

## The patterns and causes of elevational diversity gradients

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A major focus of research in spatial ecology over the past 25 years has been to understand why the number of species varies geographically. The most striking, and perhaps best documented, pattern in spatial ecology is the latitudinal gradient in species diversity in which the number of species, for most taxa, declines with increasing latitude. Understanding the underlying cause(s) of the latitudinal gradient has proven challenging, perhaps because there are really only two latitudinal gradients (in the northern and southern hemispheres), and because it is often difficult to perform experiments at latitudinal scales.

Elevational gradients in species diversity are nearly as ubiquitous as latitudinal gradients, and they offer many characteristics that make them perhaps more suitable for uncovering the underlying cause(s) of spatial variation in diversity. First, there are many replicates of elevational diversity gradients – essentially each mountain or mountain range is a replicate, so it is possible to test for the generality of the underlying cause(s). Second, it is possible to carry out manipulative experiments along elevational gradients. Third, field data can be collected more readily along elevational gradients than along latitudinal gradients, simply because the

spatial extent of elevational gradients is small relative to latitudinal gradients. Finally, many of the potential underlying causes that covary along latitudinal gradients (history, climate, time since glaciation, area) do not covary along elevational gradients (Körner 2007).

Given the benefits of elevational gradients relative to latitudinal gradients, it seems clear that they can be useful tools to understand the underlying cause(s) of diversity gradients. And, in fact, there is a growing appreciation of the utility of elevational gradients as tools to uncover the mechanisms that shape both patterns of biodiversity and the functioning of ecosystems (Fukami and Wardle 2005, Nogues-Bravo et al. 2008).

Ecography has played a major role as an outlet for many studies of elevational gradient studies, and in fact such studies are one of the strengths of the journal. Since its inception, Ecography has published more than 25 papers that have explicitly focused on elevational diversity gradients. The papers highlighted in this Virtual Issue indicate that Ecography has been, and will continue to be, an important outlet for papers at the cutting edge of documenting and explaining elevational gradients in diversity.

Here, our goal is to highlight some elevational diversity gradient papers published in Ecography (bold-face in reference list) that we feel have made long-lasting contributions to the study of spatial ecology. This Virtual Issue (<http://tinyurl.com/cr2lkew>) is about elevational diversity gradients, though we recognize that a number of key papers have been published in Ecography on topics ranging from montane diversity at regional or continental scales (Parra et al. 2004, Ricklefs et al. 2004, Ruggiero and Kitzberger 2004, Ruggiero and Hawkins 2008), population dynamics (Ramirez et al. 2006, Gimenez-Benavides et al. 2011), interactions among species (Fuentes et al. 1992, Mazia et al. 2004), adaptation (Berner et al. 2004), and climate change (Dollery et al. 2006).

### The patterns

Nearly 20 years ago, one of us (Rahbek 1995) asked whether the conventional wisdom about elevational diversity gradients – that they mirrored the latitudinal gradient and declined with elevation – was supported by the data.

Examining all of the literature (at the time, 97 papers) on elevational diversity gradients showed that the answer was, for the most part, 'no'. Most studies, when sampling effort was corrected for, showed hump-shaped diversity gradients, with diversity peaking at mid-elevations.

The quantitative review of published studies by Rahbek (1995) to document the generality (or lack thereof) of the pattern was illuminating. The studies in Rahbek's paper were from various mountain ranges, and on various taxa. One reason that different patterns of elevational diversity might occur in different systems may be that the scale and extent of the elevational gradients varied among studies (Rahbek 2005, Nogues-Bravo et al. 2008) or because different mountain ranges are embedded in different regional climatic areas with different evolutionary histories. This is an under-appreciated fact in comparative studies of elevational diversity gradients.

Another approach to examine generality of elevational diversity gradients is to focus on several replicate elevational gradients within the same region, so that species occurring along the gradient might come from the same regional species pool and share similar evolutionary histories. This was the approach of Grytnes (2003), who sampled plant diversity along seven transects in northern Norway, Wang et al. (2009) who sampled tree and herb communities along six elevational gradients in northeast China, and of Sanders (2002) who compiled regional lists of the ants of Colorado, Nevada and Utah. In those studies, the patterns differed slightly among replicate samples, but the underlying causes were similar within each gradient. These results contrast with a study on non-volant mammals in several mountain ranges in Utah by Rowe (2009). In that study, the patterns of diversity with elevation were similar, but the underlying mechanisms differed among mountain ranges.

But most of the elevational diversity gradient studies that have been published in *Ecography* have come from investigators who have compiled empirical data for a given taxon in a particular mountain range. These studies might differ in the extent and scale at which diversity is sampled, ranging from Herzog et al.'s (2005) data on bird diversity in 250 m elevational bands in the Andes to Grytnes's (2003) 25 m<sup>2</sup> plots in Norway. Regardless of the differences in sampling and extent among studies, most agree with the results from Rahbek's (1995) review of the literature: in most instances, diversity peaks at mid-elevations, with a few notable exceptions (Brehm et al. 2003, Machac et al. 2011).

## The underlying causes

A number of factors have been implicated as underlying causes of elevational diversity gradients. Some of the most frequently tested are climate and productivity (Rahbek 1995, Odland and Birks 1999, Grytnes 2003, Fu et al. 2006, Rowe 2009, Wang et al. 2009), source-sink dynamics (Kessler et al. 2011), area (Rahbek 1995, Sanders 2002, Jones et al. 2003, Bachman et al. 2004, Herzog et al. 2005, Romdal and Grytnes 2007), disturbance (Escobar et al. 2007, Bunn et al. 2011), geometric constraints (Sanders 2002, Bachman et al. 2004, Herzog

et al. 2005, Fu et al. 2006, Rowe 2009) and evolutionary history (Machac et al. 2011). The diversity of results among studies, and even within studies, suggests that no single mechanism is responsible for all elevational diversity gradients. Future studies, many of which are likely to be published in *Ecography* (we hope), will move the field forward, perhaps by examining the interplay between contemporary and past climate (Hortal et al. 2011), integrating ecology and evolution (Graham et al. 2009, Machac et al. 2011), employing new tools (Levanoni et al. 2011) and demonstrating the effects of climatic change on current (Forister et al. 2010) and future patterns of biodiversity (Colwell et al. 2008).

Papers published in *Ecography* have been some of the first to test explicitly many of these mechanisms, and their generality. As the number of studies on elevational diversity gradients continues to grow (more than 300 as of 2011), *Ecography* will continue to play a role in shaping the field and helping to uncover the mechanisms which shape broad-scale variation in species richness, especially along elevational gradients.

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