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# Tree-line changes along the Andes: implications of spatial patterns and dynamics

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The Andes provide an extensive latitudinal and topographical framework for studying the factors that control the spatial patterns of forests (timberlines) and their species components expressed through the presence of tree growth forms (tree lines). Despite consistent overall similarities in landscape patterns, many processes must be unique, given the dramatic differences in species richness and biophysical constraints along the Andes. In all cases evaluated to date, morphological plasticity is a common trait of plant species that dominate at tree lines. In fact, many changes observed can be related to species-specific traits. Physiological limitations on tree growth form only explain species limits, while disturbances and cyclical climate fluctuations interact to affect many landscape patterns. Over long periods of time, tree lines provide unique habitats and perhaps opportunities for speciation. Understanding the spatial organization of tree-line dynamics is one viable research approach for evaluating the likely past fluxes and possible future changes.

**Keywords:** Andes Mountains; biodiversity; timberline; tree line

## 1. INTRODUCTION

Tree lines delimit spatially the Andean forest biodiversity hotspots. Their presence marks points along complex environmental gradients, where tree life forms are replaced as dominants by graminoids, forbs or shrubs. Understanding their spatial patterns, structures, composition and dynamism through time should provide insights into the ecological and biogeographical processes at work in creating and maintaining vegetation patterns and species range limits. A comparative framework is useful, permitting the evaluation of general theories for tree line by examining whether spatial patterns are shared and whether similar processes are involved.

Tree lines can be defined, demarcated and evaluated in terms of their spatial and temporal dimensions. In particular, insights into the processes that control the distributions and abundances of tall woody plants (tree lines) and forests (timberlines) can be derived from examination of changes in the composition, life histories and structure of those plants and vegetation types along spatial environmental gradients and through time.

The Andes Mountains form a series of long north–south trending mountain ranges over a distance of more than 7000 km from northern South America at about 10° N to roughly 57° S in Tierra de Fuego. Tree lines are found at most of these latitudes and one crucial question is whether similar spatial patterns are to be found. In addition, this and other comparative research questions need to be framed within a temporal framework that includes a range of mechanisms, from evolutionary processes acting over millennia to many vegetation ecological processes that affect plants over years and decades, and ecophysiological functions that occur in hours or even minutes. Detailed vegetation ecology studies at different latitudes in the Andes have revealed the importance of climatic processes and of disturbances such as fire which might be part of land-use practices. Thus, the dynamism of tree lines gives insights into both biophysical and anthropogenic processes. Projecting likely future trends and interpreting palaeoevidence of changes over long time periods require additional data and assumptions, presenting both challenges and opportunities for further research.

This paper begins with a brief review of recent research from tropical, subtropical and middle latitudes in the Andes, summarized with the goal of searching for shared patterns, processes and explanations. Next, the ecological processes involved are identified in relation to research done at tree lines globally. Finally, all of these aspects are related to needed research initiatives, including better clarifying the spatial and temporal dimensions of change, particularly as biodiversity conservation concerns and the role of human agency become increasingly involved in explanations and outcomes.

## 2. ANDEAN TREE LINES

Several researchers have recently examined these issues at various sites along the Andes, principally examining altitudinal tree lines. Here, we examine three case studies located in three latitudinal belts that have predictable differences in biophysical controls (table 1), even though all sites have similar general inverted timberline landscape patterns of valley bottom grasslands and forest on valley sides. We begin with a temperate, middle latitude example in southern South

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Table 1. Major latitudinal trends in the patterns and processes that characterize the tree lines of the Andes Mountains.

| biophysical control | tropical | subtropical | temperate |
|---|---|---|---|
| growing season | probably aseasonal | perhaps 280 days $yr^{-1}$ | perhaps 60–180 days $yr^{-1}$ |
| tree diversity | 20–> 100 | several | usually one |
| importance of snow | none | occasionally | can be significant |
| influence of ENSO | possible | yes | yes |

America, accompanied by examples of complementary studies nearby. We then examine the subtropics, with landscape and regional studies in northwestern Argentina. Finally, we summarize the work at a tropical timberline forest studied in northern Peru by the authors.

### (a) *Temperate Andes*

Undoubtedly, the ecological dynamics of tree line in the Andes have been most investigated at middle latitudes (e.g. Villalba *et al.* 1997; Cuevas 2000, 2002; Daniels & Veblen 2003; Frangi *et al.* 2005). In the temperate Andes, *Nothofagus pumilio* has been the model (modal) species discussed for tree line, because it tends to become a dominant species at high altitudes, defining the upper tree limit (Cuevas 2002). It apparently occupies undisturbed sites (Daniels & Veblen 2003) or as the main element of disturbed and regrowth forest (Szeicz *et al.* 1998). This species is deciduous, morphologically plastic, wind pollinated and has cyclic mast fruiting and wind dispersal (Cuevas 2000). Plasticity is manifested in changes in its growth form, with some individuals growing as trees up to 20 m tall and others found in a shrubby krummholz form at the highest elevations. By default, tree-line explanations here revolve around the autecology of this species.

Physical settings for this part of the temperate Andes include a tectonically active terrain, with a climatic gradient from oceanic wet climates in the westernmost areas to drier seasonal precipitation towards the eastern parts and with a decrease of mean annual temperature from north to south (Villalba *et al.* 1997; Szeicz *et al.* 2003; Lara *et al.* 2005), with implications for explaining tree growth (e.g. Kitzberger *et al.* 1995).

The most evaluated biophysical controls on tree growth have been temperature and moisture in southern South America. Thus, Lara *et al.* (2005) looked along a latitudinal transect in Chile for patterns of changes in radial growth in relation to temperature and precipitation. Their analysis used dendrochronology to reveal the spatial pattern related to those two factors. Tree growth was mostly positively correlated with precipitation and negatively with temperature in the northern parts, while there was an opposite relationship on the southern parts of their transect. Presumably, this means that trees are more limited by temperature at higher latitudes.

How structure and position of tree lines are influenced by an array of biological and physical factors at the regional and local scales were questions addressed by Daniels & Veblen (2003, 2004). Their goals were to distinguish the effects of local natural disturbances from climatic influences and to evaluate structure and growth differences at a scale corresponding to regional and local climatic variation. Observed changes in position and structure of tree lines tended to correspond with a global increase in temperature, which supports the idea of tree lines being environmental indicators. However, other conditions might also be important, such as disturbance at the regional and local scales, temporal variation in some climate aspects and asynchrony between climate change and vegetation response.

Daniels & Veblen (2003) examined 150 sites in Patagonia (40°44′–41°15′ S) along a cool-wet to warm-dry transect, from Chile in the west to Argentina to the east of the Andes. They made two predictions: (i) that local disturbance will initially lower tree-line elevations and simultaneously reduce vegetation cover and growth rates, with the further prediction that recovery and re-establishment growth rates may increase upslope and (ii) in regards to temperature or moisture controls, an expectation that if temperature were the control for their study area, it would be manifested in regional changes with greater growth rates to the east due to a more continental temperature regime, while if moisture was the controlling factor then such changes will be conspicuous towards the west. This second prediction also had a local component, namely that if temperature was the controlling factor then elevation and growth would be greater on warm, north-facing slopes, but if moisture was important then elevation and productivity would be greater on cool, south-facing slopes.

Their study analysed size, density and growth rates of *Nothofagus* trees during a 5-year period, in addition to cover of herbs and shrubs, in order to estimate overall vegetation productivity. Six physical features were recorded for each site, in addition to species composition and structure of the tree line. Their data were statistically analysed for occurrences and differences in and between biological and disturbance classes in relation to categorical and continuous variables, using contingency tables and one- to three-way ANOVAs. They found that although *N. pumilio* was the dominant species in all the sites except one, two other species were also present on the west side of the transect: *N. antarctica* was growing at four sites at timberline, and as krummholz plants it was found together with *N. betuloides*. They also found that most sites without disturbance were located on upper slopes, with warm aspects, straight configurations, relatively simple microtopography, low slope angles and low topographic relative moisture index values. These undisturbed sites had short ecotones, high krummholz growth rates, high cover of herbs and shrubs and low percentages of bare ground. In addition, six out of seven features of tree-line ecotone varied significantly at regional and/or local spatial scales. Regionally, tree lines had tree density and plant cover greater in westerly sites, with greater amounts of bare ground in drier areas in the eastern part of the transect. Additionally, tree-line elevation was significantly lower in the west side than on the east of the transect. Locally, herb and shrub cover was higher in undisturbed sites, and interaction between aspect and disturbance resulted in higher tree line on the west side with warmer aspects. Increased tree-line vegetation and growth rates for the krummholz forms of *N. pumilio* supported their hypothesis that low temperature limits tree-line dynamics. On the other hand, the presence of higher forest density and more understory on the west side was interpreted as showing moisture as the main climatic control.

Regional and global climatic controls undoubtedly have an effect on altitudinal tree lines in the temperate Andes. As Daniels & Veblen (2003, 2004) discussed, structure and dynamics of timberline receive regional climatic influences and will be exacerbated by more global factors, with different spatial responses mostly based on differential availability of moisture. Switches in tree dominance have been interpreted locally in relation to disturbance, for example, shifts from *N. betuloides* dominance to *N. pumilio* in southwestern Chile has been attributed to recovery after fire (Szeicz *et al.* 2003). Community structure and biomass decline with altitude and nutrient cycling features (accumulation, uptake, requirement and recycling) in temperate Andean forests conform to the observations made outside of the Andes. However, architectural plant growth form changes, from trees to shrubby krummholz, appear to be due to advantages of the krummholz life form (Frangi *et al.* 2005). There might be additional life-history differences needed to understand species persistence and dominance patterns at the landscape level (Pollmann 2004). Physical factors (gravity and wind) may also affect fruit and seed dispersal, especially in limiting the success for establishing of new individuals outside of the borders of the timberline (Cuevas 2000).

At timberline, the dynamics of biological processes requires a consideration of both temporal and spatial scales. Cuevas (2000, 2002) studied demographic features and recruitment for *N. pumilio*, which forms an abrupt tree line along an altitudinal transect in southern Chile. Using ecological and dendrochronological techniques, he found that establishment had long-term dynamics and fluxes, referring to time periods of decades to centuries. Population dynamics tended to vary with altitude regarding abundance of individuals at different stages, but age structures were multimodal regardless of altitude, probably corresponding to differing recruitment events. Fruit production varied interannually, with maximum production every 7 years; and regardless of seed production, fruit production increased with altitude.

As a result, temporal and spatial scale considerations were important for interpreting seed production and seed survival. Both factors varied annually and diminished with altitude as a result of resource limitation linked to a short growing season and low photosynthetic rates. Site variation regarding microclimate and density of a seedling bank were also important for the success of tree establishment and the shape of tree line. Cuevas (2000) proposed the need for longer-term studies to examine additional restrictions along the different stages of the life-history cycle of timberline species, since longevity of the species may also contribute to temporal shifts in the dynamics of recruitment.

### (b) *Subtropical Andes*

Most of the recent explanations for the variability and dynamics of altitudinal tree lines and tree expansion into non-forest vegetation in the subtropical Andes come from mesic seasonal localities, where a temporal perspective can be evaluated through the studies of annual tree rings (e.g. Grau & Veblen 2000; Grau *et al.* 2003; Morales *et al.* 2004).

Climatic influences on radial growth of tree species were studied by Morales *et al.* (2004) along an altitudinal gradient in northern Argentina (22–23° S). These authors tested whether variation in seasonal and/or annual precipitation affected growth of four tree-line species at their highest limits, predicting a positive association between these variables. They used correlation function analysis of climatic data and with dendrochronological techniques. Along this gradient, precipitation diminishes with increases in altitude, and the growing season is associated with a summer precipitation regime. They found that for all the four studied species (*Alnus acuminata*, *Juglans australis*, *Polylepis tarapacana* and *Prosopis ferox*), there was a positive association between growth and precipitation. However, species responses were different in timing. Thus, *J. australis* growth responded to precipitation during the previous and the current growing season, while *P. ferox* and *P. tarapacana* responded statistically only to precipitation from the previous growing season. Therefore, species traits matter, contributing to a more complex relationship between temperature and water availability, and being influenced by the scale and temporal features examined.

Disturbance is another kind of factor that may play a role in the stasis or flux of tree abundance and plant species richness in the Andes, and thus in the presence of a tree line and its composition. Overall, the effect of disturbance is dependent on the spatial scale and will manifest itself in different patterns of physical and biological associations (Grau 2001, 2002; Grau *et al.* 2003). For example, Grau & Veblen (2000) studied a mid-elevation site in Argentina, where amount of area burned affects tree invasion into non-forested areas. They used dendrochronological, photographic and demographic data in relation to spatial and temporal parameters, and analysed them with statistical tests including correlation and principal component analysis. They showed that for a pioneering fire-resistant species such as alder, *A. acuminata,* demographic changes and especially recruitment are affected by precipitation variability and by fire occurrence. They also demonstrated that these factors will vary according to sites, showing that fire generally increases in years following an increase in precipitation, although drier sites might not show this relation owing to smaller overall fuel loads.

At high altitudes in the subtropical Andes, the approach proposed by Körner (1998; see also Handa *et al.* 2005), in which thermal constraints may affect the physiology of carbon balance or limit growth, could provide a theoretical framework for testing how species may respond to limiting conditions. The environmental setting in the drier parts of the subtropical Andes is defined by a daily climatic variability rather than strong seasonal shifts (e.g. Rada *et al.* 2001; García-Núñez *et al.* 2004), and thus differs from the more mesic sites discussed above. For example, in southern Bolivia, *P. tarapacana*, a frost-tolerant subtropical Andean tree forms woodlands in semi-arid sites, reaching altitudes above 5000 m (Liberman-Cruz & Baied 1997; Navarro *et al.* 2005). The physiological responses of this species have been studied by Rada *et al.* (2001) and García-Núñez *et al.* (2004) who measured air temperature, relative humidity, photon flux density, leaf conductance and transpiration and also contents of non-structural carbohydrates and proteins (praline) in order to consider limitations of water stress upon net photosynthetic rate due to seasonality and to determine resistance mechanisms to low temperatures. Their results show that *P. tarapacana*, regardless of climatic variability, had a range of net photosynthetic rates comparable to other timberline species at low latitudes and that interseasonal change in content of non-structural carbohydrates and protein may be correlated to changes in higher metabolic activity and growth. Hoch & Körner (2005) report data suggesting limited growth rather than limited photosynthesis for this same species.

### (c) *Tropical timberlines*

Tropical timberlines differ from other sites in the Andes by their species richness and details of their structural composition. Young and colleagues evaluated the inverted tree lines found in a previously glaciated area of northern Peru. This is a biodiverse area overlooking the cloud forests and Amazon rainforests of the upper Huallaga River Valley, characterized by high rainfall (over 2000 mm) and highly acidic soils. Some 120 species of trees and shrubs form the tree lines (Young 1993*a*,*b*). There are several species of *Ilex* (Aquifoliaceae); *Oreopanax* (Araliaceae); *Baccharis*, *Diplostephium* and *Gynoxys* (Asteraceae); *Hedyosum* (Chloranthaceae); *Clusia* (Clusiaceae); *Weinmannia* (Cunoniaceae); *Disterigma*, *Gaultheria* and *Vaccinium* (Ericaceae); *Ocotea* (Lauraceae); *Brachyotum* and *Miconia* (Melastomataceae); *Myrsine* (Myrsinaceae); *Myrcianthes* (Myrtaceae); *Piper* (Piperaceae); *Monnina* (Polygalaceae); *Hesperomeles* (Rosaceae); *Meliosma* (Sabiaceae); *Solanum* (Solanaceae) and *Symplocos* (Symplocaceae).

Spatial heterogeneity is notable in this site, and probably the best way to characterize these timberlines and their landscapes. Using a series of vegetation plots along an altitudinal gradient and with distance from the forest–grassland borders, Young (1993*b*,*c*) observed that changes at forest edges were expressed through the structure and composition of the woody plants. Densities of the trees, shrubs and lianas increased with elevation and changed inversely with distance from the forest margins. But, overall, there were also many species-specific differences with, for example, forest interior and forest edge specialists. He proposed that because tropical tree lines are located on habitat edges in landscapes with ecotonal characteristics, at those borders biophysical changes occur and are expressed in the structure and composition of the plants. Edges differ from continuous forest features in structure and microclimate.

Scandent species include species from *Bomarea* (Alstroemeriaceae); *Jungia*, *Mikania* and *Munnozia* (Asteraceae); *Centropogon* (Campanulaceae); *Stellaria* (Caryophyllaceae); *Dioscorea* (Dioscoreaceae); *Alloplectus* (Gesneriaceae); *Ribes* (Grossulariaceae); *Fuchsia* (Onagraceae); *Passiflora* (Passifloraceae); *Muehlenbeckia* (Polygonaceae); *Rubus* (Rosaceae); *Calceolaria* (Scrophulariaceae); *Tropaeolum* (Tropaeolaceae); *Pilea* (Urticaceae) and *Valeriana* (Valerianaceae). Typically they did not appear to be habitat specialists, at least in terms of their relative abundances along sampled transects, but their high abundance and density towards tree-line edges may play a role in the dynamics of other life forms, helping to understand the processes shaping timberline. Towards the edge, Young (1993*b*) recorded densities of scandent plants equivalent to 6000–10 000 stems ha$^{-1}$. The presence of relictual individuals at edges, as in the case of large stems of resprouting scandent plants, also occurs in other life forms like ferns (Young & León 1993). The abundant understory bamboo in some of the timberline forests (an apparently undescribed species of *Chusquea*) was sun intolerant and reached densities of 260 000 stems ha$^{-1}$, but did not appear to negatively affect tree recruitment (Young 1991).

Size and location of forest patches also influence the dynamics of the edge that by nature varies through time, affecting or shaping landscape patterns (Young 1993*a*–*c*). Furthermore, as for many tree-line situations, disturbance was also shown to be an important force, although most frequently manifested through grassland fires set to improve grazing for livestock. Young (1998*a*) discussed and outlined the different processes associated with the heterogeneous shaping of Andean landscapes in relation to human intervention. Through millennial and centennial processes, humans in the central Andes have profoundly changed forested habitats in highlands, while a more recent deforestation process is occurring in the wettest areas. The patterns in the landscape vary spatially, with complex consequences in highlands due to an increase in fragmentation and a shift from forests to scrublands, while in wetter areas the elevational limit of forest is moved downward and depressed often by 500 m in altitude.

## 3. TREE LINES AS DYNAMIC SPATIAL PHENOMENA

Given these latitudinal changes along the Andes, what can be currently stated about shared patterns and processes? Tree lines can be mapped. Depending on the grain and the extent represented, they would appear on paper or in digital form as the edges of forests, as the last one of a series of isolated forest patches or isolated individual trees, or alternatively as contour lines that signify the outer limits to the presence of the particular species involved. Each of these abstract cases potentially involves a variety of ecological processes and historical events. In addition, particular plant species might have the potential to grow in more than one growth form, meaning, for example, that the location of 'tree line' may not be a species limit if that plant can grow as a shrub instead of a tree under more extreme environmental conditions.

The diversity of tree lines is sometimes overlooked in the search for general biogeographical explanations (Körner & Paulsen 2004). For example, experimental evaluation of the Körner (1998) hypothesis, which states that worldwide altitudinal tree lines are found in situations where carbon balance limitations do not permit large woody structures in plants, has revealed that this explanation may work for some species but not others (Handa *et al.* 2005). Recently, Holtmeier & Broll (2005) clarified the major landscape-scale patterns and processes expected at high-latitude and high-altitude tree lines. Our review begins to do so for Andean locations.

Limits to tree growth might often be species specific, found along spatial gradients associated with changes in biophysical constraints that do not permit establishment or survival of plants in a tree growth form. In addition, community level interactions along both physical and biological gradients might shape the fate of some species (e.g. Dullinger *et al.* 2005). A species-specific response to physical parameters has been described by Biondi & Galindo Estrada (2005). Moisture availability and potential transpiration (e.g. Leuschner 2000) might also be associated with both species-specific and individualistic responses. Some altitudinal tree lines, for example, have seedlings growing above tree line that never mature or that are kept in a low shrubby form by winds or ice damage that is called krummholtz in middle latitude sites. Here, a temporal perspective will be critical, as those biophysical constraints that prevent tree development may change cyclically with intradecadal and decadal fluxes or directionally with progressive climate changes, in addition to community structure, species and individual adaptability.

Other tree lines are found in deep intermontane valleys or along other gradients to semi-arid conditions where montane forests are replaced by shrublands or grasslands, often due to drier conditions, fires and rainshadow effects (Kitzberger *et al.* 1997). There are also lowland tree lines, where prairie, steppe or savannah replaces forest formations. Finally, inspiration and conceptual challenges can be found in studies of the high-latitude tree lines that demarcate tundra from coniferous boreal forests (MacDonald *et al.* 1998). For example, Epstein *et al.* (2004) describe the spatial patterns that typify the Arctic landscapes, with many cases that would have Andean equivalents. Young (1998*a*) differentiated two main regions of tropical Andean forests, one in dissected mountainous terrain with highly fragmented forests and the other with forest occurring in large continuous belts on the humid outer flanks of the Andes. Young & León (1995, 2001) showed that biodiversity status and conservation goals would differ across these geographical and environmental gradients.

Forest limits have some additional ecological processes acting upon them, because the microclimate inside is typically ameliorated compared with nearby non-forest environments, with lower wind speeds, higher and less variable atmospheric humidity and soil moisture, moderated solar radiation, and increased organic matter and nutrient inputs to the soil by leaf fall and by fog capture and drip (e.g. Bekker 2005; Maheer *et al.* 2005). Conversely, some plant species might find the within-forest biophysical conditions more stressful due to less solar radiation. As a result, there will be some species sorting at forest limits not expected at tree limits. One consequence is that isolated forest patches can be found occasionally in places where isolated trees cannot currently grow, due to establishment under previous conditions and continued survival due to amelioration by and within the forest itself. The dendrochronological methods now used in subtropical and temperate areas of the Andes can also provide evidence of whether tree recruitment is proceeding under current biophysical conditions.

Another general expectation will be non-equilibrium conditions (e.g. Alftine *et al.* 2003; Walsh *et al.* 2003). Thus, a tree line may have a unique set of biophysical constraints that act upon the available species pool resulting in particular spatial patterns. But there is no particular reason to expect that the spatial patterns at one point in time represent dispersal, establishment and growth processes that have reached some sort of stable or quasi-stable endpoint. In fact, it may be more realistic to assume some degree of flux and some likelihood of a past disturbance that (temporarily) has removed woody plants from places they previously dominated. This complication may require qualifying tree-line explanations in reference to a local and regional disturbance regime context, as is already being done in the southern Andes.

There are also some interesting qualifications to make for environments and locales where human land use alters those disturbance regimes. For example, fire regimes, in the sense of their timing, frequency, magnitude and extent, and ecological consequences, are altered by many land-use practices with implications for tree lines. In many middle latitudes, fires have been actively suppressed over the past century (Baker 1992; Houghton *et al.* 1999). In other places, traditional grazing practices have encouraged fires that act to limit woody plant invasion and produce resprouting grass leaves (Young 1993*a*). Other land uses, such as road construction and settlement expansion (Young 1994), change land cover in ways that can alter connectivity and hence the spread of fires or other agents of change. A rule of thumb is that sharp tree lines, with a narrow ecotone between non-forest and forest vegetation, are likely to be maintained by human intervention, for example, by burning or cutting (Forman 1995).

Troll (1968, 1973) proposed that tropical timberlines had different spatial configurations compared with temperate timberlines and their respective tree lines, based on the observations in the Alps and the Andes. Young (1993*b*,*c*) modified this generalization to state that previously glaciated terrains at all latitudes with broad U-shaped valleys had multiple tree lines with upper elevational limits high on valley sides, but with valley floors covered down to lower elevations by herbaceous vegetation. Tropical timberlines with these spatial relations include his study area in northern Peru and those described by Hope (1976) and Corlett (1984, 1987) for Papua New Guinea. Many middle latitude montane sites also show these 'inverted' timberlines (Fensham & Kirkpatrick 1992; Lloyd & Graumlich 1997). However, there are situations such as those described by Troll (1968, 1973), found in places where the highest elevation trees are found in ravines and other protected microsites. These locales tend to be places with slope processes dominated by gulley formation and the V-shaped valleys that result are mostly products of erosion, deposition and transport by interactive soil–stream watershed systems. These tend to be places where the glacial imprint on geomorphology is minimal or non-existent.

Valley-bottom herbaceous vegetation can also commonly be found occupying poorly drained sites that favour non-woody plants. Again, this creates conditions with inverted timberlines, with forests on the well-drained slopes, and herbaceous vegetation types covering the valley bottoms. Often in mountainous terrain, low gradient slopes have saturated and/or fine grained soils, while steep slopes rarely support wetlands and often instead have rocky, shallow soils. The former typically have dominance by forbs and graminoids, while the latter can have shrubs or trees. Parallels can be found among the tree lines that make up complex ecotones, where tropical savannahs and tropical forest intergrade (Kellman &Tackaberry 1997; Jeltsch *et al.* 2000; Sternberg 2001).

The spatial processes involved include habitat fragmentation, observed among the patches and corridors formed by both woody and herbaceous vegetation formations. Fragmentation might result from tree-line contraction, which expands areas with non-woody plants and reduces the size of forest patches while increasing the degree of edge effect they experience. Alternatively, tree lines could expand into areas previously covered by grasses, wetlands or shrubs. Forest patches would grow and eventually coalesce. Among these landscape ecology processes (Watson 2002; Holtmeier 2003), there are possibilities for interactive feedbacks involving perturbations, plant–animal interactions and human-mediated alterations.

Current tree-line theory is often described in terms of overall carbon balance and plant life form (Körner 1998, 1999), including relations of effective carbon sequestration in the course of yearly or decadal climate change. But this review points to the need to also expect three-way ecotonal movements: tree-line expansion or contraction, and processes that result in habitat fragmentation, coalescence, percolation and persistence in hostile environments in non-reproductive states (as seeds, juveniles or adults). Even if photosynthesis and tissue allocation by plants are the ultimate explanations over evolutionary time of adaptations successful in tree-line environments, the proximate factors involved could result in a host of additional ecological conditions and limitations. A comparative framework helps in identifying similarities and differences along major latitudinal and biogeographical gradients.

## 4. TOWARDS A COMPARATIVE FRAMEWORK FOR UNDERSTANDING TREE-LINE DYNAMICS

Despite overall similarity in many landscape patterns found at altitudinal tree lines along the Andes, there are also unique patterns and processes with latitude (table 1). For example, tropical tree lines are much more diverse, not affected much by snow or ice, have numerous mutualisms with animals for pollination and dispersal, have many scandent and epiphytic species and have 365 days per year of growing season.

Daniels & Veblen (2003) conclude that in general, research on climate influences on tree lines needs to be stratified according to the influence of local disturbances, which affect location and length of ecotones. In addition, the magnitude of the disturbance was an important variable to consider. Using the annual tree ring records in their trees, they were able to distinguish climate effects after considering the effects of disturbance. Their four conclusions were that tree-line elevation increases from west to east, tree-line elevation and krummholz growth were greater on warmer slopes than those in cool aspects, tree lines and krummholz growth did not vary significantly in the east, and forest density and cover were greater towards the west.

In tropical tree-line environments, research approaches lack the ability to measure past timing and amount of growth, except on permanent plots with individual trees tracked through time. Young (1998*b*) used inferences from tree and shrub population structures to evaluate possible trajectories of forest succession and expansion of tree lines. Future work from his site and others can test those inferences with actual growth and mortality measures. Young (1998*a*) and Sarmiento & Frolich (2002) noted the importance of considering additional influences from historical and current land-use effects on these and other Andean forests. Young & Keating (2001) pointed out that some tree-line species can be found as shrubs, trees or scandent plants depending on local conditions, demonstrating the potential for great plasticity in growth forms within single species.

The subtropical environments have more species-rich mixtures of trees and shrubs than at middle latitudes, but also show strong seasonal shifts and offer the advantage of permitting dendrochronological approaches (Grau *et al.* 2003). Grau & Brown (2000) place these issues in a broader context for Northwest Argentina, both geographically and in terms of current and future land use.

The importance of temporal scale, at least in terms of current ecological processes, is evident in the temperate Andean studies reviewed, because many of their underlying processes and dynamics tend to alter over decades and even centuries (Cuevas 2000, 2003; Pollmann 2004). Szeicz *et al.* (2003) have shown that the current mosaic of vegetation is the result of environmental changes at different time-scales, such as millennial climatic changes interacting with recent, annual or decadal changes and anthropogenic disturbances. It appears that each factor shaping vegetation expansion and/or contraction has a particular span in time, although distinguishing interacting factors might require compilation of additional neo- and palaeoecological data.

Over millions of years, species appear, disappear and sometimes diversify in the fossil record (Young *et al.* 2002). One consequence for reconstructions of past environmental conditions based on micro- or macrofossils is that the specific taxa fossilized may no longer be present or its descendents may have evolved different climate–abundance relationships. Changes over this great length of time also include climate changes, differences in intercontinental connectivity and hence source areas for possible new colonizing species, and changes in mountain topography relating to uplift and downwasting. Perhaps, at least some diverse lineages will be eventually associated with speciation processes in tree-line situations. If those kinds of environments have always been found somewhere in the uplands of tropical South America, then it seems that tree lines in general also must be an ancient habitat type, reminiscent of recent re-evaluations of how some speciation has occurred in the Amazon lowlands (Maslin *et al.* 2005).

The dynamic landscape mosaic that characterizes all the Andean altitudinal tree lines studied so far, despite differences in the number of component species, permits much beta diversity to exist in the form of species turnover from place to place. One site may contain a structural gradient from open shrubby plants to relatively tall, closed forest over distances of 20–1000 m. Additional habitat variation comes from disturbances, both exogenous (winds and fire) and endogenous (tree mortality), while often underlying soils vary in terms of coarseness and moisture levels. Steep slopes imply large changes in biophysical conditions over short vertical distances. In addition, the aspect affects solar radiation, moisture stresses and exposure to winds and fog.

Also tree lines would seem to provide opportunities for speciation over evolutionary time, given sharp environmental gradients, changing habitat connectivity and the influence of mountainous topography. Fetcher *et al.* (2000) reported little evidence of ecotypic variation along elevational gradients in Puerto Rico, but recently Premoli (2003) found that there was clinal variation along elevational gradients in Patagonian populations of *N. pumilio* as evaluated using isozyme evidence. For that matter, partially interconnected mosaic tree-line landscapes may form long ‘metacommunities’ over evolutionary time in the sense of Lavin *et al.* (2004), leading to additional speciation along latitudinal and other spatial gradients.

New methods allow for some refinements in information on temporal cycles and causality; for example, Bush *et al.* (2005) recently used wavelet analysis on lake sediment magnetic susceptibility to show statistically significant 210 year cycles, apparently associated with a centennial-scale solar cycle affecting precipitation. These and other techniques offer means for disentangling centennial cycles from El Niño-Southern Oscillation (ENSO) and other cycles operating on a decadal or subdecadal rhythm. Veblen *et al.* (1999) and Veblen & Kitzberger (2002) used dendrochronology to pull out a subtle landscape and disturbance legacy left by ENSO in Argentina: more rainfall in El Niño years creates more fuel load and so more fires burn several years later when dry spells occur. These studies imply that species distributions and abundances are constantly shifting. In this context, tree line is an inherently unstable phenomenon, with both trees and forests shifting spatially with changes in environmental constraints acting upon species involved. Assuming that tree lines are only controlled by climate and that they are in some sort of equilibrium might be simplifying assumptions necessary for some kinds of palaeoclimatic reconstructions, but they are unlikely to be completely satisfying, given the data now available for Andean tree-line ecology.

## 5. CONCLUSIONS AND IMPLICATIONS FOR A RESEARCH AGENDA

Shifts in the location and composition or structure of tree lines may be indications of directional climate changes (e.g. MacDonald *et al.* 1998; Lloyd & Fastie 2002; Camarero & Gutiérrez 2004). However, there are likely to be species-specific changes (Melcher *et al.* 2000), complications resulting from past and existing disturbance regimes (e.g. Landhäusser & Wein 1993; Cullen *et al.* 2001; Motta & Nola 2001), the possibility of asynchrony between cause and effect (Lloyd 2005) and some limitations on possible research approaches, especially in the more biodiverse lower latitudes.

The careful separation of disturbance-related fluxes from those induced by temperature or precipitation signals offers a productive approach, as does the acquisition of more case studies covering more sites and species assemblages. The presence of morphological plasticity among many tree-line plant species cautions against simplistic generalizations with the necessarily coarse identification of species groups in the case of fossil pollen and other palaeoclimatic and palaeoecological indicators. Evolution of that plasticity was likely an important source of diversity (West-Eberhard 1989; Scheiner 1993) for tree-line environments.

In addition, when possible, evaluation of land-use systems is critical for places with a human role in fire frequency or direct alterations to forest cover or composition, especially when those alterations are unique in kind or magnitude, as is suspected to be the case for current changes in lowland sites (Mayle *et al.* 2004). These kinds of observations also lend themselves to planning ecological restoration in damaged environments and environmental monitoring in the case of protected areas (e.g. Kintz *et al.* 2006). At regional scales, applied biogeography applications would include the evaluation of how conservation corridors can be used to connect together distant protected areas, especially given ongoing climate change (e.g. Young & Lipton 2006).

A landscape ecology perspective on tree lines suggests that resilience is a characteristic of this ecosystem type. Ecotonal movements will include the advance and retreat of forest margins, but also forest patches that become isolated or coalesce into larger patches. Plant species adapted to open environments thrive, but forest interiors are only several metres within forests, so species needing forest interior sites will also be found adjacently. Woody plants can often survive periods when new recruitment is impossible, thus prolonging the time that a species can be present in a tree-line situation even under inhospitable conditions. Thus, a transect across a tree line might not only reveal spatial changes from forest interior to forest edge, but also, in fact, be sampling along a chronosequence or even a multiple chronosequence if tree line has shifted repeatedly. Tree-line studies will likely reveal evidence of both historical legacies and ecological succession.

Species adaptations to tree-line habitats would be of interest to evaluate further, especially given that morphological plasticity is apparently one of the defining traits of species across the latitudinal gradient in the Andes. Tree lines shift over time, but like other major ecotonal environments, while their specific location may vary their presence somewhere in a region or landscape is predictable. Somewhat like the dynamic mosaic created by large fluvial systems, the landscape mosaics formed by tree lines offer numerous resources suitable for species requiring shady conditions, those thriving in the full sun, those needing dense forests, those that need the specific habitat conditions of forest edges and those that are habitat generalists. Over evolutionary time, tree lines have always offered this range of possibilities for selective pressures to act upon species adaptations, especially given the likelihood of population fragmentation or coalescence following habitat fragmentation or coalescence (e.g. Smith *et al.* 2001; Hinojosa & Villagran 2005).

## REFERENCES

Alftine, K. J., Malanson, G. P. & Fagre, D. B. 2003 Feedback-driven response to multidecadal climatic variability at an alpine treeline. *Phys. Geogr.* **24**, 520–535.

Baker, W. L. 1992 Effects of settlement and fire suppression on landscape structure. *Ecology* **73**, 1879–1887. (doi:10.2307/1940039)

Bekker, M. F. 2005 Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic Antarct. Alp. Res.* **37**, 97–107. (doi:10.1657/1523-0430(2005)037[0097:PFBTEA]2.0.CO;2)

Biondi, F. & Galindo Estrada, I. 2005 Daily weather and tree growth at the tropical treeline of North America. *Arctic Antarct. Alp. Res.* **37**, 16–24. (doi:10.1657/1523-0430(2005)037[0016:DWATGA]2.0.CO;2)

Bush, M. B., Hansen, B. C. S., Rodbell, D. T., Seltzer, G. O., Young, K. R., León, B., Abbott, M. B., Silman, M. R. & Gosling, W. D. 2005 A 17,000 year history of Andean climatic and vegetation change from Laguna de Chochos, Peru. *J. Q. Sci.* **20**, 703–712. (doi:10.1002/jqs.983)

Camarero, J. J. & Gutiérrez, E. 2004 Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Clim. Change* **63**, 181–200. (doi:10.1023/B:CLIM.0000018507.71343.46)

Corlett, R. T. 1984 Human impact on the subalpine vegetation of Mt. Wilhelm, Papua New Guinea. *J. Ecol.* **72**, 841–854. (doi:10.2307/2259535)

Corlett, R. T. 1987 Post-fire succession on Mt. Wilhelm, Papua New Guinea. *Biotropica* **19**, 157–160. (doi:10.2307/2388738)

Cuevas, J. G. 2000 Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego Chile. *J. Ecol.* **88**, 840–855. (doi:10.1046/j.1365-2745.2000.00497.x)

Cuevas, J. G. 2002 Episodic regeneration at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego Chile. *J. Ecol.* **90**, 52–60. (doi:10.1046/j.0022-0477.2001.00636.x)

Cuevas, J. G. 2003 Gap characteristics in relation to forest structure and implications for southern beech forest dynamics. *Can. J. For. Res.* **33**, 1915–1922. (doi:10.1139/x03-114)

Cullen, L. E., Stewart, G. H., Duncan, R. P. & Palmer, J. G. 2001 Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *J. Ecol.* **89**, 1061–1071. (doi:10.1111/j.1365-2745.2001.00628.x)

Daniels, L. D. & Veblen, T. T. 2003 Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *J. Veg. Sci.* **14**, 733–742. (doi:10.1658/1100-9233(2003)014[0733:RALEOD]2.0.CO;2)

Daniels, L. D. & Veblen, T. T. 2004 Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology* **85**, 1284–1296.

Dullinger, S., Dirnboeck, T., Koeck, R., Hochbichler, E., Englisch, T., Sauberer, N. & Grabherr, G. 2005 Interactions among tree-line conifers: differential effects of pine on spruce and larch. *J. Ecol.* **93**, 948–957. (doi:10.1111/j.1365-2745.2005.01036.x)

Epstein, H. E. *et al.* 2004 The nature of spatial transitions in the Arctic. *J. Biogeogr.* **31**, 1917–1933. (doi:10.1111/j.1365-2699.2004.01140.x)

Fensham, R. J. & Kirkpatrick, J. B. 1992 The eucalypt forest grassland/grassy woodland boundary in Central Tasmania. *Aust. J. Bot.* **40**, 123–138. (doi:10.1071/BT9920123)

Fetcher, N., Cordero, R. A. & Voltzow, J. 2000 Lack of ecotypic differentiation: plant response to elevation, population origin, and wind in the Luquillo Mountains, Puerto Rico. *Biotropica* **32**, 225–234. (doi:10.1646/0006-3606(2000)032[0225:LOEDPR]2.0.CO;2)

Forman, R. T. T. 1995 *Land mosaics: the ecology of landscapes and regions*. Cambridge, UK: Cambridge University Press.

Frangi, J. L., Barrera, M. D., Richter, L. L. & Lugo, A. E. 2005 Nutrient cycling in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego Argentina. *Forest Ecol. Manage.* **217**, 80–94. (doi:10.1016/j.foreco.2005.05.051)

García-Núñez, F., Rada, F., Boero, C., González, J., Gallardo, M., Azócar, A., Liberman-Cruz, M., Hilal, M. & Prado, F. 2004 Leaf gas exchange and water relations in *Polylepis tarapacana* at extreme altitudes in the Bolivian Andes. *Photosynthetica* **42**, 133–138.

Grau, H. R. 2001 Regional-scale spatial patterns of fire in relation to rainfall gradients in sub-tropical mountains, NW Argentina. *Global Ecol. Biogeogr.* **10**, 133–146. (doi:10.1046/j.1466-822x.2001.00220.x)

Grau, H. R. 2002 Scale-dependent relationships between treefalls and species richness in a neotropical montane forest. *Ecology* **83**, 2591–2601.

Grau, A. & Brown, A. D. 2000 Development threats to biodiversity and opportunities for conservation in the mountain ranges of the Upper Bermejo River Basin, NW Argentina and SW Bolivia. *Ambio* **29**, 445–450.

Grau, H. R. & Veblen, T. T. 2000 Rainfall variability, fire and vegetation dynamics in neotropical montane ecosystems in north-western Argentina. *J. Biogeogr.* **27**, 1107–1121.

Grau, H. R., Easdale, T. A. & Paolini, L. 2003 Subtropical dendroecology—dating disturbances and forest dynamics in northwestern Argentina montane ecosystems. *Forest Ecol. Manage.* **177**, 131–143. (doi:10.1016/S0378-1127(02)00316-X)

Handa, I. T., Körner, C. & Hättenschwiler, S. 2005 A test of the treeline carbon limitation hypothesis by *in situ* $CO_2$ enrichment and defoliation. *Ecology* **86**, 1288–1300.

Hinojosa, L. F. & Villagran, C. 2005 Did South American mixed paleofloras evolve under thermal equability or in the absence of an effective Andean barrier during the Cenozoic? *Palaeogeogr. Palaeoclim. Palaeoecol.* **217**, 1–23. (doi:10.1016/j.palaeo.2004.11.013)

Hoch, G. & Körner, C. 2005 Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. *Funct. Ecol.* **19**, 941–951. (doi:10.1111/j.1365-2435.2005.01040.x)

Holtmeier, F.-K. 2003 *Mountain timberlines: ecology, patchiness, and dynamics*. Dordrecht, The Netherlands: Kluwer.

Holtmeier, F.-K. & Broll, G. 2005 Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecol. Biogeogr.* **14**, 395–410. (doi:10.1111/j.1466-822X.2005.00168.x)

Hope, G. S. 1976 The vegetational history of Mt. Wilhelm, Papua New Guinea. *J. Ecol.* **64**, 627–663. (doi:10.2307/2258776)

Houghton, R. A., Hackler, J. L. & Lawrence, K. T. 1999 The U.S. carbon budget: contributions from land-use change. *Science* **285**, 574–578. (doi:10.1126/science.285.5427.574)

Jeltsch, F., Weber, G. E. & Grimm, V. 2000 Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecol.* **161**, 161–171. (doi:10.1023/A:1026590806682)

Kellman, M. & Tackaberry, R. 1997 *Tropical environments: the functioning and management of tropical ecosystems*. London, UK: Routledge.

Kintz, D. B., Young, K. R. & Crews-Meyer, K. A. 2006 Implications of land use/land cover change in the buffer zone of a national park in the tropical Andes. *Environ. Manage.* **38**, 238–245. (doi:10.1007/s00267-005-0147-9)

Kitzberger, T., Veblen, T. T. & Villalba, R. 1995 Climatic influences on fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. *J. Biogeogr.* **24**, 35–47.

Kitzberger, T., Veblen, T. T. & Villalba, R. 1997 Climatic influences of fire regimes along a rainforest-to-xeric woodland gradient in northern Patagonia, Argentina. *J. Biogeogr.* **24**, 35–47.

Körner, C. 1998 A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**, 445–459. (doi:10.1007/s004420050540)

Körner, C. 1999 *Alpine plant life: functional plant ecology of high mountain ecosystems*. Berlin, Germany: Springer.

Körner, C. & Paulsen, J. 2004 A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* **31**, 713–732.

Landhäusser, S. M. & Wein, R. W. 1993 Postfire vegetation recovery and tree establishment at the Arctic treeline: climate-change–vegetation response hypothesis. *J. Ecol.* **81**, 665–672. (doi:10.2307/2261664)

Lara, A., Villalba, R., Wolodarsky-Franke, A., Aravena, J. C., Luckman, B. H. & Cuq, E. 2005 Spatial and temporal variation in *Nothofagus pumilio* growth at tree line along its latitudinal range (35°40′–55° S) in the Chilean Andes. *J. Biogeogr.* **32**, 879–893. (doi:10.1111/j.1365-2699.2005.01191.x)

Lavin, M., Schrire, B. P., Lewis, G., Pennington, R. T., Delgado-Salinas, A., Thulin, M., Hughes, C. E., Matos, A. B. & Wojciechowski, M. F. 2004 Metacommunity process rather than continental tectonic history better explains geographically structured phylogenies in legumes. *Phil. Trans. R. Soc. B* **359**, 1509–1522. (doi:10.1098/rstb.2004.1536)

Leuschner, C. 2000 Are high elevations in tropical mountains arid environments for plants? *Ecology* **81**, 1425–1436. (doi:10.2307/177219)

Liberman-Cruz, M. & Baied, C. 1997 *Desarrollo sostenible de ecosistemas de montaña: manejo de áreas frágiles en los Andes*. La Paz, Bolivia: Editorial Instituto de Ecología.

Lloyd, A. H. 2005 Ecological histories from Alaskan tree lines provide insight into future change. *Ecology* **86**, 1687–1695.

Lloyd, A. H. & Graumlich, L. J. 1997 Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology* **78**, 1199–1210. (doi:10.2307/2265869)

Lloyd, A. H. & Fastie, C. L. 2002 Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Clim. Change* **52**, 481–509. (doi:10.1023/A:1014278819094)

MacDonald, G. M., Szeicz, J. M., Claricoates, J. & Dale, K. A. 1998 Response of the Central Canadian treeline to recent climatic changes. *Ann. Assoc. Am. Geogr.* **88**, 183–208. (doi:10.1111/1467-8306.00090)

Maheer, E. L., Germino, M. J. & Hasselquist, N. J. 2005 Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. *Can. J. For. Res.* **35**, 567–574. (doi:10.1139/x04-201)

Maslin, M., Malhi, Y., Phillips, O. & Cowling, S. 2005 New views on an old forest: assessing the longevity, resilience and future of the Amazon rainforest. *Trans. Inst. Br. Geogr. NS* **30**, 477–499. (doi:10.1111/j.1475-5661.2005.00181.x)

Mayle, F. E., Beerling, D. J., Gosling, W. D. & Bush, M. B. 2004 Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Phil. Trans. R. Soc. B* **359**, 499–514. (doi:10.1098/rstb.2003.1434)

Melcher, P. J., Cordell, S., Jones, T. J., Scowcroft, P. G., Niemczura, W., Giambelluca, T. W. & Goldstein, G. 2000 Supercooling capacity increases from sea level to tree line in the Hawaiian tree species *Metrosideros polymorpha*. *Int. J. Plant Sci.* **161**, 369–379. (doi:10.1086/314271)

Morales, M. S., Villalba, R., Grau, H. R. & Paolini, L. 2004 Rainfall-controlled tree growth in high-elevation subtropical treelines. *Ecology* **85**, 3080–3089.

Motta, R. & Nola, P. 2001 Growth trends and dynamics in sub-alpine forest stands in the Varaita Valley (Piedmont Italy) and their relationships with human activities and global change. *J. Veg. Sci.* **12**, 219–230.

Navarro, G., Molina, J. A. & De la Barra, N. 2005 Classification of the high-Andean *Polylepis* forests in Bolivia. *Plant Ecol.* **176**, 113–130. (doi:10.1007/s11258-004-0025-1)

Pollmann, W. 2004 Regeneration dynamics and life history differences in southern Chile *Nothofagus* forest: a synthesis. *Plant Ecol.* **174**, 353–369.

Premoli, A. C. 2003 Isozyme polymorphisms provide evidence of clinal variation with elevation in *Nothofagus pumilio*. *J. Hered.* **94**, 218–226. (doi:10.1093/jhered/esg052)

Rada, F., García-Nuñez, C., Boero, C., Gallardo, M., Hilal, M., González, J., Prado, F., Liberman-Cruz, M. & Azócar, A. 2001 Low-temperature resistance in *Polylepis tarapacana*, a tree growing at the highest altitudes in the world. *Plant Cell Environ.* **24**, 377–381. (doi:10.1046/j.1365-3040.2001.00685.x)

Sarmiento, F. O. & Frolich, L. M. 2002 Andean cloud forest tree lines. *Mount. Res. Dev.* **22**, 278–287. (doi:10.1659/0276-4741(2002)022[0278:ACFTL]2.0.CO;2)

Scheiner, S. M. 1993 Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* **24**, 35–68. (doi:10.1146/annurev.es.24.110193.000343)

Smith, T. B., Schneider, C. J. & Holder, K. 2001 Refugial isolation versus ecological gradients. *Genetica* **112–113**, 383–398. (doi:10.1023/A:1013312510860)

Sternberg, L. & da Silveira Lobo 2001 Savanna-forest hysteresis in the tropics. *Global Ecol. Biogeogr.* **10**, 369–378. (doi:10.1046/j.1466-822X.2001.00243.x)

Szeicz, J. M., Zeeb, B. A., Bennett, K. D. & Smol, J. P. 1998 High-resolution paleoecological analysis of recent disturbance in a southern Chilean *Nothofagus* forest. *J. Paleolimnol.* **20**, 235–252. (doi:10.1023/A:1007950905200)

Szeicz, J. M., Haberle, S. G. & Bennett, K. D. 2003 Dynamics of North Patagonian rainforests from fine-resolution pollen, charcoal and tree-ring analysis, Chonos Archipielago, Southern Chile. *Austral. Ecol.* **28**, 413–422. (doi:10.1046/j.1442-9993.2003.01299.x)

Troll, C. 1968 The cordilleras of the tropical Americas: aspects of climatic, phytogeographical and agrarian ecology. *Colloq. Geogr. (Bonn)* **9**, 15–56.

Troll, C. 1973 The upper timberlines in different climatic zones. *Arctic Alp. Res.* **5**, A3–A18.

Veblen, T. T. & Kitzberger, T. 2002 Inter-hemispheric comparison of fire history: the Colorado front range U.S.A., and the northern Patagonian Andes, Argentina. *Plant Ecol.* **163**, 187–207. (doi:10.1023/A:1020905823901)

Veblen, T. T., Kitzberger, T., Villalba, R. & Donnegan, J. 1999 Fire history in northern Patagonia: the roles of humans and climatic variation. *Ecol. Monogr.* **69**, 47–67. (doi:10.2307/2657194)

Villalba, R., Boninsegna, J. A., Veblen, T. T., Schmelter, A. & Rubulis, S. 1997 Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. *Clim. Change* **36**, 425–454. (doi:10.1023/A:1005366317996)

Walsh, S. J., Butler, D. R., Malanson, G. P., Crews-Meyer, K. A., Messina, J. P. & Xiao, N. 2003 Mapping, modeling, and visualization of the influences of geomorphic processes on the alpine treeline ecotone, Glacier National Park, MT, USA. *Geomorphology* **53**, 129–145. (doi:10.1016/S0169-555X(02)00350-1)

Watson, D. M. 2002 A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems. *J. Biogeogr.* **29**, 823–834. (doi:10.1046/j.1365-2699.2002.00726.x)

West-Eberhard, M. J. 1989 Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**, 249–278. (doi:10.1146/annurev.es.20.110189.001341)

Young, K. R. 1991 Natural history of an understory bamboo (*Chusquea* sp.) in a tropical timberline forest. *Biotropica* **23**, 542–554. (doi:10.2307/2388392)

Young, K. R. 1993*a* National park protection in relation to the ecological zonation of a neighboring human community: an example from northern Peru. *Mount. Res. Dev.* **13**, 267–280.

Young, K. R. 1993*b* Woody and scandent plants on the edges of an Andean timberline. *Bull. Torrey Bot. Club* **120**, 1–18. (doi:10.2307/2996657)

Young, K. R. 1993*c* Tropical timberlines: changes in forest structure and regeneration between two Peruvian timberline margins. *Arctic Alp. Res.* **25**, 167–174. (doi:10.2307/1551809)

Young, K. R. 1994 Roads and the environmental degradation of tropical montane forests. *Conserv. Biol.* **8**, 972–976. (doi:10.1046/j.1523-1739.1994.08040972.x)

Young, K. R. 1998*a* Deforestation in landscapes with humid forests in the central Andes: patterns and processes. In *Nature's geography: new lessons for conservation in developing countries* (eds K. S. Zimmerer & K. R. Young), pp. 75–99. Madison, WI: University of Wisconsin Press.

Young, K. R. 1998*b* Composition and structure of a timberline forest in north-central Peru. In *Forest biodiversity in North, Central and South America and the Caribbean: research and monitoring*, vol. 21 (eds F. Dallmeier & J. A. Comiskey). *Man and the biosphere series*, pp. 595–613. Carnforth, Lancashire, UK: Unesco and the Parthenon Publishing Group.

Young, K. R. & León, B. 1993 Observations on *Botrychium virginianum* (Ophioglossaceae), a fern uncommon in the eastern Andes of Peru. *Am. Fern J.* **83**, 93–96. (doi:10.2307/1547459)

Young, K. R. & León, B. 1995 Connectivity, social actors, and conservation policies in the central Andes: the case of Peru's montane forests. In *Biodiversity and conservation of neotropical montane forests* (eds S. P. Churchill, H. Balslev, E. Forero & J. L. Luteyn). Bronx, NY: New York Botanical Garden.

Young, K. R. & Keating, P. L. 2001 Remnant forests of Volcán Cotacachi, northern Ecuador. *Arctic Antarct. Alp. Res.* **33**, 165–172. (doi:10.2307/1552217)

Young, K. R. & León, B. 2001 Perú. In *Bosques Nublados del Neotrópico* (eds M. Kappelle & A. D. Brown), pp. 549–580. Heredia, Costa Rica, DC: INBio.

Young, K. R. & Lipton, J. K. 2006 Adaptive governance and climate change in the tropical highlands of western South America. *Clim. Change* **78**, 63–102. (doi:10.1007/s10584-006-9091-9)

Young, K. R., Ulloa Ulloa, C., Luteyn, J. L. & Knapp, S. 2002 Plant evolution and endemism in Andean South America: an introduction. *Bot. Rev.* **68**, 4–21. (doi:10.1663/0006-8101(2002)068[0004:PEAEIA]2.0.CO;2)