The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences

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The upper elevational range edges of most tropical cloud forest tree species and hence the ‘treeline’ are thought to be determined primarily by temperatures. For this reason, the treeline ecotone between cloud forests and the overlying grasslands is generally predicted to shift upslope as species migrate to higher elevations in response to global warming. Here, we propose that other factors are preventing tropical trees from shifting or expanding their ranges to include high elevation areas currently under grassland, resulting in stationary treelines despite rising mean temperatures. The inability of cloud forest species to invade the grasslands, a phenomenon which we refer to as the ‘grass ceiling’ effect, poses a major threat to tropical biodiversity as it will greatly increase risk of extinctions and biotic attrition in diverse tropical cloud forests. In this review, we discuss some of the natural factors, as well as anthropogenic influences, that may prevent cloud forest tree species from expanding their ranges to higher elevations. In the absence of human disturbances, tropical treelines have historically shifted up- and down-slope with changes in temperature. Over time, increased human activity has limited forests to lower elevations (i.e. has depressed treelines), and often broken the equilibrium between species range limits and climate. Yet even in areas where anthropogenic influences are halted, cloud forests have not expanded to higher elevations. Despite the critical importance of understanding the distributional responses of tropical species to climate change, few studies have addressed the factors that influence treeline location and dynamics, severely hindering our ability to predict the fate of these diverse and important ecosystems.

Tropical montane cloud forests (hereafter referred to as cloud forests) are considered to be some of the world’s most diverse ecosystems due to the large number of endemic and endangered species that they support (Myers et al. 2000). Many cloud forest species at low and middle elevations have already begun responding to contemporary increases in temperatures by shifting their distributions upslope (Freeman and Class Freeman 2014, Rehm 2014). In order to sustain biodiversity in the face of climate change, cloud forest species must be able to continue to shift their distributions upslope and expand their ranges into the grassland areas found above the current upper elevational distribution limit of the cloud forest ecosystem. This distributional limit, or ecotone, is known as the treeline and in the tropics is formed by the convergence of dozens of cloud forest species’ upper range edges (Gentry 1988).

Interest in treelines as indicators of climatic change has been growing because treeline locations are thought to be controlled by low mean temperatures (Körner 1998, Jobbágy and Jackson 2000, Körner and Paulsen 2004) and therefore treelines are expected to shift upslope with warming. A shift in treeline elevation would provide a clear and visible indication that cloud forests are responding to climate change by expanding or shifting their ranges into the overlying grasslands and alpine areas (Harsch et al. 2009). In contrast to this expectation, global-scale studies have shown that only half of all studied treelines are shifting upslope and that in some cases, treelines are actually retreating downslope (Harsch et al. 2009).

Our ability to predict the future persistence and distribution of cloud forests under climate change is highly dependent on understanding the factors that control treeline location and dynamics. In a recent global meta-analysis, Harsch et al. (2009) found that only 52% of the 166 treeline study sites worldwide have reported upslope treeline movement with modern climate change. Due to geographic research biases, the included studies focused primarily on European and North American locations, with only seven treeline sites (4.2%) from the tropics – all from the Andes. Not a single one of these seven tropical sites reported an upslope movement of treeline in response to the recent rise in global temperatures.

In this review, we examine the possible mechanisms that limit the upper elevational distributions of cloud forest
tree species (and hence the factors that determine treeline elevation) and the potential movements of tropical treelines during climate change. Most information related to tropical treelines comes from the Andes, especially within the context of climate change. In addition, in the Andes there exists very large expanses of land area above tropical treelines (Fig. 1). In other tropical regions, such as east Africa and the Malay archipelago, mountains generally do not reach sufficient heights to form a climatic treeline or, when present, treelines are restricted to isolated mountains that are separated from each other by large non-forested habitats. This review will therefore focus primarily on the tropical Andes, but we will draw on available examples from other tropical montane systems and temperate treelines when appropriate. While we rely on some general information from temperate treeline studies (reviewed by Holtmeier 2009, Körner 2012), one goal of this review is to focus explicitly on tropical systems and to explore how factors controlling treeline location and dynamics differ between tropical and temperate systems. By focusing on cloud forest biodiversity and the upslope shift of tropical treelines we do not discount the value of the diverse high elevation grasslands and the ecosystem services they provide. However, plant diversity and endemism tends to peak at mid-elevations (1500–3500 m a.s.l.) within the cloud forest belt (Kessler 2002) and hence we emphasize the importance of tropical treeline shifts for the maintenance of tropical biodiversity.

What determines the location of treelines in the tropics

Climate

The locations of natural treelines worldwide are believed to be largely determined by mean temperature, with most treelines occurring at elevations associated with the 5–8°C soil root zone mean growing season temperature (Körner and Paulsen 2004). Tree growth is severely reduced below the 5°C soil formation threshold of higher plants and hence the 5°C isocline may represent the thermal limit for woody plant growth (‘growth limitation hypothesis’ – Körner 1998, 2003; but see Wiley and Helliker 2012). Low soil temperature is also linked to slowed soil nutrient cycling and mineralization rates in cloud forests below treeline (Tanner et al. 1998). To our knowledge, however, there has been no attempt to experimentally test for possible controls on tropical treeline position due to edaphic conditions. Therefore soil limitations will not be discussed further.

Tropical treelines mostly occur between 3000 and 4000 m a.s.l., although some woody species (Polylepis spp.) can extend their ranges up to 5000 m a.s.l but not forming continuous forests (Körner 1998). At higher elevations, where mean annual temperatures are below 5°C, upright woody species are commonly replaced by open grasslands. However, many tropical treelines occur at elevations below

Figure 1. The area of land in the tropics and above 1000 m a.s.l. (a) per 100 m elevational bands under different habitat types in (b) the neotropics, (c) tropical Africa, Madagascar and southwest Asia, and (d) tropical southeast Asia, Australia, and India. Elevations are based on the SRTM digital elevation model (Rabus et al. 2003) with a resolution of 30 arc seconds and habitat types are based on WWF biome classifications (Olson et al. 2001). In the neotropics, the extent of land area increases at high elevations due to the shift from steep, forested slopes to a relatively-flat hill and valley topography dominated by montane grasslands (locally referred to as puna and páramo) above ~3600 m a.s.l. Coloring is consistent between all panels. For clarity we grouped the high elevation grasslands of South America (e.g. puna and páramo), Africa (e.g. Ethiopian Highlands and moorlands), and southeast Asia, Australia and India (e.g. subalpine heathlands) into one category of montane grasslands and shrublands.
this 5°C thermal isocline. We do not contend that cold temperature growth limitations are not applicable to these low elevation treeline forests. Rather, we suggest that the presence of tropical treelines at elevations lower than what is predicted based on the ‘growth limitation hypothesis’ indicates that additional factors beyond mean temperature are needed to explain treeline growth form and location in many areas.

One striking difference in climate at temperate versus tropical treelines is the degree of seasonality. At temperate treelines, there are often large seasonal fluctuations in temperature, with winters being relatively harsh and plants entering into a state of dormancy during the coldest months of the year (Körner 2012). In addition, there is often an insulating layer of snow cover during the winter at temperate treelines that protects young seedlings from extreme cold temperatures. In contrast, at tropical treelines there is little or no seasonality, with daily temperature fluctuations exceeding mean annual temperature variation.

The lack of seasonality in the tropics means that plants occurring in treeline forests maintain actively growing tissue, which is known to be more sensitive than dormant tissue, throughout the year even during mild freezing events (Sakai and Larcher 1987). In addition, microclimate is known to be ‘harsher’ in the grasslands above treeline than in the forests below treeline. For example, frost events are typically more frequent and more severe in these grasslands relative to nearby closed-canopy forests, especially at ground level where seedlings maintain most of their leaves (Rada et al. 2009, Rehm and Feeley 2013, in press). Therefore, extreme low temperature events may be more important than mean temperatures in determining the upper elevational limits of some tropical treeline-forming species and overall treeline dynamics (Wesche et al. 2008, Harsch and Bader 2011). Wesche et al. (2008) demonstrated that the frequency and severity of frost events, coupled with water stress, limit tree recruitment above Andean and African treelines. It has also been suggested that freezing temperatures directly limit elevational distributions of some Venezuelan treeline species while not affecting others (Cavieres et al. 2000). Similarly, Rehm and Feeley (in press) found that juveniles of several dominant treeline forming species in Peru were vulnerable to tissue damage due to low temperatures common in the grasslands above the treeline. Extreme cold temperature events may prevent trees from recruiting into the grasslands outside of the relatively well-buffered thermal environment of the forest, leading to large-scale mortality events, potentially killing entire cohorts of seedlings and providing a possible explanation for the abrupt nature of many tropical treelines (Fig. 2; Harsch and Bader 2011).

Beyond just temperature, the importance of precipitation in determining tropical treeline locations can not be overlooked, especially given the unique hydrology of cloud forest systems. Cloud forests occur in areas where cloud mist and immersion are frequent, and significant moisture inputs come from fog interception and horizontal precipitation (Grubb 1977, Bruijnzeel and Proctor 1995, Goldsmith et al. 2013). The location of the ‘cloud immersion zone’ may therefore be the ultimate determinant of cloud forest distributions. However, cloud patterns and associated precipitation vary widely between tropical mountains, with precipitation increasing with elevation at some sites (Kitayama 1992, Schawe et al. 2010) and decreasing with elevation at others (Veneklaas and Van Ek 1990, Rapp and Silman 2012). While cloud occurrence is generally more variable and less frequent at tropical treelines compared to lower elevations, cloud immersion at and above treeline forests is still a regular event (Halladay et al. 2012a).

A closed-canopy treeline cloud forest presumably creates a wetter understory microclimate than the open grasslands, thereby potentially allowing for regeneration of drought-sensitive cloud forest species within the forest but not outside. Indeed, even with regular cloud immersion and significant moisture inputs above tropical treelines, the high mortality of seedlings recruiting into the grasslands has been attributed in part to water stress at some sites (Smith 1977, Wesche et al. 2008), but not at others (Rada et al. 1996). It has been posited that high-elevation tropical systems are generally more arid than temperate systems due to higher evaporative demand and decreasing rainfall in tropical mountains (Leuschner 2000), which may partially explain the presence of water stress in grasslands above the treeline forest. In addition to the direct effects, water availability may indirectly influence treelines through natural or anthropogenically set fires (see more on fires below; Hemp 2005). Yet it is difficult to determine the exact role that precipitation and moisture play in influencing treeline elevations due to the limited information available about water relations at tropical treelines (e.g. soil moisture data across tropical treelines ecotones) and the overall lack of long-term climatic records from tropical mountains.

**Solar radiation**

Treelines typically occur at higher elevations in the tropics than in temperate systems. Exposure to solar radiation under clear sky is thus elevated at tropical treelines since radiation...
increases with elevation and decreases with latitude. The regular occurrence of freezing nights followed by intense morning light at tropical treelines may also lead to increased risk of low-temperature induced photoinhibition and thus have a large effect on treeline dynamics (Bader et al. 2008). Bader et al. (2007) found that forest seedlings transplanted into the open grasslands above Ecuadorian treelines had higher survival and showed lower photooxidative tissue damage when planted in the shade than did seedlings planted without shade. The abundance of adaptive mechanisms (e.g. increased antioxidants) that high elevation trees possess to deal with excess insolation (reviewed by Körner [2003]) suggests that light levels in tropical mountains play an important role in treeline dynamics. It is possible that adaptations to high light environments allow trees to persist within, or just outside of, the cloud forest canopy but are insufficient to protect trees in the open grasslands above tropical treelines, where light intensities are greater.

**Forest species interactions with grasses**

Given the harsh environmental conditions at and above treeline, theory predicts that grasses should play a more facilitative than competitive role in seedling establishment within the grassland matrix above treeline (Bertness and Callaway 1994). It has even been argued that forests will advance upslope only in cases where ecological facilitation by alpine vegetation allows tree recruitment beyond the current treeline ecotone (Smith et al. 2003). However, grasses and alpine vegetation have been shown to play both facilitative and inhibitory roles in seedling establishment outside of some temperate treeline forests (Noble 1980, Ball et al. 2002, Callaway et al. 2002). It is difficult to apply observations from temperate systems to tropical treelines due to the drastically different climatic and environmental conditions between the two regions (e.g. presence vs absence of snow, strong vs no seasonality).

Information specific to the role of plant interactions in determining the location and dynamics of tropical treelines is severely limited. At two separate Andean treeline sites, temperatures in the open grassland were colder near the ground than at the grassland canopy height or in the free atmosphere (Rada et al. 2009, Rehm and Feeley in press), suggesting that grasses do little to buffer tree seedlings against the low temperature extremes that can occur outside of the closed forest canopy. In addition, Smith (1977) concluded that forest seedlings transplanted above a Venezuelan treeline suffered higher mortality due to the combination of climatic stress and competition with grasses for water during the brief dry season. Grasses may, however, provide shading, which can facilitate the establishment of tree seedlings above the established treeline forest (Bader et al. 2007). Conversely, grasses may also promote fire and increased grazing pressure, both of which have overall negative effects on the establishment of forest species in the grassland matrix (see below). Therefore grasses appear to have only minor facilitative effects on tree species recruitment and may actually play an inhibitory role in the recruitment of trees beyond established tropical treeline – the opposite of what is believed to occur in most temperate treeline systems.

**Seed dispersal, germination, and survival**

Some research suggests that reduced dispersal and survival of tree seeds outside of the forest may potentially limit upslope shifts of cloud forest species and treeline with climate change (Dullinger et al. 2004). In Peru, Rehm and Feeley (2013) showed that overall seed rain abundance and diversity decreased markedly with distance above the treeline. Cierjacks et al. (2007) found that sowing additional seeds of two *Polylepis* species increased the number of recruiting seedlings for one species both inside and outside of the cloud forest while having no effect for a second species. These studies suggest that seed limitation and germination rates may restrict recruitment above the established treeline. Conversely, Körner (2012) argued that seed limitation and recruitment is unlikely to play an important role in determining treeline formation, but this argument was based largely on studies of temperate sites. Our understanding of how seed limitations influences the ranges of cloud forest species and tropical treelines is still very restricted and would greatly benefit from additional studies that investigate seed dispersal, survival, and germination across the treeline ecotone and in adjacent grasslands.

**Human impacts**

Past and ongoing human disturbances have likely reduced the occurrence of tropical forest at high elevations and artificially lowered, or ‘depressed’, the elevation at which many tropical treelines occur (Ellenberg 1979, Young 2009). Human activities at high elevations are diverse and the temporal and spatial scale of such activities can have long-lasting and profound effects on cloud forests and their treelines. Probably the most prevalent activity around tropical treelines is the grazing of livestock within alpine grasslands (Ellenberg 1979, Young 2009). Livestock can directly limit tree recruitment into grasslands by the grazing and trampling of seedlings and saplings, and indirectly by increasing soil erosion. Fires associated with livestock grazing may have an even larger impact on tropical treeline location than the livestock themselves (Wesche et al. 2000, Hemp 2005). Fires are often used by pastoralists to stimulate new grass growth and reduce the presence of undesirable forage species such as woody vegetation. If the return interval of fires is shorter than the the time necessary for the slow-growing trees to reach a sufficient height to escape the fire kill zone, then forest succession into the grasslands is essentially reset with each re-occurring fire (Wakeling et al. 2012). Even after fires are suppressed or removed, forest invasions into grasslands may be significantly delayed (Di Pasquale et al. 2008). In addition to livestock activities, clearing of tropical cloud forests to expand agricultural areas and the cultivation of crops in the high elevation grasslands could further stabilize or even lower treeline elevations (Young 2009). Treelines that were once depressed by anthropogenic activities may be maintained at lower elevations even after human activities are halted due to inhibitory mechanisms (e.g. solar radiation, freezing events) that prevent tree establishment and forest encroachment into the grasslands, reinforcing the stability of the forest boundary (Harsch and Bader 2011).
All told, throughout the tropics the locations and dynamics of treelines are likely to be driven by a complex mix of past and present ecological and anthropogenic processes working at different spatial and temporal scales (Young and León 2007). Although the processes determining species ranges and treeline elevations are clearly complex, we may look at how natural factors and human activities have shaped tropical treeline distributions in the past as a means towards increasing our understanding of how tropical cloud forests and their treelines may be affected by ongoing and future climate change.

**Past and present tropical treeline shifts and conditions**

Since the Last Glacial Maximum (LGM), cloud forests and their associated treelines have shifted up and downhill as temperatures changed (Bush et al. 2004, Valencia et al. 2010). Even in regions where temperature fluctuations are highly correlated with past cloud forest shifts (e.g. the Andes), extended dry periods may represent a temporary switch to systems driven more by moisture than by temperature (Bush et al. 2004). Regardless, past cloud forest shifts are mostly attributed to fluctuations in temperature.

Beginning several thousand years ago, natural vegetation patterns in many tropical regions became masked and difficult to interpret from the palaeo-ecological record due to the increased influence of humans across the landscape (Hillyer et al. 2009, Valencia et al. 2010). Even though temperatures remained fairly stable or even increased during this period, increased human activities above treeline may have prevented cloud forests from shifting uphill, and possibly even driven them downhill (Bakker et al. 2008, Di Pasquale et al. 2008, Valencia et al. 2010). However, starting approximately 500 yr ago, human influence over many tropical montane landscapes declined markedly with the influx of European colonizers (e.g. Spanish conquest throughout the Andes), leading to pronounced reductions of fire activity in some tropical grasslands over the last several centuries (Urrego et al. 2010). This trend may have been reversed over the last century as humans once again began to utilize high elevation areas. Even if human impacts had been reduced, at present, tropical treelines remain remarkably stationary even though climates have continued to become more favorable to upslope shifts of cloud forest species ranges (Harsch et al. 2009; but see Bakker et al. 2008). The lack of treeline movement most likely indicates that inhibitory mechanisms other than mean temperature and/or the effects of past and continuing human activities may be stabilizing treelines by preventing cloud forest species from expanding their ranges to include areas currently under grassland.

Most recent analyses of cloud forest species migrations and treeline movements in response to contemporary climate change are restricted to the Andes. The mean annual temperature in the tropical Andes has increased by an average of 0.10–0.39°C per decade since the mid-1900s, but warming has accelerated through time and was up to three times faster during the end of the 20th and start of the 21st centuries than during previous decades (Vuille and Bradley 2000, Vuille et al. 2003). This means that temperature increases over the past several decades are occurring at rates faster than after the LGM, representing a major increase in the velocity at which cloud forest species must migrate upslope to track temperatures (Bush et al. 2004, Loarie et al. 2009).

In what we believe to be the most detailed assessment of tropical treeline shifts in any region to date, Lutz et al. (2013) found that only 18% of the treeline segments that they examined in Peru had shifted upslope over a 42 yr study period. The majority of treelines that shifted upslope were located within protected areas relatively-free from human impacts. Even then, upslope treeline forest shifts were at a rate of < 2% of the pace required for forest species to remain at equilibrium with rising mean temperatures. In contrast to the protected areas, the majority of treelines in unprotected areas remained stationary or even retreated further downslope, possibly due to continuing human disturbances (Lutz et al. 2013). These results indicate that even in protected areas with presumably decreased human disturbance, mean annual temperature may be a poor predictor of tropical treeline position and other factors are determining the location of the treeline ecotone. However, we are unaware of any attempt to model current or future tropical treeline positions based on any climatic or environmental variable other than mean annual temperature.

The influence of precipitation on tropical treeline locations in any elevations has been severely understudied in tropical mountains, with the exception of some in-depth analyses from the Andes. It appears that over the past half century, areas in northern Peru are becoming wetter overall while areas to the south are becoming drier (Vuille et al. 2003). There is also a trend of decreasing cloud cover throughout the Andes with increasing north Atlantic sea surface temperatures and frequency of El Niño events (Halladay et al. 2012b). Of particular interest is that cloud cover, and hence precipitation, appears to be decreasing over the southwest Amazon during the dry season, which in turn reduces moisture in the cloud forest zone of Peru and Bolivia, intensifying the dry seasons experienced by tropical cloud forests (Halladay et al. 2012b). Changes in precipitation and cloud inundation may be increasing water stress and fires near tropical treelines, perhaps preventing forest species from expanding into the drier, more seasonal grasslands, as has been documented in African mountains (Hemp 2005).

Deforestation and land-use change can also influence local and regional climates around treeline, especially temperature and water availability (Garcia-Carreras and Parker 2011). In the Peruvian Andes, cloud forests located near deforested areas had warmer and drier climates than areas far from deforested zones (Larsen 2012). In addition to deforestation within the cloud forest zones themselves, drying effects from deforested lowland landscapes may carry over and reduce precipitation in nearby cloud forests and associated treelines (Lawton et al. 2001). Therefore, aside from just global patterns of climate change, regional and local land-use change might have significant effects on local climate patterns, preventing forest species from establishing beyond the current treeline or even causing downslope shifts of the treeline. How these changes are affecting other biotic (e.g. competition with grass, seed dispersal) and abiotic (e.g. nutrient cycling) components of tropical treeline environments has yet to be addressed.
Tropical treelines in the future

The recent patterns of climate change are projected to intensify over the next century (IPCC 2013). In the tropical Andes, temperature is predicted to increase by an additional 4.5–5.0°C by 2100, with faster warming at higher elevations (Vuille et al. 2008, Urrutia and Vuille 2009). If the distributions of cloud forest species and associated tropical treelines are determined primarily by temperature, then upslope cloud forest migrations of 900–1000 vertical meters will be needed to track temperatures over the next 100 yr (Vuille et al. 2003). However, this predicted migration does not account for changes in precipitation and cloud cover. In some tropical regions, such as the Andes, precipitation is predicted to increase during the wet season and decrease during the dry season, increasing the seasonality experienced by cloud forest species (Vuille et al. 2008, Halladay et al. 2012b). Exacerbating this issue is the projection that cloud cover will continue to decrease throughout the tropical Andes into the future, especially during the dry season (Halladay et al. 2012b).

Precipitation and climatic patterns at local scales are also linked to regional changes in land-use. Human impacts in many tropical treeline systems have remained stable or even decreased due to shifting economic and social drivers of land-use (Aide et al. 2010), but effects of land-use change from adjacent lowland systems on the climates of tropical montane systems may intensify. For example, even with slowing deforestation rates (Hansen et al. 2013), any clearing of lowland rainforests could lead to further drying of adjacent tropical cloud forests and associated treelines. Reduced precipitation means that drought-sensitive cloud forest species will be exposed to longer and more intense dry periods in the future, especially near treeline. Furthermore, prolonged dry seasons will increase the rate of natural and human-caused fires in the already fire-prone grasslands above treeline.

In addition to changes in temperature and precipitation, atmospheric concentrations of CO₂ are also increasing rapidly but it remains unclear how treeline vegetation will respond to increased CO₂ concentrations. Young trees of some species grown at and above temperate treelines experienced net carbon gains when exposed to elevated CO₂, but the enrichment effect diminished after just a few years (Dawes et al. 2011). This evidence, along with an analysis of non-structural carbohydrates in trees growing at treeline, suggests that the majority of individuals at treeline are not carbon limited and therefore are not predicted to benefit significantly from increased carbon availability (Hoch and Körner 2012). However, little to no effort has focused on testing the potential effects of CO₂ enrichment for tropical treeline species (but see Hoch and Körner 2005).

Unlike growth, freezing tolerances of many plant types, including trees at treeline, appear to be reduced by rising CO₂ concentrations (Woldendorp et al. 2008, Martin et al. 2010). This is largely due to changes in plant phenology (Repo et al. 1996) or alterations to physiological processes which in turn lead to reduced freezing tolerances (Loveys et al. 2006). Therefore, as CO₂ concentrations continue to rise, trees growing at treeline may become more susceptible to freezing events. However, freezing resistance is strongly linked to temperature (Sakai and Larcher 1987), so concurrent increases in temperatures at treeline elevations complicate the predictions of CO₂ effects.

Given our general lack of knowledge, it is also difficult to predict how other factors such as competition with grasses, seed dispersal, and soil nutrient cycling will change at and above tropical treeline forests during future climate change. Without additional studies addressing the basic ecological processes related to species distributions and ecotone formation, predictions of how these complex interactions will change with climate are tenuous at best.

Stationary tropical treelines and cloud forest biodiversity

Areas where cloud forests are currently distributed have served in the past, and could potentially serve in the future, as climate refugia for tropical lowland species requiring cooler climates in the face of increasing global temperatures (Bush et al. 2004, Feeley et al. 2012). Evidence of distributional shifts of cloud forest plant species is currently limited to two studies – one from Costa Rica and one from the Peruvian Andes (Feeley et al. 2011, 2013). Both of these studies found that cloud forest trees are currently shifting their distributions upslope an average of 2 to 3 times slower than expected based on concurrent warming (Feeley et al. 2011, 2013). It is not surprising that we find cloud forest species’ upslope migrations lagging behind concurrent shifts in temperature, because the majority of plant species globally are shifting at a slower pace than required to perfectly track mean temperature changes (Chen et al. 2011). The fact that the migration rates of many species are lagging behind warming creates the potential for a future extinction debt (Dullinger et al. 2004). Compounding the potential negative effects of slow migrations, the leading edge of many high-elevation cloud forest species distributions are not shifting upslope, as indicated by stationary treelines. In the few cases where tropical treelines have been observed to shift upslope, they are moving at rates of 12 to >100 times slower than the shifts in species’ mean elevations (Feeley et al. 2011, Lutz et al. 2013). This lack of change in species’ upper elevational limit indicates that biome boundaries, such as the treeline ecotone, can pose formidable barriers to species migrations, further slowing or preventing species movements (Feeley et al. 2014).

It remains unclear how the inability of cloud forest species to expand their ranges to higher elevations will have cascading effects on other taxonomic and trophic groups. Cloud forest animals are generally shifting their ranges upslope faster than are plants (Freeman and Class Freeman 2014, Rehm 2014). These differential migration rates suggest that forest-dependent animal species are either less tolerant of rising temperatures and/or are more capable of shifting their distributions to track climates. However, if trees do not shift their distributions upward, there will be no forest for these animal species to move into at higher elevations. What’s more, a large number of plant species (e.g. arboREAL EPHYTES) depend on cloud forest trees for structure and water capture, and presumably these species will be able to shift to higher elevations only after trees have expanded their ranges into the grasslands above current treeline.
Like other alternative stable-state systems, it is possible that tropical cloud forests will respond to climate change in a punctuated fashion, resulting in rapid upslope shifts of treeline, followed by relatively long periods of stasis (Wilson and Agnew 1992, Bader et al. 2008). It has even been suggested that tropical cloud forests are still responding to temperature increases from the late-Holocene (Urrego et al. 2010). If this is true, then tropical treeline shifts will be much too slow to keep pace with current and future warming. Given sufficient time, cloud forest communities and their associated treelines may reach elevations at which they are in equilibrium with climate. In the interim, discordant rates of species range shifts could have major implications for populations and range sizes.

An important, but often overlooked consideration is that, in much of the neotropics, land area increases above current treeline because of the presence of large high elevation plateaus or hill-valley systems (Fig. 1). If cloud forest species do indeed shift their ranges upslope past current treeline then the potential exists for some cloud forest species to gain habitat and potentially benefit from climate change in the future (Feeley and Silman 2010). The palaeo-ecological record indicates that such shifts have occurred in the past, but as already discussed here, treeline does not appear to be shifting upslope in response to modern climate change.

Stationary tropical treeline forests will result in one of two scenarios for cloud forest species’ ranges; 1) ranges can stay relatively stable and individuals can acclimate or adapt to the changing environmental conditions in situ, or 2) species can lose range area at their lower elevational limit while failing to gain area at their high elevational limit, resulting in decreasing range area and population sizes (Feeley et al. 2012). Current evidence suggests that acclimation or adaptation of tropical cloud forest trees is unlikely, especially considering the rate of current climate change and the long life span and generation times of most tree species (Clark et al. 2003, Feeley et al. 2012). In addition, many tropical cloud forest species are already exhibiting range shifts or contractions, especially at their low elevation limits, in response to rising temperature (Feeley et al. 2011, 2013). Therefore, the latter, more dire scenario appears to be the more likely of the two. For example, in the Andes, cloud forest species are predicted to experience average population losses of 45% if they are prevented from expanding into high-elevation grasslands above current treelines (vs a potential gain of 20% if they do shift upslope into current grassland areas with warming; Feeley and Silman 2010). Even if species are able to expand their ranges upwards in the future, many species will still be at increased risk of extinction or will experience severe population bottlenecks in the meantime.

Across the tropics, human impacts play a significant role in determining the location and dynamics of treeline. Yet even in protected areas that are relatively free from human disturbances, shifts in treeline elevation lag well-behind a priori expectations (Lutz et al. 2013). These patterns match those found in temperate montane systems, where treeline forests are observed to respond only slowly after the cessation of human disturbance (Camarero and Gutiérrez 2004). These observations suggest that tropical treeline forests may respond by shifting distributions upslope once free of human influences, but that even forests occurring well below their predicted climatic limit may, at best, respond slowly to rising temperatures.

Overall, we still have only a rudimentary understanding of the ecology of tropical cloud forests and their constituent tree species and how these diverse systems will respond to ongoing and future climate change. Research in the Andes provides the most comprehensive understanding of cloud forest and tropical treelines — but even in this relatively well-studied region information remains extremely sparse. Based on the available information, we can surmise that the grassland matrix found above treeline is a harsh environment for individual tree seedlings to establish into and grow. Unlike at temperate treelines, mean temperature may not be the primary driver of dynamics at tropical treelines. High temperature variation and extreme cold events above tropical treelines appear to reduce survival and recruitment of tree seedlings in the open grasslands (Rehm and Feeley in press). In addition to temperature, water stress during certain times of year may also negatively affect seedlings growing above treeline. High levels of solar radiation, competition with grasses, and low seed dispersal into the grasslands may also prevent forest seedlings from establishing beyond the forest canopy. Human activities above treeline, such as livestock grazing and fires, can further limit the ability of seedlings to recruit in the grasslands. All of these factors work to stabilize tropical treelines and may create a ‘grass ceiling’ that will prevent cloud forest tree species from shifting their leading range edges upslope in response to climate warming.

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References


Hemp, A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. – Global Change Biol. 11: 1013–1023.


IPCC 2013. Climate change 2013: the physical science bases. – Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.


