
Verbenaceae	<i>Citharexylum joergensenii</i>					15
	<i>Duranta serratifolia</i>				60	14
Ximeniaceae	<i>Ximenia americana</i>	2				
	morphospecies 1		1		1	3
	morphospecies 2	25				
	morphospecies 3				23	