

Community and Ecosystem Responses to Elevational Gradients: Processes, Mechanisms, and Insights for Global Change

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Abstract

Community structure and ecosystem processes often vary along elevational gradients. Their responses to elevation are commonly driven by changes in temperature, and many community- and ecosystem-level variables therefore frequently respond similarly to elevation across contrasting gradients. There are also many exceptions, sometimes because other factors such as precipitation can also vary with elevation. Given this complexity, our capacity to predict when and why the same variable responds differently among disparate elevational gradients is often limited. Furthermore, there is utility in using elevational gradients for understanding community and ecosystem responses to global climate change at much larger spatial and temporal scales than is possible through conventional ecological experiments. However, future studies that integrate elevational gradient approaches with experimental manipulations will provide powerful information that can improve predictions of climate change impacts within and across ecosystems.

1. INTRODUCTION

Ecologists and biogeographers have long been aware of the value of elevational gradients for understanding how plant and animal communities respond to macroclimate (von Humboldt 1849, Merriam 1899). For example, Grinnell (1914) was among the first to point out that elevational gradients can provide powerful information on how the ranges of plant and animal species are restricted by environmental conditions. Subsequently, he highlighted the utility of studies along environmental gradients for understanding how evolutionary dynamics and adaptations are governed by environmental factors (Grinnell 1924). Similarly, the classic studies by Whittaker (1956, 1960) in the Smoky and Siskiyou Mountains of the United States explored factors that shape communities along elevational gradients. More recent work along elevational gradients has led to many insights about how patterns of species diversity respond to environmental gradients (Rahbek 2005, Colwell et al. 2008).

Despite these advances, as experimental ecology developed, the use of environmental gradients for testing ecological questions fell into some disfavor because many experimental ecologists became persuaded that observational studies were somehow less rigorous than manipulative experiments (Diamond 1986). Over the past few decades, manipulative experiments have provided useful information on community and ecosystem responses to environmental conditions at smaller spatial and temporal scales (e.g., Wu et al. 2011a). However, there is increasing recognition that such experiments may underestimate some community- and ecosystem-scale responses to variation in climate (Wolkovich et al. 2012). Further, community and ecosystem dynamics often change both over longer timeframes and across larger spatial scales than those captured in most experimental studies. For this reason, natural gradients can act as powerful study systems for understanding longer-term, larger-scale, community and ecosystem responses to environmental changes in a manner that cannot be achieved by experiments alone (Fukami & Wardle 2005, Walker et al. 2010). Indeed, ongoing climatic changes and predictions of average global surface temperatures rising by at least 2°C (and probably considerably more) by the year 2100 (IPCC 2007) provide an impetus for a better understanding of how long-term, large-scale variation in climate influences community and ecosystem processes. Elevational gradients can serve as natural experiments for studies on community and ecosystem responses to long-term changes in climate and as test beds for models about the future of biodiversity in a changing world (Fukami & Wardle 2005, McCain & Colwell 2011).

In this review, we outline and discuss recent advances in understanding the responses of communities and ecosystems to elevation, as well as the mechanisms underpinning these responses. First, we explore how organismal abundances, community composition, diversity, and biotic interactions vary with elevation for plants and above- and belowground consumers. We then explore how ecosystem-level variables driven by these organisms respond to elevation. Next, we discuss whether these responses to elevation can be used reliably to predict the effects of temperature increases caused by global climate change on community and ecosystem processes and how elevational gradients can be used in combination with experimental approaches for aiding these predictions. In doing this, we aim to highlight the potential of using elevational gradients to address ecological responses to ongoing climate change as well as major knowledge gaps and to identify topics that could usefully serve as important future directions in this quest.

2. INTERPRETATIONS OF ELEVATIONAL GRADIENTS

Increasing elevation is associated not only with a decline in temperature, but also with a decline in land area (because there is generally less total area at higher elevations) and changes in other abiotic factors. Many of these factors and their possible implications for organisms and communities across elevational gradients have been synthesized and discussed elsewhere (e.g., Körner 2007).

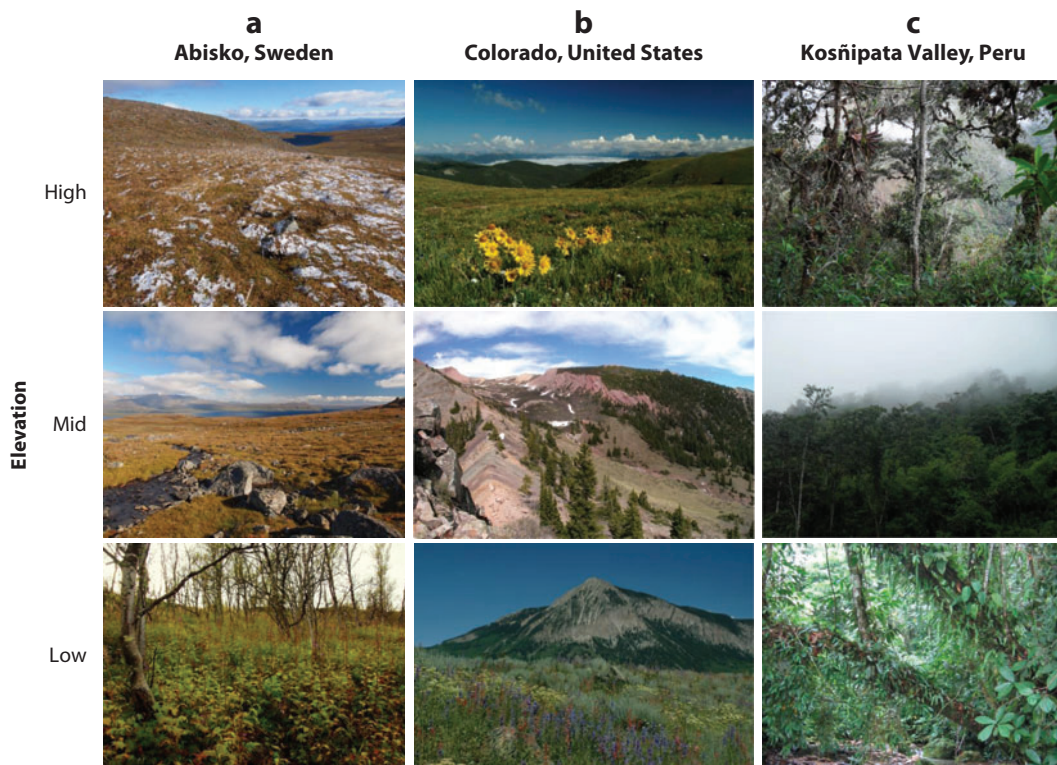


Figure 1

Low, mid-, and high elevations for each of three gradients ranging from the subarctic to the tropics: (a) Abisko, Sweden (500–1,000 m), (b) the Rocky Mountains, Colorado, USA (2,700–3,700 m), and (c) the Kosñipata Valley, Peru (200–3,000 m). Photo credits: (a) Tyler Logan, (b) David Inouye, and (c) Daniel B. Metcalfe and the Global Ecosystems Monitoring project (<http://gem.tropicalforests.ox.ac.uk/>).

Briefly, temperature declines associated with increasing elevation influence ambient humidity. In addition, total atmospheric pressure declines with increasing elevation whereas (under cloudless conditions) both total radiation and UV-B radiation increase (Körner 2007). Similar to latitudinal gradients, elevational gradients can be associated with changes in other abiotic factors, including precipitation, wind velocity, seasonality, geological substrates, soil formation processes and disturbance history (Pickett 1989, Körner 2007), and nitrogen (N) deposition (Lovett & Kinsman 1990). Some of these factors can be controlled within a single study system, whereas others inevitably covary with elevation at least for some gradients.

Mountains occur on every continent and harbor a wide array of terrestrial ecosystem types (e.g., **Figure 1**), and one of the attractions of investigating elevational gradients upon them is that studies can be repeated at multiple locations around the world (e.g., Callaway et al. 2002, Harsch et al. 2009, McCain 2009). Furthermore, although temperature and other abiotic factors often covary with elevation, they need not vary with elevation in a similar manner across different elevational gradients, either regionally or globally. Temperature and land area are often highlighted as the most important factors influencing organisms along elevational gradients (Körner 2007). The role of temperature in driving responses across elevational gradients is further supported by growing numbers of studies reporting consistent global effects of elevation-associated declines in

temperature on organismal growth (Hoch & Körner 2012), community diversity (Rahbek 2005), biotic interactions (Callaway et al. 2002) and ecosystem processes (Whittaker et al. 1974, Raich et al. 1997). When one carefully considers factors that may covary with temperature, elevational gradients serve as useful systems for exploring how temperature influences communities and ecosystems over large spatial and temporal scales. Therefore, the large and growing number of studies along elevational gradients worldwide provides powerful information on the effect of broad-scale variation in macroclimate, and especially temperature, on ecosystem properties and processes among disparate ecosystems (**Figure 1**).

3. COMMUNITY-LEVEL RESPONSES TO ELEVATION

3.1. Community Composition

Elevation influences the structure of communities through differential effects on their component species. These effects can be either direct and reflect physiological responses to temperature and associated abiotic factors that change with elevation or indirect and reflect temperature effects on resources or on coexisting organisms. We now explore the nature of these community responses and the mechanisms underpinning them.

3.1.1. Plants. Plant communities frequently show distinctive responses to elevation (Whittaker 1956, 1960). Often the most obvious response is the tree line switch from forest to treeless vegetation (Körner 1998) that represents a distinct transition of plant growth forms at an elevational threshold. However, both above and below these tree lines (as well as for gradients that lack trees), there is often a continuous turnover of plant species and functional groups, although the rate of turnover differs among vegetation types (**Figure 2a,b**) and regions (Whittaker 1956, Sundqvist et al. 2011a). Higher elevations are commonly dominated by plants of lower stature (Körner 1999) and functional groups that are characterized by inherently slower growth rates and adaptations to more stressful environments (Whittaker 1956), although there are notable exceptions (Díaz & Cabido 1997). These patterns are often associated with changes in plant functional traits, both among and within dominant species with increasing elevation, that are commonly associated with greater stress, such as decreasing specific leaf area (Salinas et al. 2011), decreasing leaf nutrient concentrations (Vitousek et al. 1988, Tanner et al. 1998), and increasing nutrient amounts per leaf area (Körner 1989).

Our knowledge of the mechanisms underpinning plant community responses to elevation is growing. For example, temperature directly regulates both plant photosynthesis and metabolism and is increasingly recognized as a key controller of the metabolic processes essential for tree tissue production, and thereby the elevational tree line (Hoch & Körner 2012). Furthermore, temperature controls nutrient mineralization rates and therefore plant nutrient supply from the soil. For this reason, increasing elevation can select for plant species and functional groups possessing functional traits that are better adapted to nutrient limitation (Vitousek et al. 1988, Sundqvist et al. 2011b). Plants also respond to changes in other abiotic factors, such as moisture availability, which can result in functionally distinct plant communities across elevational gradients (Díaz & Cabido 1997). The patterns of specific plant community responses to elevation are thus strongly controlled by the relative importance of different abiotic factors, as well as by the interactions among them (Vitousek et al. 1988, Díaz & Cabido 1997, Sundqvist et al. 2011a).

3.1.2. Aboveground consumers. Responses of aboveground consumer communities to elevational gradients arise from shifts in the relative abundances of species (Sanders et al. 2007) and

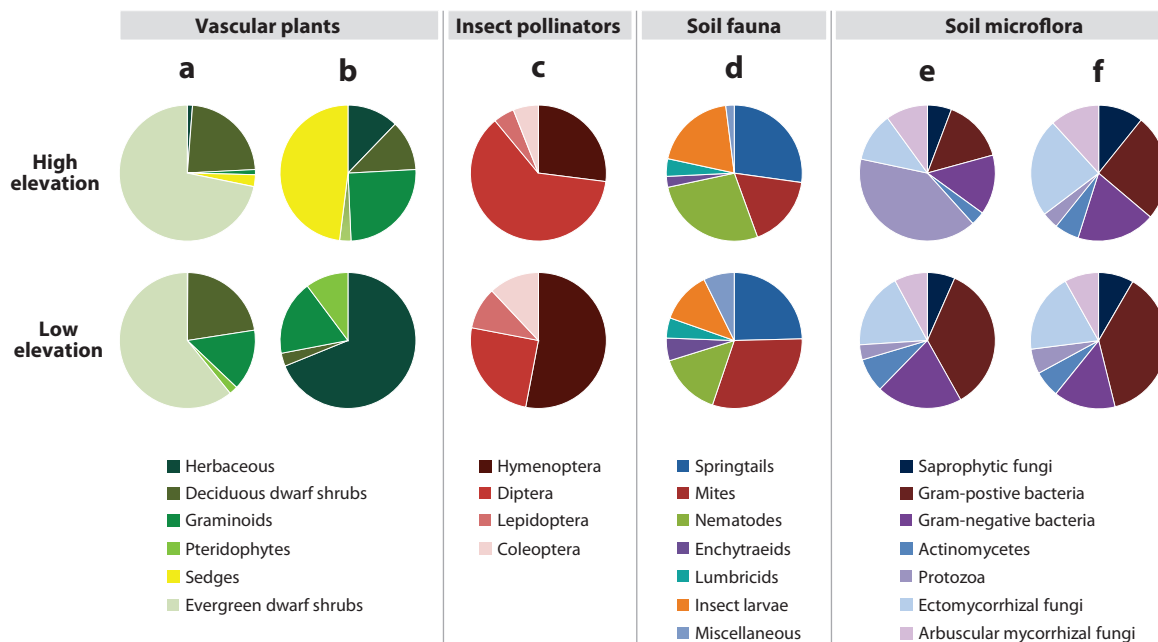


Figure 2

Changes in relative abundances of functional or taxonomic groups of organisms from low to high elevational sites. (a,b) Plant functional groups in (a) heath and (b) meadow vegetation, Abisko, Sweden, modified from Sundqvist et al. (2011a) with permission of John Wiley and Sons. (c) Insect pollinators, Utah, USA, from Warren et al. (1988). (d) Soil fauna, the High Atlas Mountains, Morocco, from Sadaka & Ponge (2003). (e,f) Soil microbes in soils on (e) ultrabasic and (f) metasedimentary parent material on Mt. Kinabalu, Borneo, modified from Wagai et al. (2011) with permission of Springer Japan.

species replacement (Hodkinson 2005, McCain 2009). The rate of species turnover with elevation can vary greatly both among communities and across regions. Within any one gradient, individual species that occupy a large elevational range may therefore co-occur with different sets of species at different portions across that range (Hodkinson 2005). Furthermore, the relative abundance of different animal functional groups commonly changes with elevation. Examples include shifts in the dominant groups of pollinators (Warren et al. 1988; **Figure 2c**), reduced abundances of keystone seed dispersers (Zelikova et al. 2008; **Figure 3b**), and lower densities of insect parasitoids per unit host (Randall 1982a,b; **Figure 3d**) as elevation increases. Body size and functional traits also vary with elevation both within and among species for a variety of animal taxa from insects to mammals, but the direction of such shifts varies greatly both among and within taxa (Badgley & Fox 2000, Hodkinson 2005).

Aboveground consumers differ in their thermal limits, and temperature therefore has a fundamental role in determining the elevational range limit for many species (Hodkinson 2005, Moritz et al. 2008) and the responses of communities to elevation (Sanders et al. 2007, McCain 2009). In combination with temperature, water supply operates as a driver of animal community responses to elevation (McCain 2007), but its importance varies among both taxa and regions (Badgley & Fox 2000, Powney et al. 2010). Other factors that drive aboveground consumer responses to elevation are plant productivity and the availability of food resources (McCain 2007), which in turn are often driven by temperature (see Section 4.1). For example, de Sassi et al. (2012) recently showed that although warmer temperatures at lower elevations along an elevational gradient in New Zealand

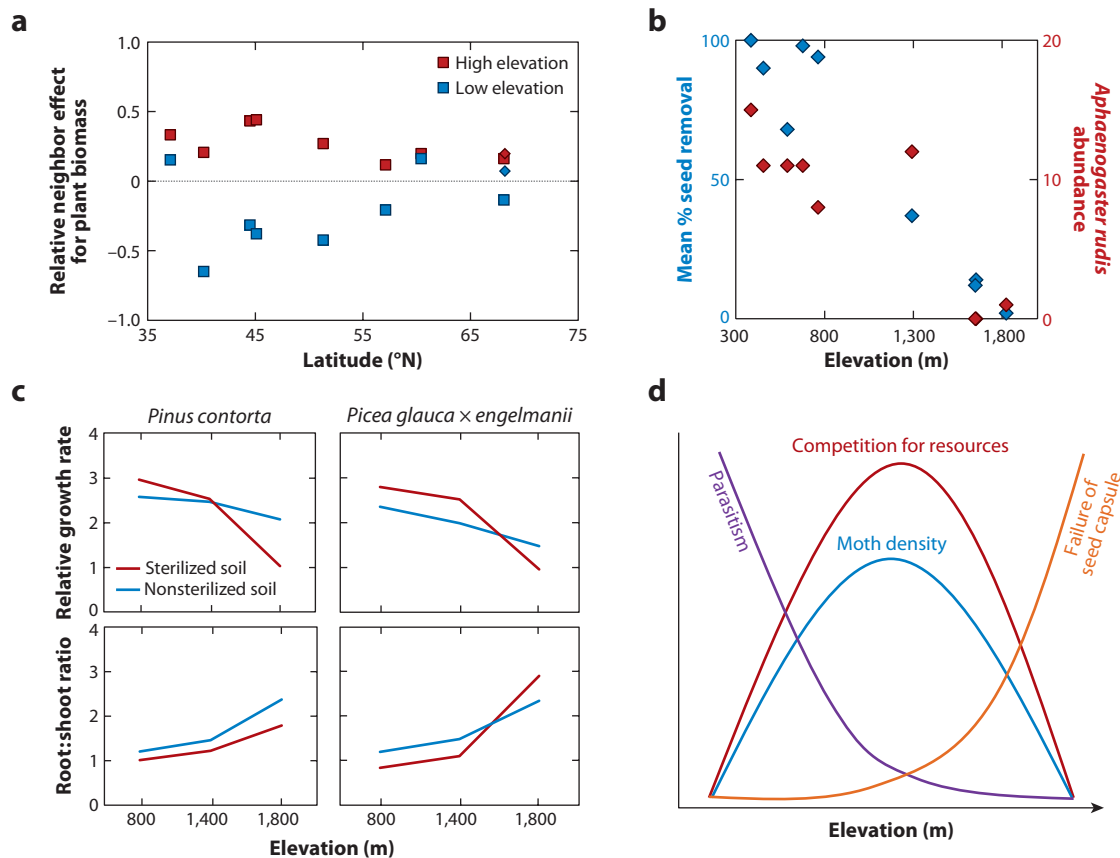


Figure 3

Examples of changes in biotic interactions across elevational gradients. (a) Plant-plant interactions: relative neighbor effects for plant biomass at high and low elevations across latitudes. Positive values denote facilitation (positive effect of neighbor plants on plant biomass) and negative values denote competition (negative effect of neighbors on biomass). At 68°N, sites are distinguished using squares (Central Brookes Range, Alaska) and diamonds (Abisko, Sweden). Modified from Callaway et al. (2002) with permission of Nature Publishing Group. (b) Plant-animal interactions: variation in mean percentage of seeds from *Trilium undulatum* removed by the keystone seed dispersing ant, *Aphaenogaster rudis*, during a 24-h period (blue diamonds, left y-axis), and abundance of *A. rudis* (red diamonds, right y-axis), with elevation. Data from Zelikova et al. (2008). Copyright © 2013 Elsevier Masson SAS. All rights reserved. (c) Plant-soil organism interactions: the mean relative growth rates and root to shoot ratios for *Pinus contorta* and *Picea glauca* × *engelmannii* seedlings grown in sterilized and nonsterilized soil from three elevations. Modified from Wagg et al. (2011) with permission of the authors and Springer. (d) Tritrophic interactions: variation with elevation in density of the moth *Coleophora alticolella*, parasitism of *Coleophora alticolella*, failure of the host plant *Juncus squarrosus* to set seeds, and moth larval competition for food (note that x- and y-axis scales are arbitrary). Modified from Randall (1982b) with permission of John Wiley and Sons.

significantly increased biotic homogenization in insect herbivore communities, these patterns were largely mediated by changes in plant community composition.

3.1.3. Belowground consumers. Many taxonomic groups of belowground consumers respond to elevation (Olson 1994, González et al. 2007, Bahram et al. 2012), but these responses vary both among and within groups (Decaëns 2010). Although some studies find distinct microbial communities at specific elevations (Gómez-Hernández et al. 2012), others do not (Sundqvist et al. 2011a). Likewise, though total turnover in species composition of termite communities may be low

(Palin et al. 2011), other litter-dwelling species may have a relatively high turnover across elevational gradients (Olson 1994). Furthermore, the relative biomass or abundance of dominant functional groups of soil organisms can be highly responsive to elevation (**Figure 2d-f**). For instance, the ratio of fungal to bacterial biomass can increase with elevation (Wagai et al. 2011), which is consistent with microbial communities in more stressful environments supporting a fungal-based food web associated with more conservative nutrient cycling (Wardle 2002). There is, however, much variation in the responses to elevation by major groups of soil biota at both local (Sundqvist et al. 2011a) and regional scales. For example, Lessard et al. (2011) found that abundances of arthropod detritivores declined with increasing elevation in the Great Smoky Mountains (USA), whereas Sadaka & Ponge (2003) found that both the total abundance of soil biota and the dominance of litter feeders increased with elevation in the Moroccan Atlas Mountains.

Although the mechanistic basis for belowground community responses to elevation remains poorly understood, variations in temperature and precipitation are important drivers for many soil-dwelling taxa (Palin et al. 2011, Bahram et al. 2012). Furthermore, belowground consumers are intrinsically linked to aboveground communities (Wardle 2002). Changes in vegetation can therefore shape the responses of soil communities to elevation (Richardson et al. 2005, Bahram et al. 2012), for instance, by influencing habitat and food resources, and this can help explain turnover of soil animal communities across elevational gradients (Sadaka & Ponge 2003). However, the role of vegetation in driving responses to elevation by soil communities can be less important in arid environments, where moisture availability instead plays a greater role (Clark et al. 2009). Other soil abiotic properties (e.g., pH, nutrients) can also influence the responsiveness of microbial communities to elevation, either separately or in combination with vegetation (Wagai et al. 2011, Sundqvist et al. 2011a). Because soil microbes and animals drive soil processes affecting carbon and nutrient cycling (**Figure 4**; see also Sections 4.2 and 4.3), increased understanding of their responses to elevation and the underlying mechanisms can provide insights into how changes in climate and other environmental factors may influence ecosystem functioning.

3.2. Relationships between Elevation and Species Diversity

It was long thought that diversity declined linearly with elevation in much the same way that it does with latitude (e.g., MacArthur 1972). However, more recent work highlights that this is not the case: Rahbek (2005) demonstrated that the most common pattern (~50% of all studies) is a peak in diversity at mid-elevations, and when only studies that are standardized for the effect of area and sampling efforts are considered, ~75% of all elevational gradients reveal this pattern for both plants and animals. However, there is some variation around this pattern, as it can vary among taxa, depend on spatial scale, or differ among mountain ranges embedded in different climatic regimes (McCain 2009, Sanders et al. 2009). Importantly, the mechanisms that shape these patterns are still the subjects of considerable debate (Dunn et al. 2007).

Although plant diversity often peaks at mid-elevations (Rahbek 2005, Kessler et al. 2011), the mechanisms underlying these patterns, as well those that cause diversity to differ between local and regional scales, are only just beginning to be explored in a systematic way (Rahbek 2005, Nogués-Bravo et al. 2008). One possibility is that though the patterns differ among taxa, functional groups, and gradients, the mechanisms that shape them are the same; temperature and precipitation may both act to regulate plant diversity across elevational gradients, but temperature and precipitation need not covary in the same way with elevation among different gradients (McCain & Colwell 2011). For example, elevational diversity patterns can differ between arid systems and tropical systems because water is likely to be less limiting at high elevations in arid systems, whereas temperature is more likely to be limiting at high elevations in tropical systems (Kessler et al. 2011).

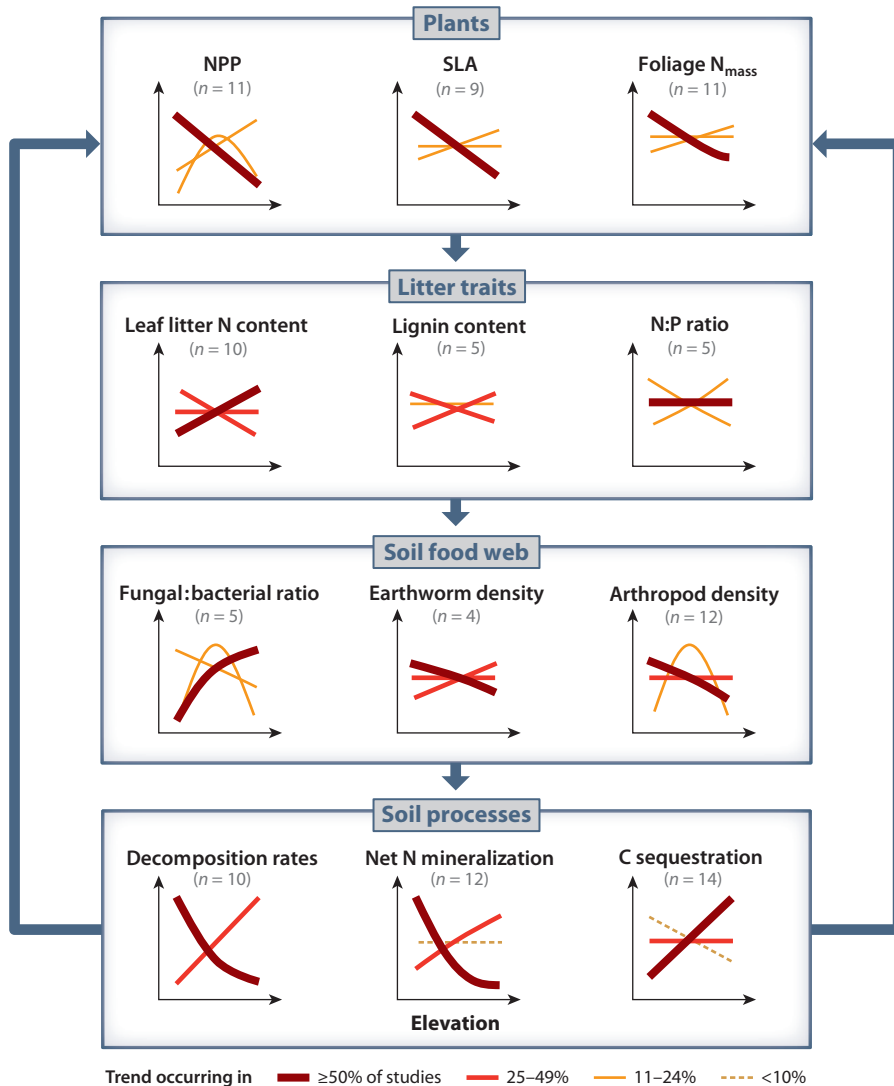


Figure 4

Summary of commonly found changes in aboveground and belowground properties and processes (y-axes) in response to elevation (x-axes) derived from data in 64 published studies. Plant traits determine the amount and quality of litter entering the soil food web at different elevations, which influences soil processes that in turn feed back to plant nutrition and growth. n = number of studies that the trends for each property or process are summarized from. Abbreviations: C, carbon; N, nitrogen; NPP, net primary production; P, phosphorus; SLA, specific leaf area.

Aboveground consumer diversity sometimes tracks with plant diversity along elevational gradients because of either increased productivity or increased resource heterogeneity, or because of both of these factors, which has been shown for birds in the Eastern Himalayas (Acharya et al. 2011). However, it is likely that the interplay between the biotic and abiotic environment shapes consumer diversity along elevational gradients. For example, studies on hummingbirds in the Andes (Graham et al. 2009) and ants in the United States and Europe (Machac et al. 2011)

suggest that cold climates filter species at high elevations, whereas interspecific interactions shape diversity patterns at lower ones.

There is a paucity of studies on the response of soil biodiversity to elevation, and most focus on soil invertebrates. These studies often find that soil faunal diversity either decreases with increasing elevation (due to temperature, energy, or area effects) or peaks at mid- and high elevations (due to changes in soil abiotic factors) (Decaens 2010). Furthermore, studies on soil microflora have shown microbial diversity to peak at mid-elevations on Mt. Fuji in Japan (Singh et al. 2012); acidobacterial diversity to decline with elevation in the Colorado Rocky Mountains, USA (Bryant et al. (2008); and bacterial diversity to show no consistent response to elevation in Peru (Fierer et al. 2011). Additionally, recent findings show that elevational diversity patterns vary among different macromycete functional groups along a gradient spanning from 100 m to 3,500 m in central Veracruz, Mexico (Gómez-Hernández et al. 2012). Specifically, diversity for xylophagous species peaks at 1,000 m, whereas ectomycorrhizal fungal diversity peaks at 1,500–2,000 m. In total, the available evidence indicates that for both aboveground and belowground consumer biota, responses of diversity to elevation are not governed by the same mechanisms in disparate systems. However, because such studies are still in their infancy (especially for microbes), our capacity to generalize about the responses of soil biodiversity to elevation remains limited.

3.3. Biotic Interactions

The strength and the direction of biotic interactions within and across trophic levels can vary greatly with elevation (**Figure 3a–c**). For example, Callaway et al. (2002) found for several sites around the world that interspecific interactions between plants were positive (i.e., facilitative) at high elevations, but negative (i.e., competitive) at low elevations (**Figure 3a**). In addition, Jankowski et al. (2010) showed that interspecific competitive interactions limited elevational ranges for several tropical bird species. Interactions between plants and their consumers can also respond to elevation. For instance, increased herbivory at lower elevations can limit the lower elevational range limit for some plant species (Galen 1990). In addition, Miller et al. (2009) found that the effect of insect herbivory on the tree cholla cactus (*Opuntia imbricata*) was lower at higher elevations in central New Mexico owing to greater defense of the cactus by ants. With regard to belowground interactions, Defosse et al. (2011) showed that negative effects of soil biota (e.g., pathogens) on the survival of *Fagus sylvatica* in the French Alps declined with elevation. Similarly, it is recognized that particular ectomycorrhizal fungal species can promote tree establishment in stressful environments (Nara & Hogetsu 2004), and a study from the Canadian Rocky Mountains revealed that these positive effects could be more important for promoting tree establishment at higher elevations (Wagg et al. 2011; **Figure 3c**). In sum, in addition to variation in abiotic factors, biotic interactions greatly affect the composition of species and growth forms across elevational gradients.

The importance of multitrophic interactions in influencing community structure is well established (Hunter & Price 1992), and a handful of studies have explored the dynamics of such interactions along elevational gradients. As a classic example, the density of seed-feeding larvae of the moth *Coleophora alticolella* is controlled more by parasitism at low elevations (Randall 1982a) and more by food availability at high elevations through lower seed production by its host plant. This generates a mid-elevation peak in both the density of the moth larvae and its predation of seeds of the host plant (Randall 1982a,b, 1986; **Figure 3d**). However, the dearth of studies on the role of multitrophic interactions in influencing organisms other than insects across elevational gradients limits our understanding of how broad-scale variation in climate structures community composition and ultimately ecosystem processes.

As we have discussed, patterns of community responses to elevation are commonly driven by temperature and, especially in arid environments, also by precipitation. However, much remains to be learned about the relative roles of climate, biotic interactions, and other factors (as well as the interactions among them) in shaping the responses of species, whole communities, and diversity patterns to elevation. Although important recent advances have been made in understanding the relative roles of some of these underlying mechanisms (e.g., Dunn et al. 2007, Graham et al. 2009, Machac et al. 2011), further developments are most likely to arise through combining observational data across elevational gradients with experimental manipulations designed to tease apart these mechanisms, as we discuss in the final sections of this review.

4. ECOSYSTEM-LEVEL RESPONSES TO ELEVATION

Ecosystem properties and processes are governed by the interactions between abiotic factors such as climate and soil properties, and biotic factors such as the composition and trait spectra of the component species (see Section 3). All of these factors vary, sometimes systematically and concomitantly, along elevational gradients (**Figures 2–4**). In this section, we discuss what is known about how properties and processes that occur at the ecosystem level respond to changes in elevation-associated factors, both above- and belowground.

4.1. Plant Biomass and Production

Ecosystem productivity often varies with climate, which in turn varies with elevation. Therefore, common responses to increasing elevation are declines in aboveground plant biomass and aboveground net primary production (NPP) (**Figure 4**; Whittaker et al. 1974, Raich et al. 1997), which are usually attributed to declining temperature. However, there is some variation in these patterns among gradients that differ in bedrock type (Kitayama & Aiba 2002), soil age (Raich et al. 1997), and precipitation regime (Whittaker & Niering 1975, Pérez & Frangi 2000). Furthermore, some studies in forest ecosystems have found that understory vegetation and tree biomass do not necessarily decline in tandem, especially when the growth of the two components is limited by different factors (Whittaker 1966, Barrera et al. 2000). Non-unidirectional responses to elevation can also occur when different portions of the gradient are dominated by functionally different plant life forms. One example is from Tierra del Fuego, Argentina, where the tree species *Nothofagus pumilio* forms monocultures from sea level to the tree line. Here, an overall decline in aboveground NPP with increasing elevation is reversed in the krummholz zone, where *N. pumilio* has greater productivity per growing season day and per unit leaf area compared to trees at lower elevations (Barrera et al. 2000, Frangi et al. 2005).

Although fewer studies have explored how root biomass and production vary with elevation, Luo et al. (2005) found a decline in root biomass with increasing elevation in Tibet, and Girardin et al. (2010) showed that mean annual belowground productivity was highest at the more fertile low-elevation sites along an elevational gradient in the Andes, Peru. However, Oleksyn et al. (1998) grew seedlings of Norway spruce (*Picea abies*) originating from elevations ranging from 600 m to 1,500 m in a common garden in southern Poland to show that populations adapted to higher elevations allocated a greater proportion of fixed C to roots than to shoots. This result has also been supported by studies that show both a decline in aboveground plant biomass and an increase in root biomass with increasing elevation (Pérez & Frangi 2000). Increases in root relative to shoot allocation are commonly associated with declining soil fertility (Chapin 1980), such as is frequently observed with increasing elevation (see Section 4.3.4).

4.2. Plant Litter Decomposition and Leaf and Litter Nutrient Dynamics

Temperature is a well-known direct driver of litter decomposition, and litter mass loss rates are often greater at lower elevations due to warmer conditions (**Figure 4**; Wang et al. 2009, Salinas et al. 2011). Greater rates of nutrient release from decomposing litter also occur at lower elevations (Vitousek et al. 1994), potentially enhancing the supply rates of available nutrients from the soil. However, precipitation, which may also promote litter decomposition rates (Vitousek et al. 1994), can play a more prominent role than temperature across elevational gradients in arid ecosystems. For instance, decomposition rates increase toward the colder but more humid higher elevations in northern Arizona in the United States (Murphy et al. 1998). Furthermore, in the Himalayas, Upadhyay et al. (1989) showed that monthly precipitation was the best abiotic predictor of monthly litter mass loss, whereas annual temperature and evapotranspiration were the best predictors of annual litter mass loss, suggesting that different or interacting climatic variables that covary with elevation can drive decomposition at different temporal scales.

It is well recognized that litters with high nutrient concentrations and low levels of structural and chemical defense compounds on average decompose fastest. Thus, the decline in litter quality that can occur with increasing elevation (**Figure 4**) and the changes in plant functional traits that determine this quality (Vitousek et al. 1988, Salinas et al. 2011) should in turn lead to reduced litter mass loss and nutrient release rates at higher elevations (Vitousek et al. 1994). However, both the shifts in litter quality with elevation and the role of litter quality in driving mass and nutrient loss rates across elevational gradients can vary greatly both within and among plant species (Sundqvist et al. 2011b). As a consequence, even when some leaf and litter traits shift toward values commonly associated with low litter quality at high elevations, these traits are not always the same as those that actually drive litter decomposition (Salinas et al. 2011, Sundqvist et al. 2011b). Furthermore, studies in disparate ecosystems reveal that the responsiveness of leaf and litter traits to elevation and their role in driving litter mass loss and nutrient release rates depends on environmental context and can be influenced by vegetation type, soil conditions, and substrate age (Vitousek et al. 1994, Kitayama et al. 2004, Sundqvist et al. 2011b).

As discussed earlier, decomposer organism densities and community composition often respond to elevation (**Figure 4**), but few studies have explicitly tested the consequences of this fact for litter decomposition rates. However, Wang et al. (2009, 2010) performed decomposition experiments on tree leaf litters both with and without microarthropod exclusion along an elevational gradient in southern China. They showed that the effect of soil fauna on mass loss became increasingly positive toward lower elevations for litter from the tree *Castanopsis carlesii*, but not for litter from *Pinus taiwanensis*, which has a higher litter C:N ratio. This indicates that decomposer organisms can greatly influence the response of litter decomposition to elevation, but this effect may depend on litter quality.

4.3. Nutrient Cycling Processes and Nutrient Availability

Key components of nutrient cycling can vary with elevation. Below we examine these patterns and how they may impact major ecosystem processes along elevational gradients.

4.3.1. Nutrient inputs. A major pathway by which N enters ecosystems is via atmospheric N deposition, and this input can vary with elevation though not in a consistent manner. This is because within mountain chains N deposition can show considerable spatial variability owing to local variation in precipitation, wind speed, and canopy structure (Lovett & Kinsman 1990).

For example, though N deposition increases with elevation in parts of North America (Lovett & Kinsman 1990), it declines with elevation in parts of the Swiss Alps (Jacot et al. 2000a). Other than atmospheric deposition, the primary means of ecosystem N input is through biological N fixation, but the response of this process to elevation remains little studied. However, Jacot et al. (2000a,b) showed that the proportion of plant N derived from symbiotic N₂ fixation for legumes in the Swiss Alps increased toward their upper elevational limit, whereas N-fixation per unit area declined because of a reduction in legume abundance with elevation. Furthermore, Cusack et al. (2009) found higher N-fixation rates by free-living N-fixers at a low-elevation site in a Puerto Rican forest, likely as a result of declining temperatures with elevation.

Nutrients other than N, such as P and K and trace elements, become available for organismal uptake through weathering of bedrock, which is strongly influenced by climatic factors. Weathering rates are impaired by lower temperatures at higher elevations (Kitayama et al. 2000) and sometimes also by lower precipitation rates at lower elevations (Rasmussen et al. 2010). These climatic factors further interact with bedrock type (Kitayama et al. 2000) and age (Idol et al. 2007), leading to contrasting responses to elevation of plant-limiting nutrients, notably P, from weathering of different parent materials.

4.3.2. Internal nutrient fluxes. Studies spanning a wide range of ecosystems frequently show a decline in flux rates of some important steps in the N cycle with increasing elevation, including both N mineralization (conversion of organic N to ammonium) and nitrification (conversion of ammonium to nitrate) (e.g., Sveinbjörnsson et al. 1995, Kitayama et al. 1998; **Figure 4**). Values of $\delta^{15}\text{N}$ for surface soils and plants often become more negative at higher elevations, which indicate lower rates of microbial release of mineral forms of N (Liu & Wang 2010). However, there are exceptions, and examples also exist of net N mineralization rates increasing with elevation (Groffman et al. 2009). Additionally, Averill & Finzi (2011) found that though net mineralization declined with increasing elevation, plant uptake of organic N increased. Although flux rates of other nutrients are less studied, there is evidence that they can also decline with increasing elevation. For example, in a dry tropical forest in Mexico, Campo-Alves (2003) found that inputs of P, K, and Ca via litter fall and canopy through-fall declined with increasing elevation, which was matched by a decline in the available forms of nutrients in the soil. Likewise, Johnson et al. (2000) found that the cycling of K was most rapid at low elevations in a watershed in the Hubbard Brook Experimental Forest, New Hampshire, USA. However, nutrient fluxes vary in their response to elevation when soil substrates differ (Kitayama et al. 1998), and fluxes for different nutrients can respond differently along the same gradient. For instance, in the Swedish subarctic, Jonasson et al. (1993) found that net N mineralization rates increased whereas net P mineralization rates declined with elevation.

Declining temperature frequently drives reductions in net nutrient mineralization and nitrification rates with increasing elevation because of the role of temperature in regulating both biological activity and chemical process rates (e.g., Sveinbjörnsson et al. 1995, Liu & Wang 2010). However, variation in soil abiotic properties, such as pH and moisture availability, as well as snow depth, can also be important in regulating nutrient flux rates across elevational gradients. For example, Groffman et al. (2009) showed that net N mineralization and nitrification rates in the Hubbard Brook Experimental Forest increased with elevation during the summer owing to enhanced soil moisture status (probably through reduced evapotranspiration) and during the winter due to thicker snow cover and therefore less soil freezing. Increasing elevation also often influences the amount of nutrient inputs from litter by driving declines in aboveground NPP and thus litter production (Whittaker et al. 1974, Campo-Alves 2003), although again there are notable exceptions (Frangi et al. 2005). Furthermore, changes in the quality of soil organic matter can greatly influence nutrient flux rates along elevational gradients. For instance, across an elevational gradient on

Mt. Kinabalu, Borneo, though net N mineralization and nitrification rates were mainly controlled by temperature for sites on sedimentary rocks, mineralization was regulated by declining soil organic matter quality for sites on ultrabasic rocks (Kitayama et al. 1998). In addition, soil fauna and microbial communities play a large role in governing nutrient cycling (Wardle 2002), and shifts in belowground communities with elevation (**Figure 2d-f**) could therefore potentially influence nutrient flux rates along elevational gradients, although to our knowledge this hypothesis has not been explicitly tested.

4.3.3. Nutrient outputs. Outputs of N from the biosphere to the atmosphere occur via denitrification (release of nitrous oxides) and volatilization (release of ammonia). Although these processes can be an important pathway for N loss from terrestrial ecosystems, few studies have explored their responses to elevation. However, one study from a Brazilian Atlantic forest showed that N₂O fluxes increased with decreasing elevation due to warmer and moister soils (Sousa Neto et al. 2011). In contrast, N₂O flux did not vary with elevation at the Hubbard Brook Experimental Forest, whereas potential denitrification increased with elevation because soils at high elevations were moister and supported greater nitrification rates (Groffman et al. 2009).

Another relatively unexplored pathway by which nutrients can be lost along elevational gradients is via leaching or by overland transport, which may be particularly important on steep slopes. With regard to N, losses of nitrate from soil to stream water declined with increasing elevation during the winter months in the Catskill Mountains, USA, despite N deposition increasing with elevation (Lawrence et al. 2000). This was most likely due to declining nitrification rates and a greater accumulation of organic matter and increased nutrient retention capacity due to impairment of litter decomposition rates with increasing elevation. Furthermore, along an elevational gradient in New Mexico, USA, net losses of a wide range of nutrients (e.g., N, K, Mg, Ca) via stream water were generally lowest at mid-elevations, although the precise elevation at which maximal losses occurred varied among elements (Gosz 1980). These mid-elevation peaks resulted from a large influence of evapotranspiration on stream discharge and through evapotranspiration being greatest at mid-elevations owing to low temperatures at high elevations and low precipitation at lower elevations.

4.3.4. Consequences for soil fertility and feedbacks to plant growth. Data on how soil fertility varies with elevation are accumulating, and a common trend across a range of ecosystems is a decline in the concentrations and supply rates of plant-available mineral nutrients in the soil with increasing elevation (Sveinbjörnsson et al. 1995, Johnson et al. 2000). This pattern is often associated with changes that occur in other variables frequently associated with reduced soil fertility as elevation increases (**Figure 4**). For example, soil mineral and foliar nutrient concentrations, aboveground NPP, and rates of decomposition and nutrient mineralization all decline with elevation across the Mauna Loa environmental matrix in Hawaii (Vitousek et al. 1988, 1994; Raich et al. 1997). However, there are several exceptions to this general pattern (**Figure 4**), and as discussed previously, increasing elevation does not always lead to reduced soil fertility or impaired plant growth (Körner 1989, Frangi et al. 2005, Averill & Finzi 2011). Little is currently known about which abiotic or biotic factors control plant growth across those elevational gradients for which temperature and its consequent effects on soil fertility are not the major drivers.

The relative importance of different nutrients (notably N versus P) in limiting plant growth can vary substantially with elevation, and results to date suggest that these relationships vary across contrasting elevational gradients. Foliar N:P ratios decline sharply with increasing elevation for tropical trees in Peru (Fisher et al. 2013), which is consistent with the hypothesis that tropical lowland forests are limited by P, whereas tropical montane forests are limited by N (e.g., Tanner et al. 1998).

By contrast, foliar and litter N:P ratios increase with elevation both within and across species, as well as at the whole community level, in Swedish subarctic treeless tundra (Sundqvist et al. 2011b). However, the extent to which N versus P limitation of plants changes with elevation across contrasting gradients, and the mechanistic basis for contrasting patterns, remains largely unresolved.

5. COMPLEMENTARY APPROACHES FOR UNDERSTANDING GLOBAL CHANGE EFFECTS

5.1. Retrospective Studies

The fingerprint of climate change is clear: Many species have moved poleward and up mountain slopes in response to increasing temperatures over the past century (Parmesan & Yohe 2003). Several retrospective studies in both tropical and temperate systems demonstrate that these shifts are in line with what would be predicted if organisms were tracking their optimal temperatures. For example, Moritz et al. (2008) repeated Grinnell's early-twentieth century surveys across a 3,000-m elevational gradient in California, USA, and showed that approximately half of all small mammal species have moved up in elevation by ~500 m. In temperate forests in the United States, Beckage et al. (2008) found that the ecotone between northern hardwood and boreal conifers shifted upslope by more than 90 m between 1962 and 2005. However, a recent global meta-analysis of long-term tree line records from 166 locales around the world showed that tree lines moved upslope in only about half of all cases (Harsch et al. 2009). Though retrospective studies can provide insights into the factors that govern the distribution of species along elevational gradients, they are at their core purely observational, and would therefore benefit when used in combination with experimental approaches.

5.2. Experiments along Elevational Gradients

Experimental manipulations along elevational gradients can disentangle the relative roles of biotic and abiotic drivers, and local and regional processes, on community structure and ecosystem processes (Fukami & Wardle 2005). Although experimental studies have provided much information on the drivers of community and ecosystem dynamics along other types of natural gradients (Vitousek 2004, Wardle & Zackrisson 2005), few have been conducted along elevational gradients. Perhaps the most compelling example is that of Callaway et al. (2002), which involved experimental removal of neighboring vegetation to examine the relative roles of positive and negative interactions on survivorship and seed/fruit production for a variety of plant species at low and high elevation sites around the world (**Figure 3a**). Furthermore, experiments manipulating resource availability along elevational gradients can elucidate how resource availability varies with elevation. For instance, N and P fertilizer additions across an elevational gradient in the forests of the Peruvian Andes revealed increasing N limitation toward higher elevations (Fisher et al. 2013). In another example, the response of insect herbivore abundance and community composition to elevation was found to be mediated in part by plant community responses to both temperature and fertilizer addition (de Sassi et al. 2012). Similarly, experimental addition of food resources across an elevational gradient in the southern Appalachians illustrated that decreasing abundance and richness of detritivorous arthropods with elevation were largely independent of food availability (Lessard et al. 2011). Although there are only a handful of these types of experiments, they are key for improving our understanding of how environmental context mediates ecological responses to elevation and, more broadly, of ecological responses to interactions between multiple drivers of global change.

Many experimental warming studies have demonstrated that increased temperatures can lead to changes in community composition (Walker et al. 2006), nutrient cycling (Rustad et al. 2001), and phenology (Wolkovich et al. 2012), but few studies have explored the effects of temperature manipulation along elevational gradients. However, Jonasson et al. (1993) found that experimentally warming air and soil using mini-greenhouses at a low and a high elevation site in subarctic Sweden did not increase net N and P mineralization at either elevation. Further, Lessard et al. (2011) used shade tables to lower temperatures by $\sim 2.8^{\circ}\text{C}$ across an elevational gradient and found that the effect of this treatment on arthropod richness and abundance was independent of elevation. Similarly, few studies have experimentally manipulated other climatic factors such as precipitation regimes along elevational gradients. One notable exception is that of Wu et al. (2011b, 2012), who studied an elevational gradient in northern Arizona, USA, where warming was simulated by transplanting intact plant-soil mesocosms to lower elevations, and where precipitation was experimentally manipulated. They revealed that warming was the main factor influencing ecosystem C cycling but that the effect of warming was mediated by its influence on soil moisture and soil temperature (Wu et al. 2011b). Such experiments, especially if repeated across multiple elevational gradients, have considerable potential to determine the relative and collective importance of multiple climate change factors in driving community and ecosystem processes across contrasting systems.

6. FUTURE DIRECTIONS

We propose four areas that merit particular attention to understand better how communities and ecosystems respond to the climatic factors that vary along elevational gradients. First, there is a need for studies on how multiple contrasting taxa respond to elevation along the same gradient at scales that are appropriate for each of the taxa being investigated (Sanders et al. 2009), as well as on how the same taxa respond to different elevational gradients (Kessler et al. 2011). Given increasing recognition of the role of soil microbes and soil fauna in driving ecosystem responses to environmental gradients (Wardle 2002), there is a particular need for data on the responses of belowground communities to elevational changes. These knowledge gaps limit our capacity to predict how biotic interactions and community-level properties respond to changes in climatic factors. Second, there is a dearth of data on how community-level responses to elevation gradients in turn influence ecosystem properties and processes. Studies exploring this topic are important because they can inform us about how organism responses to changes in climate (such as through warming) may alter nutrient cycling and ultimately plant growth. Third, a greater emphasis on experimental manipulations of abiotic factors (e.g., temperature, precipitation, soil fertility) and biotic factors (e.g., species removals, animal exclusions) across elevational gradients is essential for disentangling the mechanistic bases through which elevation affects community and ecosystem properties (Dunne et al. 2004). Finally, we emphasize the need for better understanding of when and why the same variables respond differently to increasing elevation, and therefore climatic factors, across contrasting elevational gradients. We note that experimental manipulations along multiple elevational gradients have considerable potential to enhance this understanding and should help reveal the mechanistic basis through which the ecological effects of climate change may be manifested in disparate systems. The past century of work along elevational gradients has helped explain numerous fundamental concepts in ecology, but much work remains to be done along these gradients in contrasting mountain systems to better predict and perhaps help mitigate the effects of ongoing global climate change.

DISCLOSURE STATEMENT

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