Altitudinal gradients in biodiversity research:
the state of the art and future perspectives under climate change aspects

*Höhengradienten in der Biodiversitäts-Forschung:
Eine Übersicht unter Berücksichtigung des Klimawandels*

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Abstract

Mountains, with their isolated position and altitudinal belts, are hotspots of biodiversity. Their flora and fauna have been observed worldwide since the days of Alexander von Humboldt, which has led to basic knowledge and understanding of species composition and the most important driving forces of ecosystem differentiation in such altitudinal gradients. Systematically designed analyses of changes in species composition with increasing elevation have been increasingly implemented since the 1990s. Since global climate change is one of the most important problems facing the world this century, a focus on such ecosystem studies is urgently needed. To identify the main future needs of such research we analyze the studies dealing with species changes of diverse taxonomical groups along altitudinal gradients (0 to 6,400 m a.s. l.) on all continents, published during the past one to two decades. From our study we can conclude that although mountains are powerful for climate change research most studies have to face the challenge of separating confounding effects driving species assemblages along altitudinal gradients. Our study therefore supports the view of the need of a global altitudinal concept including that (1) not only one or a few taxonomical groups should be analyzed, but rather different taxonomical groups covering all ecosystem functions simultaneously; (2) relevant site conditions should be registered to reveal direct environmental variables responsible for species distribution patterns and to resolve inconsistent effects along the altitudinal gradients; (3) transect design is appropriate for analyzing ecosystem changes in site gradients and over time; (4) both the study design and the individual methods should be standardized to compare the data collected worldwide; and (5) a long-term perspective is important to quantify the degree and direction of species changes and to validate species distribution models. (6) Finally we suggest to develop experimental altitudinal approaches to overcome the addressed problems of biodiversity surveys.

Keywords: altitudinal gradient, biodiversity, climate change, transect, species richness

Zusammenfassung

Gebirge mit ihrer mehr oder weniger isolierten Lage und ihren vielfältigen Höhenstufen stellen „Hotspots der Biodiversität" dar. Ihre Flora und Fauna wird seit den ersten Beschreibungen durch Alexander von Humboldt immer wieder untersucht. Systematisch angelegte Studien zur räumlichen Verteilung von Arten bzw. Artengruppen in Höhengradienten erlangen eine zunehmend größere Bedeutung seit den 1990iger Jahren, insbesondere im Rahmen der Klimafolgenforschung. Um für die zukünftige Biodiversitätsforschung die heute als wesentlich angesehenen Forschungsansätze zu identifizieren, wurden in dieser Studie Literaturangaben der letzten zwei Jahrzehnte über die sich verändernden Artenzusammensetzungen in Höhengradienten aus allen Kontinenten, verschiedenen Artengruppen und einem Höhenbereich von 0 bis 6.400 m ü. NN ausgewertet. Diese Zusammenstellung zeigt, dass Untersuchungen der Muster der Biodiversität von Höhengradienten in Gebirgen einen wichtigen Beitrag für das Verständnis der Herausbildung und Änderung von Biodiversitätsmustern gerade im Rahmen des zu erwartenden Klimawandels leisten können. Die Musterbildung im Höhengradienten ist für verschiedene Artengruppen durchaus unterschiedlich.

Diese Literaturauswertung macht aber auch die Notwendigkeit eines weltweit einheitlichen Konzeptes für die Forschung in Höhengradienten deutlich. Ein solches Konzept sollte folgende Gesichtspunkte beinhalten: (1) Nicht nur ausgewählte Artengruppen, sondern mehrere verschiedene Artengruppen gemeinsam analysieren; nur so lassen sich die vielfältigen Ökosystemfunktionen und Prozesse berücksichtigen. (2) Begleitend möglichst viele Umweltfaktoren erfassen, um herausarbeiten zu können, welche der Umweltfaktoren für die Musterbildung wirklich maßgeblich sind. (3) Die Transekte so anlegen, dass sie nicht nur eine einmalige räumliche Analyse ermöglichen, sondern auch zukünftig im Sinne von Zeitreihen zur Verfügung stehen. (4) Sowohl das Erhebungsflächendesign als auch die Aufnahmemethoden für die einzelnen Artengruppen standardisieren, um die Daten weltweit vergleichen zu können. (5) Langzeitstudien starten; denn nur sie bieten die Möglichkeit, erwartete oder aus Modellen abgeleitete Veränderungen der Artenzusammensetzungen bzw. von Verschiebungen von einzelnen Arten im Höhengradienten zu validieren. (6) Gezielt konzipierte Experimente einsetzen, um offene Fragen zur Verteilung der Arten in Höhengradienten untersuchen zu können.

Schlüsselwörter: Höhengradienten, Artendiversität, Klimawandel, Artenverteilung, Transekte

1   Introduction

The expeditions of Alexander von Humboldt (1799–1804) and Charles Darwin (1831–1836) and their reports on the mosaic of habitats along spatial and especially altitudinal gradients piqued the interest of scientists and have held their interest since then. During the last two decades, the focus has been on species diversity along such gradients. Already in 1995

Rahbek summarized 97 publications representing 163 research studies on species diversity in altitudinal gradients.

The focus of such studies has changed with time to factors forming the patterns of species diversity and especially the influence of human impact. Approaches include comparing and modeling species diversity patterns worldwide in relation to human-induced environmental factors, such as land use and climate change (Sala et al. 2000). Today, the main parameters of climate, e.g., temperature and precipitation, are changing rapidly (IPCC 2007), with drastic consequences for ecosystems, such as species extinction, species shift, changes in species composition, and phenologically driven mismatch (for reviews, see Walther et al. 2002, Parmesan 2006). Altitudinal gradients are especially suited to study these effects owing to the short distances between different ecosystems. It is not expected that whole ecosystems will move as a consequence of changing environmental factors, e.g., temperature increase, but rather that certain species or species groups will respond in different ways, with the consequence that community compositions will be disrupted (Parmesan 2006). Transect analyses of altitudinal belts represent climate gradients in time. They thereby may help to identify the current responses of species to climate changes and to develop a better understanding of how ecosystems change in a changing world.

The taxonomic groups analyzed, the methods used, and the goals in altitudinal gradient studies vary greatly, as do the results of these studies. Many species groups have been studied: mostly flowering plants (Odland & Birks 1999, Kessler 2001, Vetaas & Grytnes 2002, Grytnes & Vetaas 2002, Grytnes 2003, Doran et al. 2003, Bachman et al. 2004, Fisher & Fulé 2004, Küper et al. 2004, Kreft et al. 2004, Lovett et al. 2006, Erschbamer et al. 2006, Behera & Kushwaha 2007, Pauli et al. 2007, Wang et al. 2007, Milla et al. 2008, Chawla et al. 2008, Nogués-Bravo et al. 2008, Ibisca 2008, Sang 2009, Shimono 2010, Desalegn & Beierkuhnlein 2010, Zhang et al. 2011), but also ferns (Parris et al. 1992, Kessler 2001, Hemp 2002, Bhattarai et al. 2004, Kluge et al. 2006, Watkins et al. 2006, Desalegn & Beierkuhnlein 2010), bryophytes (Frahm 1990, Frahm & Gradstein 1991, Wolf 1993, Nogués-Bravo et al. 2008), lichens (Grytnes et al. 2006, Ibisca 2008, Nogués-Bravo et al. 2008), microfungi (Widden 1987) and plant communities (Moscol Olivera & Cleef 2009); also bats and small mammals (Mccain 2005, Mccain 2007, Rowe 2009), birds (Altshuler 2006, Mccain 2009), fish (Jaramillo-Villa et al. 2010), reptiles (Cettri et al. 2010), insects (Olson 1994, Fleishman et al. 1998, Sanders 2002, Axmacher et al. 2004, Wilson et al. 2007), littoral benthic macroinvertebrates (Ciamporová-Zat'ovicová 2010), land snails (Hausdorf 2006, Müller et al. 2009), testate amoebae (Krashevs'ka 2008), myxomycetes (Rojas & Stephenson 2008)

and the plant-pollinator networks (Ramos-Jiliberto et al. 2010). Plant species are well represented in these studies, but the high number of insect species are greatly underrepresented (Fig. 1).

About 30 % of the publications available are analyses of published data on selected groups. Mountain areas of all continents are represented, including the large Himalayas, Rocky Mountains, Andes, and Alps, but also isolated high mountains such as Mt. Kilimanjaro in Tanzania (Hemp 2002, Axmacher et al. 2004), Mt. Kinabalu on Borneo in Malaysia (Frahm 1990, Parris et al. 1992), and San Francisco Peaks in Arizona (Fisher & Fulé 2004). Both the latitudinal position and the elevation extent of the studies mentioned here are summarized in Fig. 2.

With this review, we (i) outline both the diversity patterns and hotspots of research in this field, especially with respect to the ongoing discussion of changing species distributions in altitudinal gradients driven by climate change and (ii) point on future research needs. We concentrate on publications since 1990 and especially since 2000.

2   Research goals

The biodiversity in altitudinal gradients has been studied for a number of reasons: (1) to obtain better knowledge and general understanding of biodiversity and biodiversity change along gradients (Vetaas & Grytnes 2002, Axmacher et al. 2004, Küper et al. 2004, Mccain 2005, Davies et al. 2005, Watkins et al. 2006, Bässler et al. 2009, Moscol Olivera & Cleef 2009, Müller et al. 2009, Ciamporová-Zat'ovicová 2010, Desalegn & Beierkuhnlein 2010, Jaramillo-Villa et al. 2010, Shimono et al. 2010, Nagaike 2010), (2) to construct schemes of altitudinal zones (Frahm & Gradstein 1991), (3) to compare the behavior of different taxa in the same altitudinal gradient (Grytnes et al. 2006) or to find reasons why different groups react differently (Bhattarai et al. 2004), (4) to verify ecological and biogeographical hypotheses, both generally and with a focus on endemic species (Behera & Kushwaha 2007), (5) to understand changes in species assemblages along landscape boundaries, e.g., the boundary between tropical rain forests and agriculturally used areas or heath lands (Axmacher et al. 2004), (6) to determine whether biodiversity is changing either continuously or discretely, e.g., whether the changes are greater at the timberline (Odland & Birks 1999), (7) to test the hypotheses of generally decreasing species number with altitude (Rahbek 1995) and the increase in space range settled by species with increasing distance to the equator (Rapoport rule, Hausdorf 2006), (8) to analyze interactions between different groups of taxa (e.g., forest density and arbuscular mycorrhiza of herb-layer plants (Fisher & Fulé 2004), plant-pollinator networks (Ramos-Jiliberto et al.
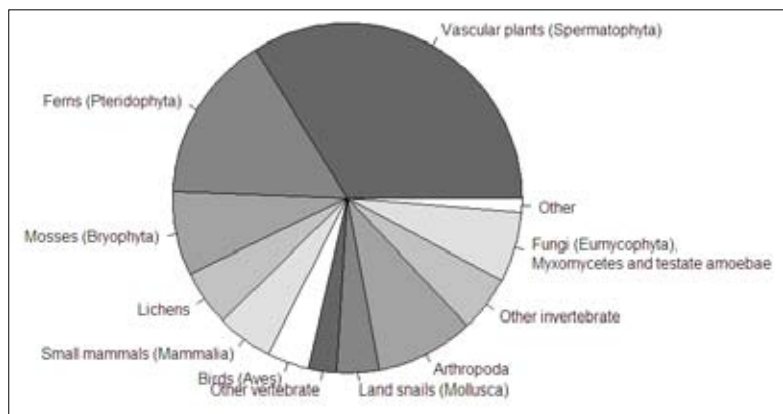

Fig. 1: Representation of the different taxonomic groups studied in the cited publications. (If a study deals with more than one taxonomical group, each counts for its own.)

Abb. 1: *Anteile der einzelnen taxonomische Gruppen im Rahmen der hier zitierten Studien zu Höhengradienten. (Für Studien, die mehrere taxonomische Gruppen bearbeitet haben, wurde jede Artengruppe für sich gezählt.)*
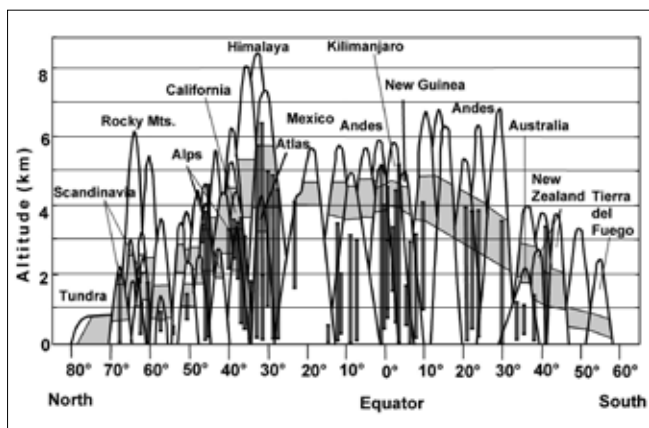
Fig. 2: Global latitudinal position and altitudinal gradients under study in relation to our focus (background of the diagram modified from Körner 1999; with alpine life zone light grey shaded); dark-grey bars: altitudinal sections studied.

Abb. 2: *Lage der hier betrachteten Höhengradienten zum Äquator und ihre Höhenausdehnung (dunkelgraue Balken); (Grundlage des Diagramms verändert nach Körner 1999 mit der Lage der alpinen Zone in hellgrau).*

2010) including the effect of human impact (Rowe 2009), (9) to gather basic information for developing concepts of nature protection (Olson 1994, Grytnes 2003), and (10) to provide data for the calculation of the total global number of species (Schmidl & Corbara 2005). The goals of biodiversity studies in altitudinal gradients therefore range from basic research (species diversity, diversity distribution patterns) to applied research (planning and management, nature conservation).

Since the mid-1990s, the consequences of global climate change for biodiversity in altitudinal gradients have become increasing important (Fleishman et al. 1998, Odland & Birks 1999, Grytnes 2003, Bässler et al. 2009, Müller at al. 2009, Ciamporová-Zat'ovicová 2010, Malhi et al. 2010, Shimono et al. 2010). There is broad evidence that increasing temperatures will lead to an upward migration of species in montane systems. Indeed, the abundance of various species at their lower limit of altitudinal range is decreasing, whereas thermophilous species are moving to higher elevations (e.g., Walther et al. 2005, Pauli et al. 2007, Kelly & Goulden 2008, Lenoir et al. 2008). These and other observed changes in the phenology and physiology of plants and animals in all well-studied marine, freshwater, and terrestrial taxa are tending strongly in the directions predicted for "global warming" and have been linked to local or regional climate change by correlation of changing climate parameters with biological variation, field and laboratory experiments, and physiological research (for reviews, see Walther et al. 2002 and Parmesan 2006). Especially the alpine and nival mountain belt seems to be greatly affected by climate change (e.g., Erschbamer et al. 2006, Thuiller 2007, Kudernatsch et al. 2008). For this reason, a program for long-term documentation and analysis of vegetation changes in high mountains was successfully implemented in the 1990s (GLORIA, Grabherr et al. 2000).

3   Sampling, mapping, and analysis methods

In general, studies of diversity depend strongly on the grain (plot) size investigated. Studies using a large grain integrate across space, and, therefore, the variation apparent in studies using a small grain disappears (Schreiner et al. 2000). Grain

size and extent vary widely between studies and depend on specific hypotheses.

Only a few publications provide information on the number of replications of the surveys, even though this is critical to assess the generality of the results (Pauli et al. 2007). Only few describe the techniques used to measure environmental variables, such as the climatic parameters temperature, precipitation, and relative humidity, which are used to reveal predictors responsible for observed species diversity patterns (e.g., Kluge et al. 2006, Ibisca 2008, Bässler et al. 2009, GLORIA).

The number of studies in which more than one taxonomical group was considered simultaneously has increased in recent years (Grytnes et al. 2006, Ibisca 2008, Bässler et al. 2009). Nevertheless, still in 2006 Grytnes et al. mentioned that they did not find any elevational study that included vascular plants, lichens, and bryophytes together.

Different methods are used to survey different taxonomical groups in altitudinal gradients. Most of the studies on vascular plants (e.g., Odland & Birks 1999, Doran et al. 2003, Grytnes 2003, Fisher & Fulé 2004, Erschbamer et al. 2006, Kluge et al. 2006, Pauli et al. 2007, Chawla et al. 2008, Ibisca 2008, Bässler et al. 2009, Sang 2009, Shimono et al. 2010, Desalegn & Beierkuhnlein 2010) follow the (modified) phytosociological method of Braun-Blanquet (1964) or corresponding methods (Zhang et al. 2011). In some cases, only one group of plants is studied, e.g., trees or palms (Bachman et al. 2004, Lovett et al. 2006, Behera & Kushwaha 2007, Nagaike 2010). In most cases, the study design is plot based, with a plot of several square meters. In a few studies, continuous lines were used for sampling and mapping (Fleishman et al. 1998). Sampling and recording of object-related taxonomic groups, e.g., wood-inhabiting fungi, bryophytes, and lichens, require a special design dependent on the questions to be answered (see Stokland & Sippola 2004). Invertebrates are surveyed using various kinds of traps (Doran et al. 2003, Ibisca 2008, Bässler et al. 2009), such as flight-interception traps (Bässler et al. 2009), pit-fall traps (Olson 1994, Bässler et al. 2009), light traps (Axmacher et al. 2004, Bässler et al. 2009), Malaise traps (Bässler et al. 2009) and Hess sampler for littoral benthic macroinvertebrates (Ciamporová-Zat'ovicová 2010). Hand sampling is still a common method, especially when used to complete the data obtained with traps, e.g., for saproxylic beetles and land snails (Müller et al. 2009). The visual encounter survey (VES) for reptiles (Cettri et al. 2010) followed this sampling method. Bird surveys require special methods, e.g., sound mapping to determine species (Bässler et al. 2009) or observations during a fixed time frame and video recording to analyze behavior (Altshuler 2006). To collect fish electrofishing was used (Jaramillo-Villa et al. 2010). Other methods used include litter sifting to specify invertebrates (Olson 1994), analyzing soil samples to determine the arbuscular mycorrhiza (Fisher & Fulé 2004) or soil microfungi (Widden 1987, Bachman et al. 2004), using moist chamber cultures of dead plant material to specify myxomycetes (Rojas & Stephenson 2008), or measuring or to describe functional traits to characterize the differences of plants along the elevational gradient (Palacio & Montserrat-Martí 2006, Milla et al. 2008, Albert et al. 2010).

Biodiversity pattern analyses, especially by combining species number related data with environmental parameters just increase. For example, Kluge et al. (2006) regressed species richness patterns against climatic variables, area, and predicted species numbers in a geometric null model (the mid-domain effect). Gorelick (2008) provided an explicit mathematical

model of the area hypothesis of species richness along altitude gradients, described by the geometry of a cone.

Many authors have used data on elevational diversity from the literature or extracted from databases for such analyses (Rahbek 1995, Odland & Birks 1999, Vetaas & Grytnes 2002, Bachman et al. 2004, Hausdorf 2006, Mccain 2007, Wang et al. 2007, Nogués-Bravo et al. 2008, Rowe 2009).

4 Results

The studies mentioned above have addressed two main research questions of general importance related to the effect of altitudinal gradients on biodiversity: (1) Does the maximum biodiversity regularly peak in a particular mid-elevation of the altitudinal gradient and then decrease both above and below this area? (2) Are there any disruptions in biodiversity connected with ecological boundaries, e. g., tree lines?

Peaks of diversity. There is strong evidence that in many cases biodiversity reaches a maximum at a particular middle elevation; this elevation, however, depends on the geographical position of the mountains or mountain ranges. Chawla et al. (2008) found a biodiversity peak for vascular plants at middle elevations in the western Himalayas in India, as did Kluge et al. (2006) for ferns in Costa Rica (maximum around 1,700 m a. s. l.), Wang et al. (2007) for seed plants in Tibet, Zhang et al. (2011) with two different plot-based methods for vascular plants in the Qinling Mountains in central China, Mccain (2007) for bats in a temperate climate, Olson (1994) for leaf-litter invertebrates in western Panama (750–1,000 m a. s. l.) and for Carabidae and Cucurlionidae around 1,750 m a. s. l., Hausdorf (2006) for land snails in Switzerland (400–800 m a. s. l.; starting research at 115 m a. s. l.), and Rowe (2009) for small mammals in Utah (2,100–2,900 m a. s. l). Such a pattern, with a peak of biodiversity at a particular elevation, according to Colwell & Hurtt (1994) and Colwell et al. (2004), allows a prediction of the biodiversity based on elevation (Kluge et al. 2006; mid-domain effect). Also Rahbek (1995) concluded that this type of pattern is the most common one.

However, different patterns have been found in other studies. Some studies have revealed two peaks of biodiversity along an altitudinal gradient. Sang (2009) found one maximum of vascular plant species diversity in the continental part of northwestern China at around 1,500 m a. s. l., where the steppe turns into forest, and a second maximum at 2,700–3,300 m a. s. l. in alpine meadows above the tree line. Similarly, Behera & Kushwaha (2007) in the eastern Himalayas found one maximum of tree species diversity between 600 and 1,000 m a. s. l. and a second maximum between 1,600 and 1,800 m a. s. l. In contrast, Frahm & Gradstein (1991) in tropical rain forests found the maximum number of bryophyte species and the maximum amount of bryophyte biomass close to the upper limit. Jaramillo-Villa et al. (2010) collected highest diversity of fish although at the upper limit of the streams in the Andes of Columbia. Odland & Birks (1999) found that vascular plant species diversity in western Norway does not change up to around 900–1,000 m a. s. l., at which it then starts to decrease above this level. Peaks of biodiversity have also been found in the lowlands, as demonstrated by Mccain (2007) for bats in the tropics (but see different results from the same publication for bats in a temperate climate), by Cettri et al. (2010) for reptiles and by Olson (1994) for leaf-litter invertebrates.

Transition zones. Whether ecological boundaries disrupt biodiversity has been addressed in some studies. As mentioned above, the vascular plant species diversity in western Norway remains unchanged up to 900–1,000 m a. s. l. and then starts to decrease (Odland & Birks 1999). There are clear correlations of this transition with some climatic para-meters, i. e., mean July temperature (11 °C), mean January temperature (–5 °C), and 1,000 mm annual precipitation, but there is no correlation with the tree line. Bässler et al. (2010a) studied the community composition of understorey vascular plant species in forests along a low mountain range gradient of 650–1,450 m a. s. l. in southeastern Germany and found a discrete change between 1,100 and 1,200 m a. s. l. within the forest belt. Further analysis revealed that temperature, which correlates linearly with altitude, is the most important factor explaining the observed patterns. However, according to this study, other factors also contribute to this pattern, such as canopy cover and tree species composition. Nevertheless, direct and short-term effects on understorey vascular plant species composition are expected owing to an increase in temperature, but also long-term effects triggered by climate change that change the forest structures (tree species) are expected (Sang 2009).

5 Discussion

The studies reported in this review represent different continents, different mountain ranges, and different latitudes of the world rather well (Fig. 3). Because of the global uneven distribution of high mountains, many studies were concentrated at latitudes between 25 °N and 50 °N (Alps, Himalayas, Rocky Mountains).

One main aspect addressed by these studies is the altitudinal zonation of biodiversity in mountains. The pattern most often observed is hump shaped, which can be described well by the mid-domain effect. The essential, single, main reason for this pattern, however, has not been elucidated (Rahbek 1995). And a general distributional pattern does not hold for all taxonomic groups. The reasons for a hump-shaped distribution pattern may be the higher diversity of different site types per area (e. g., different inclinations, exposures, and geological substrates; many different micro-sites) in mountains compared to flatlands. At higher altitudes, however, the area available for plant settlement decreases disproportionately (Körner 2000), and therefore, also the possibility for species to live there decreases. From the perspective of population ecology, such hump-shaped patterns may result because of the dispersal of species from lower and higher elevations, resulting in the highest overlap of such dispersing populations at mid-elevations, whereas the extremes of the gradient only receive dispersing species from one side (Kessler 2009). Also human impact has reduced species diversity mainly at lower altitudes and in flatlands (Nogués-Bravo et al. 2008, Chawla et. al. 2008). According to Sang (2009), in a continental climate water availability may be relevant at lower altitudes, but temperature is relevant at higher altitudes. Generally, climatic parameters are strongly correlated with species diversity (Mccain 2005, Bässler et al. 2010b). Therefore, to make general predictions of the biodiversity of a mountain or mountain range, the taxonomic groups that do not follow the most common patterns of diversity in altitudinal gradients need to be identified and separately analyzed.

What will happen when the climate changes? The most important climatic parameters, i. e., temperature and precipitation, may change independently of each other. Precipitation is expected to become highly variable, both spatially and
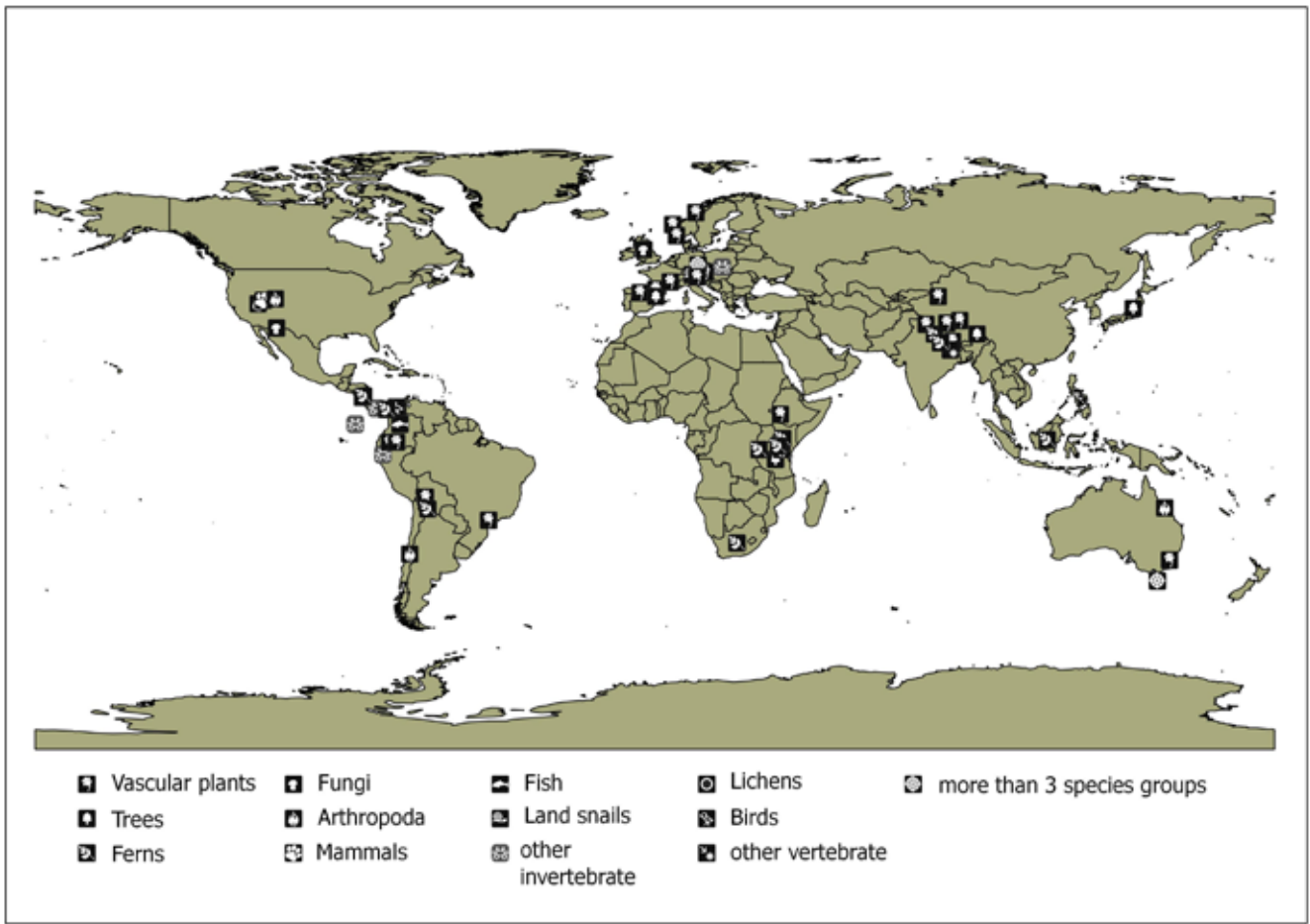
Fig. 3:   Position of altitudinal gradients analysis studies of different species groups in the world.

Abb. 3:   *Lage der Höhengradient-Studien zu diversen Artengruppen der Erde.*

temporally (IPCC 2007). The parameters might also become overlaid with effects of other anthropogenic changing parameters (Thuiller 2007), such as nitrogen emission (Sala et al. 2000, Galloway & Cowling 2002). And both, within an altitudinal gradient and along a mountain range, the climatic parameters and their direction of change may also change. This makes changes in species composition and species diversity in such gradients hard to predict.

Since humans contribute to global warming and therefore to the location of climate zones, there has been considerable effort to predict the future distribution of species, ecosystems, and biomes (Thomas et al. 2004, Parmesan 2006, Jensen et al. 2008, Svenning, Kerr & Rahbek 2009, Kölling et al. 2009, Malhi et al. 2010). Most studies in this area focus on coarse resolution data, which is useful in identifying vulnerable regions or taxa (e.g., Thomas et al. 2004). However, such models based on macroclimate are not appropriate for smaller spatial scales. Currently, the most relevant spatial and temporal scales for the management of biodiversity in the context of global warming or changes in land use are local and span less than three decades (Walther et al. 2002, Ojeda et al. 2003). On large spatial scales, predictions based on relationships between species or communities with macroclimate are certainly helpful. However, on a local scale, the picture may be quite different because other factors may override macroclimate (e.g., Hemp 2005). For this reason, especially on a local scale, we need more models considering not only climate variables but also other local predictors to resolve inconsistent effects observed

in studies of biodiversity along altitudinal gradients. Nevertheless, using transects is a successful methodological study approach for analyzing changing altitudinal limits of species as a response to climate change.

Not only the site conditions differ along altitudinal gradients, but also to a certain degree the species pools. Therefore, the same factors may cause different consequences because they interfere with different species (Rowe 2009). This in turn has consequences for the design of field studies (see below).

Recent movements of some species to higher elevations have been recorded, especially of species in high alpine habitats (Hofer 1992, Grabherr et al. 1994, Burga et al. 2004, Walther et al. 2005, Parolo & Rossi 2008), but also of species of the mountain belt (Penuelas & Boada 2003). For a few alpine species a movement of a few meters per decade could be verified (Grabherr et al. 1994, Erschbamer et al. 2006, Parolo & Rossi 2008), but for most of the species exact measurements have not been made. Obtaining sound data on which species change their lower or upper distribution limits could become one of the most important tasks for transect analysis on permanently marked plots.

Another aspect to consider is species composition. It cannot be expected that whole species assemblages or biocoenoses will start to move upwards. On the contrary, because of the diversity of different site conditions that will be created by changing climate and because of the different qualitative

and quantitative response traits of species during climate change (e. g., Kudernatsch et al. 2008), one would expect the affected assemblages to rearrange, with weighting of the involved species to extents not yet known (Scholes & Van Bremen 1997). In this case, permanently marked transects may also help to detect and document the ongoing changes in species composition.

In studies of altitudinal gradients, focus is often placed on the site factor considered to be the most important, namely temperature, but this is a rough approximation. Indeed, many other ecologically important site factors change with increasing altitude, e. g., precipitation, relative air humidity, air pressure, airborn particles, and water balance, some for the entire year and some for certain time periods. We therefore agree with Lomolino (2001) that clines in environmental variables must be analyzed concurrently to be able to connect the species distribution pattern in gradients with environmental patterns, and to do so on a statistically sound basis. Correlating species distribution patterns with many such parameters and identifying which is the ecologically most important parameter is an important task to be tackled. To date, only few studies have attempted to analyze the distribution patterns of different taxonomic groups in altitudinal gradients simultaneously (e. g., Bässler et al. 2009, Ibisca 2008). Such an approach would clarify whether only selected species react to certain environmental changes or whether certain ecological groups react together, and functional traits important for the reaction could be identified (e. g., plant functional types; PFT). Such information could contribute to answering two of the many questions important to the conservation of global biodiversity posed by Sutherland et al. (2009), i. e., whether there are critical thresholds at which the loss of particular species or species diversity disrupts ecosystem functions, and how the thresholds can be predicted.

One problem of transect studies is methodological and concerns the number of replications. It will not be possible to enlarge the number of plots or the number of transects extensively, especially if many different taxonomic groups are being studied. Even if the number of plots or transects could be enlarged, they would be concentrated on one mountain or a certain part of a mountain range. Both mountains and mountain ranges, however, are ecological islands with a particular and unique species pool. The larger the area under study, the more heterogeneous the species pool will be. This will lead either to a limited number of replications per ecological unit, or to the acceptance of an interpretation, e. g., at the level of ecological traits, such as PFT. Therefore, such studies generally have the character of case studies, sometimes with limited sections of the gradient, i. e., cut gradients.

A standardized field record design for such studies has been developed for climate change research on high mountain tops (see www.gloria.ac.at), but only for vascular plants. A standard method for different taxonomic groups and different ecosystems may be difficult to set up, but such combined analyses would be useful in critical areas such as the transition zones of boreal forest and tundra, mediterranean-type and temperate ecosystems, dry flatlands and moister shrub and wood mountain ecosystems. The results obtained would help to better understand ecosystem change in a changing world.

Based on our review of the literature on biodiversity and climate change in altitudinal gradients, we propose the following guidelines for future research in this area:

1. Not only one or a few taxonomic groups should be analyszed, but rather different taxonomic groups covering different ecosystem functions simultaneously. Models could be examined by repeating the analyses every 5 or 10 years.

2. Relevant site conditions are important to be recorded to reveal direct environmental variables responsible for species distribution patterns along the altitudinal gradients.

3. An appropriate field study design in an altitudinal gradient involves transects, which not only record the recent species composition under one set of site factors but also under a series of different ecological situations, which might be relevant for other locations with a changing climate.

4. A standard method developed in a global joint action would help to overcome the problem of case-study character of past studies and would allow a more regional or in the best case a global joint data analysis.

5. A long-term perspective is essential to determine the extent and direction of species changes and to validate species distribution models.

6. As shown by our review, biodiversity surveys are certainly helpful in order to detect the direction and magnitude of changes in species distribution patterns. However, in such studies confounding effects are hard to uncover and evidence about the reason of changes is clearly limited. We therefore support the view of developing and establishing experimental approaches to test specific hypothesis related to climate change arisen from biodiversity survey studies (Thuiller 2007). Therefore a "global altitudinal concept" should necessarily encompass both, biodiversity surveys as well as experimental approaches.

6   Acknowledgement

Literature

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Appendix / Anhang

Tab. 1: Overview of the altitudinal gradient studies mentioned in this review.

Tab. 1: *Übersicht der Höhengradient-Analysen in dieser Studie.*

Author	Region	Elevation m a.s.l.	Taxa	Method	Plot-Design	Number of species
ALBERT et al. (2010)	French Alps	1200–3000	plants	functional traits		16
ALTSHULER (2006)	Andes, Peru and Colorado Rockies, USA	400–3860 1875–2900	hummingbirds	time formal observations, video filmed	8 field sites in Peru, 2 in Colorado	29
AXMACHER et al. (2004)	Mt. Kilimanjaro (Tanzania)	1650–3300	geometrid moths	Manually sampling at a UV-emitting light trap	26 plots with homogeneous vegetation of 400 m² at 9 elevation levels	188
BÄSSLER et al. (2008), MÜLLER (2009)	Bavarian Forest NP, Germany	650–1420	25 investigated taxa	manually sampling and different kind of traps	293 sampling plots (180 flight interception traps, 36 light traps malaise traps, 180 pitfall traps)	n.d.
BEHERA & KUSHWAHA (2007)	Eastern Himalaya	200–2000	tree	measurement on quadrates	80 plots of 20 x 20 m	336
BHATTARAI et al. (2004)	Himalaya (Nepal)	100–4800	ferns	review of literature	n.d.	293
BHATTARAI et al. (2004)	Himalaya, Nepal	100–4800	ferns	literature survey	n.d.	200
CHAWLA, A. et al. (2008)	Bhabha Valley, Western Himalaya (India)		higher plants	vegetation sampling	n.d.	313
CHETTRI et al. (2010)	Eastern Himalaya, India	300–4800	reptiles	visual encounter survey (VES)	7 elevation zones	42
CIAMPOROVÁ-ZAŤOVICOVÁ et al. (2010)	High Tatra	1725–2157	littoral benthic macro invertebrates	modified Hess sampler	3 lakes	60
DESALEGN & BEIERKUHNLEIN (2010)	Southwest Ethiopian highlands	1000–3546	vascular plants	vegetation sampling	74 plots	475
DORAN et al. (2003)	Tasmania, Australia	70–1300	vascular plants and invertebrate	vegetation sampling and traps	4 transects with 24 plots and 240 subplots	155 plants
ERSCHBAMER et al. (2006)	South Tyrol and Trentino, Italy	2199–2893, 2180–3287	vascular plants	vegetation sampling	Two areas with 4 sites of 4 plots 3 x 3 m² and subplots of 0.1 x 0.1 m²	198 and 137
FISHER & FULÉ (2004)	San Franzisko Peaks, Arizona	2442–3569	understory vegetation and arbuscular mycorrhizae	vegetation sampling	121 Plots 50 x 20 m²	200 understory plants
FLEISHMAN et al. (1998)	Great Basin, Nevada	1900–3275	butterflies	walking transects	105 elevational bands	40

Author	Region	Elevation m a.s.l.	Taxa	Method	Plot-Design	Number of species
GRYTNES (2003)	Norway	0–543 0–504 300–1461 0–1271 450–1952 360–2060 600–1666	vascular plants	vegetation sampling	7 transects with each 38–48 plots 5 x 5 m	n.d.
GRYTNES & VETAAS (2002)	Himalaya (Nepal)	60–6400	vascular plants	review of literature	n.d.	4928
GRYTNES et al. (2006)	Western Norway	310–1135	vascular plants, bryo-phytes and lichens	vegetation sampling	42 plots 5 x 5 m²	n.d.
HAUSDORF (2006)	Austria and Switzerland	115–3798; 195–4634	land snails	review of literature	n.d.	222 and 197
HEMP (2002)	Mt. Kilimanjaro, Tanzania	760–4400	ferns	Plotless sampling	n.d.	140
IBISCA (2008)	Lamington NP, Australia	300–1100	Vegetation (vascular plants, ferns and bryo-phytes) and invertebrate	vegetation sampling and different traps	20 sites with up to 9 traps	140 Lepi-doptrea, 229 Cole-optrea
JACOBSEN & JACOBSEN (1989)	Southern Africa	0–3482	ferns	literature survey	n.d.	296
JACOBSEN & JACOBSEN (1989)	East Africa, Rwanda-Burundi-Kivu	700–4507	ferns	literature survey	n.d.	254
JACOBSEN & JACOBSEN (1989)	East Africa, Kenya Uplands	0–5195	ferns	literature survey	n.d.	219
JARAMILLO-VILLA et al. (2010)	Central Anden of Columbia	258–2242	freshwater fish	sampling with electro fishing	32 streams	62
KESSLER (2001)	Bolivian Andes	220–3950	Acanthaceae, Araceae, Bromeliaceae, Melasto-mataceae, Palmae and Pteridophyta	204 plots of 400 m²	23, 57, 51, 180, 25 and 493	
KESSLER (2001)	Carrasco National-park, Bolivia	200–3950	ferns	vegetation sampling	Plots 20 x 20 m²	493
KLUGE et al. (2006)	Carrillo NP, Costa Rica	100–3400	ferns (Pteridophytes)	vegetation sampling	156 plots 20 x 20 m²	484
KRASHEVS'KA (2008)	Andes, Southern Ecuador	1000–3000	Testate amoe-bae (Protista)	Litter and soil samples	3 areas at 1000, 2000 and 3000 m of ca. 150 m² and 6 samplings	166 (135 in soil and 115 epiphytic)
KREFT et al. (2004)	Western Amazonia, Ecuador	230	vascular epiphytes	compare field data with inventories	16 published inventories and representatively sampling of 650 ha	313

Author	Region	Elevation m a.s.l.	Taxa	Method	Plot-Design	Number of species
Küper et al. (2004)	Ecuadorian Andes	30–3150	vascular epiphytes	review of literature	11 studies and to catalogue	4026
Lellinger (1985)	Panamá	0–3250	ferns	literature survey		687
Lovett et al. (2006)	Udzungwa Mountains, Tanzania	470–1700	woody vegetation	vegetation sampling	6 plots 100 x 25 m with 4 subplots 25 x 25 m and 78 variable-area plots with 20 trees	204
McCain (2005)	global	n.d.	small mammals	global meta-analysis	data from 56 elevational gradients	n.d.
McCain (2007)	global	n.d.	bats	global meta-analysis	data from 27 elevational gradients	n.d.
McCain (2009)	global	n.d.	birds	global meta-analysis	data from 190 elevational gradients	n.d.
Milla et al. (2008)	northern Spain	100–1872	Saxifraga	leaf traits	6 study sites 100 x 25 m and 78 Points of 20 trees	2
Müller et al. (2009)	Bavarian Forest NP, Germany	651–1420	land snails	pitfall traps and hand collection	111 plots 1000 m²	46
Nagaike (2010)	Central Japan, Mt Kushigata	1300–2000	woody vegetation	vegetation sampling	59 plantations and 26 natural forests 10 x 10m	45 in natural forests and 65 in plantations
Nogués-Bravo et al. (2008)	Pyrenean, France and Spain	400–3100	vascular plants, bryophytes and lichens	review of literature		3046
Odland & Birks (1999)	Western Norway	0–1764	vascular plants	Floristic inventories and literature data	18 altitudinal 100 m bands	444
Olson (1994)	Western Panama	300–2020	leaf litter invertebrates	litter sifting and test tube pitfall traps	8 transects of 180 m elevation	718
Palacio & Montserrat-Martí (2006)	North-east of Spain	340–1380	subshrubs	morphology and shoot growth	4 plots	4
Parris et al. (1992)	Mt. Kinabulu, Borneo	400–4000	ferns	Literature and herbarium survey	613	
Pauli et al. (2007)	Schrankogel, Tyrol, Austria	2912–3457	vascular plants	vegetation sampling	362 plots 1 x 1 m with repeated recording after 10 years	54 and 56
Ramos-Jiliberto et al. (2010)	Central Chile	1800–3600	Plant-pollinator networks	review of literature and record of insect visitation on flowers	4 plots	45–88 plants and 31–110 insects
Rojas & Stephenson (2008)	Cocos Island, Costa Rica	5–575	Myxomycete	Moist chamber cultures and field collection	6 study sites	41

Author	Region	Elevation m a.s.l.	Taxa	Method	Plot-Design	Number of species
Rowe (2009)	Utah, USA	1564–4118 1540–3440 1571–3448 1482–3449	small mammals	multiple trap types and review of literature	73 sites	37
Sanders (2002)	Colorado, Utah and Nevada, USA	150–4400	ant	review of literature	n.d.	226
Sang (2009)	Tianshan Mountain, Xinjiang, China	450–3400	vascular plants	vegetation sampling	87 plots 20 x 20 m with four subplots	341
Santos & Costa (2010)	Southeastern Brazil	100–2300	liverworts	vegetation sampling and literature data	6 areas	736
Shimono et al. (2010)	Qinghai-Tibetan Plateau	3200–5200	vascular epiphytes	vegetation sampling	23 study sites	191
Vetaas & Grytnes (2002)	Himalaya (Nepal)	1000–5000	vascular plants	review of literature	n.d.	4928
Wang et al. (2007)	Gaoligong Mountain, Tibet	215–5791	seed plants	review of literature	n.d.	4156
Watkins et al. (2006)	La Selva Volcán, Costa Rica	30–3000	ferns (epi-phytic and terrestrial)	vegetation sampling	six study sites with four transects 100 x 2 m	264
Widden (1987)	Northern England	350–880	microfungi	soil survey	6 plots 2 x 2 m	34
Wilson et al. (2007)	Queensland, Australia	100–1200	Schizophoran flies	malaise traps	6 sites with 3 traps each	203
Wolf (1993)	Northern Andes, Columbia	1000–4130	epiphytic bryo-phytes and lichens	canopy trees	15 sites with 59 conopy trees	473 (108 mosses, 187 lliver-worts, 178 lichens)