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The use of 'altitude' in ecological research

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Altitudinal gradients are among the most powerful 'natural experiments' for testing ecological and evolutionary responses of biota to geophysical influences, such as low temperature. However, there are two categories of environmental changes with altitude: those physically tied to meters above sea level, such as atmospheric pressure, temperature and clear-sky turbidity; and those that are not generally altitude specific, such as moisture, hours of sunshine, wind, season length, geology and even human land use. The confounding of the first category by the latter has introduced confusion in the scientific literature on altitude phenomena.

Introduction

Approximately 25% of the land surface of the Earth is covered by mountains, which host at least a third of terrestrial plant species diversity [1], supply half of the human population with water [2,3] and, by offering steep environmental gradients, represent exciting biological experiments of nature which have stimulated research for centuries [4–7]. As one ascends a mountain, environmental conditions change, and one finds organisms that are commonly well adapted to the local conditions along an altitudinal transect, thus offering ideal conditions for exploring evolutionary adaptation over short spatial distances. However, the interpretation of results obtained from such works becomes difficult when the gradients selected include environmental changes that reflect local or regional peculiarities, such as fire [8], land use [9] or drought [10], not generally associated with altitude above sea level. Much of what has been discussed as being a discrepancy between findings (and supposed mechanisms) from different altitudinal gradients by different researchers, in reality reflects confusion between rather different environmental drivers under the umbrella term 'altitude'. If the general geophysical phenomena (e.g. temperature, pressure or turbidity) had been separated from coincidental phenomena, the supposed contrasts might not have become an issue and the scientific endeavor would have become much more fruitful.

Here, I summarize the main geophysical drivers along altitudinal gradients from an ecological point of view and contrast these with other drivers not generally associated with altitude. For practical reasons, I address 'mountains' as any elevation of land mass from the plains 300 m above sea level [11]. The climatological considerations presented

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also apply to the vast high-altitude plateaus (e.g. parts of the North American prairie, the Tibetan plateau and the Andean Altiplano), although these are commonly not included in the term 'mountain' because of the lack of steepness of the slope [11,12]. For land area-related biological phenomena such as biodiversity and speciation, large plateaus have to be considered as a special case, not covered by the term 'mountain'. A clear concept of the meaning of 'altitude' in an ecological context is essential – and is advocated here – to advance the altitude-related theory of life.

Highlighting the problem

If, for instance, one aims at testing theories of adaptation to altitude but selects a gradient along which the moisture regime varies in a peculiar way (precipitation and evaporative forcing might increase or decrease, depending on region), results are likely to reflect the moisture gradient rather than an altitude gradient in its strict sense, or a combination of the two [13–15]. A functional (mechanistic) interpretation would either require data from altitudinal gradients with ample water supply throughout [16,17] or a combination of gradients differing in moisture trends [18,19], so that altitude phenomena can be separated from moisture phenomena statistically. Done correctly, such comparisons become complicated because altitude effects on temperature interact with the architecture of plants (e.g. tree versus shrub versus grass versus cushion), land surface characteristics (inclination and direction of slopes) and concurrent solar radiation, producing evaporative forcing that differs strongly from standard meteorological data [6,20]. Data on actual temperature and moisture conditions would be needed for such comparisons to make sense but soil moisture data are commonly hard to obtain and thus, mostly missing.

This example clearly illustrates the difficulties of distilling a general (global) altitude-related theory of biological phenomena, such as the reduction of species number [6,21], productivity [6,13,22], body or organ size [23], trends in certain physiological [24] and morphological traits [14,25], or gene-ecological [26,27] and life-history characteristics [15]. It is obvious that practicality becomes an issue when so many variables can co-vary with the small set of general altitude-related trends. However, theory testing will become fruitless unless a rigorous account of the driving variables is applied, as holds for other 'proxy' drivers such as latitude [28]. A common escape route, which addresses biological altitude phenomena as a syndrome in response to the combined action of all possible

variables ('everything matters'), is neither assisting theory formation nor enabling meaningful comparisons of works conducted on mountains across the globe.

Global geophysical changes with altitude
Land area changes
Available land area is a major driver of organismic diversity and its evolution [29,30]. With increasing altitude, land area is shrinking (Figure 1), thereby narrowing opportunities for life [31–33]. The concurrent fragmentation of the land area by geological and gravity-related processes into an 'archipelago' of climatic mountain 'islands' further reduces the uniform space for any type of habitat conditions [34]. Yet, habitat diversity or 'geodiversity' and spatial isolation are also enhancing the segregation of populations and, thus, potentially speciation [35]. However, geodiversity does not always increase with altitude and depends on geological age (degree of erosion, steepness) and type of bed rock. In plants, the plus and minus effects of high-altitude geodiversity tend to cancel each other out, so that near-linear species-to-area relationships result in altitudinal clines above the tree line, with a mean reduction of 40 angiosperm species per 100 m [7,32,36].

The reduction of land area is thus a global altitude-related phenomenon, with some local modification. Above the altitudinal tree limit (see later), land area, on average, is halved for every further increase of altitude by 167 m (means for the Alps and Andes are 150 and 178 m, respectively). As altitude increases, the associated climatic changes (discussed later) thus apply to a dramatically diminishing fraction of land.

General climatic trends with altitude
In addition to the altitudinal reduction of land area, there are four primary atmospheric changes associated with altitude: (i) decreasing total atmospheric pressure and partial pressure of all atmospheric gases (of which O_2
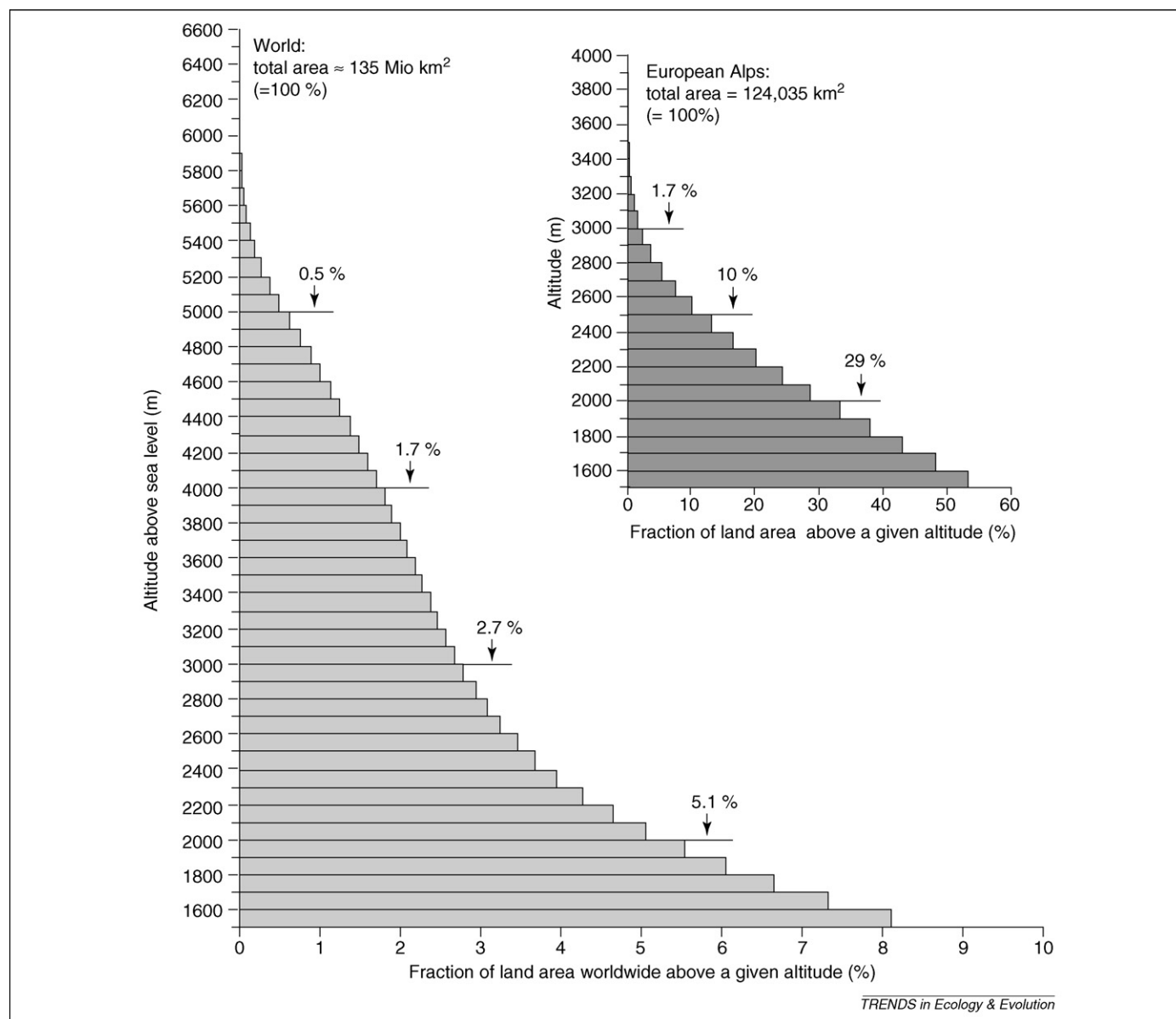

Figure 1. The global pattern of land area outside Antarctica per altitude in 100 m steps above sea level (a.s.l.), starting from 1500 m a.s.l. (land area above 1500 m = 10.94 million km²). The inset depicts the situation in the European Alps as a regional example (total mapped area >1500 m a.s.l. = 66 000 km²).

and CO_2 are of particular importance for life); (ii) reduction of atmospheric temperature, with implications for ambient humidity; (iii) increasing radiation under a cloudless sky, both as incoming solar radiation and outgoing night-time thermal radiation (because of reduced atmospheric turbidity); and (iv) a higher fraction of UV-B radiation at any given total solar radiation. There are no other climatic factors relevant for organisms which exhibit globally unidirectional trends with altitude, such as is the case with the four factors discussed here.

Atmospheric pressure

For every kilometer gain in altitude, atmospheric pressure (and the partial pressure of all other gases) declines by ~11%, starting from 1013 hecto-Pascal (hPa) at sea level, and reaching 900, 798, 705 and 621 hPa at an altitude of 1, 2, 3 and 4 km in a standard (20°C) atmosphere, respectively [37]. In reality, the exact mean pressure gradients vary with temperature and humidity and exert some regional trends, although the general pattern is universal [38,39].

This reduction in pressure and partial pressure has a significant impact on respiration in animals and on gas exchange in plants. For instance, the O_2 and CO_2 partial pressure (p) is ~21% lower at 2000 m than at sea level, although the effects of pressure reduction are partly mitigated by faster molecular gas diffusion at any given temperature. The increase in the mean free path of molecules reduces collisions and, thus, enhances the rates at which CO_2 arrives at the cell surface in the leaf. However, this effect is not proportional to the drop in pressure, and the lower atmospheric temperature at high altitudes counteracts the diffusivity effect (molecules also move more slowly). In plants, the net effect is further reduced by the fact that 70–80% of the total CO_2 transfer resistance between air and the chloroplasts is in the liquid phase, which is not influenced by pressure. Pressure effects on photosynthesis are, thus, smaller than predicted from the decline in the ambient pCO_2 alone [40,41]. Most alpine plants have increased numbers of stomata [6], and one could argue that this is to counteract the low ambient pCO_2; however, such a trend was not seen in cloudy tropical high mountains, suggesting light, rather than pCO_2, as the primary cause [42,43]. Natural abundance of stable carbon isotopes in plants from humid regions around the globe suggests biochemical adjustments to the reduced pCO_2 (more efficient CO_2 fixation at high altitude [16]).

In animals, for example, the egg shells of birds become more porous with altitude, thus facilitating higher rates of O_2 diffusion to the developing embryo [44]. Warm-blooded animals, with their actively pumping respiratory systems, counteract reduced pO_2 by enhanced ventilation (breathing faster) and adjustments in blood composition (more or more efficient red blood cells) [45]. Whenever molecular gas diffusion comes into play, reduced temperature (slowing diffusion) is counteracting the effect of reduced pressure alone (increasing the rate of diffusion).

Temperature

On average, air temperature drops by 5.5 K per kilometer of altitude [46]. However, this is not necessarily the temperature reduction experienced by all organisms. Whereas trees, owing to their height, are closely coupled to atmospheric circulation and, thus, ambient temperature, low-stature vegetation can effectively decouple from free convection (create an aerodynamic resistance against heat exchange) and warm significantly under solar radiation. Adapted to these thermal conditions during sunny days, the optimum temperature for photosynthesis does not differ between low-stature alpine and lowland plants (~23°C), whereas it does in trees (dropping from ~23°C at low elevation to ~16°C near the high-altitude tree limit in a temperate climate [6,40]).

A reduction in ambient air temperature reduces the saturation vapor pressure (the capacity of the air to hold moisture), which also sets lower boundaries for vapor pressure deficit, thus reducing evaporative forcing at high elevation when the temperature of the evaporating surface is close to (or cooler than) air temperature. When evaporating surfaces are warmer than air (human skin or solar-heated, low-stature plant carpets – cushion plants in particular), the driving forces for vapor loss can become as strong or even stronger than at low elevation [20,42]. This deviation from free atmosphere conditions depends on solar radiation (i.e. cloudiness), wind speed, aerodynamic roughness and availability of soil moisture (and, thus, degree of transpirational cooling). Under full solar irradiance, alpine cushion plants commonly reach surface temperatures of 25–30°C at air temperatures of ~10°C [6].

Hence, across all plant life forms, there is no common altitudinal temperature trend to be expected, and local and/or life form-specific, rather than global, patterns are likely to govern the degree of such departures from ambient conditions. Yet, such solar warming of surfaces does occur in low-stature vegetation of all mountains; hence, such periodic thermal contrasts between ambient air and low-stature, high-altitude vegetation are a general, high-altitude phenomenon. By contrast, tall plants (trees) are exposed to and exhibit (with minor deviations) similar altitudinal reductions in temperature than the free atmosphere around the globe, which explains the uniform position of natural climatic tree lines near a common isotherm of the mean temperature during the growing period of between 6°C and 7°C [47].

For altitudinal thermal gradient analysis to become biologically meaningful, the temperatures that need to be considered are those that become physiologically effective – that is, occur during the growing season. Thus, mean annual temperature is unsuitable because it is confounded with the degree of climatic continentality (distance to the sea) and the length of the dormant season, particularly along altitudinal gradients outside the tropics. Altitudinal comparisons of absolute minimum temperatures make sense in a stress physiological context, provided that target organisms are not snow covered (and, thus, thermally insulated). However, owing to temperature inversion in valleys and night-time radiative cooling, the absolute minima of air temperature and plant surface temperature do not follow a uniform altitudinal cline.

Solar radiation

Meteorological text books draw a misleading picture, by traditionally referring to clear-sky altitudinal profiles only. Under such conditions, solar radiation increases with altitude because of reduced atmospheric turbidity (increased transmissivity) with altitude. However, for solar radiation in general, and the dose per day in particular, there is no global altitudinal trend. The actual dose seen by organisms depends on clouds and fog, both often increasing with altitude. In New Guinea, for instance, alpine plants see only a third of the daily radiation intercepted by lowland plants [42]. In the Swiss Alps, the average global radiation in July does not change significantly with altitude, although peak radiation is more intense at high altitude [6].

UV-B radiation

Although commonly contributing a higher fraction at any given incoming irradiance at high compared with low altitude (for clear-sky conditions, see Blumthaler [48]), more frequent clouds and fog can negate or even reverse this effect [6,49].

For peak solar radiation, there is a consistent (increasing) global trend with altitude; for mean daily or seasonal dose, there is none.

Climatic trends that are not generally related to altitude

In addition to situations where the steepness, but not the general direction, of altitudinal trends varies, other meteorological parameters show regional variation in the direction of change, with precipitation and seasonality exerting the largest influence.

Precipitation

Moisture availability is one of the most difficult and confusing components of altitudinal environmental gradients, as reflected by the published literature on altitude

phenomena. There is no rule on altitudinal precipitation trends, and gradients can go in any direction, as they do at low elevation [6,50,51] (Figure 2). There are regions that are dry at low altitude and moderately humid at high altitude (e.g. the slopes surrounding the Intermountain Basin in the western USA), whereas others show a mid-altitude moisture peak (e.g. Mount Kilimanjaro) or start from moist foothills and than sharply convert to a mountain desert (e.g. parts of the Andes and Tenerife).

Thus, it seems unwise to quote regional altitudinal moisture trends as 'altitude phenomena', as such gradients could also be studied in non-mountain regions. Specific regional moisture gradients are best addressed as such, although they might locally be following an altitudinal gradient. If such regional trends are referred to as 'altitude effects', comparisons with altitude-related data from studies in which moisture gradients differ, become a lottery. For example, altitudinal gradient work in the western USA always reflects moisture gradients that are peculiar to this region (i.e. dry at low altitude and humid at high altitude [10,52]). Data from such gradients can neither prove nor disprove any general altitude-related ecological theory for non-moisture-limited transects, such as reflected, for instance, in stable carbon isotope data (e.g. increased CO_2 uptake efficiency in high-altitude plants [16]). Organismic responses to altitudinal moisture gradients [10,18,19,53,54] should not be referred to as 'mountain phenomena' or 'altitude effects' as such. Cavieres et al. [55] showed for transects in the Chilean Andes that moisture gradients can reverse generally assumed altitudinal trends [56], in their case a reduction rather than an increase in plant–plant facilitation with altitude.

Wind velocity

Contrary to popular belief, mountains, as a whole, are among the less windy places on Earth, owing to the topographic shelter between or within mountain ranges, except for exposed crests, summits and isolated mountains on
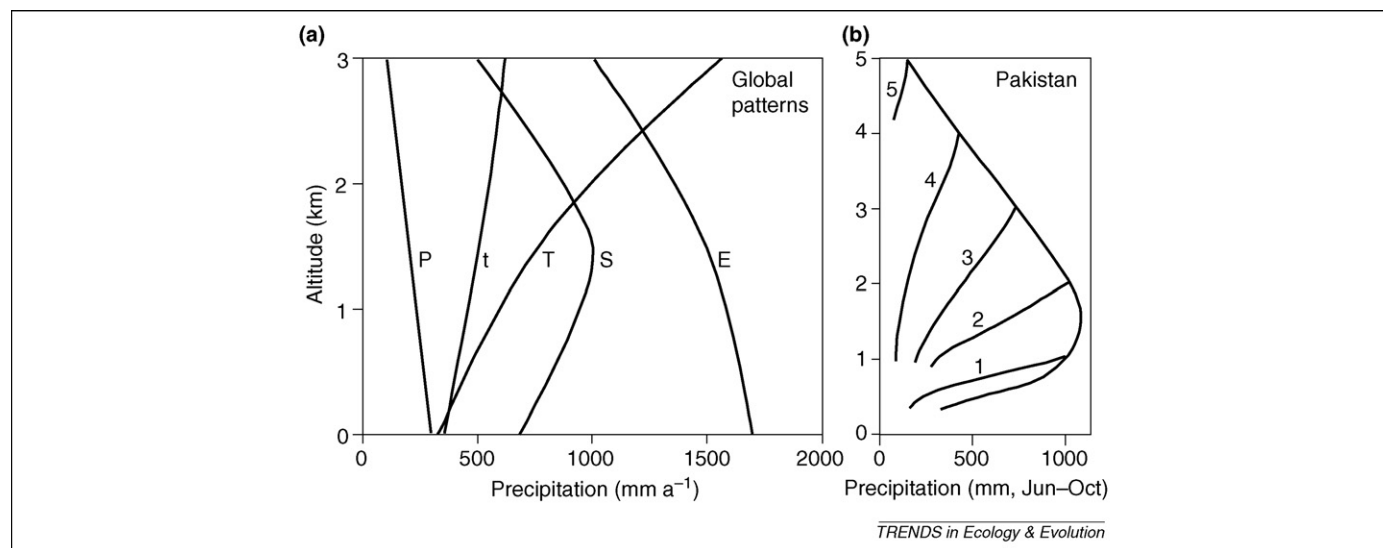

Figure 2. **(a)** A global typology of altitudinal trends in precipitation. E, equatorial (0–10° latitude); S, subtropical (10–30° latitude); t, transition (30–40° latitude); T, temperate (40–60° latitude); and P, polar (Greenland). Modified, with permission, from Ref. [50]. **(b)** Altitudinal trends in precipitation across various mountain ranges in Pakistan as a function of the average height of a mountain range during the monsoon period (June to October). Note the variable breakpoint altitudes from increasing to decreasing precipitation. Modified, with permission, from Ref. [51].

islands [46,57]. In addition, compact low-stature alpine vegetation produces calm plant canopy conditions. It is the plains, coastal ones in particular, which see the windiest climate. The few high-altitude meteorological stations are commonly built in rather exposed places. In fact, all of the high-altitude stations in the European Alps are on such 'extreme' sites (Jungfrau- and Weissfluh-Joch in Switzerland, Zugspitze in Germany and Sonnblick in Austria). Tropical mountains are particularly calm [57]. Hence, there is no general altitudinal pattern of ecologically relevant wind velocity that one could refer to [6].

Seasonality

It is a common perception that seasons become shorter as altitude increases. This reflects the perspective of people living at high latitudes and commonly refers to a temperature-driven seasonality in humid climates. There is no pronounced altitudinal change in seasonality in the humid equatorial tropics. In regions with a dry low-altitude climate, the length of the growing period can become longer with increasing altitude because of improving moisture conditions (e.g. the eastern slopes of the Sierra Nevada of California). Interactions of regional thermal and moisture seasons can thus produce a variety of altitudinal seasonality trends. Ecological tests for general season-length effects in mountain biota, therefore, need to account for confounding moisture effects. Altitudinal gradients in season length (irrespective of whether these are driven by temperature or moisture) are ecologically decisive. In humid, temperate mountains, the altitudinal reduction in productivity and evapotranspiration is exhaustively explained by the duration of the growing season [6,58].

Conclusion

There is a need for a consistent 'altitude concept' in comparative ecology. Because there is no 'standard mountain', any data collected along altitudinal gradients will reflect the combined effect of regional peculiarities and general altitude phenomena. This distinction becomes crucial when the results of different studies are compared and trends are commented on as being different or similar to those found by others along altitudinal gradients elsewhere. To distill general altitude-related organismic responses, data from altitudinal gradients with little confounding by moisture gradients are particularly valuable (humid mountains). Alternatively, multivariate analysis of data from altitudinal gradients replicated across a variety of regions contrasting in moisture regimes can assist in separating moisture from thermal effects. The actual physical conditions must be well documented, however, for such an analysis. Extrapolations from base-station precipitation data alone are completely insufficient because it is the actual soil moisture which drives plant responses – data which are hardly ever reported.

The mountains of the world provide many opportunities to develop and test theories of adaptation by comparative observations, manipulative experiments and data mining in legacy archives [59]. Modern Geographical Information Systems (GIS) for topography and climate enable large-scale comparisons of life conditions along altitudinal clines [60]. Electronic archive data provide a broad arena for testing such theories [61–63]. Large-scale comparative empirical works will remain the most convincing tests [13,16,24,47,55,63–66] but they must account for covariables unrelated to altitude as such, for their results to contribute to a furthering of the theory of altitude-related life phenomena.

The two most important factors for life that are globally associated with increasing altitude are the decline in air temperature and the reduction of land area per bioclimatic belt (for a given range of altitude, Figure 1). It seems, with these two geophysical components, one related to climate, one related to mountain geometry, and with the variable history (age) and isolation of mountain biota, that the mechanisms of physiological and morphological adaptation [16,43], in addition to evolutionary trends and resultant biodiversity in mountains [33,67], can be explored. For example, a comparison of subarctic tundra (no land area constraints) versus temperate alpine ecosystems (archipelago-type, land area constrained) enables an examination of the effect of low temperature on species traits and species diversity, irrespective of space limitation. Environmental influences other than these globally altitude-related factors either need to be reduced by clever site selection, or data need to cover a well-documented, broad spectrum of such potentially confounding, not strictly altitude-related, covariables.

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