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Forest patches and the upward migration of timberline in the southern Peruvian Andes

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ABSTRACT

Montane plant species around the globe are predicted to shift their distributions upslope in response to increasing temperatures associated with climate change. In the tropical Andes, which are one of the most diverse and threatened of all biodiversity hotspots, many plant and animal species have already started to shift their distributions to higher elevations in response to warming. However, a variety of biotic and abiotic factors may stabilize Andean timberlines and halt further upslope migrations into the high elevation grasslands (referred to as "puna" in southern Peru) above the forest. One possibility is that small forest patches that occur above-timberline throughout the Andes may facilitate forest expansion into newly suitable areas in the puna, yet little is known about the ecology or function of these patches. In this study, we examined seedling recruitment patterns, seed dispersal, and microclimate at the timberline, in and around above-timberline forest patches, and in the puna. The above-timberline forest patches had similar patterns of seed dispersal as the timberline but overal <1% of captured seeds were dispersed 10 m into the puna. At both the patch edges and the forest timberline, seedling abundances were lower in the puna relative to the adjacent forest and forest–puna ecotone. This reduction may be a result of reduced seed dispersal across the forest–puna ecotone and/or decreased germination of dispersed seeds due to the harsh microclimatic conditions occurring in the puna (daily temperature fluctuations are greatly elevated in the puna relative to the forest and frost events are more frequent and severe). While increasing temperatures associated with climate change may ameliorate some of the severe climatic conditions occurring in the puna, it will not directly affect other potential recruitment limitations such as reduced seed dispersal, high levels of UV radiation, and anthropogenic activities (cattle grazing and fires) in the puna. With the reduction of anthropogenic activities, above-timberline forest patches may serve as nucleating foci for future forest expansion into the puna. However, our results indicate that any upslope migration of the timberline into the puna will likely occur at a rate that is slower than what is required to keep pace with warming because recruitment is restricted to a narrow strip along the forest–puna borders. Slowed forest expansion into the puna could act as a barrier to the upslope migration of Andean cloud forest species leading to extreme losses of Andean biodiversity.

1. Introduction

Temperature is commonly believed to be one of the most important environmental factors determining the upper elevational limit of closed canopy forests, i.e., the timberline (Körner, 1998, 2012; Körner and Paulsen, 2004; Berdanier, 2010). Accordingly, with global warming, it is expected that montane forest species will shift their distributions upslope and colonize the currently unforested alpine zones (Grace et al., 2002; Harsch et al., 2009). However, in a recent meta-analysis conducted by Harsch et al. (2009), timberlines showed no consistent response to past climate warming; upward shifts were observed at 52% of sites, downslope shifts were observed at 1% of sites, and no shifts were observed at 47% of sites. While only a relatively small number of tropical sites were included in this meta-analysis (7 of 166), none shifted their timberline elevations through time (Harsch et al., 2009). More specifically for the tropical Andes, an analysis of remotely-sensed Landsat images taken from 1980–2010 has indicated no measurable change in the location of timberline despite the approximate 0.55 °C increase in temperatures that occurred over the same time period (assuming an approximate adiabatic lapse rate of $-5.5\,^{\circ}\mathrm{C\,km^{-1}}$, this warming should have resulted in a ~100 m upslope shift in timberline; Zelazowski, 2010).

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The reason that the timberline in the tropics, and specifically in the tropical Andes, is not migrating upslope despite rising temperatures remains unknown. However, it may be due to a combination of biotic and abiotic factors that prevent the recruitment and/or the growth of tree species above the timberline. For instance, increased frost severity and frequency (Körner and Paulsen, 2004; Wesche et al., 2008), elevated intensity of UV solar radiation (Bader et al., 2007a), reduced seed dispersal (Primack and Miao, 1992; Dullinger et al., 2004), low germination rates of timberline species (Cierjacks et al., 2007a), competition with established grasses (Tilman, 1997), high levels of seed predation (Hillyer and Silman, 2010), altered edaphic conditions (Zimmermann et al., 2010), and anthropogenic disturbances such as livestock grazing combined with fire (Kessler, 2000; Suarez and Medina, 2001; Cierjacks et al., 2007b) and agriculture clearing (Sarmiento and Frolich, 2002) can all potentially restrict forest tree recruitment above timberline. In addition, shifts in species distributions may lag behind temperature changes, and therefore it is possible that some timberlines are still responding to past climatic changes or have not yet begun to respond to more recent warming (Wardle and Coleman, 1992; Dullinger et al., 2012).

Regardless of the causes, if Andean timberlines continue to remain fixed despite future climate change, then this ecotone may act as a barrier halting the migration of high-elevation forest species (Feeley and Silman, 2010; Feeley and Rehm, 2012). This could have dire consequences to global biodiversity since the tropical Andean cloud forests are some of the most diverse ecosystems on Earth (Myers et al., 2000; Hobohm, 2003) and since many Andean cloud forest species have already been observed to be shifting their distributions upslope within the forests (Feeley et al., 2011, 2012b; Forero-Medina et al., 2011; Feeley, 2012). Additionally, cloud forests are expected to act as future cool temperature refugia for species shifting their distributions upslope from the Amazonian lowlands (Feeley et al., 2012b), but are already highly threatened by other anthropogenic disturbances such as deforestation and conversion for other landuses (Sarmiento and Frolich, 2002; Purcell and Brelsford, 2004; Kintz et al., 2006; Cierjacks et al., 2008; Bruijnzeel et al., 2010; Martin et al., 2011; Román-Cuesta et al., 2011; Feeley and Rehm, 2012; Feeley et al., 2012a).

In the southeastern Peruvian Andes, the vegetation above the timberline is comprised mainly of a grassland matrix (hereafter referred to by the local name of "puna" a drier less-widespread version of "páramo") that eventually gives way to alpine vegetation and bare rock, culminating in snow at extreme elevations. Within the puna matrix, there exist small mixed-species forest patches that are similar to *Polylepis* spp. forest patches that grow up to several hundreds of meters above the principle timberline throughout the Andes (Miehe and Miehe, 1994; Kessler, 2002). The origin of these above-timberline forest patches is debatable, but they are often hypothesized to be the remnants of more extensive forests that were destroyed by past human activity (Miehe and Miehe, 1994; Kessler, 2002; Sarmiento and Frolich, 2002; White, 2013). Alternatively, they may be an advancing front of expanding forest vegetation halted through the recent increase of fire frequency associated with grazing (Di Pasquale et al., 2008). Regardless of their origin and history, these patches may play a crucial role in any future forest expansion above the current timberline, for example, by acting as nucleating foci for the establishment of forest seeds and seedlings in the puna (Yarranton and Morrison, 1974; Schlawin and Zahawi, 2008). As an analogy, patches of tropical lowland trees in abandoned fields act as seed sources, and areas in the immediate vicinity of "nurse" trees have higher rates of seedling establishment than occurs in nearby fields (Janzen, 1988; Nepstad et al., 1996; Turner and Corlett, 1996). These lowland forest patches also alter microclimate, promoting seed germination and forest expansion into surrounding pasture habitats. Similarly, the above-timberline forest patches in the Andes may potentially facilitate forest expansion into the puna under future climate change, especially if other human impacts (e.g., cattle grazing and fires) are decreased or completely removed from the puna (Cierjacks et al., 2007b; Aide et al., 2010). For example, in some central Andean forests, there are more seedling microsites available within forest patches than outside (Renison et al., 2004) and patches buffer against extreme climatic events, reducing seedling mortality (Cierjacks et al., 2007b; Wesche et al., 2008). Furthermore, seedling abundance is often highest at the patch–puna ecotone (Byers, 2000; Cierjacks et al., 2007b), indicating the potential for these patches to expand outwards.

To increase our understanding of the ecology of these above-timberline forest patches, as well as their potential role in facilitating the expansion of montane forests past the current timberline and into the puna of the southern tropical Andes, we investigated the structure and function of several above-timberline forest patches and adjacent timberline forests within Manu National Park, Peru. We specifically addressed the following questions: (1) Could changes in the patterns of seed dispersal and microclimate across the forest–puna ecotone limit forest expansion into the puna? (2) What are the current tree recruitment patterns at the forest to puna and patch to puna ecotones? and (3) Can forest patches potentially act as nucleating areas for future forest expansion above the current timberline into the puna? It is increasingly clear that high Andean landscapes have experienced long term and intensifying human alterations (Young, 2009; White, 2013). While human impacts were not an explicit aspect of this study, results are interpreted in the context of a human modified landscape.

2. Materials and methods

2.1. Study area

Data were collected along 14 transects located on three ridges on the eastern slope of the Peruvian Andes in the Kosñipata Valley within Manu National Park, in the political department of Cusco in southeastern Peru (~13°6′18″S, 71°35′21″W). The three study ridges occur at the boundary between tropical montane cloud forests, which are characterized by heavy precipitation caused by orographic lifting of warm, moisture-laden air from the Amazon, and the relatively dry, unforested altiplano found to the west. Rainfall in the high elevation portions of the park averages 1900–2500 mm yr^{-1} with a distinct wet season from October to April (Rapp and Silman, 2012). Forest soils below the timberline are characterized by a 20–70 cm thick organic layer over a 10 cm organic humic Ah layer, which are underlain by a 10–70 cm mineral layer (Zimmermann et al., 2010). Puna soils are much simpler with a 20–30 cm thick organic A layer underlain by a stony B layer (Zimmermann et al., 2010).

Manu National Park was designated as a national park in 1973, but even before this time the study areas were relatively conserved due to inaccessibility. Cattle grazing and associated fires do occur within the study area but cattle density and fire frequency is lower than in areas outside of Manu National Park and throughout other parts of the Andes (Gibbon et al., 2010). Although the study sites have had low levels of human impacts for at least the past 40 years relative to the surrounding landscape, current and past anthropogenic disturbances must be considered when investigating the timberline location. Therefore, results from the chosen study sites may be seen to offer a "best case scenario" for timberline shifts in the Peruvian Andes in response to climate change.

The 14 study transects were chosen in order to cover a wide range of timberline elevations (3146–3663 m a.s.l.) and by the requirement for nearby above-timberline forest patches. All tran-