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Review Article

A global framework of mountain ecology

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Abstract

In this contribution, I will summarize a number of features of mountain ecosystems that apply globally. After providing a brief statement on mountain definitions and some mountain statistics, I will recall the major climatic and atmospheric drivers and how their action is modified by geomorphology and type of vegetation. I will close by highlighting the power of sharp microenvironmental gradients in mountains to test ecological hypothesis and elaborate projections on future developments in a global warming context.

Keywords:

1 | Mountains

Mountains are geomorphological features resulting from plate tectonics (including volcanism). They can neither be defined by elevation, given the many elevated table lands, nor by a certain climate, given the latitudinal and elevational climatic gradients. The unifying principle is topographic roughness often addressed as ruggedness. Which degree of ruggedness one considers mountainous is a matter of scale and common sense, and cannot, in a strict sense, be defined from first principle. A widely held approximation that meets most peoples' perception is a minimum vertical amplitude of somewhere between 150 m and 300 m of elevation within an area of around 2 x 2 km, commonly obtained from 9 adjacent grid points in a 30 arcsec geographical grid. One can attribute the ruggedness obtained from such a core area to variable sizes of surrounding land, causing the terrain globally considered to be mountainous to vary between 12.5% and 30% (Körner et al. 2021). With the narrower concept preferred here, using a ruggedness threshold of 200 m projected onto a 21 km^2 reference window at the equator, 16.5 Mio km^2 of land outside Antarctica is mountainous. This definition includes c. 2 km of non-rugged foreland and all valleys less 4 km wide. Statistically, this land area is home to c. 0.5 billion people, 3/4th of which living close to mountains and 1/4th are actually living on mountains, mostly at lower, warmer elevations (Körner et al. 2017). So, Kathmandu, La Paz, or Innsbruck are clearly mountain cities. Some of the wider mountain definitions include for instance Hong Kong and other megacities, because they have some hills on their outskirts, and the reference area is so large, and thus inclusive for such mountain features. This is to be kept in mind when judging the various statistics published in the literature (Körner et al. 2021). 21.5% of that land is above the climatic treeline (by definition alpine) and 78.5% below (montane). The alpine fraction corresponds to 2.6% of the global land area outside Antarctica but hosts an over-proportional fraction of global biodiversity (Körner 2004). In terms of terminology, elevated land should be addressed by elevation, while altitude applies to the free atmosphere only (McVicar & Körner 2013), something non-native speakers like myself had long ignored.

2 | Principles of mountain climate

There are only four climatic factors that change with altitude (in the free atmosphere) in all mountains: (1) barometric pressure (and with it, partial pressures of oxygen and CO_2) declines by about 10% per 1000 m. (2) Due to the expansion of the atmosphere, air temperature declines by c. 0.55 K per 100 m (the use of the Kelvin is encouraged for differences, irrespective of the °C scale for temperature, to avoid confusion between the two), but this 'laps rate' of air temperature varies with season and differs between means and extremes of temperature (Kollas et al. 2014). (3) clear sky turbidity diminishes, hence clear sky solar radiation increases with altitude, and (4) the fraction of UV-B radiation of any given total solar radiation increases with altitude (Körner 2007). All other changes reflect local peculiarities. While the atmosphere can hold less vapor the cooler the air (saturation vapor pressure declines with altitude), the actually effective humidity (best expressed as saturation vapor pressure deficit, vpd) depends on local circulation, fog and land surface temperature. Depending on cloudiness, solar radiation may increase or decrease with altitude. There are also no rules for precipitation, although many temperate mountains receive increasing precipitation with elevation, there may be a sharp decrease above the condensation layer in subtropical and tropical mountains. These patterns may change from front range to inner ranges, as is well exemplified by data for Pakistan (Körner 2007). While summits can be quite windy, the mountains of the world belong to the least windy environments, because their roughness slows atmospheric circulation, and inner mountain valleys belong to the calmest regions globally. Isotherms, that is lines of a given air temperature, rise in elevation from front to inner ranges, called the 'mass elevation effect', because this effect is larger, the greater the mass of a mountain range is. The important message for ecologists is: do not use elevation as a surrogate for change in temperature or other atmospheric factors (except for the four listed above) but measure or use the actual environmental conditions.

There is one common geomorphological feature that applies to all mountain ranges: The land area becomes smaller with elevation. While globally 5.1% of all land area is above 2000 m, 2.7% are above 3000 m, 1.7% above 4000 m, and only 0.5% above 5000 m (Körner 2007). This is an ecologically important point, because biodiversity correlates with available land area. As one moves upslope elevational belts occupy less space. As the climate warms, upslope moving biota risk some crowding. To some extent, this effect becomes moderated by the microclimate effects of micro-topography, discussed in the next paragraph.

3 | Climate-Topography interaction and the role of plant size for micro-climate

The above climatic trends apply to the free atmosphere. The climate actually experienced by plants, animals and microbes cannot be approximated by these trends, except for trees. By their upright architecture that evolved for outcompeting neighbors, trees are aerodynamically well coupled to the free atmosphere and experience, in a first approximation, a climate as it is measured by a nearby weather station. This is also the reason for treeline formation, often exhibiting patterns like the shore line of a hydrolelectic reservoir, reflecting the thermal layering of the atmosphere. The treeline is often fragmented by disturbances or trees may be absent from the treeline due to land use, though (Körner 2021a). Indeed, the global treeline phenomenon follows a common isotherm of air temperature (Paulsen & Körner 2014), with a seasonal mean near 6 °C the best approximation. As the vegetation above treeline becomes shorter and shorter, the thermal decoupling from the free atmosphere becomes more pronounced. Hence, by reducing their size, alpine plants trap solar heat (by slowing heat convection) and arrive at much warmer daytime temperature than treeline trees, not dissimilar from temperatures in plants growing at much lower elevation. Being 'small by design' the high elevation vegetation above treeline and all other small organisms associated with them, is 'engineering' a micro environment that is so different from the free atmosphere that weather station data become useless (Scherrer & Körner 2011). These effects become accelerated by topography, that is, exposure to the sun (slope and compass direction) and by shelter (microtopographic roughness). Topography also influences moisture and snow distribution, the latter is a key driver of species distribution at higher latitude mountains. Snow pack protects against freezing but shortens the season in so called snowbed habitats. The message for alpine ecologists: obtain your own micro-environmental data. While modern, cheap and reliable instrumentation makes this easier, the handling of such tools requires training in basics of microclimatology. For instance, sensors must never be exposed to full sunshine, and non-professional shelters and screens can make things worse (Körner & Hiltbrunner 2019).

Above the treeline, topography becomes a dominant factor of life. Life conditions may change over a few meters of horizontal distance by more than for trees across 1000 m of elevation (Scherrer & Körner 2011, Körner 2021b). These mosaics of life conditions are not tied to elevation and associated isotherms of air temperature, but to micro-topography. A sheltered niche on an equator-facing slope at 5000 m elevation in the Himalayas may be warmer or as warm during the day as a treeless habitat on a poleward or wind exposed location at 3000 m elevation. Scherrer and Körner (2011) illustrated that the alpine vegetation on a single mountain slope of 2 km width may host thermal habitats at close proximity that differ by 8 K seasonal mean plant temperature (corresponding to c. 1500 m elevation in the free atmosphere). This enormous thermal habitat diversity within a small area is one of the reasons, why alpine organism can be expected to be far less vulnerable to climatic change than any other type of biocoenosis. Alpine organisms can escape unfavorable temperature conditions by moving over very short distances. For that reason, the alpine flora has been considered most robust against climatic warming, an effect that becomes enhanced by the predominant clonal nature of these plants (Körner and Hiltbrunner 2021).

4 | Experiments by nature

Protozoa These sharp micro-environmental gradients host organismic assemblages for thousands of years. Hence, these communities and the associated soils can be considered a long-term answer of nature to these conditions. No experiment in an experimental garden or in a growth chamber can ever arrive at such a steady state situation. Thermal or moisture gradients, but also season length gradients in regions with regular snow cover, produce species range limits at the 0.1 m scale. Exploring such micro-range limits and relating these limits with microclimatic data helps formulating and testing hypothesis. Such 'experiments' by nature can help to unravel the controlling mechanisms of range limits, which can than be applied to larger scales. Long-term monitoring of such micro-patterns of species distribution can help visualizing responses to ongoing global change. The only problem is the year-to-year stochasticity of weather conditions, calling for sufficiently long-time frames for initial data collection. Embedded in a permanent plot concept, such data collection can also serve as a reference for future re-visitations (Körner et al. 2022).

Conflicts of interest

Author declares no conflict of interest.

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