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Many species risk mountain top extinction long before they reach the top

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perspective

Many species risk mountain top extinction long before they reach the top

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Abstract. Analyses of topography show that mountains do not monotonically decrease in area with elevation as is commonly believed and that in reality land area often increases at higher elevations. This finding bodes well for the future of biodiversity since it means that in many parts of the world there are sufficient upslope areas for low- and mid-elevation species to migrate into as temperatures increase. However, more attention needs to be given to determining if migrating species can actually reach these expansive high-elevation areas. Many factors can prevent species from migrating upslope including stable ecotones. Often ecotonal boundaries are not set by mean temperatures alone and thus are not shifting upslope with warming. An example of this are tropical alpine treelines, which are not shifting upslope despite rapid warming potentially due to the stabilizing influences of climatic factors other than mean temperatures (e.g., extreme cold events) or non-climatic factors (e.g., soil or human disturbances). Stable ecotones can potentially prevent species from expanding their ranges into upland areas in which case the amount of land at higher elevations is irrelevant and species may face “mountain top extinctions” long before they reach the actual tops of the mountains.

During climate change, the fate of many montane species will depend on two main factors: (1) the existence of sufficient areas upslope for species to migrate into, and (2) the ability of species to reach those areas. By analyzing the topographic profiles of mountain ranges around the world, Elsen and Tingley (2015) show that the caricature of pyramid-shaped mountains monotonically decreasing in area with elevation does not hold true for the majority of ranges. In reality, land area often increases at higher elevations, at least up to a point. In other words, while high-elevation species may still face risks of “mountain top extinctions”, in many parts of the world there are large areas upslope for low- and mid-elevation species to migrate into. This potentially bodes well for the future of biodiversity since these species’ ranges will not necessarily contract as they migrate upslope and as such their risk of extinction may be reduced (Elsen and Tingley 2015).

However, more attention needs to be given to determining if species can actually reach the expansive high-elevation areas. There are a number of different factors that can prevent species from shifting their ranges upslope. For example, many species are dispersal-limited and therefore are incapable of rapidly shifting their ranges to keep pace with contemporary climate change regardless of the location or size of suitable habitats (Pearson 2006, Dullinger et al. 2012). Likewise, species interactions can influence the ability of species to migrate and establish in new habitats (Tylianakis et al. 2008) especially at high elevations (Callaway et al. 2002, Alexander et al. 2015). Another important factor that can potentially prevent even highly-vagile species from migrating are ecotones. As species shift their distributions upslope to remain at equilibrium with rising temperatures, they are almost certain to encounter multiple ecotones (Figure 1). In some cases, ecotones themselves may be shifting upslope and therefore they will not impede upward species migrations. In other places, ecotones may remain stationary or move in different directions or rates than the migrating species. In these cases, species that cannot cross the ecotones will be prevented from reaching higher elevations and the amount of area upslope is irrelevant (Feeley et al. 2014). Under this latter scenario, many species may experience range retractions and risk mountain top

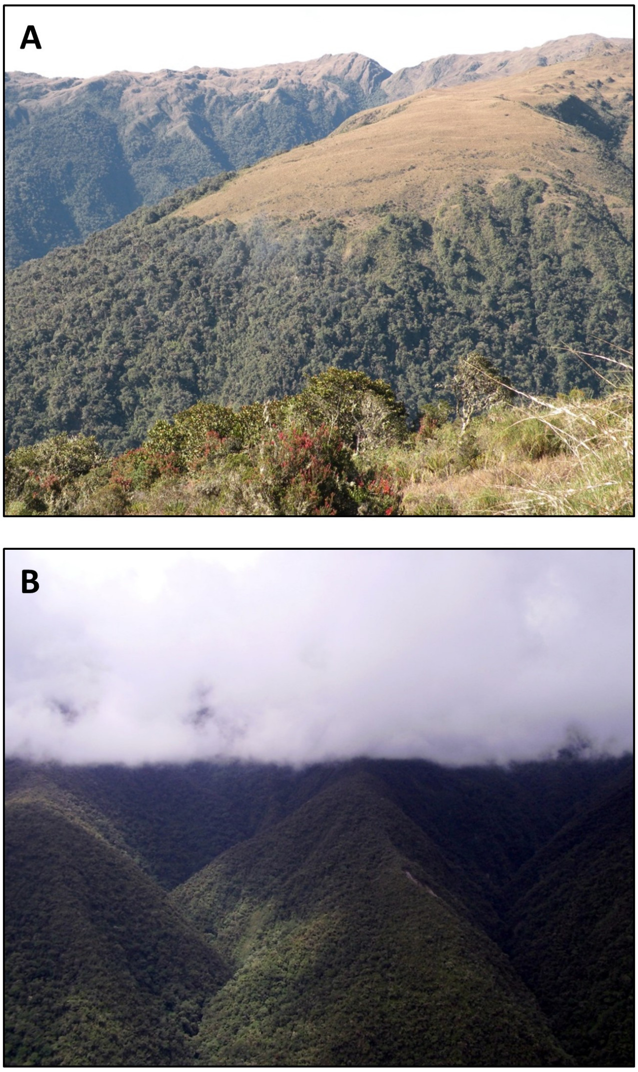

Figure 1. If ecotone boundaries such as A) the alpine treeline, or B) the lower boundary of the cloud immersion layer, do not shift to higher elevations with global warming, then many species occurring below the ecotone will be prevented from expanding their ranges into upland areas. In these cases, the amount of land at higher elevations is irrelevant and species may face "mountain top extinctions" long before they reach the actual tops of the mountains. Photographs are at approximately 3700 m a.s.l. and 1700 m a.s.l. in Manu National Park, Peru, respectively. Photographs by K. J. Feeley.

extinctions well before they reach the actual tops of the mountains.

An example of an ecotone that may prevent some species from migrating to higher elevations is the treeline – i.e., the point where montane forests abruptly give way to high-elevation alpine habitats (Körner 2012). It has long been presumed that the elevations where treelines occur is related to average temperatures (Körner 1998) and as such treelines are generally predicted to shift upslope in accord with global warming (Grace et al. 2002). In contrast to expectations, only about half of the world's treelines are shifting upslope, and in some cases treelines are actually retreating downslope (Harsch et al. 2009, Lutz et al. 2013). The possible causes for stationary or retreating treelines are complex and vary between geographic areas (Rehm and Feeley 2015a). For example, in the tropical Andes, treeline locations may be determined more by the magnitude and frequency of extreme cold events than by average temperatures (Rehm and Feeley 2015b). Extreme cold events are not necessarily becoming less severe or less frequent through time, thereby potentially explaining why treelines have remained stationary in the Andes despite rising mean temperatures (Rehm and Feeley 2015b). In other cases, the location of the treeline may be determined by non-climatic factors such as soil conditions or human-mediated disturbances (e.g., burning and cattle grazing above the treeline; Young and León 2002). Whatever the cause(s), stationary or retreating treelines will prevent forest-dependent species from migrating into higher elevations and thereby raise the risk of species extinctions below the treeline (Rehm and Feeley 2015a). For example, in the Andes, studies have estimated that if the treeline shifts upslope (current treeline elevation is generally between about 3500 and 3800 m asl), many montane forest species can potentially expand their population sizes by migrating upslope and taking advantage of the sharp increase in land area above the current treelines (Feeley and Silman, 2010). In contrast, if the treeline remains stable, as is the case in many places, none of the montane forest species are predicted to benefit and they are instead predicted to decrease in population sizes by an average of >45% under a 5^{o}C warming scenario (Feeley and Silman 2010). If the treeline is pushed downslope (Feeley and Rehm 2015), then rates of range contractions for forest species will be even faster.

The importance of ecotones is almost certainly not unique to the Andes Mountains. As quantified by Elsen and Tingley (2015), the increases in land area that occur on mountains are often at high elevations near or above regional treelines (e.g., in the Himalayas, the extent of land area begins to increase above approximately 4000 m asl which is approximately the same elevation as the treeline). Furthermore, the treeline is only the most visible of ecotones. There are likely to be many other ecotones even within the different ecosystems that can possibly prevent or slow upward species migrations. For example, in tropical mountains there is often a distinct break in species composition at the lower boundary of the cloud immersion zone (generally between approximately 1500-1700 m asl; Fig. 1B) associated with the transition from lower montane forests to cloud forests (Terborgh 1971, Gentry et al. 1995). If the cloud immersion zone does not shift to higher elevations with warming, then any lower montane species that are unable to prosper under cloud forest conditions may soon be at risk of mountain top extinctions as they are prevented from shifting their ranges upslope at the same time that the lower elevations become intolerably hot.

The notion that land area always decreases monotonically with elevation and that all species will have smaller range areas as they migrate upslope is clearly overly-simplistic and unrealistic. While there is still a worrisome risk of rapid range contractions and mountain top extinctions for the highest-elevation species, in many cases there are actually extensive land areas for low- and mid-elevation species to migrate into. If species are able to migrate upslope and reach these areas, then they can potentially expand their population sizes and avoid extinctions or even benefit under warming (Feeley and Silman 2010). However, it must not be forgotten that many factors including dispersal limitation, species interactions, and stationary ecotones can effectively make these higher elevations invisible to some species. In other words, many species may run out of room long before they reach the top.

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