

Land-use and climate change effects on population size and extinction risk of Andean plants

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Abstract

Andean plant species are predicted to shift their distributions, or 'migrate,' upslope in response to future warming. The impacts of these shifts on species' population sizes and their abilities to persist in the face of climate change will depend on many factors including the distribution of individuals within species' ranges, the ability of species to migrate and remain at equilibrium with climate, and patterns of human land-use. Human land-use may be especially important in the Andes where anthropogenic activities above tree line may create a hard barrier to upward migrations, imperiling high-elevation Andean biodiversity. In order to better understand how climate change may impact the Andean biodiversity hotspot, we predict the distributional responses of hundreds of plant species to changes in temperature incorporating population density distributions, migration rates, and patterns of human land-use. We show that plant species from high Andean forests may increase their population sizes if able to migrate onto the expansive land areas above current tree line. However, if the pace of climate change exceeds species' abilities to migrate, all species will experience large population losses and consequently may face high risk of extinction. Using intermediate migration rates consistent with those observed for the region, most species are still predicted to experience population declines. Under a business-as-usual land-use scenario, we find that all species will experience large population losses regardless of migration rate. The effect of human land-use is most pronounced for high-elevation species that switch from predicted increases in population sizes to predicted decreases. The overriding influence of land-use on the predicted responses of Andean species to climate change can be viewed as encouraging since there is still time to initiate conservation programs that limit disturbances and/or facilitate the upward migration and persistence of Andean plant species.

Keywords: bioclimatic niche, climate change, conservation biogeography, distribution, land-use, range size, REDD, tree line

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Introduction

Climate change causes species to shift their distributions, or 'migrate,' in order to remain within the bounds of their climatic tolerances (Thomas *et al.*, 2004; Walther *et al.*, 2005; Beckage *et al.*, 2008; Colwell *et al.*, 2008; Chen *et al.*, 2009). Beyond changing where species occur, these migrations may lead to large changes in the amount of habitat area available, which in turn may cause changes in species' population sizes and influence extinction risk (Thomas *et al.*, 2004; Feeley & Silman, 2010). Changes in species range sizes are especially likely in montane areas, which are also home to many of Earth's richest biodiversity hotspots (Myers *et al.*, 2000).

The ability of species to persist in the face of climate change will however be influenced by many factors other

than changes in available habitat area, including patterns of abundance within a species' range, the rate at which species are able to migrate in relation to the pace of climate change, and interactions with human land-use and other anthropogenic disturbances. These factors are often excluded from studies predicting species' risks of extinction due to climate change (Ibanez *et al.*, 2006).

The eastern slope of the Andes harbors Earth's highest biodiversity and is also one of the areas most threatened by climate change. Future scenarios of climate change – even the most sanguine – present unprecedented challenges to plants and ecosystems on the Andean slope (Bush *et al.*, 2004). In the southwestern Amazon and adjacent Andes, major climate models are consistent in predicting an approximate 4–6 °C temperature increase by 2100 (Cramer *et al.*, 2001; Urrutia & Vuille, 2009). Given the decrease in temperature of approximately 5.5 °C per 1000 m gain in elevation (Bush *et al.*, 2004), this will require plants to migrate >900 m elevation within a single generation to remain

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in equilibrium with climate. The speed and magnitude of climate change raises acute questions regarding the future of biodiversity in hotspots: What are basic species range sizes and plant–climate relationships? Do species have distributions or migratory abilities that allow them to keep pace with changing climate? Are there barriers – natural or anthropogenic – that might hinder migration? The last point takes on singular importance in the high Andes where tree line is presently depressed ~500 m by anthropogenic activities such as cattle grazing and fires (Sarmiento, 2002; Sarmiento & Frolich, 2002) and where increasing temperatures may increase fire frequency. Under these conditions, anthropogenic tree line may present a hard barrier to upward plant migration, imperiling high-elevation Andean biodiversity. Here we explore the potential distributional responses of Andean plant species to changes in temperature incorporating different scenarios associated with plant population distributions, migration rates, and land-use change.

Distribution of individuals within species' ranges

Within a species' range limits, the density of individuals will vary greatly, often in relation to climate (Shoo *et al.*, 2005; Murphy *et al.*, 2006; Sagarin *et al.*, 2006; Purves, 2009). The specific density distribution pattern will strongly affect how range shifts translate into changes in total population size (Iverson & Prasad, 1998) and the species' resultant risks of extinction (Shoo *et al.*, 2005). Previous studies modeling climate-driven species migrations and extinction risks have generally used variations of the bioclimatic envelope approach, thus making the assumption that population density is independent of location within a species' range (Fig. 1), and consequently that there is a direct translation between change in habitat area and change in population size (Pearson & Dawson, 2003; Thuiller, 2003). This assumption, however, is often not true. Species have long been demonstrated to show changes in amplitude along environmental gradients (Whittaker, 1956), and a

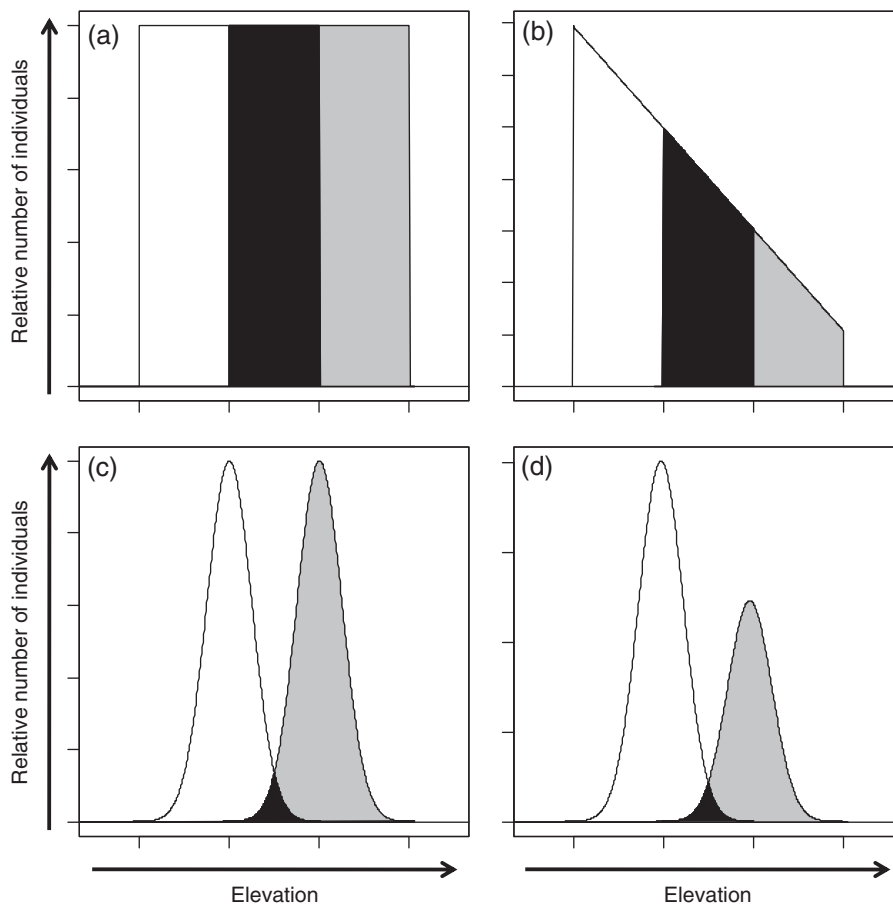


Fig. 1 For a hypothetical species, the current (clear areas), future (gray areas), and overlap (black areas), number of individuals per elevation with a uniform density distribution of individuals (a), or a normal density distribution of individuals (c) and showing the corresponding effects of decreasing available land area under future conditions (b and d) as is typically the case for species shifting their distributions upslope.

central result of macroecology is that population densities for a species are generally greater in the core than along range edges (Brown, 1984; Brown *et al.*, 1995; Murphy *et al.*, 2006; Sagarin *et al.*, 2006; Purves, 2009). Nonuniform responses to environmental gradients and geographic distributions suggest that the translation between change in habitat area due to migration and change in population size will be complex, depending on the specific shape of the species' density distribution and how the distribution of individuals relates to the distribution of available land area under both current and future climate (Shoo *et al.*, 2005; Fig. 1).

Migration scenarios

The ability of species to migrate significantly affects the predicted changes in habitat area and extinction risk. If species are capable of 'perfect migration' – the ability to remain in equilibrium with shifts in climate – they are assumed to completely occupy all habitat area that is suitable under the new climate. With perfect migration, species experience changes in population size directly proportional to the change in habitat area within their ranges under the different climatic conditions. In contrast, if species are incapable of migrating (i.e., 'no migration'), either due to limited dispersal abilities or the influence of limiting factors other than climate (Ibanez *et al.*, 2006), then species will be in disequilibrium with climate and will occupy only the habitat that is suitable under both current and future climate (Fig. 1), greatly reducing the amount of land available and increasing extinction risk. In some cases, changes in climate may be so severe that there will be no overlap between current and future habitat areas of many species, in which case certain extinction is predicted for nonmigrating species (Thomas *et al.*, 2004). True migration rates will likely be intermediate between 'no' and 'perfect' migration and will be highly variable between species. Given the lack of data for most species, few studies have attempted to incorporate known migration rates into their species migration models. The perfect- vs. no-migration scenarios are therefore commonly used to represent extreme or best- vs. worst-case scenarios.

Human land-use change

Patterns of human land-use change may affect the ability of species to persist in the future. Land-use effects will be especially pronounced in the context of changing climate as species may migrate into or out of areas that will experience disproportionate levels of human land-use change, thereby either increasing or decreasing the relative benefit of migrating. For example, a disturbance model of Soares-Filho *et al.* (2006)

predicts high rates of deforestation throughout the Amazon and along the base of the Andes but decreasing rates of disturbance at higher elevations. Upward migrating species may therefore actually 'escape' highly disturbed areas and benefit by moving upslope even if the amount of total land area decreases.

In the tropical Andes, however, human land-use may have an additional effect on species migrations in that the upper elevational limit of forest growth, or tree line, is potentially set not by climate but instead by human-associated activities such as cattle grazing and accidentally or intentionally set fires which are used to increase fodder for cattle (Keating, 2007; Cierjacks *et al.*, 2008). With anthropogenic effects on tree line, increasing temperatures may not cause tree line to move upslope as would be predicted if tree line were set by climate alone. This places a fixed upper limit to the distributions of forest species and may greatly reduce range sizes from those predicted based on climate alone. Under this fixed tree line or 'grass ceiling' scenario, upward migrating Andean species will have less area available to them than if tree line was allowed to move upslope in response to temperature increases. An anthropogenically fixed upper limit to the distribution of forest species will have pronounced effects in the Andes as the region above current tree line is relatively flat compared with the forested slopes with the amount of land area actually increasing at high elevations between ~3500 and 4500 m. If tree line moves upslope in response to climate change, species may increase their range size and increase their ability to persist. If, on the other hand, tree line is anthropogenically determined and/or remains fixed or lowers in the future, species will be prevented from colonizing the high-elevation plateau and as such future range predictions may switch from increases to decreases in habitat area following migration.

Here we model the effects of climate change on the distributions, population sizes, and associated relative extinction risks of 223 forest plant species from the tropical Andes incorporating information about within-range density distributions, migration rates, and human land-use change. We show that while all of these factors have significant impacts on predictions, the fate of Andean species with climate change will likely depend primarily on patterns of human land-use. This is potentially good news if conservation policy measures can be enacted now to change patterns of land-use and help reduce the loss of Andean species due to climate change.

Methods

We modeled the distributions of tropical Andean plant species on the basis of natural history collections which indicate the known locations and hence abiotic conditions where species

occur. We downloaded all herbarium collections data available through the Global Biodiversity Information Facility (<http://www.gbif.org>; for a list of all contributing herbaria, see supporting information Table S1) for vascular plants from Columbia, Ecuador, Peru, and Bolivia. Data were screened to exclude duplicate records (those with identical species name and geographic coordinates) and to include only records identified to species and including information on collection elevation. In estimating species ranges, we did not use elevations inferred on the basis of collection coordinates to minimize the potential influence of geo-referencing errors which we have elsewhere shown to be severe in mountainous areas (Feeley & Silman, 2010). After filtering, we selected species represented by ≥ 30 records and occurring exclusively between 500 and 4000 m elevation. This provided us with a database of 223 well-collected Andean forest species.

For each of our 223 study species, we estimated the relationship between relative population density and elevation by fitting a density distribution to the list of collection elevations with bandwidth set using the biased cross validation technique (Oh, 1996). In fitting a density distribution to collection elevations we make the implicit assumption that the relative number of collections per species at a given elevation is indicative of the relative density of individuals at that elevation. One potential concern with this method is that collection intensity may be biased, for example due to differential access and/or proximity to field stations and population centers, consequently biasing the inferred species–elevation relationship (Kadmon *et al.*, 2004; Moerman & Estabrook, 2006; Tobler *et al.*, 2007; Loiselle *et al.*, 2008). To correct for possible collection biases, we divided each species' population density distribution by the density distribution estimated for all collection records (including samples of nonstudy species and samples not identified to species). Owing to differences in collection intensities between species, we only estimate the relative density of individuals within species across their elevational ranges which in the context of scenarios of climate- and land-use change, allows us to calculate proportional changes in a species' population, even if the actual population densities of the species is unknown.

For current distributions of each species, we calculated the relative population size at each elevation by multiplying the corrected population density distribution by the distribution of land area with respect to elevation. The amount of land area per elevation was only tabulated within the 'Tropical and Subtropical Moist Broadleaf Forest' biome (Olson *et al.*, 2001) in order to effectively limit species' current ranges to just within areas that are presently forested. We also estimated each species mean elevation, or 'center of gravity' as the weighted mean elevation of the relative population distribution (Chen *et al.*, 2009).

Migration scenarios

To estimate how species ranges and population sizes will change in response to global warming, we looked at species migration under three scenarios: (1) perfect-migration, (2) no-migration, and (3) observed-migration rates calculated from repeated cen-

suses of forest inventory plots in the Peruvian Andes (K. J. Feeley and M. R. Silman, unpublished data; see below).

Perfect-migration scenario

To model perfect migration, we shifted the density distribution of each species upslope 910 m. This is elevational shift expected under a 5 °C warming scenario based on the adiabatic lapse rate of -5.5 °C per 1000 m of elevation gain measured for the region (Terborgh & Weske, 1975; Bush *et al.*, 2004). 5 °C is the approximate increase in temperature predicted for tropical South America over the next 100 years (Malhi *et al.*, 2009; Urrutia & Vuille, 2009). We also conducted all analyses per degree temperature increase ranging from 1 to 8 °C; the results for these warming scenarios are presented in the supporting information Table S2. When shifting species upslope, we allowed them to move onto areas of land above current tree line by including the 'Puna' biome when tabulating future land area. Within the Puna, we excluded the 'Dry Puna' ecoregion under the assumption that these areas will be unable to support forest growth in the future even with increased temperatures due to low water availability. Likewise, we excluded all extra-tropical Puna areas. The changes in species population sizes were also estimated while not allowing migration above current tree line. An important caveat to our methods is that we did not incorporate changes in climatic factors other than temperature, such as precipitation or seasonality. Changes in these climatic variables will certainly have important impacts on the future distributions of Andean species and will be explored in future studies.

No-migration scenario

We also looked at the changes in population size expected due to climate change if species are unable to migrate (i.e., 'no migration'). Here we counted the percent of each species' population currently occurring at elevations that will remain suitable under future climate (i.e., the overlap between the distributions of elevations occupied under current and the perfect-migration scenarios).

Observed migration scenario

We modeled the effects of climate change on species distributions assuming migration rates consistent with observations for Andean tree species in the region. Based on repeated analysis of forest inventory plots in the Andes of Southeastern Peru, we have estimated the annual migration rates under contemporary climate change for 145 Andean tree genera including 51 of our study species (K. J. Feeley & M. R. Silman, unpublished data). For the few species estimated to have negative migration rates (i.e., migrating downslope; $n = 8$), we assumed no migration, and for species with observed migration rates meeting or exceeding the expected rate under the observed temperature changes ($n = 18$), we assumed perfect migration. For those study species for which no specific migration rate estimates are available ($n = 191$), we used the

mean migration rate of 2.5 m yr^{-1} as estimated across tropical Andean tree genera from this region (because observed migration rates were annualized we assumed a time frame of 100 years). We then calculated the proportion of the population within each species that will migrate to elevations that will be suitable under future climate (i.e., the area of overlap between future distribution curves predicted under observed and perfect migration).

Scenarios of land-use

The above calculations exclude deforestation and allow species to migrate above the current tree line and thus represent a future with massive intervention to halt deforestation and alter land-use practices (e.g., suppression of fire) so that forests are allowed to colonize Puna habitat. We repeated each of the above migration scenarios incorporating a perhaps more realistic business-as-usual (BAU) scenario of future human land-use. We estimated the amount of forest area that will be lost in the future due to deforestation by calculating the annual rate of deforestation vs. elevation within the study area as predicted over the next 40 years in the Soares-Filho *et al.*'s (2006) BAU land-use model. Based on this annual rate, we extrapolated the amount of forest that will be lost at each elevation over the next 100 years and modified the estimates of species' current and future habitat area, population sizes, and population size changes accordingly. We also incorporated the possibility that tree line will remain at its current elevation due to anthropogenic activities at high elevations by setting the amount of land area that will be available to species in the future equal to the amount of currently forested land (i.e., by tabulating future land areas with suitable climate just within the 'Tropical and Subtropical Moist Broadleaf Forest' and excluding all 'Puna' areas).

For all migration and land-use change scenarios, we calculated the resultant relative change in population size per species based on the ratio of future to current total population size. This ratio also provides a measure of relative extinction risk since threat of extinction is predicted to increase with greater relative population decline (O'Grady *et al.*, 2004).

Results

Perfect-migration scenario

Under an ideal scenario of perfect migration and excluding deforestation and allowing species to migrate past tree line, we predict that an approximate 900 m upslope migration in response to a 5°C temperature increase will cause changes in the population sizes of our study species ranging from -45% to $+133\%$ (mean = $+20\%$; Fig 2a, Table S2). There is a strong relationship between the predicted change in populations size and species mean elevation such that population loss is predicted to be greatest in low-elevation species while all species with mean elevations $>2400 \text{ m}$

are predicted to increase in population size as they migrate from steep, low-area mountain slopes onto the rolling terrain and high-elevation plateaus found above 3200–3500 m (Fig. 2a). Relative population size increases are predicted to be greatest in the very highest-elevation species, those with populations centered close to current tree line (Fig. 2a, Table S3).

No-migration scenario

If species are incapable of migrating to remain in equilibrium with climate, predictions change significantly with all species expected to experience large population losses ranging from -53% to -96% (mean = -72% ; Fig. 2). Under the no-migration scenario, population loss tends to be greatest in high-elevation species (Fig. 2a, Table S3) indicating that the ability to migrate will be of greatest importance to high-elevation species.

Observed migration scenario

As expected, we find that using the observed migration rates predicts population changes that are intermediate between the perfect- and no-migration scenarios and more variable due to intraspecific differences in migration rates (Fig. 2a, Table S2). With observed migration rates, all but 19 species (all estimated to have migration rates exceeding the required rate under future climate change and thus assigned 'perfect migration') are predicted to decrease in population size, with predicted population change averaging a 42% loss across all species (Fig. 2a, Table S3).

Scenarios of land-use

Under the BAU scenario of future human land-use change including deforestation and a fixed tree line, the predicted fates of species change significantly. With deforestation and a fixed tree line, we predict that all Andean plant species will decrease in population size regardless of their current mean elevation or their ability to migrate (Fig. 2b, Table S2). Even with perfect migration, population losses average $>45\%$. There is a strong relationship between the magnitude of population change and species' current mean elevation such that population loss is greatest in low-elevation species and relatively less in high-elevation species (Fig. 2b). However, the effect of human land-use change on population change is greatest in high-elevation species (i.e., compare Fig. 2a and b), causing species that potentially could have more than doubled in population size to decrease in population size by more than 50% (Table S3). The extreme difference in predicted population changes for high-elevation species is

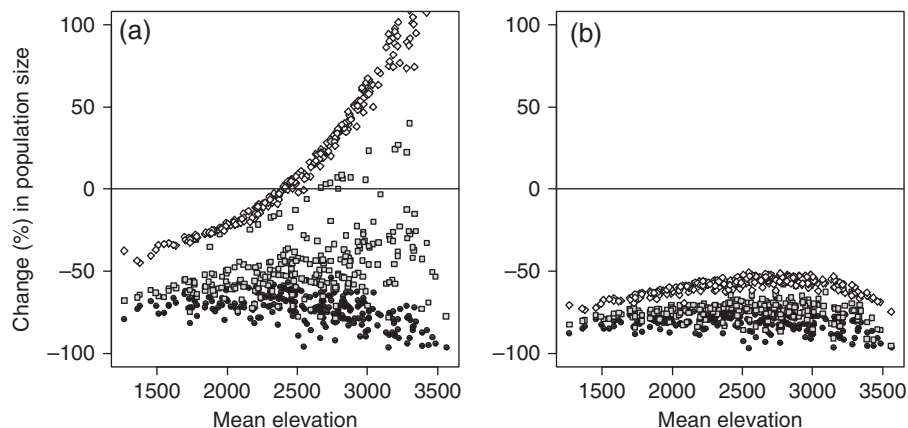


Fig. 2 Predicted percent change in population sizes of Andean plant species following a 5 °C temperature increase with perfect (white diamonds), no (black circles), and observed (gray squares) migration rates and with (a) no future deforestation and allowing species to migrate past current tree line or (b) under a business-as-usual future land-use scenario including deforestation and a fixed tree line. Positive values indicate an increase in population size.

primarily due to human activities above tree line which prevent species from crossing tree line and reaching the expansive rolling plateaus of the high Andes. Under the no- and observed-migration scenarios, incorporating human land-use change similarly causes elevated population losses, though deforestation within existing ranges has the greater effect as, even in the absence of human land-use, species would be unable to expand their ranges above tree line due to the absence of upward migration.

Discussion

Our results demonstrate several striking patterns. First, if deforestation is halted and land-use change practices are adapted which allow forests to pass tree line and colonize areas currently under Puna, species from the high Andean forests (those with current mean elevations greater than ~2400 m) may actually 'benefit' from climate change and expand, and in some cases more than double, their population sizes if they are capable of migrating at the pace required to remain in equilibrium with the changing climate. If, on the other hand, the pace of future climate change greatly exceeds species' abilities to migrate (equivalent to the 'no-migration scenario'), all species in the study experience large population losses and consequently face high risks of extinction; 45 species (19%) to below 20% of original population sizes and 11 species (5%) to below 10% of their original population sizes. These aforementioned results represent best- and worst-case scenarios, respectively, and provide boundaries on expectations under temperature changes predicted to occur over this

century. If we use migration rates consistent with those observed in the region over the past several years, again all but a few species will experience population losses. However, in many cases these losses will be relatively minor (Fig. 2a).

The relatively sanguine predictions under the observed and perfect-migration scenarios change qualitatively if a more realistic scenario of human land-use is incorporated. In the complete absence of any climate change over the next century, deforestation alone could cause average declines of >50% in the current population sizes of Andean forest species. Because most deforestation is concentrated in the lowlands and along the base of the Andes (Soares-Filho *et al.*, 2006; Feeley & Silman, 2009), any benefit of migrating upslope is heightened (or any cost of migrating decreased).

Given that temperatures are rising (Vuille & Bradley, 2000; Malhi & Wright, 2004; Hansen *et al.*, 2006) and will likely continue rising in the Andes over at least the next century (Urrutia & Vuille, 2009), and that species will be pushed upslope as a consequence, a perhaps even more important impact of human activities on Andean forest species is through land-use effects on tree line. If current patterns of human land-use above tree line continue and prevent species from migrating to higher elevations, the amount of land area available to species in the future, and their consequent range sizes, will be significantly reduced. Indeed, if tree line is permeable, many species could experience significant increases in population size (assuming perfect migration) but if tree line presents a hard barrier to migration all species found above ~2400 m will experience a net decrease in population size regardless of their potential migration rates.

The fact that human land-use has such an overriding influence on predictions of how Andean species will respond to future climate change can be viewed as encouraging in that there is still time to change many of our land-use activities. Even if climate change proceeds at the projected rates we have the opportunity to decrease the loss of Andean species, and possibly even create a situation in which population sizes of some species increase, by reducing rates of deforestation and encouraging the adaptation of land-use practices above tree line that allow or facilitate the upward migration of forest species above current tree line. The single most important land-use change to allow tree species to migrate is the elimination or amelioration of anthropogenic fire from high Andean ecosystems. Fire is pervasive in Puna ecosystems and mainly are started to increase the quality of fodder for grazing, or simply escape during routine clearing of fields for agriculture.

Economic and social incentives for changing land-use practices in the Andes are also central to conservation goals. One example of such an activity is 'carbon farming.' Under the Clean Development Mechanism (CDM) statute of the Kyoto Protocol, developing nations can receive funds for carbon sequestered through afforestation (Smith, 2002). While not currently a CDM, Reducing Emissions from Deforestation and Degradation projects are currently being developed which produce carbon offsets sold on the voluntary carbon market. Under both types of activities tropical Andean countries, as well as local communities, can profit by simply allowing forests to move upslope, and even more so by encouraging the upslope migration of Andean plants through active forestry projects involving native montane cloud forest species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of all herbaria and collections contributing plant collection records used in this study as accessed through the Global Biodiversity Information Facility (12/2008–1/2009).

Table S2. Changes in Andean plant population size predicted under incremental 1 degree warming from +1° to +8 °C incorporating different migration and land-use change scenarios. Positive values (bold) indicate predicted population increases.

Table S3. Changes in population size predicted for individual Andean tree species due to 5 °C warming.

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