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perspective



The responses of tropical forest species to global climate change: acclimate, adapt, migrate or go extinct?

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Abstract. In the face of ongoing and future climate change, species must acclimate, adapt or shift their geographic distributions (i.e., “migrate”) in order to avoid habitat loss and eventual extinction. Perhaps nowhere are the challenges posed by climate change more poignant and daunting than in tropical forests, which harbor the majority of Earth’s species and are facing especially rapid rates of climate change relative to current spatial or temporal variability. Considering the rapid changes in climate predicted for the tropics, coupled with the apparently low capacities of tropical tree species to either acclimate or adapt to sustained changes in environmental conditions, it is believed that the greatest hope for avoiding the loss of biodiversity in tropical forest is species migrations. This is supported by the fact that tropical forests responded to historic changes in climate (e.g., post glacial warming) through distributional shifts. However, a great deal of uncertainty remains about whether tropical forest plant species can migrate, and if so, whether they can migrate at the rates required to keep pace with accelerating changes in multiple climatic factors in conjunction with ongoing deforestation and other anthropogenic disturbances. In order to resolve this uncertainty, as will be required to predict, and eventually mitigate, the impacts of global climate change on tropical and global biodiversity, more basic data are required on the distributions and ecologies of tens of thousands of plant species, in combination with more directed studies and large-scale experimental manipulations.

Keywords. Acclimation, adaptation, biotic attrition, climate change, conservation biogeography, dispersal, diversity, extinction, global warming, land-use change, phenotypic plasticity, species migrations

Understanding the effects of climate change on natural systems has been referred to as “a grand challenge in ecology” (Thuiller 2007). Nowhere is this challenge more poignant, and perhaps more daunting, than in tropical forests. Despite covering a tiny fraction of the Earth’s surface, tropical forests harbor the majority of known and unknown species (Raven 1988, Dirzo and Raven 2003, Joppa et al. 2011a), sequester vast amounts of carbon (Saatchi et al. 2011, Baccini et al. 2012), and support many millions of humans directly through the production of food and other resources (Fa et al.

2002, Milner-Gulland and Bennett 2003), or indirectly through a diverse range of ecosystem services (Costanza et al. 1997, Cincotta et al. 2000, Naidoo et al. 2008). In this review, we discuss the potential effects of ongoing and future climate change on tropical forests and specifically tropical forest tree species, with an acknowledged bias towards Amazonian and Andean species.

There are only four possible responses of any species, including tropical trees, to global climate change: (1) individuals can acclimate to changes in climate through phenotypic plasticity

(Chambers et al. 1998), (2) species can adapt to climate change through genetic changes (Davis and Shaw 2001), (3) species can shift their distributions, or “migrate”, to remain at equilibrium with climate (Parmesan 2006), or (4) failing to do any of these first three, species will go extinct. As such, the real challenge that ecologists and conservation biologists face is trying to predict which of these options species will “choose” (Bawa and Dayanandan 1998, Hughes 2000, Aitken et al. 2008, Williams et al. 2008, Wright et al. 2009, Corlett 2011).

Can individuals of tropical tree species acclimate to climate change?

While studies of tropical rainforest trees are hindered by the general scarcity of definable annual growth rings (Lieberman et al. 1985, Worbes 2002, Rozendaal and Zuidema 2011), studies employing demographic models, ¹⁴C dating, and other techniques, have suggested that Amazonian canopy tree species have average life spans of several hundred years (Martinez-Ramos and Alvarez-Buylla 1998, Worbes and Junk 1989, Worbes and Junk 1999, Fichtler et al. 2003, Laurance et al. 2004), with some individuals occasionally reaching ages of more than 1000 yrs (Chambers et al. 1998, Laurance et al. 2004). Therefore, many individuals will see significant changes in climate within their lifetimes (for example, most climate models are consistent in predicting a minimum of 2–4°C warming in tropics over the next century alone; IPCC 2007). This will necessitate that individuals acclimate to changes in climate through phenotypic plasticity in order to survive, grow and reproduce (Jump and Peñuelas 2005). The fact that many tropical trees are more than a century old indicates that they have necessarily tolerated past climatic fluctuations; however, the changes in climate that are currently underway present an entirely new challenge in that individuals will be required to acclimate to rapid and sustained warming coupled with significant changes in precipitation, seasonality and other climatic variables.

While direct studies of phenotypic plasticity or acclimation in large, long-lived tropical trees are sparse or non-existent, it may be possible to

test for evidence of acclimation to changes in climate and other environmental conditions using space-for-time substitutions or through analyses of long-term records of tree growth and other measures of physiological performance (Bawa and Dayanandan 1998). For example, a study of Hawaiian plant communities occurring across a broad precipitation gradient showed differences in the dominant sources of nitrogen used by individuals within species. These spatial shifts in nitrogen use may indicate an ability of these tropical plant species to acclimate to changes in nitrogen cycling through time that may be caused by future climate change (Houlton et al. 2007). Contrasting this are studies of tree growth rates which may suggest an inability of tropical species to acclimate to increased temperatures. Tropical tree growth rates are expected to decrease at high temperatures because of increased respiratory costs relative to photosynthetic gains (Way and Oren 2010, Ghannoum and Way 2011). However, if individuals are able to acclimate to increasing temperatures through shifts in their photosynthesis and respiratory response curves, then tree growth rates may remain relatively stable through time, despite warming (Ghannoum and Way 2011). This does not appear to be the case. Long-term studies of forest dynamics in Costa Rica, Panama and Malaysia, for example, have indicated declining tree growth rates correlated with increasing regional temperatures (Clark et al. 2003, Feeley et al. 2007, Clark et al. 2010). Likewise, other studies have indicated decreases in tropical tree growth rates and forest net primary productivity, as well as increased tree mortality, when water availability is reduced (Nepstad et al. 2007, Clark et al. 2010, Zhao and Running 2010). Thus, while still uncertain, it appears that tropical trees will have only a limited ability to acclimate to the high-magnitude, sustained changes in climate predicted for the tropics over the next decades to centuries (Cunningham and Read 2003).

Can species adapt to climate change?

As indicated above, many tropical trees are long-lived; they are also generally slow to reach maturity and have long generation times (Swaine et al.

1987). Given the speed at which climate change is occurring (Malhi and Wright 2004) and predicted to occur in the future (Loarie et al. 2009, Urrutia and Vuille 2009), this may rule out adaptation as a possible response to climate change since adaptation, by definition, is a heritable change in phenotype occurring across multiple generations (Hoffmann and Sgro 2011). However, even if we disregard time as a limiting factor, adaptation to climate change may still not be possible for many tropical forest species. This is because, in addition to multiple generations, adaptation requires the existence of suitable and sufficient heritable genetic variation in the trait of concern – in this case, climatic tolerance (Chown et al. 2010). For tropical species in general, and for lowland rainforest tree species in particular, intra-specific variation in climatic tolerance is expected to be low because of a high degree of specialization on a narrow range of climatic conditions which are stable both in space (Janzen 1967, Terborgh 1973) and time (Fine and Ree 2006, Sunday et al. 2010, Sandel et al. 2011). As such, it is predicted that future climates will rapidly change beyond the range of conditions currently experienced by tropical forest species, resulting in the emergence of novel climates. This potential emergence of novel climatic conditions is well illustrated in studies which show that, despite the fact that rates of climate change measured in absolute terms (e.g., °C yr⁻¹) are generally predicted to be faster at high latitudes vs. the low latitude tropics (IPCC 2007), rates of climate change when measured as relative dissimilarity between current and future climates will generally be fastest in the tropics (Williams and Jackson 2007, Williams et al. 2007, Beaumont et al. 2011). Another illustration of this phenomenon is the high likelihood (>90% probability) that by 2080, average growing season temperatures in the tropics will be hotter than even the most extreme seasonal temperatures currently experienced in these areas (Battisti and Naylor 2009).

As climatic conditions rapidly move outside the range of conditions currently experienced by tropical species (even in extreme years), the likelihood that these species will have the genetic

variation required to adapt to these conditions decreases. Indeed, if the observed distributions of species reflect the true breadth of their climatic tolerances (Colwell and Rangel 2009), then it is probable that most species will not have the sufficient and suitable variation required to adapt to future changes in climate. However, the observed distributions of species may not accurately reflect the full breadth of their fundamental climatic tolerances, possibly as a result of adaptation to past “no analog” climatic conditions (Dick et al. 2003, Woodruff 2010, Veloz et al. 2012).

In order to investigate this hypothesis, Feeley and Silman (2010a) analyzed the observed thermal distributions of several thousand Amazonian plant species. Using the metadata associated with online herbarium records, they showed a strong relation between the observed thermal ranges of species and where the species occur. Specifically, species that occur in areas with either the hottest or coldest mean annual temperatures (lowland rainforests or high elevation Andean cloudforests, respectively) tend to have thermal ranges which are several degrees narrower than those of species inhabiting mid-elevations/temperatures (Feeley and Silman 2010a). There are several possible explanations for this pattern. One is that the observed thermal ranges are in fact reflective of species’ true climatic tolerances and that the decreases in the thermal niche breadths of the hottest and coldest species reflect increased climatic specialization in species from these areas. A decrease in the niche breadth of species from the hot tropics is consistent with the long-standing hypothesis that species from the lowland tropics have narrower climatic niches than species from higher latitudes or higher elevations because of specialization on stable climatic conditions (Janzen 1967). This hypothesis is supported by a recent analysis of the geographic ranges of tropical vertebrates (McCain 2009) as well as by a meta-analysis which showed that thermal tolerances of ectotherms, as measured in experimental trials (and thus likely to reflect their true thermal tolerances), do in fact increase with latitude and altitude (Sunday et al. 2010). It must be noted, however, that this same hypothesis can-

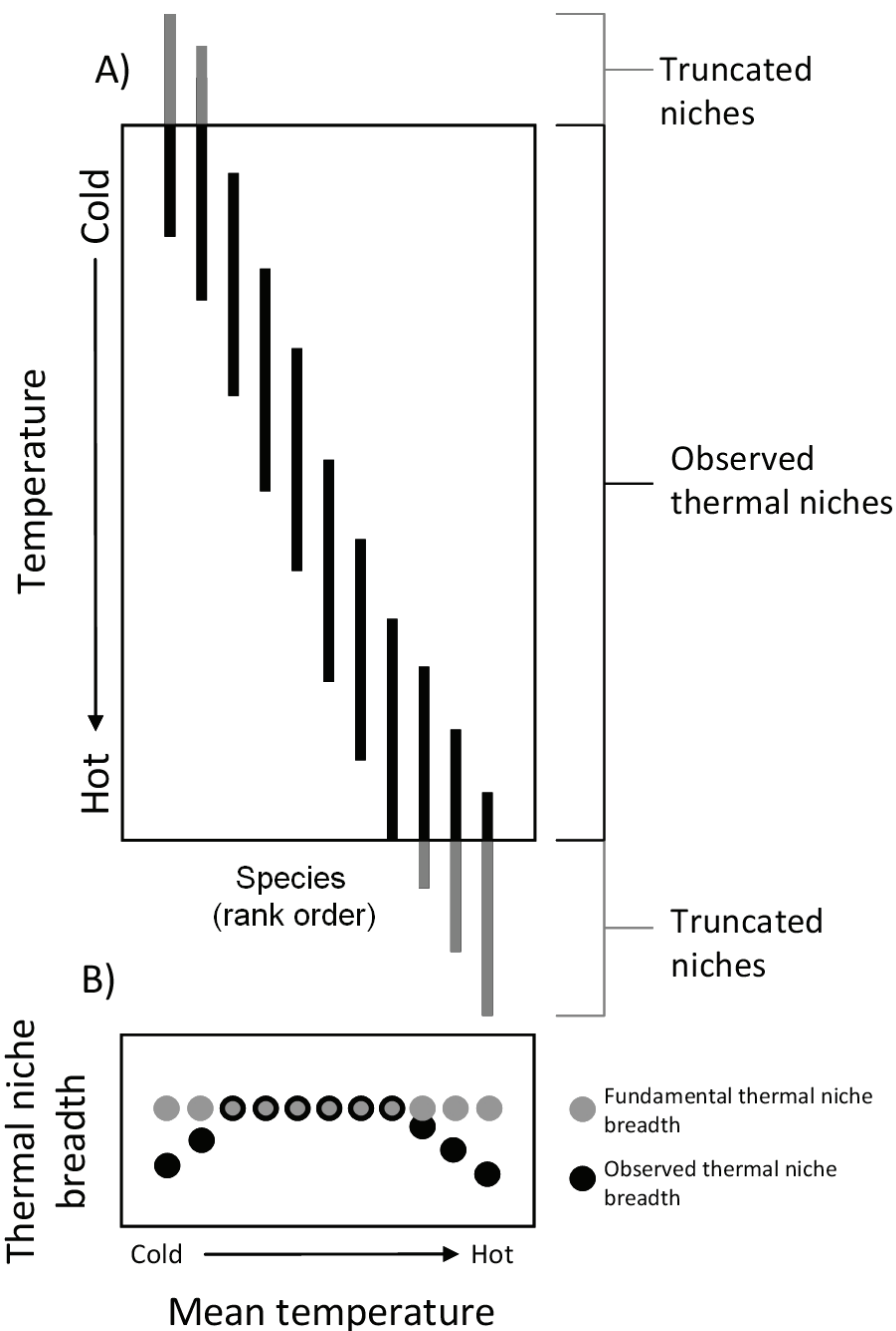


Figure 1. A schematic representation of how truncation of same-sized fundamental thermal niches resulting from the lack of available hotter and/or colder habitats (A) could result in species from mid elevations/temperatures having broader observed/realized niches than species occurring at the thermal extremes (B).

not account for the decrease in niche breadths of species collected from the coldest/highest parts of tropical South America since it predicts that these species will have wider niches than their lowland counterparts because of the greater diurnal and seasonal variation in climate at high elevations.

An alternative hypothesis, which can potentially explain the decreases in niche breadths observed for species collected from both the hot and cold tropics, is the idea of “niche truncation” (Feeley and Silman 2010a; Figure 1). According to the niche truncation hypothesis, even if fundamental niche breadths are relatively constant

between species, realized niches will be reduced in species occurring at the thermal extremes, simply as a result of a lack of opportunity. For example, species from the hottest lowland areas of the tropics may have climatic niches which encompass even hotter conditions, but they are unable to exhibit this tolerance because there are no hotter areas on the continent (Figure 1). Niche truncation is consistent with the observation that invasive species are sometimes able to occupy a wider range of climatic conditions than would have been predicted based on the range of conditions under which they occur in their native habitats

(Broennimann et al. 2007, Beaumont et al. 2009).

Whether or not the observed niches of tropical tree species accurately reflect their fundamental niches has important implications for how these species will respond to future climate change (Colwell et al. 2008, Colwell and Rangel 2009, Feeley and Silman 2010a, Hoffmann and Sgro 2011, Veloz et al. 2012). As stated above, if realized niches accurately reflect fundamental niches, then species will likely not have the genetic capacity to adapt to future climate change and will therefore go extinct from any areas where the newly arising conditions are beyond the range of conditions they currently experience. Under this scenario, we would predict that even relatively modest rises in temperatures would cause catastrophic losses of diversity (i.e., “biotic attrition”; Colwell et al. 2008) throughout much of the lowland tropics (Feeley and Silman 2010a). If the alternative is true, and the fundamental thermal niches of lowland tropical species are wider than reflected in their current distributions, then they may be able to adapt to rising temperatures, thereby decreasing the rates at which areas will become unsuitable to species and hence rates of biodiversity loss caused by global warming (Kearney et al. 2009, Feeley and Silman 2010a, Veloz et al. 2012).

Another set of factors that may limit the ability of tropical species to adapt to climate change is deforestation, land-use change, and the associated fragmentation of natural habitats. Approximately half of tropical forests worldwide have already been cleared or converted to other uses (Achard 2002, Wright 2005), with agriculture and grazing being the leading drivers of tropical deforestation (Geist and Lambin 2002, Gibbs et al. 2008, Rudel et al. 2009). Between 1980 and 2000, more than 55% of new agricultural land was developed from intact tropical forests and another 28% from disturbed tropical forests (Gibbs et al. 2010). The increasing world population (expected to reach 9 billion by 2050) combined with increasing levels of affluence and meat consumption in developing nations is predicted to necessitate an additional 10^9 ha of natural ecosystems (an area larger than the United States of America) being

converted into new agricultural lands (Tilman et al. 2001). This expansion of agricultural lands is expected to occur primarily in Latin America, sub-Saharan Africa, and other tropical regions currently containing large tracts of primary forests (Alexandratos 1999). Deforestation can directly reduce population sizes through reductions in habitat area, possibly leading to reduced genetic diversity and loss of plasticity in the remaining population (Young et al. 1996, Fowler and Whitlock 1999). Deforestation also leads to fragmentation and isolation of the remaining forest (Skole and Tucker 1993), breaking species into isolated populations and thus disrupting gene flow and possibly decreasing the ability of species to successfully respond to new selective pressures such as climate change (Young et al. 1996, Jump and Peñuelas 2005, Lowe et al. 2005). However, current empirical evidence does not suggest that isolated plant populations are experiencing genetic degradation, possibly because long-distance gene-flow events (e.g. seed dispersal or pollination) can link geographically disparate populations (Lowe et al. 2005, Bacles et al. 2006), or alternatively because most populations have not yet been isolated for long enough (Kramer et al. 2008). Even if fragmented populations are linked through gene-flow events, the spatial and temporal scale over which these events occur may be smaller than what is necessary, given the relatively recent destruction of tropical forests, rates of current and predicted future deforestation and climate change, and the expanding distances between isolated forest fragments (Peres 2001, Lowe et al. 2005).

Can tropical tree species shift their distributions to remain at or near equilibrium with climate?

Given the constraints of long-lived individuals, long generation times, potentially low genetic variation in climatic tolerances, high levels of habitat/population fragmentation and accelerating rates of climate change, it appears unlikely that many tropical tree species will be able to either acclimate or adapt to future climate change. As

such, a great deal of attention is now focused on understanding how species may be able to compensate for changes in climate by changing the locations of their geographic ranges – “migrating”. For example, a widely predicted outcome of global warming is that species’ distributions will shift towards cooler areas – usually either through poleward and/or upslope migrations (Parmesan and Yohe 2003, Parmesan 2006, Thuiller 2007, Chen et al. 2011a), thereby keeping the species’ distributions at or near equilibrium with temperature.

Migrations of tropical plant species in response to past climate change are evident in the paleo records. For example, Bush et al. (2004) and Urrego et al. (2010) documented changes in the composition of pollen through time, as recorded in the sediment of a mid-elevation lake in the tropical Andes (Lago Consuelo at 1,360 m.a.s.l.). The observed changes in species composition were non-directional until approximately 21,000 years ago, after which lowland taxa slowly became more abundant while highland taxa decreased in abundance or disappeared altogether. The observed changes in composition are consistent with an upward migration of plant species in response to ~6°C postglacial warming (Bush et al. 2004, Urrego et al. 2010).

A large and growing number of studies have documented recent upward and poleward shifts in the distributions of different taxonomic groups (Chen et al. 2011a). Unfortunately, the tropics remain vastly underrepresented in these studies. For example, a recent meta-analysis by Chen et al. (2011a) included data from over 50 studies representing over 2,000 different species, yet only two studies, representing just 160 species (30 species of herpetofauna on Tsaratanana Massif, Madagascar [Raxworthy et al. 2008], and 130 moth species on Mt. Kinabalu, Borneo [Chen et al. 2009, Chen et al. 2011b]) were included from the tropics. No studies of tropical plant species or of any species from the tropical lowlands were included.

In the case of modern tropical plant communities, perhaps the only documentation we

have of species migrations comes from a trio of studies that Feeley (2012) and Feeley et al. (2011a, b) conducted, looking at changes in plant species’ distributions at local, regional and continental extents, respectively.

To examine the effects of climate on species’ distributions at a local scale, Feeley worked with the Center for Tropical Forest Science (CTFS¹) to analyze census records collected at five-year intervals from 1980 to 2005 in the 50-hectare forest plot on Barro Colorado Island, Panama (Feeley et al. 2011a). These analyses showed that there have been consistent and directional changes in the composition of tree species in the BCI forest towards an increased relative abundance of drought-tolerant species (Condit et al. 1996a, Condit et al. 1996b, Hubbell 2004, Feeley et al. 2011a). One possible explanation for these directional shifts in species composition is climate change and especially decreases in water availability through time, related to warming.

At a regional extent, Feeley et al. (2011b) analyzed recensus data that they had collected from a network of fourteen 1-ha tree plots established by the Andes Biodiversity and Ecosystem Research Group (ABERG²) along a *ca.* 3,000-meter elevational gradient on the eastern slopes of the Peruvian Andes (Feeley et al. 2011b), four years after the previous census. These recensus data revealed increases in the mean elevations at which most tree genera (>85%) occur, indicating upward migrations in the distributions of most species groups (Feeley et al. 2011b). Likewise, when they analyzed the changes in species composition that had occurred within each of the tree plots, they found that the relative abundance of lowland taxa had increased in most plots (80%) through time (Feeley et al. 2011b).

To test for the possibility of continent-wide distributional shifts, Feeley (2012) used herbarium collection records to determine whether the mean, maximum and minimum temperatures from which approximately 250 Amazonian plant species have been collected have changed directionally through time. After correcting for geo-

1. <http://www.ctfs.si.edu/>

2. <http://andesresearch.org/>

referencing errors and collecting biases (potentially confounding factors that must be accounted for in these studies using natural-history records; Schulman et al. 2007, Tobler et al. 2007, Boakes et al. 2010, Feeley and Silman 2010c, Feeley and Silman 2011b), Feeley found that the majority of species that he examined (55%) did in fact show some evidence of distributional shifts in accord with the *a priori* expectations under global warming (Feeley 2012).

These three studies all suggest that many tropical plant species are shifting their geographic distributions potentially in response to changes in climate; however, it remains unknown whether species will be capable of migrating fast enough to keep pace with current and future climate change (Sandel et al. 2011). During the height of the Pleistocene–Holocene transition (approximately 11,000 years ago), temperatures in the Amazon rose by approximately 0.01°C per decade (Bush et al. 2004). Since the 1970s, temperatures in the Amazon have increased by approximately 0.25°C per decade (Malhi and Wright 2004) and warming rates over the next 100 years are predicted to accelerate, with many models predicting rates of 0.6°C per decade (IPCC 2007) or up to 0.9°C per decade (Urrutia and Vuille 2009). From their research in Peru, Feeley et al. (2011b) estimated that Andean tree genera are currently shifting their mean elevations upslope at an average rate of approximately 2.5–3.5 vertical meters per year. Given the adiabatic lapse rate of -5.5°C per 1000 m of elevational gain, this equates to an average migration of <0.02°C per year. This is significantly slower than required to keep pace with current temperature increases and is less than one third of the rate that will be required to keep pace with predictions of future warming (IPCC 2007), even fairly conservative ones. Likewise, the study of herbarium records indicated that the mean elevations of Amazonian plant species are changing at an average of less than one third of what is predicted based on concurrent changes in temperature (Feeley 2012).

The disparity between observed and required migration rates is even greater if variables other than just temperature are considered, since

climatic factors will not necessarily all change in concert (Crimmins et al. 2011). To demonstrate this, Feeley and Rehm (*in review*) generated spatial maps of required migration distances by calculating the distances from several thousand points in the Amazon rainforest to their closest analog climates, as predicted for 2050. Future analogs were first identified on the basis of just mean annual temperature and then considering both temperature and annual precipitation. They found that the inclusion of precipitation increased the median required migration distance by approximately 50%. This finding is consistent those of McCain and Colwell (2011), in which predicted effects of climate change on tropical species were significantly greater when multiple climatic factors were considered, compared with temperature alone.

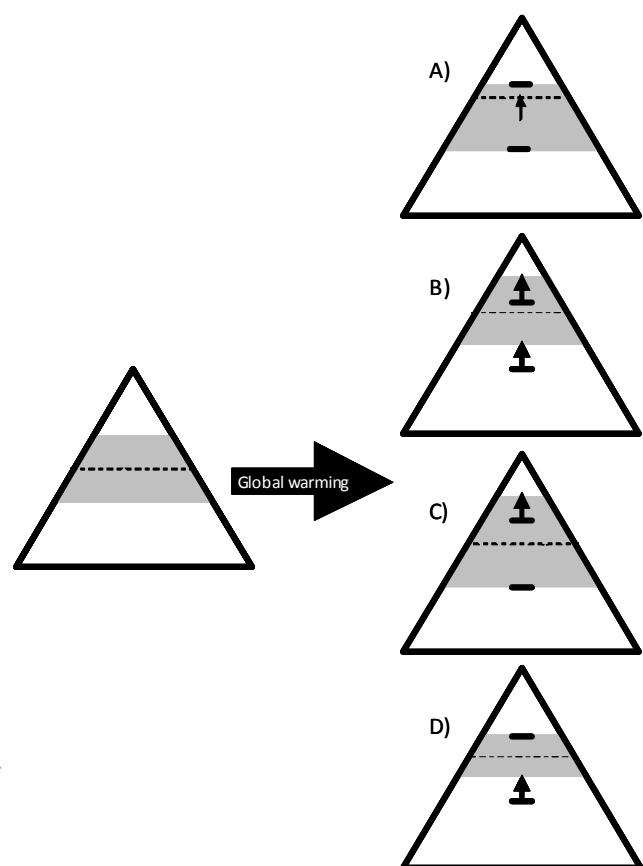
Perhaps even more important than the pace at which mean elevations of species are changing, is how the leading and trailing edges of these distributions are changing through time, since it is these margins which define species' ranges (Figure 2). A migrating species will experience range movement if both its leading and trailing distributional edges shift at the same pace, range expansion if its leading edge shifts faster than its trailing edge, range contraction if its leading edge shifts more slowly than its trailing edge, or an increasingly skewed distribution if the abundances of individuals shift within the species' current range boundaries. In all of these cases, the species' mean elevation would increase, but with very different outcomes for the species' range and population sizes (Figure 2). From his study of herbarium specimens, Feeley (2012) estimated that the majority of the Amazonian plant species that exhibit range movements have contracting ranges resulting from faster loss of habitat along the hotter, lower-elevation portions of their ranges than is compensated for by immigration into new areas at higher elevations. This is consistent with patterns observed for tree species in temperate North America (Zhu et al. 2012) and supports the hypothesis that species' observed ranges are indicative of their fundamental climatic tolerances (see above and Figure 2).

Another important factor which will influence the ability of species to respond to climate change through species migrations is deforestation and human land use. Deforestation will not only decrease the total amount of habitat available to species in the future, but may also create barriers to migrations or extend the distances that species must migrate in order to reach suitable habitats. To quantify how deforestation may influence the required distances for species that cannot utilize or disperse through large expanses of non-forest habitat, Feeley and Rehm (*in review*) recalculated their required migration distances (see above), avoiding all areas which are predicted to be deforested by 2050 (Soares-Filho et al. 2006). Relative to their previous predictions that included both temperature and precipitation, they predicted that, if deforestation poses a barrier to migration, median migration distances will increase by 85%, and that 46% of the Amazon will have no reachable future climate analogs. These results clearly indicate that in addition to the many other problems associated with habitat loss, land-use change has the potential to cause even further reductions in tropical and global biodiver-

sity by limiting the ability of species to respond to climate change through distributional migrations.

Even species capable of rapid migration, and thus able to keep pace with current and future climate change, may experience reductions in habitat area and population sizes because of topographic effects. Given the lack of a latitudinal gradient within the tropics, equatorial species will need to shift their distributions upslope. Since most mountains tend to be approximately conical, habitat area at high elevations is reduced relative to lower elevations. In the Andes, topography is steep up to elevations of approximately 3,000–3,500 m.a.s.l., at which point the slopes level off to a flatter inter-Andean hill–valley system. As such, there is actually an increase in land area from 3,000 up to 4,000 m.a.s.l., above which land area decreases again towards the tops of the mountains. Consequently, species which are currently distributed along the high eastern flanks of the Andes may potentially expand their ranges, if they migrate further upslope (Feeley and Silman 2010b). These range expansions will depend largely on the nature of the timberline (i.e., the upper elevational limit of forest habitats), which in

Figure 2. Differential relative elevational migration rates at different portions of a species' range (shaded area) can all result in increases in the species' mean elevation (dashed line) but with different effects on range extent and hence population size. (A) range skew = no movement along the species' trailing or leading edges but a shift in the relative abundance of individuals at different elevations within the range, (B) range movement = the leading and trailing edges of the species' distribution migrate at the same pace, (C) range expansion = the leading edge moves faster than the trailing edge, and (D) range contraction = the leading edge moves more slowly than the trailing edge. A range expansion may indicate that the species is capable of tolerating climate change through adaptation or acclimation. In contrast, a range contraction will be caused by dieback along the species' trailing edge, resulting from an inability to adapt or acclimate to climate change coupled with an unavailability of newly suitable habitats and/or an inability to rapidly invade newly suitable habitats.



the Andes occurs at approximately 3,500 m.a.s.l. In order for tree species to shift their distributions from the forested slopes onto the grasslands above, the timberline will have to shift to higher elevations. If the timberline ecotone is set by climatic conditions then it is possible that it will move with increasing temperatures (Körner 1998, Grace et al. 2002, Körner and Paulsen 2004). However, there is also the possibility that the timberline in the Andes and other tropical montane systems is set not by temperature but instead by edaphic conditions or by human activities such as grazing of cattle and burning to increase fodder (Sarmiento 2002, Sarmiento and Frolich 2002). Under these latter scenarios, the timberline may not shift upslope with climate change, in which case migrating forest species would be unable to shift their ranges upslope, leading to rapid range contractions (Feeley and Silman 2010b).

In all montane systems, including the Andes, habitat area inevitably decreases at extremely high elevations. For species which currently reside at high elevations there may consequently be no future climate analogs (Williams et al. 2007) which could lead to numerous mountaintop extinctions (Laurance et al. 2011b, Pounds et al. 1999). Indeed, predictive models show that future range contractions for tropical montane species will be especially severe for this reason (Williams et al. 2007), and also because of the large horizontal distances between isolated mountain ranges that may have suitable future climate (Sekercioglu et al. 2008, La Sorte and Jetz 2010).

Beyond climate, land use and topography, there are many other factors which will influence the distances that species will be required to migrate in order to reach suitable future habitats, as well as the amount of habitat that will be available to them. For example, the distributions of many tropical species are determined mainly by soil type and/or other non-climatic environmental factors (Harms et al. 2001, Phillips et al. 2003, Russo et al. 2005, Silman 2007, Bader and Ruijten 2008). Since these factors will not necessarily change in direct relation to climate, the availability of suitable habitat in the future will likely be less than predicted by models which only consider

climate (Ibanez et al. 2006). Furthermore the migration distances required to reach suitable habitats may be increased. To illustrate this effect, Feeley and Rehm (*in review*) recalculated their required migration distances while restricting the future analogs to occur only within the same ecoregion (Olson et al. 2001) as the origin points (i.e., they assumed ecoregion to be a proxy for soil type or other non-climatic variables; Feeley and Silman 2009). Under this set of assumptions, less than 30% of the Amazon rainforest is predicted to have future analogs that are reachable, regardless of migration rate.

Finally, complex species interactions are a defining characteristic of tropical forest communities (Darwin 1859), and interactions have been shown to have important effects on the distributions of many tropical species (Fine et al. 2004, Hillyer and Silman 2010, Jankowski et al. 2010, Wyatt and Silman 2004). As species shift their distributions in response to changes in climate, some communities will become disassociated and novel biological communities will be formed (Williams and Jackson 2007, Sheldon et al. 2011, Urban et al. 2012). These changes in species interactions will likely decrease the availability of suitable areas in the future and increase required migration distances and rates even further. Likewise, while it has not yet been observed in tropical systems, climate change may also lead to phenological mismatches between plants and their animal associates (Miller-Rushing et al. 2010), thereby decreasing the ability of some species to persist under altered climates.

Conclusions

All told, it appears likely that most tropical forest species will be unable to successfully respond to climate change through acclimation, adaptation or migration – leading to possible large-scale extinctions (Thomas et al. 2004) and potentially massive losses in global diversity (Feeley et al. 2012). That said, there remains a great deal of uncertainty and a large number of unanswered questions. For example, will some tropical plant species be able to persist through combinations of acclimation, adaptation and migration? Are tropical plant species

capable of rapid migrations through long-distance dispersal events? What species trait(s) will determine the ability of species to persist in the face of future climate change? It is critical that we resolve questions such as these if we hope to predict, and eventually mitigate, the impacts of climate change on our richest and most diverse ecosystems (Feeley et al. 2012).

Towards this end, we must increase the number of studies which are directed at understanding the impacts of climate change on tropical systems. Even with the addition of the three tropical plant studies (Feeley et al. 2011a, b, Feeley 2012), as well as a new study of Andean bird species (Forero-Medina et al. 2011), tropical organisms represent less than one quarter of the species for which modern species migrations have been investigated (Chen et al. 2011a). More generally, the vast majority of studies on climate change and conservation are focused on temperate North America and Europe and relatively few studies are directed at tropical systems (Felton et al. 2009), which is clearly out of sync with diversity patterns and conservation priorities (Myers et al. 2000). Likewise, there is a dire need for experimental studies to help untangle and elucidate the influences of individual, climatic or environmental factors on plant performance. Large-scale global-change experiments are generally lacking from the tropics; for example, to date there are no CO₂ enrichment studies in any natural tropical systems (Norby and Zak 2011), nor are we aware of any warming experiments that have been conducted in the tropics (Aronson and McNulty 2009). The lack of large-scale experiments in the tropics is due in large part to the difficulties inherent in working in biodiverse and developing nations, but there are several notable examples of studies in Brazil which have successfully overcome these difficulties including the Biological Dynamics of Forest Fragmentation Project (Laurance et al. 2011a), a large-scale drought simulation experiment (Nepstad et al. 2007), and the large-scale experimental burns being conducted through the Woods Hole Research Center³. Clearly, more such

studies are required.

Perhaps an even more important factor limiting our understanding of how tropical forest species will respond to climate change is the simple lack of information or raw data from most tropical systems (Pitman et al. 2011) and for most tropical species (Feeley and Silman 2011a). For example, one of the most powerful tools used to predict responses of species to climate change is species' distribution models (SDMs). These build from the observed relationships between environmental variables and species' presence-only or presence-absence data. They estimate the ranges of species and thus provide valuable information on the importance of different climatic and environmental factors in limiting species' distributions (Franklin 2009). In addition, SDMs can be used to predict range locations/extents under future climate-change scenarios and thereby estimate extinction vulnerabilities and guide management strategies (Franklin 2009, Richardson and Whittaker 2010, Feeley et al. 2012). The accuracy of SDMs generally increases with the number of occurrences included and all models are unreliable below a certain minimum sample size (Elith et al. 2006, Wisz et al. 2008, Feeley and Silman 2011b). Unfortunately, the amount of data available for most tropical plant species is well below any realistic minimum sample size (Feeley and Silman 2011a, b). Feeley and Silman (2011a) quantified the number of occurrence records available for plants in online data repositories across most of the tropics and found that the median number of records per species is just 2, even if we disregard the thousands of described species for which we have no occurrence data at all and the hundreds of new species being described from the tropics each year (Pimm et al. 2010, WWF 2010, Feeley and Silman 2011a, IISE 2011, Joppa et al. 2011a, b). Thus, for the vast majority of tropical plant species we simply cannot even begin to predict their ranges. This clearly illustrates the need to invest in ongoing exploration and data collection. How can we expect to conserve tropical diversity when we know so little about it?

3. http://www.whrc.org/ecosystem/amazon_fire.html

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