Mountain Ecosystems as Natural Laboratories for Climate Change Experiments

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Experimental studies are needed to empirically examine the effects of climate change on terrestrial organisms and to serve as the basis for predictions and management practices. As such, designing and implementing experimental systems that can simulate complex changes in the natural environment is currently a major area of interest of climate change science. Most climate change experiments (e.g., infrared heaters, open-top chambers) are typically performed within small, controlled environments and often manipulate just temperature and/or CO_2 concentration. Other factors are more difficult to control (e.g., wind speed, soil moisture) or are frequently ignored (e.g., biotic interactions), leading to uncertainties in the results and limiting our ability to make realistic predictions about species' responses to future environmental changes. We examined the natural variation of abiotic and biotic factors along mountain elevational gradients in order to highlight the potential for using these systems as natural laboratories for climate change research and experiments. The high variability of different abiotic and biotic factors along elevational gradients provides a good opportunity to carry out field transplant/translocation experiments aimed at answering some critical questions, including: How will new biotic assemblages affect key interactions and processes? What are the factors that influence species assemblages under novel climates? How do local abiotic factors influence the establishment of species migrating into novel and climatically suitable habitats? Based on empirical evidence, we strongly encourage researchers to take advantage of the natural environmental gradients found in mountains to study the potential direct and indirect impacts of climate change on species, communities and biodiversity as a whole.

Keywords: altitudinal gradients, common garden experiments, experimental warming, field experiments, global warming, latitudinal gradients, novel interactions, transplant experiments

INTRODUCTION

As the global climate continues to change and the effects of these changes become more pronounced, we need to prioritize studies that can provide a solid understanding of how complex environmental changes will directly and indirectly impact ecological processes. Experimental studies are critical for empirically examining the effects of climate change on terrestrial systems and organisms, and these studies may serve as the basis for many predictions and management

practices. However, designing and implementing experiments that can fully simulate multifactorial changes in the natural environment remains a daunting problem.

Most climate change experiments have been carried out in controlled environments. Heating experiments such as infrared heaters, open-top chambers, soil heating cables or glasshouses are typically employed over small spatial scales and often manipulate just temperature and/or CO_2 concentrations (Bokhorst et al., 2011; Pelini et al., 2011; Elmendorf et al., 2015; Kimball, 2016; Wang et al., 2017). Although a specific variable(s) of interest can be controlled in this type of experiments, other factors are more difficult to control (e.g., wind speed, radiation, relative air humidity, soil moisture content). In addition, simulating changes in some factors, such as biotic interactions, may be difficult or impossible within laboratory or mesocosm experiments. Several recent studies have highlighted the limitations in the results from controlled experiments that can arise due to these and other problems. For example, a large-scale comparative analysis (for 1,634 plant species) of warming experiments and observational studies concluded that heating experiments underestimate the effects of climate change on plant phenological responses (Wolkovich et al., 2012) – although a subsequent analysis suggested that this is not always true for tundra species (Elmendorf et al., 2015). Likewise, Yang et al. (2018) compared three different methods (transplants, open top chamber and field long-term monitoring) and showed that the influence of altered competition under warmer conditions was only detected in the transplant experiments. Another recent study (Ettinger et al., 2019) evaluated the alteration of microclimates within experimental warming plots (15 studies) and showed that heating experiments produce changes in soil conditions (soil drying) that can have important biological consequences, but that this indirect effect of warming was often overlooked. These limitations decrease our ability to predict species' responses to climate change, and consequently our capability to plan and effectively implement conservation actions (Pressey et al., 2007; Reside et al., 2018; Ettinger et al., 2019).

Conducting experiments within natural environments is one promising option for more realistic assessments of how species and communities will respond to climate change. There is a growing number of studies taking advantage of natural environmental gradients – including latitudinal (Frenne et al., 2013; Nooten and Hughes, 2014; Nooten et al., 2014), elevational (Alexander et al., 2015; Tito et al., 2018), geothermal (Valdés et al., 2018) or forest successional gradients (Agosta et al., 2017) – in climate change studies. The use of elevational gradients can be an especially powerful and logistically feasible tool for studying how climate and other factors influence species' distributions and physiologies (Malhi et al., 2010; Silveira et al., 2019). Field experiments using elevational gradients can reveal effects that cannot be easily detected with experiments in controlled or artificial settings (Alexander et al., 2015; Nooten and Hughes, 2017; Tito Leon, 2017; Tito et al., 2018).

One of the most important advantages of field experiments is the possibility of detecting changes in biotic interactions and their effects (Alexander et al., 2015; Nooten and Hughes, 2017; Tito et al., 2018). There is a broad consensus that climate change will modify ecological communities by driving some species locally extinct and/or by creating new assemblages among species whose ranges did not previously overlap (Hobbs et al., 2006; Lavergne et al., 2010; Lurgi et al., 2012). Indeed, some field experiments have shown that the indirect effects of altered interactions are the most important drivers of plant responses to climate change (Alexander et al., 2015; Tito et al., 2018). However, despite the clear need to understand how the combined direct and indirect effects of climate change will affect species assemblages, field studies that allow for altered biotic interactions remain scarce. Revising more than half a million studies that focused on the possible impacts of climate change on terrestrial organisms, Nooten and Hughes (2017) found only 47 that were based on field experiments.

Here, we present a brief analysis of the natural variation of abiotic and biotic factors along mountain elevation gradients in order to highlight the potential for using these systems in climate change studies. Many of the ideas presented here are based on a set of field experiments conducted along an elevation gradient in the Peruvian tropical Andes (Tito Leon, 2017; Tito et al., 2018). Our goal in presenting this perspective article is to encourage the use of field experiments in future studies focused on determining the direct and indirect effects of climate change.

ENVIRONMENTAL VARIATION ALONG MONTANE ELEVATIONAL GRADIENTS

During last few decades, there were many efforts to define mountainous areas and to map the occurrence of these areas globally (Kapos et al., 2000; Körner et al., 2011, 2017; Elsen and Tingley, 2015; Antonelli et al., 2018; Price et al., 2019). The resulting classification system, which has been employed in many studies (Elsen and Tingley, 2015; Price et al., 2019), is based on elevation (>300 m asl) and ruggedness criteria, and indicates that mountain areas occupy approximately 21–24% of the global land area (Kapos et al., 2000; Meybeck et al., 2001). However, because the criteria previously used to define mountain areas allowed the inclusion of areas (e.g., plateaus, hilly lowland terrain) that seem inappropriate in a mountain biodiversity context, the methodology was improved and refined by applying a finer spatial resolution and considering local elevation range (maximal elevation difference among neighboring grid points: 200 m across 3 × 3 grid points of 30″ within each grid cell; see Körner et al., 2011 for more detail) (Körner et al., 2011, 2017; Price et al., 2019). Using this new approach, it is now acknowledged that mountainous regions represent ~12% of the Earth's terrestrial land surface outside of Antarctica (Körner et al., 2011, 2017). One of the most outstanding characteristics of mountainous regions is the high altitudinal variability of many climatic and non-climatic factors (Körner, 2007; Rapp and Silman, 2012). The high heterogeneity of abiotic conditions over short spatial scales is also reflected in the elevational variation of the diversity and composition of many montane plant and animal communities (Körner, 2007; Farfan-Rios et al., 2015). As a consequence, mountain regions host especially high levels of diversity and

endemism (Barthlott et al., 1996; Myers et al., 2000; Körner, 2004; Rahbek et al., 2019b).
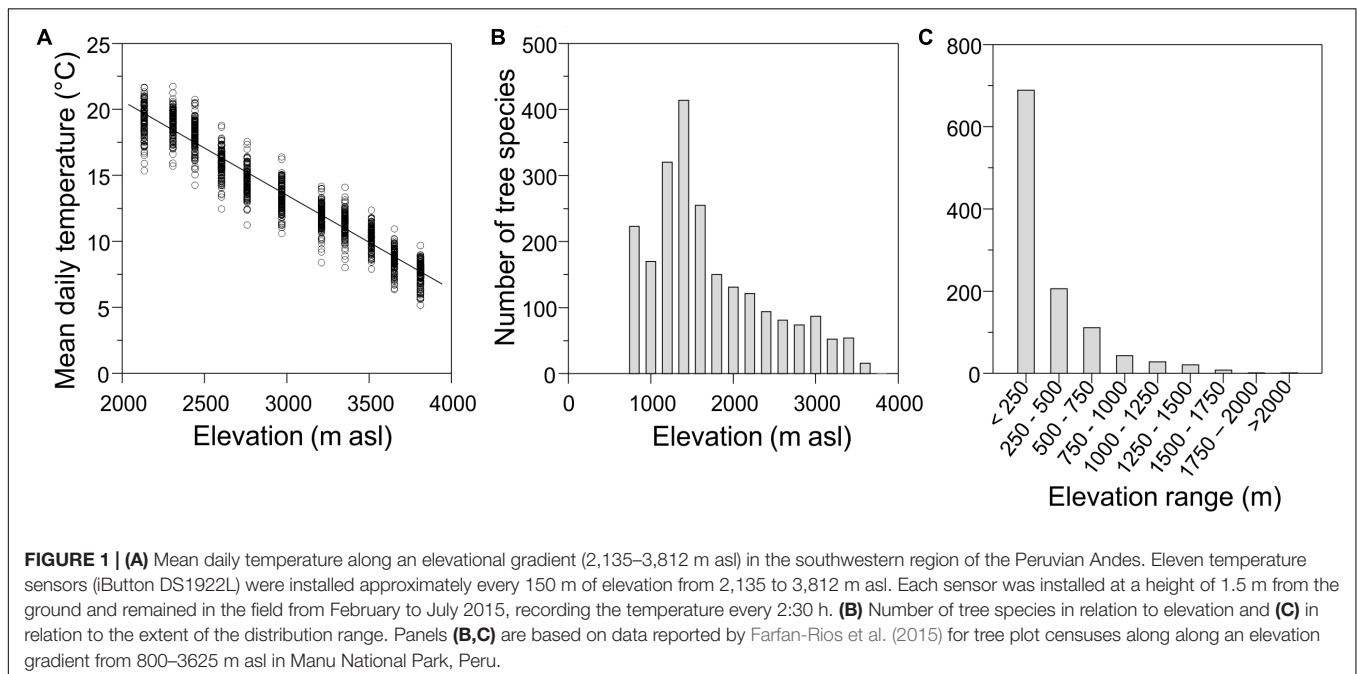
Abiotic Factors

Although the topography of mountains changes considerably from one region to another, there is a universal and steady decrease in mean air temperatures as elevation increases (Körner, 2007; Kessler et al., 2011; Rapp and Silman, 2012; **Figure 1A**). However, the rate that temperature decreases with elevation can vary depending on the slope and location of the mountain. For instance, along an elevation gradient in the southeastern slope of the Peruvian Andes, temperature decreases with an adiabatic lapse rate of approximately 5.2°C for every 1,000 m of elevation (Rapp, 2010), while on a southwestern Andean slope temperature decreases at a rate of 7.4°C per 1,000 m (Tito et al., 2018). Nonetheless, the temporal variation in temperature follows similar patterns on both the eastern (Rapp and Silman, 2012) and western slopes of the Andes (Tito et al., 2018). Several other studies also report an adiabatic decrease in temperature with elevation. For example, Kessler et al. (2011) show elevational temperature decrease for 20 other tropical and temperate regions.

Soil physical and chemical properties usually vary within mountain ranges and there is no consistency in patterns between mountain areas (Körner, 2007; Rahbek et al., 2019a). The heterogeneity of soil properties along mountain slopes depends on local characteristics such as topography, vegetation and geographic location. For example, soil organic matter increases with elevation in the Peruvian Andes (Zimmermann et al., 2010; Tito et al., 2018), in the mountains of Hawaii (Townsend et al., 1995), and in Mt. Rainier in the western United States (Zimmermann et al., 2010; Ettinger and Hillerislambers, 2017). In contrast, in the Himalayas, soil organic matter decreases at higher

elevations (Sheikh et al., 2009). In the southwestern Peruvian Andes, high concentrations of phosphorus and potassium are found at middle elevations (∼3,500 m asl), whereas calcium content increases and magnesium content decreases strongly with elevation (Tito et al., 2018). Nitrogen and phosphorus content show no trend with elevation on Mt. Rainier (Ettinger and Hillerislambers, 2017) and on the arid Tianshan Mountain in northwest China (Xu et al., 2019). In the Andes, nitrogen content decreases with elevation and is limiting for plants at high elevations (Zimmermann et al., 2010). Studies argue that many tropical mountain soils are younger and more nitrogen-limited at high elevations, and that soils are older and more phosphorus-limited at low elevations (Vitousek and Sanford, 1986; Vitousek and Farrington, 1997). In short, the existing studies indicate that soil properties vary strongly with elevation (but not necessarily in the same way in different regions) and that future studies on species' responses to climate change should take this into account.

Precipitation, relative humidity, and solar radiation are other important abiotic factors that vary in mountains, but without unidirectional elevational trends (Körner, 2007). For example, photosynthetically active radiation (PAR) on Mt. Rainier increases with elevation (Ettinger and Hillerislambers, 2017); in contrast, in tropical montane cloud forests, PAR decreases with elevation due to increased cloud cover and cloud immersion (Rapp and Silman, 2012). There is no general pattern for precipitation changes in relation to elevation (Körner, 2007). In some mountains (e.g., in the southern Peruvian Andes) the elevational variation in precipitation is not significant due to steep slopes and rapid changes in elevation over very small spatial scales (Condom et al., 2011). Humidity increases with elevation in some mountains (e.g., in the western United States) (Körner, 2007; Ettinger and Hillerislambers, 2017) but decreases with elevation in others (e.g., eastern of Neotropical Andes)

FIGURE 1 | (A) Mean daily temperature along an elevational gradient (2,135–3,812 m asl) in the southwestern region of the Peruvian Andes. Eleven temperature sensors (iButton DS1922L) were installed approximately every 150 m of elevation from 2,135 to 3,812 m asl. Each sensor was installed at a height of 1.5 m from the ground and remained in the field from February to July 2015, recording the temperature every 2:30 h. **(B)** Number of tree species in relation to elevation and **(C)** in relation to the extent of the distribution range. Panels **(B,C)** are based on data reported by Farfan-Rios et al. (2015) for tree plot censuses along along an elevation gradient from 800–3625 m asl in Manu National Park, Peru.

(Rapp and Silman, 2012) and is greatest at mid-elevations in others (e.g., Mount Kilimanjaro) (Körner, 2007). Because of their low temperatures, high elevations are generally more susceptible to frost, snow and hail.

Current Variation in Biotic Factors

There are elevated levels of species richness and endemicity in most mountain regions, and thus these systems are clear priority areas for conservation (Myers et al., 2000; Körner, 2004, 2007; Rahbek et al., 2019b). While covering just 12% of the land surface, mountains host more than 85% of the world's bird, amphibian and mammal species (Körner et al., 2011; Rahbek et al., 2019b), and at least one third of the terrestrial plant species (Barthlott et al., 1996; Körner, 2004, 2007). Most montane species have narrow elevational ranges (Rahbek et al., 2019b; **Figure 1C**).

Richness, composition and structure of plant and animal communities change along elevational gradients. Farfan-Rios et al. (2015) recorded over 1,000 species of trees, palms and lianas along an elevation gradient of ∼2,800 m, from submontane forests at 800 m asl up to the tree line at 3,625 m asl in Manu National Park, Peru. From the distributional ranges reported in this study, we observe that plant species richness generally decreases with elevation but has a marked peak at ∼1,400 m asl (**Figure 1B**), consistent with previous studies (Rahbek, 1995; Girardin et al., 2010).

Similar to the elevational variation of plant species richness, the diversity of herbivores (Hodkinson, 2005; Metcalfe et al., 2014; Rasmann et al., 2014; but see Galmán et al., 2018), frugivorous birds (Dehling et al., 2014; Bender et al., 2019), seed predators (Hargreaves et al., 2019), and soil bacteria and fungi (Nottingham et al., 2018) also decreases with elevation. In the case of geometrid moths (Beck et al., 2017), salamanders (McCain and Sanders, 2010), tropical ferns (Kessler et al., 2011) and non-volant small mammals (McCain, 2005), mid-elevational peaks in species richness are reported, but with sharp declines in richness at higher elevations. These elevational patterns of species richness and abundance can cause changes in the biotic pressures that local populations endure at different elevations within their ranges. For example, studies show that herbivory (Metcalfe et al., 2014), seed predation (Hargreaves et al., 2019), and predation rates on model caterpillars (Roslin et al., 2017) are greater at lower elevations. In addition, immigrant lowland plant species are expected to have increased competitive abilities (Yang et al., 2018). It is generally hypothesized that biotic interactions (e.g., competition, herbivory) set the lower limit of species' elevational ranges while harsh climatic conditions set species' upper elevational range limits (Ettinger et al., 2011; Hillerislambers et al., 2013).
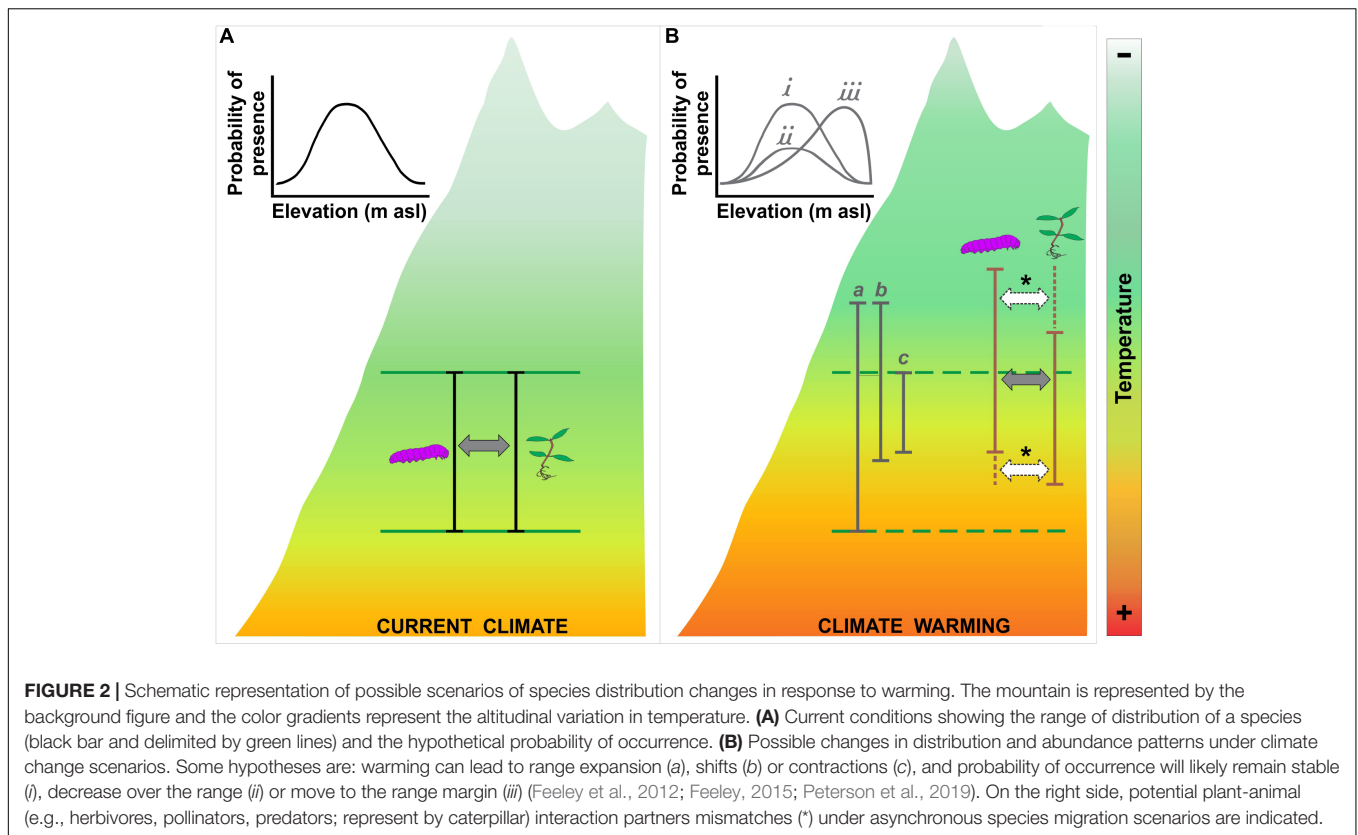
PREDICTED SPECIES RESPONSE AND FUTURE RESEARCH DIRECTIONS

Many plant and animal species are migrating to higher elevations and latitudes in response to ongoing changes in climate (e.g., Chen et al., 2011; Feeley et al., 2011b; Lenoir and Svenning, 2015; MacLean and Beissinger, 2017; Fadrique et al., 2018;

Freeman et al., 2018). However, studies suggest that migration rates are commonly slower than the rates required to track concurrent warming (Feeley et al., 2011a; Fadrique et al., 2018). Furthermore, several species appear unable to migrate due to different biological (e.g., dispersal capacity) or geographical (e.g., area availability) barriers (Hobbs et al., 2006; Rehm and Feeley, 2015, 2016; Alexander et al., 2018). However, several species may not need to migrate and may be able to persist under altered climates due to phenotypic plasticity and acclimation (MacLean and Beissinger, 2017). Overall, species vary widely in both their ability to change their geographic distributions due to climate change, but additional work is required to develop a more detailed understanding of climate-driven range shifts. For example, phytophagous insects are mobile organisms and can "migrate" faster than their associated host plants (Berg et al., 2010). Therefore, in this system, asynchronous species migrations could eventually lead to disrupted or reorganized interaction networks (**Figure 2B**).

In this context, several fundamental questions remain unanswered, including: How will new biotic assemblages affect key interactions and processes? What are the factors that influence species assemblages under altered climates? And, how do local abiotic factors (e.g., new soil conditions) influence the establishment of species migrating into novel and climatically suitable habitats? (Ibañez et al., 2006). The pronounced elevation and temperature gradients in mountains offer an ideal natural system to carry out field experiments aimed at answering these and other critical questions. Downslope translocation and transplant experiments can simulate future scenarios of climate change in the natural environment and can be used to determine the potential direct and indirect impacts of global warming on individuals, populations and communities. We summarize below some of the field transplant experiments that have used natural environmental gradients to simulate future conditions.

In order to assess the impacts of natural enemies (herbivores and pathogens) that can occur under future warming on potato and maize varieties in the Andes, Tito et al. (2018) used downslope transplants of seeds and tubers (with their home soil) to warmer areas (+1.3 and +2.6°C). This experiment revealed that the survival and productivity of both potato and maize varieties under warmer climates was strongly affected by novel pest and diseases. Other studies using latitudinal gradients have likewise shown that warming can lead to new suites of herbivore species colonizing the host plants (Nooten et al., 2014) and cause increased damage in some species (Nooten and Hughes, 2014). Beyond the obvious need for similar studies in more species and systems, these transplant studies reveal some new hypotheses that need to be addressed. For example, generalist interactions among species will likely be less constrained by the identity of the host plants (Dunn et al., 2009; Lurgi et al., 2012), while specialist enemies or mutualists with obligate interactions may be limited to asynchronous migration with their host plants (Dunn et al., 2009; Lurgi et al., 2012). Theoretical studies suggest that the risk of species extinctions consequently increases with the level of specialization (Binzer et al., 2011; Lurgi et al., 2012). Furthermore, warming also likely influences the phenology of insects and their host plants and may lead to temporal mismatches between species

FIGURE 2 | Schematic representation of possible scenarios of species distribution changes in response to warming. The mountain is represented by the background figure and the color gradients represent the altitudinal variation in temperature. **(A)** Current conditions showing the range of distribution of a species (black bar and delimited by green lines) and the hypothetical probability of occurrence. **(B)** Possible changes in distribution and abundance patterns under climate change scenarios. Some hypotheses are: warming can lead to range expansion (*a*), shifts (*b*) or contractions (*c*), and probability of occurrence will likely remain stable (*i*), decrease over the range (*ii*) or move to the range margin (*iii*) (Feeley et al., 2012; Feeley, 2015; Peterson et al., 2019). On the right side, potential plant-animal (e.g., herbivores, pollinators, predators; represent by caterpillar) interaction partners mismatches (*) under asynchronous species migration scenarios are indicated.

and alter trophic interactions (Renner and Zohner, 2018; Boukal et al., 2019). Overall, little is known about how climate change will impact the role of consumers on host plants or as prey for predators (Tylianakis et al., 2008; Lurgi et al., 2012).

To explore how the responses of plants to climate change depend on the migration of other species, Alexander et al. (2015) transplanted alpine plant communities along an elevational gradient in the Swiss Alps. This study showed that the performance of plants growing under warmer climates (simulated through downslope transplants) is strongly reduced by new competitors that emerge through upward migrations. On the other hand, high-elevation competitors had little or no effect on the plants migrating upslope. Further similar experimental studies could enable us to better understand plant community responses to altered competitive interactions under climate change (Alexander et al., 2016) and address additional areas of uncertainty, such as priority effects (Fadrique and Feeley, 2016).

In the studies of Tito et al. (2018) and Tito Leon (2017), upslope migrations were simulated by growing plants in soils translocated from higher elevations (i.e., upward migrating plants will grow under their current climate but at higher elevations and thus in different soils) allowing them to test the effect of changing soil conditions on plant performance. The productivity of maize varieties significantly decreased in high-elevation soils due to changes in soil nutrients (including altered Ca:Mg concentrations) (Tito et al., 2018); in contrast, the survival and growth of seedlings of a dominant cloud forest tree species (*Weinmannia bangii*) were not affected by changes in soil

(Tito Leon, 2017). Understanding the potential effects of climate change on soil biota and on plant microbe interactions are other important areas of study where soil translocation experiments could provide valuable information. The vast majority of plant species are associated with soil microorganisms that are critical for the growth and establishment of plants, and for dictating plant community composition (Collins et al., 2016; Sayer et al., 2017). A greenhouse warming experiment revealed that changes in soil biota due higher temperatures negatively affected the competitive capacity of *Poa trivialis*, although in the absence of competitors it favored their growth (Cardinaux et al., 2018). Another recent study (Nottingham et al., 2019) that translocated soil monoliths along an elevation gradient in the Andes showed that warming caused shifts in microbial community composition and changes in microbial physiology leading to increased carbon use efficiency.

Several authors have suggested that local adaptation may play a key role in determining species' responses to warming (e.g., Peterson et al., 2018, 2019; Solarik et al., 2018); despite this, the possibility of local adaptation is often ignored or overlooked (Feeley, 2015; Peterson et al., 2019). Transplant experiments from different local populations within species' ranges can be used to study the influence of local adaptation on species' response to climate change. In their study of *W. bangii*, Tito Leon (2017) transplanted seedlings collected from the upper edge, middle and lower edge of the species' elevational/thermal range. These transplants revealed that the responses to warming varied between populations such that the mid-range populations

were generally more sensitive to warming than the range-edge populations. This same study also showed that seedling survival increased with elevation. This suggests that the most favorable conditions for seedling survival of this species occur in areas near the upper limit of the current elevational range, contrary to expectation areas near to the middle of species' range should be the most favorable and that conditions should be more stressful near range limits (Holt, 2003; Sexton et al., 2009; **Figure 2A**). Overall, fine-scale experimental approaches such as these could help us to better predict the future abundances and distributions of species under altered climate scenarios, as well as the potential evolutionary responses of species (Verheyen et al., 2019). The possibility that the abundance patterns within species ranges could remain constant or shifted as species' ranges move, expand or contract (**Figure 2B**) under climate change (Feeley et al., 2012; Feeley, 2015; Peterson et al., 2019) also needs to be tested empirically.

CONCLUSION

There are many knowledge gaps and areas of uncertainty about how species will respond to current and future climate change. In particular, we know very little about how biotic interactions (e.g., between plants and their competitors, herbivores, pollinators, pathogens, and soil microbes) will be affected by altered climates and how these interactions will influence individual species and communities. The field experiment studies that have been conducted to date indicate that transplant and translocation experiments along natural environmental gradients in mountain systems offer a very valuable, but underutilized, approach to study species' response to climate warming. We encourage future studies to take advantage of natural gradients to help us gain a more complete understanding of the possible impacts of climate change on species, communities and biodiversity.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: http://www.scielo.org.pe/scielo.php?script= sci_arttext&pid=S1727-99332015000200004.

AUTHOR CONTRIBUTIONS

RT conceived the idea. All authors contributed to the writing and editing of the manuscript.

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