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Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research

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Tropical forests have a major influence on global patterns of biodiversity, ecosystem ecology, productivity and biogeochemical cycles, but they remain relatively understudied. Moreover, our understanding of many global patterns (e.g. of how biodiversity, ecophysiology or ecosystem function vary with latitude) are often influenced by a handful of data points from tropical latitudes (in contrast to swarms of data points from temperate regions). The result is that the wet tropics are often treated as a warm, wet 'end-point' of most global analyses. However, comparison of tropical with extratropical regions is not straightforward, because of the vast geographical separations involved that lead to complications resulting from both biogeography and climate. The sheer size of the tropical zone implies further that comparison is necessary *among* tropical biomes, not just between climate zones.

Here we argue that our understanding of ecosystem ecology and function can be greatly advanced by considering environmental gradients within the tropics, whether gradients of moisture or of other climate variables. In particular, the use of elevation gradients within the tropics is a particularly powerful tool to further understanding of the influence of temperature on the biodiversity, ecology, ecosystem function and global change response of forest ecosystems. Since the explorations of von Humboldt (von Humboldt & Bonpland, 1805), the importance of tropical elevational gradients to biodiversity has been noted, and species distribution has been recognized to be a function of climatic and edaphic factors. Now, more than ever before, we are acutely aware that these environmental factors are likely to change at rates without recent parallel (Vuille *et al*., 2003; Bush *et al*., 2004; Urrutia & Vuille, 2009). Montane forest systems are under threat of destruction and dislocation. Deepening our understanding of their composition and function is an essential step to providing an adequate baseline for evaluating future change. We identify five major justifications for investing effort in studying these systems.

First, high elevation tropical ecosystems are intrinsically interesting, being evolutionarily and ecologically distinct from the lowland tropics, but are often considered simply as an upslope extension of those systems. Tropical montane ecosystems are even more poorly researched than the lowland tropics (Bubb *et al*., 2004). Key features include unique species composition, largely unknown soil communities and processes, a climate frequently influenced by cloud immersion and low transpiration rates, large stocks of soil organic matter and litter, and temperatures that are persistently cool and aseasonal, but without freezing (Grubb, 1977).

Second, species turnover along elevation gradients accounts in large part for the high diversity in many of Earth's most important biodiversity hotspots, with ~70 000 endemic species found in 11 hotspots involving tropical montane environments. The Tropical Andes Biodiversity Hotspot alone is estimated to host one-sixth of all plant species in <1% of earth's land area (Myers *et al*., 2000). Understanding the patterns and causes of this turnover is important in understanding the biodiversity richness of these hotspots, and the fate of these hotspots under global change (Sommer *et al*., 2010).

Third, tropical montane elevation transects make excellent natural laboratories for understanding environmental controls on ecosystem function, especially temperature. Manipulations and controlled laboratory studies can yield insights into short-term responses of organisms or ecosystems to changes in climate, but understanding of longer-term responses (acclimation, adaptation, community turnover) requires the use of transect studies. When examining temperature responses of biological or biophysical processes, the temperature gradients over time or space within the lowland tropics tend to be shallow, in contrast to the large gradients in temperature and other variables that elevation transect studies offer.

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Latitudinal gradient studies (or elevation gradients in mid- or high-latitude regions) are often complicated by variations in the length and intensity of the dormant (e.g. low temperature) season. It is challenging to unravel the confounding effects of temperature seasonality from the direct effects of alterations in temperature. In most tropical elevation gradients, a dormant season driven by cold temperature is largely absent. With appropriate selection, moisture variation can also be limited in tropical elevation gradients, leading to isolation of temperature as the key driver of variation in ecological properties. Of course, such transects are still far from perfect, as many other environmental variables co-vary with elevation (e.g. cloudiness, atmospheric density, absolute O_2 or CO_2 concentrations, UV radiation), but with careful interpretation such transects do have the potential to generate new insights into temperature controls on ecosystem structure and function (Korner, 2007).

Another complication in the use of latitudinal gradients is that historical biogeographical contingencies can have a strong influence in explaining compositional differences across large, intercontinental, distances. Over the relatively short distance of elevation gradients, the potential species pool is well-mixed, and almost all shifts in function or composition are likely related to direct environmental control rather than historical contingency.

The relatively small distances in elevation gradients involved also make elevation transects good locations for translocation or transplant experiments (e.g. translocation of soil cores or litter bags, transplanting of seedlings upslope to assess migration potential, or downslope to impose experimental warming).

Fourth, tropical elevations are excellent sites for understanding past climate change in the tropics (van der Hammen & González, 1959; Hooghiemstra & van der Hammen, 2004), presenting strong gradients and relatively sharp ecotones that allow palaeoecological and palaeoenvironmental records to be highly sensitive to even small changes in climate. These palaeorecords include information not only on climate, but also describe the alterations in species distributions that may be correlated with changes in both temperature and moisture availability. Analysis of these data has also revealed teleconnections from the tropics to the arctic, linking tropical ecosystem behaviour with climate and sea surface temperatures (Baker *et al.*, 2001). Anthropogenic change is also evident in these records, and they allow fine scale reconstruction of past human effects on ecosystems, and human responses to changing climate (Chepstow-Lusty *et al.*, 2003; Valencia *et al.*, 2010).

Fifth, with their strong gradients, small spatial distances and sharp tree line ecotone, tropical elevation gradients are excellent sites for monitoring ongoing and future impacts of atmospheric change in the tropics. In terms of responses to climate, it has been argued that tropical biota may be more sensitive to change than temperate or high latitude biota, because the magnitude of projected temperature change relative to current or prehistoric temperature ranges is greater than for higher latitudes (e.g. Deutsch *et al.*, 2008). Tropical organisms may have relatively narrow thermal niches (Janzen, 1967), and therefore the responses to warming (whether by acclimation, adaptation, dispersal/migration or decline) may be relatively greater, than for their temperate or arctic counterparts, and thus these changes may be easier to detect.

Finally, tropical mountains are potential arks for biodiversity in a century of rapid warming. One of the great unknowns in our understanding of the potential impacts of atmospheric change on biodiversity in the tropics is whether many tropical species have a narrow thermal niche and are close to a thermal limit where they will experience declines in function or fitness, or whether most species are able to acclimate, acclimatize or adapt to current or future warming. If the former is true (and for some species it must be so), climate pressure in the lowlands may lead to tropical mountains being essential refugia. Indeed, they already may be, as many species now considered 'montane' were widespread in lowland Amazonia during much of the Pleistocene (e.g. Liu & Colinvaux, 1985; Bush *et al.*, 1990). As well as cooler temperatures, montane regions also host a large diversity of microclimates driven by differences in aspect and slope that are likely to provide further refuge to some species unable to cope with lowland temperatures. Microclimates play an important role in the beta-diversity of montane ecosystems, with large variability according to topography, local rain-shadows, orientation of exposure, cloud formation and hydrology. Special variants of such microclimates are those that provide microrefugia; persistent and unusual microclimates that provide potential nuclei for rapid population expansion as climatic conditions change (Rull, 2009). Other effects, though, such as shifting cloud bases, different patterns of disturbance, soil types and biotic interactions make the true potential for rapid migration uncertain. Monitoring of tropical montane regions and maintaining their connectivity to the lowlands are essential components in any conservation strategy in this warming century (IPCC, 2007).

The papers in this thematic section illustrate the potential of tropical elevation gradients as laboratories for understanding basic questions in biodiversity distributions and ecosystem ecology by presenting results from a research programme in southeastern Peru, centred on an elevation transect in the upper Madre de Dios/Madeira watershed on the boundary of Manu National Park. This research is part of a wider programme, the Andes Biodiversity and Ecosystem Research Group (http://www.andesconservation.org), which is seeking to understand biodiversity distribution and ecosystem ecology of tropical Andean montane systems and their ties to past and future climate change.

The papers selected for this special issue represent a range of articles, from studies of ecosystem ecology and species interactions across a single Amazon to Andes elevational transect, to broader-scale studies of species and ecosystem responses to land use and global climate change. The gradient studies are centred on a series of study plots ranging from 200 to 3500 m above sea level (asl), centred on the Kosñipata, Tono and Tambopata valleys of southeastern Peru. The transect encompasses a range of ca. 18 °C mean annual temperature, with several complete turnovers in both plant and animal communities in high biodiversity areas. Over 1000 species of trees $\geq$10 cm diameter at breast height (DBH) have been recorded from the study plots alone, and the transect has also recorded 1005 species of birds to date. These valleys are embedded in a larger landscape of about 9 000 000 ha in the headwaters of the Madre de Dios river in the Upper Madeira watershed. The landscape ranges from the largest tropical ice cap to the Amazonian lowlands, and contains Earth's highest biodiversity protected areas, including a large portion of the Vilcabamba-Amboro Megacorridor, and vast areas of tropical wilderness. The landscape is also home to the Interoceanic Highway Project that juxtaposes increased human migration and extractive enterprizes with the protected areas. Together, the study area provides an unparalleled landscape for studying biodiversity and ecosystem changes along major environmental gradients, and how these may respond to scenarios of global change.

The first two papers describe aspects of the production and respiration of carbon across a number of intensively studied forest plots along an elevation gradient ranging from 200 to 3025 m asl. These studies form part of a wider research programme using these plots to quantify how carbon assimilation, production, metabolism, and cycling vary with elevation, and to what extent this variation is controlled by temperature, moisture, light or other factors. Girardin *et al.* (2010) report on how the net primary productivity (NPP) and its components vary along the transect, and in comparison to a number of other sites in lowland Amazonia. They report a threefold decline in NPP with increased elevation along the transect, with evidence of a sharp transition between 1500–2000 m asl, where the cloud immersion zone begins. Despite the large variation in NPP across the montane and lowland sites, the relative allocation to NPP between its components (canopy, woody biomass and fine roots) is relatively invariant, an insight useful to ecosystem modelling and to understanding the relationship between NPP and forest biomass.

Robertson *et al.* (2010) use a subset of the same plots to explore how woody stem CO_2 efflux, a major component of ecosystem autotrophic respiration, varies along the transect. They document a two-fold decline in whole-plot stem respiration with elevation. This decline is associated with reductions in growth and maintenance respiration. Plot-level stem respiration is very sensitive to changes in forest structure, but in this study the decline in tree stature with elevation was offset by the increasing number of small trees, leading to no overall trend in stem surface area with elevation. Under current and future warming, however, changes in forest structure may be as important in influencing ecosystem autotrophic respiration as changes in ecophysiology. In both studies, temperature is found to be the main determinant of variance in ecosystem carbon cycling with elevation, though other factors (moisture and light) may also play a role.

However, forest ecosystems are more than collections of trees and their responses to abiotic factors. Biotic interactions among species can have dramatic effects on ecosystem function and biodiversity distributions, though these are little studied with respect to natural ecological gradients, save for competitive interactions. Hillyer & Silman (2010) use the elevation gradient as a laboratory for looking at the effects of seed predation on tree regeneration. The study uses 24 tree species placed in a common garden experiment at 250 m increments in elevation from 1000 to 3500 m asl. The results show that the nature of seed predation varies in fundamental ways across the gradient. When looked at in the demographic context of the species, changes in predation rate experienced by a species can potentially cause the intrinsic rate of increase to vary by a factor of seven. Moreover, these effects show size-dependence linked to specific seed predator guilds, as well as overall effects on productivity.

Predicted climate warming in the Andes is expected to be $\sim$4 °C and as high as +8 °C by 2100, and these changes will be combined with land use change including deforestation at low elevations and the use of fire to maintain open grassland at high elevations. The next three papers take a broader view of global change effects on species responses to climate change in the Andes in both space and time. In a pair of papers, Feeley & Silman (2010a,b) use species distribution models to predict future range sizes of tree species. The first paper Feeley & Silman (2010a) looks at range size and extinction probabilities under different scenarios of warming, species migration abilities and land use change. The authors find that in the absence of anthropogenic disturbance, if species can migrate at a pace that allows them to remain in equilibrium with temperature, the range sizes of many Andean species increase. Even using observed migration rates for the area, in the absence of land use change effects, species population sizes remain large enough to have low extinction rates for most species. Anthropogenic disturbance, however, changes this result fundamentally. Particularly important is the anthropogenically determined tree line, which presents a hard barrier to species migrating upwards. This result emphasizes that conservation strategies can only be successful under climate change if fire is controlled, particularly if the upper limit of species distributions are limited primarily by temperature rather than moisture.

The next paper presents a palaeoecological perspective on climate change and species migration in the Andes. Bush *et al*. (2010) use a 370 kyr palaeoecological record from Lake Titicaca to demonstrate that the environments of past interglacial periods differed markedly as a result of synergistic responses between temperature, moisture availability, biomass and fire. By using the Holocene and the previous three interglacials (marine isotope stages 5e, 7 and 9) as proxies, Bush *et al*. (2010) predict what warming scenarios might mean for species distributions and migration scenarios for Andean plant species. The results from the study are sobering, and show that while trees can colonize the high altiplano at >3800 m elevation, this only happens when the ecosystem is wet. At temperatures only 1–2 °C higher than modern, the ecosystem passes a tipping point, likely driven by sea surface temperatures, into severe and prolonged drought. The observations from the palaeorecord call into doubt forecasts of tree migration onto all but the wettest areas of the high Andes, and also point to the imperative to incorporate moisture into niche-based distribution models use to predict species responses to global change.

The final paper (Feeley & Silman, 2010b) in the special issue goes to the heart of the question of our ability to model species distributions in high-diversity tropical areas. Results from the literature show that a minimum of 20–50 data points – species collections – are needed in order to obtain useful fits for species distribution models. This paper asks a simple question: for the three major tropical regions of the world, what fraction of plant species have enough collections to be useful in species distribution models? The results show that 92–99% of tropical species are so poorly collected or so sparsely represented in databases, that they are in effect invisible to this widely used technology.

Together with a few other recent papers (van der Weg *et al*., 2009; Zimmermann *et al*., 2009a, b, 2010; Palin *et al*., 2010; Gibbon *et al*., 2010; Salinas *et al*., in press), the papers presented here are among the first of a large number of papers anticipated from this study in coming years. Other aspects being studied at this site include the climate patterns and their determinants (e.g. patterns of cloud immersion and their relation to large-scale climate), the climate and vegetation history of the region over glacial-interglacial periods, the sensitivity of various components of plant and ecosystem processes to temperature (e.g. autotrophic respiration, photosynthesis, litter and soil decomposition, soil macrofauna and microbial communities, patterns of upslope migration, the dynamics of the treeline and the role of fire, the ecology of bird communities, landslide dynamics and the influence of disturbance, the cycling of carbon, nutrients and greenhouse gases, the potential of airborne lidar, radar and other remote-sensing technologies to map forest structure and biomass, interactions between forests, climate change, and local communities, and scaling up the results from research plots and transects to understanding regional ecosystem processes. Moreover, there are tropical forest transect studies established in other regions, including Ecuador, Hawaii, Borneo, Australia and Papua New Guinea, and future comparative work and collaboration across these transects will both provide replication and likely yield fundamental new insights. We hope that this selection of papers and the wider programme will stimulate interest and research into the wonderful biology and ecology of tropical elevation gradients, and provide insights into the future of tropical ecosystems in a century of rapid climate change.

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