

## **Gradients of Plant Diversity: Local Patterns and Processes**

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Patterns of plant diversity can be studied at different spatial scales, which, for convenience, can be divided into two overlapping categories (Srivastava 1999, Magurran 2004): Regional diversity (also known as gamma diversity) concerns the number of species in large geographical regions such as countries or biomes and is explored in Jørgensen et al., Chapter 13, this volume. Local richness (also known as alpha diversity) refers to the number of species co-occurring in areas of limited size, typically  $\leq 1$  ha. Studies of plant diversity at these two scales are subject to different methodological constraints and reveal different ecological aspects shaping plant diversity. Both methodologies have their special characteristics: regional species lists are typically incomplete, especially in tropical regions, whereas local surveys tend to be much more complete. On the other hand, local inventories only cover a minute portion of the land surface and are often conducted with different sampling methods, making it difficult to compare results across different studies. Also, whereas at the local scale all recorded plant species actually co-occur and thus potentially interact ecologically with each other through competition, facilitation, etc., at the regional scale many species occur in geographically or ecologically remote sites without direct interactions. However, because of the dispersal of individuals through populations, interactions can also play out over large, environmentally heterogeneous regions rather than only within local communities in relatively uniform habitats (Ricklefs 2004). Alpha and gamma diversity are connected through the degree of change in composition from one plot to another (beta diversity).

In the present chapter, we first briefly review patterns of local plant species richness along three important geographical and ecological gradients (latitude, elevation, amount and seasonality of precipitation). We do not specifically address other gradients such as energy availability or soil fertility because relevant data are very sparse for the tropical Andes. Then, we focus on the mechanisms and processes that determine and influence these patterns, because an understanding of the underlying causes is relevant for predicting possible responses of plant assemblages to climate change. Our focus is on natural habitats without human or natural disturbance, but diversity is also influenced by the disturbance regime of the sampled area.

## Patterns

### *Latitude*

Latitude itself is not an ecological factor directly affecting plant diversity (Hawkins and Diniz-Filho 2004). Rather, numerous ecological factors that vary with latitude may be responsible for creating latitudinal diversity patterns. Latitudinal patterns of plant diversity in the tropical Andes have mainly been studied at the regional scale (Jørgensen et al., Chapter 13, this volume). In contrast, there are very few specific studies using local plots to assess latitudinal trends in plant diversity. In Ecuador, Sklenár and Ramsay (2001) used a consistent sampling scheme to study plant diversity and community composition in páramos on volcanoes spanning some four degrees of latitude, but the focus of this study was on the effect of climate, geology, and topography, rather than latitude per se. Young and León (2007) showed that the diversity of trees and shrubs was an order of magnitude greater at a tropical timberline site compared to subtropical and mid-latitude sites in the Andes.

Compilations from different studies show that the diversity of woody plants (trees and lianas) increases with decreasing latitude in similar habitats and elevation, with marked declines around the Tropics of Cancer and Capricorn (e.g., Gentry 1982, 1988, 1995, Phillips and Miller 2002, Willig et al. 2003, Macía and Svenning 2005, Schnitzer 2005, Weiser et al. 2007). Whereas different Andean forests at a given elevation are similar in floristic composition at the generic and family levels, species composition varies strongly between sites. For epiphytes, local-scale inventories show that in the lowlands highest species numbers are found in Colombia and Ecuador (Ibisch 1996, Nieder et al. 1999, Acebey and Krömer 2001, Krömer and Gradstein 2003, Arévalo and Betancur 2004, Kreft et al. 2004, Benavides et al. 2005, Krömer et al. 2005, Krömer et al. 2008). These trends are primarily driven by decreasing numbers of Araceae and to a lesser degree of Orchidaceae away from the equator. In contrast, epiphyte inventories from montane sites (Ibisch 1996, Krömer and Gradstein 2003, Krömer et al. 2005) differ much less between countries, with, e.g., 196 species found on 10 canopy trees and its surroundings in Otonga, Ecuador (Nieder et al. 1999), versus 207 species found in 9 canopy tree plots in Mosetenes, Bolivia (Krömer et al. 2008). The diversity of ferns also remains roughly constant in humid montane forests at similar elevations within the tropical regions from Costa Rica to central Bolivia, and only drops noticeably further north and south as one reaches subtropical latitudes (Kessler 2001a, Kluge et al. 2006, Kessler and Kluge unpubl. data).

### *Elevation*

As with latitude, elevation as such does not directly influence plants (Körner 2000, 2007). Rather, it is factors that are either directly related to elevation (e.g., air pressure, temperature) or that have a more complex relationship with elevation (available surface area, precipitation, etc.) that affect plants growing at different elevations.

Elevational patterns of local plant species richness have been studied much more intensively than latitudinal ones. For trees and lianas diversity is constantly high from the lowlands to about 1500 m, although a slight mid-elevation hump has also been found (La Torre-Cuadros et al. 2007). Below 1500 m, Leguminosae are the most important tree family, and Bignoniaceae and Leguminosae the most important for lianas (Gentry 1991, Macía et al. 2007, Macía 2008). Above this elevation, there is a linear decrease in species richness with elevation, and the floristic composition is dominated by montane genera and families such as Lauraceae, Melastomataceae, and Rubiaceae (Gentry 1995, Macía and Fuertes 2008). In the

case of lianas, Asteraceae become predominant. Tree ferns are much more prevalent in mid-elevation forests, at 1200–1700 m (Gentry 1995). At the highest elevations, above 3000 m and near the timberline, floristic composition again changes dramatically and Asteraceae becomes one of the most important families together with Melastomataceae and Myrsinaceae, although this family composition may change locally. Here, lianas become scarce (Young 1993). The highest montane forests (3000 to >5000 m) are patchy in distribution and consist of monospecific stands of *Polylepis* spp. (Rosaceae) from Ecuador southwards, but they are more diverse in Colombia with about 4–6 other tree species and few lianas.

Focusing on individual woody and herbaceous plant families, mid-level maxima of elevational richness have been found in Bolivia for Acanthaceae, whereas Arecaceae and Melastomataceae have roughly constant richness to about 1000 m, followed by strong declines to high elevations (Kessler 2001b). Epiphytic plant species richness typically shows a mid-elevation bulge that peaks at 1500–1700 m (Cleef et al. 1984, Wolf 1994, Muñoz and Küper 2001, Krömer et al. 2005). Ferns also show such hump-shaped patterns, with maximum richness values at 1700–1800 m (Kessler 2001a,b, Kessler et al. 2001), while richness of Bromeliaceae peaks at 1000–1900 m (Kessler 2001a, Krömer et al. 2005, 2006). Araceae deviate from this general pattern in having highest local species counts in the lowlands (Ibisch et al. 1996, Kessler and Croat 1999). The recorded upper elevational limit of vascular plants increase from around 4800 m in Ecuador to 5400 m in southern Peru and 5800 m in Bolivia (Halloy 1989, Seimon et al. 2007).

### *Amount and Seasonality of Precipitation*

Unlike the previous two factors, the availability of water, either through vertical (rain) or horizontal (fog) precipitation, or from ground water, directly affects plant growth and community composition. The tropical Andean region includes practically the entire range of humidity conditions experienced by plants on the globe, ranging from the Atacama desert, which has been practically rain-free for over 10 million years (Placzek et al. in press), to the perhumid Chocó region in Colombia, one of the world's wettest areas with up to 15 m mean annual precipitation (Galeano et al. 1998). Patterns of water availability often co-vary with other ecological or geographical gradients, making it difficult to separate the influences of different factors. Thus, the western Amazon basin experiences highest precipitation levels in Ecuador and declining values both to the north and the south, although with local pockets of high rainfall along the east Andean base (Killeen et al. 2007). Cloud condensation often peaks at mid-elevation on tropical mountains, although cloud forests can also be found at low elevations (Gradstein 2006). Although humidity shows some broad gradients, it is highly heterogeneous at a much smaller scale; within kilometers or even hundreds of meters conditions may vary from perhumid to semi-arid, and this is repeated throughout mountainous terrains.

There have been few studies specifically designed to study the influence of water availability on plant community diversity and composition in the tropical Andes. However, all available information shows that overall plant diversity typically declines with decreasing water availability, with the exception of a few drought-adapted families. In central Bolivia, e.g., in three almost adjacent plots of 1 ha differing in water availability, overall plant diversity declined from the wet to the dry site, although some specific plant families such as Bromeliaceae and Cactaceae showed opposite patterns (Linares-Palomino et al. 2008, 2009). Trees and lianas have a strong relationship with water availability, reflecting annual rainfall and rainfall seasonality at all geographical scales (Gentry 1988, Clinebell et al. 1995, Schnitzer 2005). The same pattern was also documented for palms throughout the Americas

by Bjørholm et al. (2005), an example of a large-scale study that documents local scale patterns. One of the most striking distributional patterns shown by epiphytes is a tremendous decrease in both numbers of species and individuals in drier habitats. Already Schimper (1888) considered air humidity to be the most important factor determining epiphytic plant diversity, a suggestion followed by Gentry and Dodson (1987), Kessler (2001a), Kreft et al. (2004), Küper et al. (2004), and Krömer et al. (2005), among many others. Ecophysiologicaly, this relationship appears to be well founded, as water availability is of critical importance to epiphytes (Benzing 1990, Zotz and Hietz 2001). One main difference between lowland and montane forests is that regular dry periods, but also periodically occurring events such as El Niño, reduce the abundance and diversity of epiphytes in Amazonian lowland forests. In contrast, in montane rain forests, the impact of dry periods is mitigated by 'horizontal precipitation', which in cloud forests frequently contributes 20% or more to total water input (Hölscher et al. 2004, Thies et al. 2008). Local species richness of ferns is also closely linked to water availability (León and Valencia 1989, Kessler 2001a).

## Processes

Understanding the ecological processes determining these patterns will help us make predictions with respect to the potential impacts of future environmental changes and for predicting plant diversity in undersampled regions, which is important for identifying areas of high conservation value. In addition, to give a better understanding of the most important factors in the region, studies of diversity patterns in the tropical Andes with their steep environmental gradients, have the potential to play an important role in understanding the processes behind global diversity patterns.

Recently considered, partly interlinked explanations for richness patterns involve five groups of processes and mechanisms (Grytnes and McCain 2007)(Table 14.1). As with the surveys of patterns, an analysis of the processes and mechanisms influencing the patterns must distinguish between regional and local scales. Direct ecological interactions such as competition and facilitation take place at the local scale while regional patterns are more likely to reflect historical, evolutionary, and biogeographical processes, although dispersal may link these scales and their processes (Ricklefs 2004). Several of the explanations, both at the local and regional scales, involve climatic factors, which therefore allow direct inferences to be made regarding possible effects of climate change. There is general agreement that more than one of these factors plays a role and that their relative impact depends on the spatial and temporal scale, as well as on the taxon under consideration, but it is still unclear when and how any of these factors predominate (e.g., Cornell and Lawton 1992, Gaston and Blackburn 2000, Ricklefs 2004, Shurin and Srivastava 2005). Contrasting patterns in the tropical Andes may give valuable clues to a better understanding of this.

The influence of area on species richness is well-documented at all scales (Rosenzweig 1995) and has been implicated in determining patterns of species richness through a variety of mechanisms (e.g., Losos & Schluter 2000, Stropp et al. 2009; see Table 14.1). However, area alone can probably not fully explain patterns of species richness along latitudinal and elevational gradients and typically only modifies the more basic patterns determined by climatic and other factors (Rahbek 1995, McCain 2007, Romdal and Grytnes 2007). For example, the Altiplano region of the central Andes has a larger surface area than the adjacent slopes but much lower plant diversity because of its low temperatures and aridity. Thus, although area always has to be considered (or controlled for) when interpreting patterns of species richness, it can rarely be considered to be the main cause. Population processes such as dispersal limitation or source-sink effects have a potential to modify

**Table 14.1.** Summary of some important potential processes and mechanisms that may determine or influence regional (reg) and local (loc) patterns of species richness. “+” indicates the scale at which these may become relevant, a “-” indicates that this factor is unlikely to be of major importance at a given scale.

Processes and Mechanisms	Predicted scale of impact	
	reg	loc
<b>1. Area</b>		
<i>key sources:</i> Lomolino 2001		
a Larger area – higher number of individuals – decreased extinction risks – larger number of species (" <i>Island Biogeography</i> ": MacArthur and Wilson 1967).	+	-
b Smaller area – lower number of individuals – faster genetic changes at population level – faster evolution of new species (Losos and Schluter 2000).	+	-
c Larger area – higher number of habitats – larger number of species (Kallimanis et al. 2008).	+	+
d Larger species pool due to larger area (see above) – higher local richness (" <i>Echo effect</i> ": Rosenzweig and Ziv 1999).	-	+
e Larger sampling areas – larger number of species recorded (Gleason 1922, Rosenzweig 1995).	+	+
<b>2. Climatic variables – energy – productivity</b>		
<i>Key sources:</i> Rohde 1992, Mittelbach et al. 2001, Rahbek and Graves 2001, Hawkins et al. 2003, Willig et al. 2003, Currie et al. 2004, Evans et al. 2005, Mönkkönen et al. 2006, Laanisto et al. 2008		
a More energy – higher productivity – larger number of individuals – larger number of species (" <i>Sampling Hypothesis</i> ": Srivastava and Lawton 1998, Kaspari et al. 2000).	-	+
b More energy – higher productivity – larger number of individuals – decreased extinction risks – larger number of species (" <i>Population Size Hypothesis</i> ": Kaspari et al. 2000, Hurlbert 2004, Pautasso and Gaston 2005, 2006).	+	+
c More energy – higher productivity – larger number of rare resources – larger number of niche position specialists (" <i>Niche Position Hypothesis</i> ": Abrams 1995).	-	+
d More energy – higher productivity – reduced niche breadth by focusing on preferred resource types – increased co-existence (" <i>Niche Breadth Hypothesis</i> ": Evans et al. 2005).	-	+
<b>3. Historical and evolutionary processes</b>		
<i>Key sources:</i> Wiens and Donoghue 2004, Ricklefs 2005, Roy and Goldberg 2007, Jablonski et al. 2006		
a Under specific conditions, speciation rates may be higher, increasing species richness (" <i>Tropics as a Cradle Hypothesis</i> ": Cardillo 1999).	+	-
b Under specific conditions, extinction rates may be higher, reducing species richness (" <i>Tropics as a Museum Hypothesis</i> ": Stebbins 1974).	+	+
c Phylogenetic lineages may be older in some areas than in others, thus providing more time for diversification (" <i>Out of the Tropics Hypothesis</i> ": Jablonski et al. 2006; " <i>Niche Conservatism Hypothesis</i> ": Wiens and Donoghue 2004).	+	-
<b>4. Null models and neutral theories</b>		
<i>Key sources:</i> Gotelli and Graves 1996		
a Variations in the dispersal ability of species, their population size, and the immigration (resp. speciation) rate determine the composition and abundance distribution of species (" <i>Neutral Theory of Biodiversity and Biogeography</i> ": Hubbell 2001).	+	+
b Random placement of species with different species-specific geographical or ecological amplitudes within a constrained geographical or ecological domain leads to maximum richness in the middle of the domain (" <i>Mid-Domain Effect</i> ": Colwell and Hurtt 1994, Colwell et al. 2004).	+	-
<b>5. Population dynamics</b>		
a Dispersal from suitable habitats to less suitable habitats can create non-self-supporting sink populations, especially at locations surrounded by numerous habitats such as mid-elevations on mountains (" <i>Source-sink effects</i> ": Shmida and Wilson 1985, Pulliam 1998, Kessler 2000, Grytnes et al. 2008a).	-	+
b Limitations in dispersal may limit the number of species that occur in an area or site, despite potentially suitable conditions (" <i>Dispersal Limitation</i> ": Tilman 1997, Turnbull et al. 2000).	+	+

patterns of species richness at the local scale (Grytnes et al. 2008a), but it is unclear how strong their impact is (Kessler 2009). There are essentially no studies that allow a quantitative evaluation of the importance of population processes on patterns of species richness. These require population-level studies of reproduction and dispersal, and although such studies require long-term efforts, they are indispensable and urgently needed.

In the study of the remaining factor complexes, null models are probably the most debated (Clark 2008). Mid-domain effect (MDE) models have been shown to correlate closely to diversity patterns especially along some elevational gradients (Kessler 2001b, Colwell et al. 2004, McCain 2004), but the meaning and implications of these models is hotly debated on theoretical grounds (Bokma and Mönkkönen 2000, Colwell and Lees 2000, Jetz and Rahbek 2001, Hawkins and Diniz-Filho 2002, Grytnes 2003, Colwell et al. 2004, Herzog et al. 2005). In its most extreme form, the MDE model predicts that the diversity patterns should primarily be dependent on the upper and lower boundary of the domain. This would imply that all groups of organisms should show very similar patterns and that similar patterns should be found when comparing different regions (e.g. the western and eastern slopes of the Andes), which is clearly not the case, as exemplified by the wide range of elevational richness patterns discussed above. However, the mid-domain effect may still be a modifying factor (Grytnes et al. 2008b). Hubbel's (2001) null model, which assumes that species are ecologically equivalent, has commonly been found not to apply at regional scales and across strong ecological gradients, where niche assembly models appear to be more adequate (e.g., Harms et al. 2001, Phillips et al. 2003, Tuomisto et al. 2003, Jones et al. 2006, 2007, Ruokolainen et al. 2007). However, it may still be important for the maintenance of high local diversity when the environment is homogenous (Hubbel 2001).

The remaining two factor complexes (climate/productivity and history/evolution) are most likely to include the most important processes and mechanisms, and should probably receive most research attention. One of the long-standing debates in biodiversity research is to which degree local diversity is either limited by local resources (niche or energy availability) in concert with species interactions (competition, herbivory, etc.) or by a limited regional species pool (Terborgh and Faaborg 1980, Ricklefs 1987, 2004, Cornell and Karlson 1996, Herzog and Kessler 2006, Jiménez et al. 2009). In the latter case, more species could co-occur at a given site but are simply not available within the historical and evolutionary framework of that particular region.

Ecosystems with a high level of productivity are believed to exhibit high levels of species richness, and there are several mechanisms suggested to be the link between these two ecosystem properties. These mechanisms involve the number of individuals and levels of niches and resources (see Table 14.1) and all predict a positive correlation between energy input and species richness at a local scale. However, the most challenging aspect in addressing the species-energy hypothesis is getting the appropriate measure for productivity at the ecosystem level (Waide et al. 1999) and of the amount of energy that is used by a given focal group (Gaston 2000, Chase and Leibold 2002). Important theoretical and empirical advances have recently been made, at least with regard to trees, and important insights are to be expected in the near future (Mittelbach et al. 2001, Hawkins et al. 2007).

The past few years have seen considerable effort directed at generating time-referenced phylogenetic hypotheses that may allow an assessment of historical evolutionary hypotheses (Antonelli 2008). However, only a tiny proportion of tropical Andean plants has been included in these efforts, and for those groups for which data are available, their interpretation is frequently limited by geographically or taxonomically incomplete sampling, or by difficulties in obtaining reliable age estimates. For example, Linder (2008) proposed that plant radiations may saturate (i.e., reach stable limits of species richness) after roughly 10 million years, and that young radiations are typical of young (Pliocene) environments

whereas mature radiations are characteristic of regions that have been geologically and climatically stable throughout the Neogene. He concluded that “the hyperdiverse Neotropical flora is the result of both mature as well as recent and rapid radiations”. As intriguing as it is, Linder’s (2008) study only included seven Neotropical examples. Clearly, additional efforts have to be directed at generating a larger number of geographically and temporally explicit phylogenetic hypotheses of tropical Andean plants. Further, analytical approaches have to be refined to be able to distinguish between alternative hypotheses. For example, in a case study of Neotropical frogs, Algar et al. (2009) conclude that the phylogenetic processes can only determine which species occur in a given area, but not how many species, and that species numbers may actually be determined by local ecological processes. Yet, for higher taxonomic levels (families, genera), well-resolved phylogenetic hypotheses are available for many taxa (<http://www.tolweb.org/tree/> ; <http://www.mobot.org/mobot/research/apweb/welcome.html>) and recent work has resulted in free open software that allows ecologists to make use of the available phylogenetic information (<http://www.phylodiversity.net/phylocom/>). Clearly, the time is ripe to link ecological and phylogenetic information.

## Conclusions and Research Recommendations

The knowledge of local patterns of plant diversity in the tropical Andean region remains fragmentary. Elevational patterns are documented best, while latitudinal and moisture gradients have been neglected. To complicate matters, many studies have employed different methods (plot size and shape, plant groups included), which makes it difficult to compare data from different surveys and regions.

Despite these shortcomings, it appears to be possible to arrive at some rough, preliminary generalizations on patterns of plant diversity. In the western Amazonian lowlands, overall plant diversity appears to be highest around equatorial latitudes, declining towards higher latitudes. In contrast, on the eastern Andean slope richness remains roughly constant in the tropical regions south to about 18°S, and only then declines markedly. The western Andean slope has high local diversity in Colombia and northern Ecuador which declines strongly further south. Probably, floristic turnover from site to site remains high throughout the tropical Andes, but specific studies of beta diversity along environmental gradients are needed. Above the treeline, species richness exhibits complex latitudinal patterns related to topography and its influence on moisture regimes. High species richness in the equatorial páramos declines towards the north and south as humidity decreases. South of around 10°S an east-west gradient also becomes dominant, with diverse cloud-grasslands to the east and poorer semi-arid to arid altiplano in the center and west.

Along elevational gradients, overall plant diversity appears to show a hump-shaped pattern with maximum richness at around 1000–1500 m in humid regions (Rahbek 1995, 2005) and higher in arid ones (Lauer 1976). This pattern appears to be mostly driven by terrestrial and epiphytic herbaceous taxa, whereas woody plants show a more gradual decline of richness with elevation. Above treeline, release from arboreal competition may produce a pronounced increase in species richness of herbaceous and shrub species, particularly in tussock and shrub paramo. Finally, with the exception of a few specialized taxa, plant diversity generally decreases with increasing aridity. Overall, these patterns thus closely reflect the regional patterns outlined in Jørgensen et al., Chapter 13, this volume. However, detailed comparisons of local and regional patterns have only been conducted for ferns along elevational gradients, where they reveal minor but potentially important differences of biological significance (Kessler et al. 2009).

Despite the wide range of discussion about the processes that determine richness patterns, the most promising approaches are certainly held by evolution/history at the regional and climate/productivity at the local scale. Recent literature provides hypotheses to test underlying mechanisms, but specific field studies are few, because fully resolved phylogenetic trees of study groups are rarely available and because the development of a consistent measure of productivity is a difficult task. However, comparing prevalent richness patterns with surrogates of productivity may lead to rough conclusions about the processes driving these patterns. For example, comparisons of the arid western and humid eastern Andean slopes in Peru may help to unravel the impact of water availability on local plant species richness. Because climatic factors directly influence levels of ecosystem productivity, understanding the causal relationships between productivity and species richness will be critical for predicting responses of plant assemblages to climate change (Colwell et al. 2008).

To meet the needs for documenting and monitoring levels of species richness, and to predict responses to climate change, three main lines of activity are needed. First, additional well-designed surveys aimed at testing hypotheses are necessary, ideally tackling those ecological gradients that have been neglected to date. Second, networks of permanent plots are needed to monitor future changes in plant community richness and composition to determine the effects of climate change on plant communities. The GLORIA project ([www.gloria.ac.at](http://www.gloria.ac.at)), which focuses on high-elevation sites above treeline (Halloy et al. 2008), and the extensive network of 1-ha tree plots in Amazonia are important steps in this direction, ([www.geog.leeds.ac.uk/projects/rainfor/](http://www.geog.leeds.ac.uk/projects/rainfor/)) and a similar, badly needed initiative (Rainfor-Andes) is about to start in highly diverse Andean forests. Third, well-designed experimental and observational studies on the relationship between ecosystem productivity and local species richness are needed, with the aim of distinguishing between different potential mechanisms that in turn predict different responses to climate change (Evans et al. 2005). Those data should also be linked to the increasingly available phylogenetic information.

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