TITLE: Differential Seedling Regeneration Patterns across Forest-Grassland Ecotones in Two Tropical Treeline Species (*Polylepis* spp.)

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Differential Seedling Regeneration Patterns across Forest-Grassland Ecotones in Two Tropical Treeline Species (*Polylepis* spp.)

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Abstract

Successful forest expansion into grassland can be limited by seed dispersal and adverse conditions for tree seedlings in the grassland environment. In the high-elevation Andes, human-induced fragmentation has exacerbated the patchy distribution of *Polylepis* forests, threatening their unique biological communities and spurring restoration interest. Studies of *Polylepis* forest extent in Peru suggest that forest borders have remained stable over the past century despite decreasing anthropogenic disturbance, suggesting that tree seedling recruitment is being limited in the open grassland habitat. We studied natural seedling dispersion patterns of *P. sericea* and *P. weberbaueri* (Rosaceae) at forest-grassland edges across a range of environmental conditions to examine seedling recruitment and colonization of grasslands in Huascaran National Park (Peru). Using data from 2,367 seedlings found in 48 forest-grassland edge plots (15 m x 15m) at forest patches between 3900-4500 masl, we employed generalized mixed modelling to identify the significant associations of seedling densities with environmental covariates. Additionally, we compared these associations to patterns of adult presence on the landscape. Seedling densities were associated with a combination of variables varying within (distance to forest edge) and among (elevation and dry season solar irradiation) plots across the landscape. For both species, seedling densities decreased with increasing distance away from the forest in a manner consistent with short-distance seed dispersal by wind. Our results suggest that such short-distance dispersal may slow forest expansion, but that there also appear to be substantial post-dispersal limitations to seedling establishment in the grassland. *Polylepis sericea* densities decreased with elevation, while *P. weberbaueri* increased with elevation and decreased with solar irradiation. Associations of adult presence with elevation and solar irradiation mirrored those of seedling densities. Management of areas with forest patches dominated by these species should consider these differences in their environmental tolerances, particularly during species selection and zonation for reforestation.

Keywords: seedling recruitment, *Polylepis* spp., forest-grassland boundaries, colonization, forest expansion

INTRODUCTION

While successful regeneration is essential to forest persistence, successful recruitment beyond forest edges into non-forest areas is necessary for expansion and migration of forest tree species. Both natural and anthropogenically created forest-grassland boundaries may persist with little change over time due to inadequate tree seedling colonization beyond the forest line (Holl *et al.* 2000; Aide & Cavelier 1994; Smith *et al.* 2003; Harsch & Bader 2011). Colonization into grasslands may be limited by seed dispersal from forest edges (Holl *et al.* 2000) and rates of seedling establishment under the high-stress abiotic conditions that seedlings experience under open-sky habitat (Johnson *et al.* 2011, Bader *et al.* 2007). Competition with grasses and disturbances (fire and grazing) can further limit woody plant establishment in grasslands (Aide & Cavelier 1994; Gunarante *et al.* 2010; Scholes & Archer 1997; Renison *et al.* 2015).

High-Andean *Polylepis* forests are a sub-alpine vegetation community dominated by trees of the *Polylepis* genus (Rosaceae), and define the upper treeline in the tropical and subtropical Andes and Sierras de Cordoba, Argentina. These forests are characterized by a patchy distribution at multiple scales, occurring within single valleys as islands in a grassland matrix and ranging in extent from tens to hundreds of meters. These forest patches are far above the continuous forest-line, but below the global low-temperature limit to tree growth (Korner & Poulsen 2004). There has been considerable debate regarding whether the causes of this local patchiness are primarily natural or anthropogenic (reviewed in Kessler 2002). However, the combined body of research suggests the contemporary distribution of *Polylepis* stands and surrounding grassland is the product of past climate history and topographic heterogeneity coupled with fragmentation from human land-use (e.g., Cierjacks *et al.* 2007; 2008; Williams *et al.* 2011; Renison *et al.* 2006; 2015, Toivonen 2014, Valencia *et al.* 2016).

Their island-like distribution makes these forests local hotspots of biodiversity and habitat for a unique mountain-top community of flora and fauna (Gareca *et al.* 2010, Sylvester *et al.* 2017). Concern over the conservation of these communities and the ecosystem services forests provide to local people has spurred interest in the restoration of the forest cover reduced by humans (e.g., Aucca & Ramsey 2005). Understanding the potential and constraints for *Polylepis* forests (re)establishment in grassland areas is important for this work. Studies in Peru have documented apparent stability of *Polylepis* forest boundaries even where agropastoral pressure has decreased and forests could ostensibly recover from past reduction (Byers 2000; Tohan 2000; Jameson & Ramsey 2007). This stability may be due to unsuccessful seedling establishment outside current boundaries; however, the factors governing this process have not been studied. Understanding the dynamics of natural seedling colonization is also important for assessing these forests' future under climate change, because under future climate scenarios most *Polylepis* species will need to migrate to higher elevations if they are to follow their climatic niche (Zutta 2009; Cuyckens *et al.* 2016).

The early stages and ontogenetic differences (Young *et al.* 2005) of tree recruitment niches (*sensu* Grubb 1977) are important for understanding the potential for successful seedling colonization under and outside forest canopy. Although the seedling recruitment phase (seed arrival through early growth) is only part of the entire process required to generate a forest with reproductive adults, it is inarguably the crucial one. Seeds and seedlings are the plant life-stages with the highest mortality rates (Leck & Outred 2008), representing a bottleneck that determines the initial population available for later life-stage transitions, and can determine species niche space (Young *et al.* 2005).

Studying patterns of seedling dispersion in space and their associations with environmental factors provides information about the seedling establishment niche. Seedling dispersion patterns integrate the results of all early recruitment processes and are the spatial manifestation of the early recruitment niche, where trends in seedling densities are early indicators of "effective dispersal" (Schupp *et al.* 1995; Nathan & Muller-Landau 2000; Cain 2000). Patterns of tree seedling abundance vary with spatial scale in response to seeder tree location and number, microsite conditions (e.g., microtopography), and environmental gradients varying at larger scales (e.g., elevation and precipitation). The relative influence of microsite on tree seedlings is thought to increase as overhead cover decreases, being greatest outside the forest (Dobrowski *et al.* 2015, Korner 2012). On the other hand, variation at larger spatial scales provides information about associations with global environmental conditions, the collective behaviour of forest boundaries across climatic gradients of forest distribution, and the potential response of the subalpine forest zone to climate change (Millar *et al.* 2015). Therefore, an adequate description of the recruitment niche for tree colonization of grasslands at subalpine *Polylepis* forest margins requires studying seedling patterns and their association with micro- and macro-environmental conditions.

This study describes patterns of seedling density in *P. weberbaueri* and *P. sericea* across a range of forest-grassland ecotones in Huascaran National Park (Peru) (HNP), and identify biotic and abiotic environmental factors associated with these patterns across two spatial scales. Our objectives were to establish what environmental conditions are likely to determine colonization of each species and characterize those that appear particularly favourable or detrimental to seedlings and natural colonization outside the forest. We discuss our results in the context of the role of seed dispersal and seedling recruitment in limiting colonization into non-forest habitat, differences in species tolerances and traits, and the implications they have for restoration and management of *Polylepis* forests dominated by these species.

METHODS

Study Area

Huascaran National Park (Ancash, Peru) (8.768° –10.067° S, 77.082°–77.818° W, elevational range: 2400–6768 masl), is a nationally protected area of 340,000 ha encompassing the nucleus of Huascaran Biosphere Reserve. It includes most of the Cordillera Blanca's glaciated massifs and contains much of the geomorphic and biological diversity of the Puna biogeographic region, including large tracts and patches of *Polylepis* forests within a grassland/shrubland matrix.

Mean annual precipitation across the park ranges between 640–1400 mm, with a pronounced dry season May–October (Smith 1988). The amount and strength of seasonality in precipitation varies with latitude and elevation. Precipitation generally decreases from the north to the south of the range, where the dry period is more severe, and increases with elevation on the western slope (Smith 1988, Niedertscheider 1990 in Kaser *et al.* 2003, R. Hellstrom, unpublished data 2016)

Native forest covers 3.4% of the HNP and is concentrated in the numerous (~44) major east-west glacial valleys intersecting the park, whereas grassland covers more open high-elevation areas

(SERNANP 2011). Natural forests dominated by *Polylepis weberbaueri* or *P. sericea* account for the majority of forest cover above 4000 m and are found up to 4700 masl. They are primarily located on the slopes, steep walls, and to a lesser degree, the bottoms of deep glacial mountain valleys. In more open valleys or exposed high "plains", they are rare and restricted to small depressions. Generally, patches only have one *Polylepis* species present, although some also host *Gynoxis* spp. trees and shrubs. Lone trees occur more rarely. Paralleling rainfall, forest cover diminishes from north to south along the cordillera and is generally greater on south facing slopes.

Forest cover within the HNP has been affected by past climatic fluctuations and historic, as well as contemporary, human activities (wood extraction, burning, mining and agricultural clearing, livestock grazing) dating back several millennia (Lynch 1967; Jolie 2011). Although cutting of native forests and pasture burning have been outlawed since 1975, both occasionally occur and limited extraction of downed wood by rural people living outside the park is allowed. Grazing by domestic livestock (cows, horses and donkeys) is allowed within the park, where almost all valleys serve year-round as natural "paddocks" for free-ranging, unsupervised livestock, even up to the base of glaciers (4600–5000 m).

Forest-Grassland Edge Surveys

During July and August of 2014 and 2015 we surveyed *Polylepis* forests located between 3900-4500 masl in four valleys on the western side of the Cordillera Blanca (Figure 1). Within each valley we surveyed 6-13 plots (total n=48) straddling the forest-grassland boundary (Figure 1A-D). Candidate plots were preselected using satellite imagery to cover the full range of elevation and slope orientations where forests naturally occur. Within each valley, we stratified selection within four ~150 m elevational bands starting at 3900 masl, choosing 3–4 candidate forest areas per band. Final sampling plots were selected in the field based on the absence of edaphic/topographic discontinuities at the forest edge (e.g., abrupt end of boulder fields), their accessibility, and the range of elevations and slope orientations covered by the final sample (See Table 1).

Forest plots were 15 m x15 m squares aligned parallel to the forest canopy line, half within canopy-covered area and half outside the canopy in grassland. We censused all adult *Polylepis* individuals (>1 m tall) within the plots, identifying the species present. Stems ≤ 1 m tall appearing to be individuals ('seedlings' as opposed to clonal ramets) were censused using quadrat sampling along one (19 plots) to three (29 plots) 15-m transects perpendicular to the forest edge (Figure 2). Transects were positioned 2.5, 7.5, 12.5 meters along the plot border parallel to the forest edge, and only the central transect was sampled in single-transect plots. Eight 1-m^2 quadrats were placed every 2 m along each transect (total n per plot= 8-24, forest: 4-12 grassland: 4-12). Within each quadrat, we identified and counted all *Polylepis* seedlings. Asexual ramets were extremely rare in our plots and distinguished from seedlings by exploring root connections to potential mother plants.

Environmental Covariates

Data on environmental covariates were collected at two scales, the plot and quadrat level. At the plot level, we measured elevation, slope, aspect, ground-cover classes, dung frequency and grass height in the field. Elevation and coordinates of each plot were taken at the lower-left corner of each plot using a GPS (Garmin GPSMAP 62S). We estimated percent ground cover (summing to 100%) in four cover classes: exposed rock, moss-covered rock, bare soil, covered/vegetated ground. Dung frequency was assessed by registering the presence/absence of bovine and equine dung in various states using stratified random sampling of ten 30 cm x 30 cm squares in each survey plot (grassland area: 4, transition zone: 3, under the forest canopy: 3). Within these same sampling quadrats, we measured the vertical height of vegetative parts of grass at a random point. At three plots within Rajucolta valley, we found the presence of sheep dung as well, but excluded these from our dung frequency calculations since only equine and bovine livestock are grazed in most of the park.

We calculated average solar irradiation received overhead by each plot during the dry season (JJA) using GIS. Average daily solar irradiation (Wh/m^2/day) received by each plot monthly was extracted from a map generated using the r.sun tool (QGIS 2.6 & Grass GIS 6.4.4), which allows the calculation of solar irradiation integrating topographic influences (slope and topographic shading), seasonal variation in solar trajectory, and sky conditions (cloud cover) (Hofierka & Suri 2002). We ran the calculations using a 20-m resolution digital elevation model (DEM, SPOT DEM Imagery) for the study area. For atmospheric inputs, we obtained Linke Turbidity from the SoDa solar data service (SoDa 2014; Redmund *et al.* 2003), real-sky diffuse and beam horizontal radiation fractions from NASA Surface meteorological and Solar Energy (NASA SSE 2016), and real-sky downward surface radiation from NASA GLDAS-2 (Rodell & Beaudoing 2015). Monthly average surface radiation values were created for the period 1986-2010 using the Google Earth Engine platform (Google Earth Engine Team, 2015) and downscaled to 20-m resolution with the “raster” package (V2.5-2,Hijmans 2015) in R (Version 3.2.1) (R Core Team 2014). Using r.sun, we calculated mid-month irradiation values for all 12 months and derived quarterly averages. See Appendix S1 for additional details on the methods and data.

At the quadrat level, we collected data on ground cover and soil hardness. Percentage ground cover was visually estimated for the four classes described above, where ground with either vegetation or leaf litter layer was classified as covered/vegetated ground. Soil hardness (kg/cm^2) was measured with a pocket penetrometer (AMS E-280 Pocket Penetrometer) at three randomly chosen points without rock cover, and mean values were for used for analysis.

Data Analysis

We used a multivariate generalized mixed modelling (GLMM) approach to build models associating seedling abundance with environmental variables at the quadrat and plot levels. Seedling densities were modelled using negative binomial distributions. In order to account for the hierarchical nature of the data and associate variables of different levels simultaneously, we employed study plot nested within valley as random effects terms. Using AICc criteria, we used forward and backwards model selection to choose a model with a set of variables that best explained the data from a preselected set of 10 which we expected to best capture differences in microclimatic conditions, seed availability, livestock activity, and macroclimate (Quadrat-Level: distance to forest edge and its square, exposed rock, moss-covered rock, bare ground, soil hardness; Plot-Level: elevation, dry season solar irradiation, dung frequency, number of trees > 2m)(Appendix S2). Based on the final model(s) we assessed the significance of the model terms using Log-Likelihood Ratio Tests (L-R Tests) or Wald Chi-square Test approximations when L-R Tests could not be performed due to convergence issues with the reduced model. We used Wald Tests on simplified models without additional covariates to test for significance of differences in overall seedling densities between species, valleys, and habitats.

We expected that exposed rock and bare ground would be negatively associated with seedling number per quadrat because both cover types are by definition, areas where vegetation, including seedlings, does not occur. However, these variables may have further associations with seedling density if the amount of either substrate in the neighbourhood influences the number of seedlings found in other ground cover. When model selection found significant negative associations with them, we tested for these additional effects by adding an offset term and examining if the fixed effect terms remained significant. We used log(non-rock area) as an offset term for examining extra effects of exposed rock cover and log(non-rock area- bare ground area) to test for additional effects of bare ground.

Additionally, we modelled the environmental associations of adult presence/absence of each *Polylepis* species within our study areas using the information from our sample plots and an additional 130 points sampled for vegetation structure by Sevillano-Ríos and Rodewald (2017). This dataset covered an elevational range of 3300–4700m in five valleys on the western side of HNP, including the four sampled for seedlings. We modelled the probability of adult presence using a binomial data structure and used AICc criteria to select the best model for each species from a subset of all possible models using elevation, the square of elevation and solar irradiation as covariates. All models were built using the “glmmADMB” (V 0.8.0) (Fournier *et al.* 2012; Skaug *et al.* 2014) and Wald Test were run using the “car” (V 2.5)(Fox & Weisberg 2011) package in R (Version 3.2.1).

RESULTS

Seedling density across species and valleys

A total of 1,829 *P. sericea* and 538 *P. weberbaueri* seedlings were counted. Mean seedling densities observed were several times higher in *P. sericea* than *P. weberbaueri* (Wald χ^2 Test: χ^2= 26.165, p<0.0001) and 10–60 times higher inside the forest than the adjacent grassland (*P. sericea:* χ^2= 127.23, p<0.0001; *P. weberbaueri*: χ^2= 88.47, p<0.0001; Table 2). Within each species, overall mean seedling densities across the entire border area, under the forest canopy, or in the grassland were not significantly different among valleys (Table 2). Variance partitioning indicated that most variation in seedling density occurred between quadrats (*P. sericea*> 83.6%; *P. weberbaueri*> 99.9%), rather than between plots (*P. sericea*=16.3%; *P. weberbaueri*<<0.1%), or valleys (*P. sericea*<<0.1%; *P. weberbaueri* <<0.1%), indicating a strong effect of microsites.

Environmental associations of seedling density

Seedling densities of both species were best fit by models containing both quadrat-level and plot-level variables (Table 3). The final models for both included quadrat distance to forest edge (linear and square terms), exposed rock cover, bare ground cover, and elevation. The best model for *P. weberbaueri* additionally included dry season irradiation.

For most environmental factors, seedling densities of both species responded similarly. Distance to the edge of the forest canopy was the strongest influence, with seedling density rapidly decreasing once outside the forest canopy (Table 3, Figure 3). The fitted models suggest that this decline of seedlings across the forest-grassland border begins a few meters inside the forest canopy. Seedling density also decreased with increasing exposed rock and bare ground. These are strong and significant factors for *P. weberbaueri*, but for *P. sericea* each was less strong and not a significant model component, with low additional explanatory power when added to the models independently or jointly (ΔAICc<-1) (Table 3, Appendix S3 and S4). However, these two terms had little explanatory power in the model beyond simply being areas where seedlings do not occur. Both were no longer significant when offset terms for area not covered by these two cover classes were included in the final models (*P.*

sericea: exposed rock χ^2=0.59, p=0.44; bare ground χ^2=0.05 p=0.82; *P. weberbaueri*: exposed rock χ^2=0.73, p=0.39; bare ground χ^2=1.55, p=0.21).

The two species responded differently to other environmental factors at the plot level. While *P. sericea* seedling density decreased significantly with elevation along the studied range, *P. weberbaueri* seedlings increased with elevation (Table 3, Figure 3). Additionally, dry season irradiation was negatively associated with *P. weberbaueri* seedling density, even when controlling for all other factors, whereas this variable was not included in the final model for *P. sericea*. It is worth noting, however, that dry season irradiation was positively correlated with elevation in the *P. sericea* dataset (Pearson's r=0.41, p=0.16), possibly confounding the association with seedling density with that of elevation. A model of seedling density including dry season irradiation as the sole covariate revealed a weak and marginally significant negative association (L-R Test: Deviance=5.60, p=0.058).

For both species, neither seeder tree density, livestock dung frequency, nor soil hardness were significantly associated with seedling density, and these factors were excluded in the final models.

Variation in edge effect with elevation and species

Given the strong patterns of seedling density across the forest-grassland boundary, we tested for an interaction of the magnitude (distance to edge) and shape (squared distance to edge) of the decline in seedling density with elevation by adding those interaction terms into best models for each species. There was a significant interaction between the overall edge effect and elevation in *P. sericea* (L-R Test: df=2, Deviance=6.74, p=0.034; linear term: Deviance=5.97, p=0.015; square term: Deviance=0.16, p=0.69), but not in *P. weberbaueri* (L-R Test: df=2, Deviance=0.36, p=0.84). The decline in *P. sericea* seedling density with elevation is proportionately less severe in the grassland than in the forest, although seedlings are still far more abundant within the forest at all elevations.

Although *P. sericea* has higher overall mean seedling densities in our samples than *P. weberbaueri*, the models suggest that inside the forest, this difference reverses as elevation increases. However, even at higher elevations, *P. sericea* densities outside the forest remain higher further out into the grassland than *P. weberbaueri* (Figure 3).

Adult Occupancy across the Landscape

The best adult occupancy models identified significant associations between adult presence on the landscape and elevation and dry season irradiation levels that differed between species and mirrored those associations found with seedling density (Table 4, Figure 4, Appendix S5). The probabilities of adult *P. sericea* and *P. weberbaueri* presence showed a unimodal association with elevation, but *P. sericea* peaks around 3900-4000 masl, while *P. weberbaueri* peaks at 4500 masl, such that within the elevational range surveyed for seedlings (>4000 masl), adult presence of *P. sericea* decreases while *P. weberbaueri* increases. Adult presence of both species decreases with increasing solar irradiation, however there was a significant interaction with elevation in *P. sericea* (Figure 4). This reflects that although *P. sericea* adults were less frequent at higher elevations, when present, they were more likely to be in areas with higher irradiation, most commonly found on north-facing slopes in our sample.

DISCUSSION

Our models of surveyed seedlings suggest that seedling densities of both *P. weberbaueri* and *P. sericea* are associated with a combination of biotic and abiotic environmental influences at micro- (< 1 m) and macro-environmental (100-1,000 m) scales. While seedling densities of both species were associated similarly with the same set of microenvironmental conditions, there were differences in their associations with landscape level factors (elevation and dry season solar irradiance) concordant with the current distributional associations of adults and indicative of niche differences between them. More importantly, we observed that seedling presence across the forest-grassland boundary was strongly limited over the entire elevational gradient, suggesting a strong, negative edge effect on natural recruitment of both *Polylepis* species outside the forest.

Seedling Associations with Quadrat-scale Variables and Distance from Forest

The strongest and only significant association of seedling densities at the quadrat scale was distance from the forest edge. Seedling numbers of both species decreased with increasing exposed substrate (rock and bare ground) within quadrats because they are by definition areas without seedlings. However, neither exposed rock nor bare ground cover had further association with the seedling densities within vegetated areas of the quadrats.

Overall, the patterns of seedling density at the forest edge suggest that even in areas directly adjacent to abundant seed sources (i.e., < 7 m) there are low rates of natural *Polylepis* seedling colonization into grassland areas. Seedling density of both species declined rapidly across the forest-grassland transition, with very few seedlings outside the forest canopy. Lower seedling density in the grassland may be due to either seed-rain limitation or post-dispersal conditions unfavourable for germination and seedling establishment.

The pattern of decline in seedling density is consistent with seed dispersion patterns that would result from primary seed dispersal by gravity/wind. Studies have commonly found a leptokurtic pattern of seed dispersion with distance from seeder trees or forest margins, with peaks near seed sources and sharp declines with distance, even for wind dispersed seed (Clark *et al.* 1999, Nathan & Muller-Landau 2000). In *P. australis,* which unlike the species studied here produces fruit with appendages that could assist wind dispersal, seed traps failed to capture seeds more than 6 m away from seeder trees (Torres *et al.* 2008), although studies of seedling density found that seedlings reduced to nil within 10 m of trees (Zimmerman *et al.* 2009). Cierjacks *et al.* (2007) observed similar rapid declines in *P. incana* and *P. pauta* juvenile densities at forest-grassland boundaries in Ecuador. The shorter tails of grassland seedling dispersion in *P. weberbaueri* than *P. sericea* may be related to the former's higher fruit masses (Thomson *et al.* 2011; Augspurger & Franson 1987). Seeds of *P. weberbaueri* are 2-3 times heavier than those of *P. sericea* (avg. fruit mass ± SE: *P. weberbaueri*=4.9 ± 0.2 mg, *P. sericea*=1.9 ± 0.1 mg; LVM, unpublished data).

Unfavourable abiotic and biotic post-dispersal conditions for seedling establishment can also contribute to the decline of seedlings into the grassland. Several conditions would create a more stressful environment for *Polylepis* seedlings in grassland areas adjacent to the forest edge: greater daily thermal amplitudes, higher freezing event ocurrence, intensified solar irradiation and UV, lower humidity, or higher rates of livestock grazing and trampling (Rehm & Feely 2013; Zimmerman *et al.* 2009; Cierjacks *et al.* 2007; Bader *et al.* 2007). The daily thermal oscillation typical of the high-elevation tropics is severe, requiring plants in the alpine zone to adjust physiologically to "summer every day and winter every night" (Hedberg 1964). Small, shallow-rooted seedlings are vulnerable to daily frost heaving and morning water stress under such conditions (Meinzer *et al.* 1987; Beck 1987; Johnson *et al.* 2011). Rehm and Feely (2015) suggested that rare, but extreme, low-temperature events at tropical treeline ecotones occur frequently enough at ground level to overwhelm overall low-temperature tolerances of tissues and kill tree seedlings, thereby preventing cloud forest trees from colonizing the grassland. Canopy cover of trees or other vegetation, reduces radiative cooling and increases night-time minimum temperatures at ground level, reducing this risk.

Our dung counts do not support the idea that livestock activity is generally higher in grassland; dung presence was not significantly different between grassland and forest (Overall Zone A vs Zone C: p=0.21; *P. weberbaueri* plots: p=0.21, *P. sericea* plots: p=0.11). Nevertheless, although levels of livestock activity may not differ, the influence of livestock grazing in forest and grassland may be qualitatively different. In both habitats, livestock may kill seedlings by trampling or consumption, but may favour seedling emergence by removal of litter cover and creation of open areas for colonization (Cierjacks *et al.* 2007). However, livestock alters the vertical and horizontal structure of ground vegetation (typically reducing the height and cover of grasses and shrubs) (e.g., Renison *et al.* 2015). In the absence of an overhead canopy, taller grasses and shrubs may buffer emerging seedlings from the above-mentioned abiotic stresses. Grazing by livestock in the grassland would reduce the possibility of such facilitation of seedlings.

Such contributions by these additional factors on seedling dispersion patterns into grassland are impossible to disentangle from the effects of seed dispersal in a non-experimental study (see Morales 2017). For example, the positive interaction between distance to the forest edge and elevation on *P. sericea* seedling abundance suggests that some of these factors affecting seedling establishment are stronger at lower elevations. Despite decreased seedling presence under the canopy with elevation, which may indicate decreased seed production, *P.sericea* seedling number decline into the grassland was comparatively less severe than at lower elevations. Variation in wind speed and turbulence can alter patterns of primary seed dispersal in wind-dispersed seed (Nathan *et al.* 2011), thus higher wind speeds at higher elevations might increase dispersal, but we have no evidence to support this. Instead, this might be explained by the effect of gradients in temperature and grazing activity on post-dispersal germination and establishment.

Despite the high local climatic variability in complex mountain topography, day and night-time air temperatures generally decrease with elevation. We expect lower mean night-time temperatures and extremes at higher elevations to result in lower seedling establishment in grassland and a stronger decline in *P. sericea* seedlings across the forest border. However, cooler, less desiccating, daytime climates might increase seedling survival and offset these effects, explaining the observed pattern of *P. sericea* density. Another possibility is that higher livestock activity in our lower-elevation plots altered the seedling dispersion pattern resulting from seed dispersal alone. Although local livestock activity was not associated with *P. sericea* seedling densities in our final model, dung frequency was negatively correlated with elevation in *P. sericea* plots.

The Importance of Seedling Associations with Elevation and Solar Irradiation

The relationships of seedling densities to elevation and dry season solar irradiation were markedly different between *P. sericea* and *P. weberbaueri*, having opposite trends with elevation. The changes in seedling densities also mirrored those changes in adult occupancy of each species across the landscape. This suggests that despite the potential for high topoclimate variability in our study area, elevation and dry season solar irradiation capture important niche differences between these species and the optimal environmental conditions for each occur at different elevations.

Elevation is a proxy for several environmental variables: temperature, UV exposure, and precipitation. On average, mean, minimum and maximum air temperatures decrease with elevation and frost event frequency increases. UV exposure also increases with elevation, increasing photo-oxidative stress on plants (Blumthaler 2012). On the other hand, meteorological data from our study area indicates that precipitation increases locally along this elevational gradient. Assuming this precipitation gradient is general throughout the region, the elevational trends suggest that *P. weberbaueri* is better adapted to cooler, and probably wetter, conditions than *P. sericea*. Future studies monitoring precipitation locally could confirm if there is a difference in optimal moisture conditions between these species.

Solar irradiation determines daytime temperatures, has direct biological effects on plants and reflects topographic differences between plots. Dry season irradiation was negatively associated with both adult presence and seedling density for both species (although this was not significant for *P. sericea*). Higher levels of solar irradiation provide increased energy for photosynthesis, but can also cause photoinhibition and drought stress, especially in the dry season because of higher daytime temperatures. The difference in the relationships with irradiation between the two species reinforces the idea that *P. weberbaueri* tolerates warmer and drier conditions daytime conditions less than *P. sericea*. Interestingly, although models of both species suggest lower adult presence with higher irradiation (Figure 4), they also suggested that *P. sericea* presence at higher elevations is greater where solar irradiation is higher, potentially indicating that it can successfully recruit and persist at higher elevations when daytime conditions are locally warmer and drier than at other sites at the same elevations. This has important implications for this species' future ability to colonize elevations currently occupied by grasslands or *P. weberbaueri* forest. The Cordillera Blanca is the high-elevation area of the tropical Andes expected to experience the greatest temperature increase with global warming during this century (+4-7°C), although how precipitation will change remains unclear (Urrutia & Vuille 2009). If precipitation decreases concurrently with this temperature increase, we hypothesize that the climate at the upper end of the elevational gradient studied will become more favourable for *P. sericea* and increasingly less so for *P. weberbaueri*. However, it will be important to compare species performance directly with local temperature and moisture to confirm our climatic interpretation of the observed trends.

As with forest edge patterns, associations of seedling density with elevation and solar irradiation may be due to differences in seed availability (driven by local seed production) or seedling establishment (driven by germination and early survival) along these gradients. Because static seedling abundance patterns are the combined product of the aforementioned processes over time, the trends of any one could differ from that of seedling density and from seedling density alone we cannot discern their underlying patterns. As past studies of trees along elevational gradients have documented, it is even possible for trends in reproduction, seedling germination and establishment to differ from each other (País-Bosch *et al.* 2013, Marcora *et al.* 2013, Marcora *et al.* 2008, Wesche *et al.* 2008). Studies of natural trends in reproductive output of *P. weberbaueri* and *P. sericea* adults, longitudinal studies of seedlings and adults, and manipulative field studies controlling for possible confounding factors (e.g., seed dispersal, seed predation, livestock) will help us understand how underlying demographic parameters vary along these gradients.

Implications for Management and Restoration

Our results have important implications for the management of *P. weberbaueri* and *P.* sericea, particularly in the region where their distributions overlap (Ecuador to Central Peru) (Simpson 1979, Zutta 2009). We highlight two points: 1) natural seedling recruitment into grasslands is currently rare and highly concentrated around forest edges and 2) the adult distribution and seedling densities of these two species suggest they have distinct ecological zonation and should be managed accordingly.

The highly restricted nature of natural seedling colonization of grassland suggests this stage is a serious bottleneck to natural forest expansion (at least in the HNP). Nonetheless, rare long-distance seed dispersal events may accelerate the spatial expansion of natural colonization (Cain 2000). We have observed larger juveniles (50-150 cm tall) established at distances of 50-100 m (Byers 2000 and personal observation) from at least one forest; however, this seems the exception rather than the rule. Factoring in the time for most tiny seedlings of slow-growing, high-altitude trees to recruit into the adult population, we believe unassisted forest expansion to be a *very* slow process for these species, in both the HNP and elsewhere. It will be slower if seedling survival to adulthood is low in grassland.

From this descriptive study, we cannot discern the separate role of post-dispersal conditions on seedling establishment and survival, which requires experimental transplants and seed additions. However, we believe high rates of seeding and planting could overcome such barriers. Other strategies that may facilitate establishment around forest edges, lone seeder trees, and planted areas should be considered further, such as planting near shrubs (Ayma-Romay *et al.* 2015), and reducing livestock densities (Renison *et al.* 2015). Not explored here is the risk fire poses for regenerating edges, but fire may control forest-edge expansion by killing colonizing juveniles (Scholes & Archer 1997) or reducing post-fire recruitment (Cierjacks *et al.* 2008), so management should also consider protecting forest edges from fire.

Zonation of such interventions will be important in determining both what locations and which species of *Polylepis* to plant. *Polylepis sericea* seedlings are unlikely to thrive above 4300 meters, while *P. weberbaueri* seedlings will likely do best in cooler and wetter areas, such as those above 4000 m. If seedlings are to be planted away from current forest patches, we recommend planting around lone conspecific trees, using them as indicators of climatically suitable areas for conspecific seedlings. For this, an important strategy for *Polylepis* conservation will be increasing attention to protecting isolated trees. Whether these trees are remnants of larger patches or vanguard individuals of long-distance dispersal, they may be important as indicators of potential habitat suitability for new recruits, nuclei of local recruitment, and seed sources for active restoration (Yarranton & Morrison 1974, Guevara *et al.* 1986, Corbin & Holl 2012).

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TABLES

Table 1. Summary information (ranges) for plot-level environmental characteristics of plots in the study valleys.

Plot -level Variables by Valley	***P. sericea***		***P. weberbaueri***		
	Llanganuco	**Ulta**	**Ulta**	**Llaca**	**Rajucolta**
N Plots	6	7	11	11	13
Seeder Trees†	1 - 4	1 - 10	1 - 7	1 - 11	1 - 9
Dung Frequency (proportion) †	0 - 0.7	0 - 0.5	0 - 0.7	0 - 0.2	0 - 0.6
Elevation (m.a.s.l.) †	3988 - 4282	4002 - 4321	3199 - 5314	2864 - 4470	1062 - 5838
Dry season solar irradiation (Wh/m²/day) †	4458 - 5506	3433 - 5350	4041 - 4489	4020 - 4488	4041 - 4507
Slope (°)	15.0 - 27.0	5.0 - 36.0	10.6 - 31.0	6.0 - 39.4	6.0 - 41.0
Exposed Rock (%)	5 - 15	1 - 43	2 - 22	1.5 - 40	1 - 45
Moss covered Rock (%)	5 - 15	0 - 8	0 - 11	0.5 - 40	0 - 25
Bare Ground (%)	1 - 10	0 - 25	2 - 41	0 - 10	0 - 30
Vegetated Ground (%)	65 - 89	48 - 99	42 - 91	30 - 97	35 - 98.99
Grass Height (cm)	5.2 - 40.3	8.4 - 24.0	7.3 - 42.8	0 - 25	2.5 - 37.5
Grassland Canopy Openness (%)	64.5 - 99.8	83.2 - 99.8	69.7 - 99.8	70.7 - 99.8	78.0 - 99.1
Forest Canopy Openness (%)	1.0 - 83.2	9.4 - 65	5.7 - 59.8	0.8 - 80.2	5.8 - 57.5
Total Seedlings Counted	684	1145	186	137	214

†= Plot-level variables used for model selection.

Table 2. Means of seedling densities (SE) (seedlings per m^2) of the studied forest plots in each valley and the results of Wald Tests for differences among valleys in the entire plot, and the forest and grassland zones separately.

	Valley					
	Llanganuco	**Ulta**	**Llaca**	**Rajucolta**	**Wald χ^2**	**p-value**
P. sericea:						
Overall Plot	4.78 (2.36)	8.10 (3.57)	---	---	0.94	0.333
Forest	9.31 (4.77)	14.73 (6.33)	---	---	0.77	0.380

Grassland	0.24 (0.11)	1.48 (1.11)	---	---	0.38	0.271
N	6	7	---	---		
***P. weberbaueri**:*						
Overall Plot	---	1.66 (0.65)	0.81 (0.23)	0.92 (0.24)	0.78	0.679
Forest	---	3.11 (1.34)	1.42 (0.44)	1.81 (0.47)	0.77	0.681
Grassland	---	0.21 (0.13)	0.19 (0.09)	0.03 (0.02)	3.80	0.150
N	---	11	11	13		

Table 3. Estimated coefficients of the environmental covariates included in the final models of seedling density and their statistical significance.

	Model	**L-R Test**		**Wald Test**	
Covariate†	**Coefficient (log-scale)**	**Deviance**	**p-value**	**Wald χ^2**	**p-value**
P. sericea:					
Distance to edge	-0.3508	97.02	<<0.001	117.46	<<0.001
Sq. distance to edge	-0.0281	15.36	<<0.001	16.25	<<0.001
Exposed rock cover	-0.0229	3.36	0.067	3.47	0.063
Bare ground cover	-0.0179	2.85	0.091	2.95	0.086
Elevation	-0.0067	7.90	0.005	11.47	<0.001
P. weberbaueri:					
Distance to edge	-0.4303	---	---	62.13	<<0.001
Sq. distance to edge	-0.0523	8.19	<<0.001	30.45	<<0.001
Exposed rock cover	-0.0231	14.00	<0.001	14.70	<0.001
Bare ground cover	-0.0315	7.60	0.006	7.60	0.006
Elevation	0.0029	6.30	0.012	6.77	0.009
Dry season solar irradiation	-0.0004	5.34	0.021	5.56	0.018

† Units of Variables: Quadrat Level-Distance to edge (m), Sq. Distance to Edge (m^2), Exposed rock cover (%), Bare ground cover (%); Plot Level-Elevation (m), Dry season solar irradiation ($Wh/m^2/day$).

Table 4. Model terms included in the best models of adult presence and their statistical significance.

Model Terms†	L-R Test		
	Df	**Deviance**	**p-value**
P. sericea			
Elevation	1	37.94	<<0.001
Elevation^2	1	13.32	<0.001
Dry season irradiation	1	1.14	0.286
(Elevation+Elevation^2) x Dry season irradiation	2	11.52	0.003
P. weberbaueri			
Elevation	1	44.96	<<0.001
Elevation^2	1	8.10	0.004
Dry season irradiation	1	8.38	0.004

† Units of Variables: -Elevation (m), Dry season solar irradiation (Wh/m^2/day).

FIGURE LEGENDS

Figure 1. Huascaran National Park (left) and the locations of study plots within each of the four valleys surveyed (A: Llanganuco, B:Ulta, C: Rajucolta, D: Llaca). Forest plots were monospecific with regards to *Polylepis* species present (circle: *P. sericea*, triangle: *P. weberbaueri*).

Figure 2. Sampling layout of plots indicating position of transects used to sample seedlings (numbers 1-3, quadrats in grey) and the three 5-m plot zones used to sample livestock dung frequency (A: grassland, B: transition zone, C: forest canopy interior).

Figure 3. Trend in *P. sericea* (black lines) and *P. weberbaueri* (grey lines) seedling density (seedlings per m^2) across the forest-grassland boundary at two different elevations (masl)(Solid line:4000, Dashed line:4300) as modelled by GLMMs. On the x-axis, negative numbers indicate areas under the forest canopy and positive numbers areas in the grassland. Seedling densities of both species decrease rapidly into the grassland, but seedling densities *of P. sericea* decrease proportionately less rapidly as elevation increases.

Figure 4. Modelled occupancy of adult *P. sericea* (black lines) and *P. weberbaueri* (grey lines) trees along elevation and its variation with different levels of solar irradiation (Wh/m^2/day; Dashed: 1000, Soild:

5000) received by the landscape during the dry season (JJA). Dotted vertical line indicates lower altitudinal limit of seedling surveys.

SUPPORTING INFORMATION HEADINGS

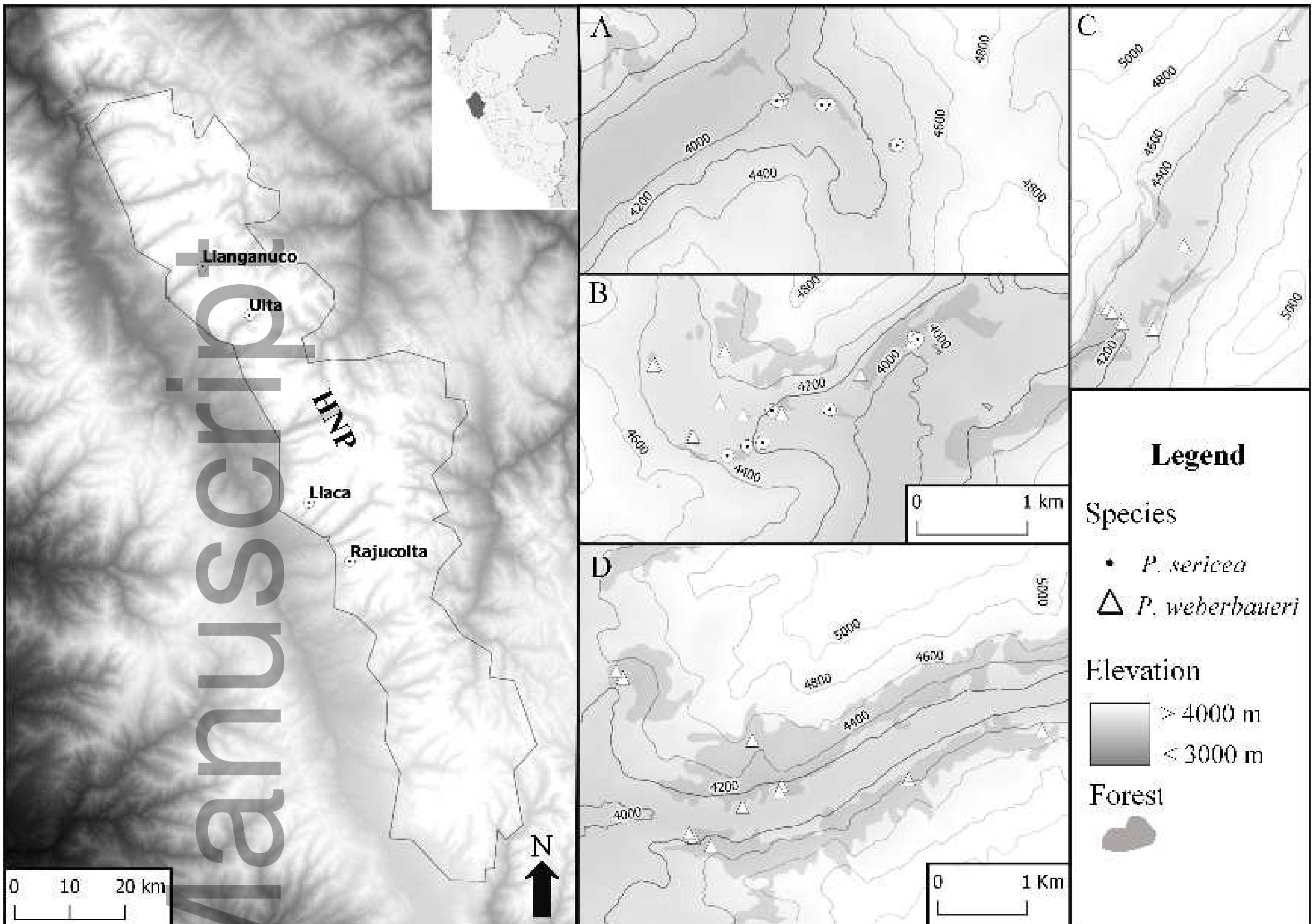
Appendix S1 Procedure for derivation of solar irradiation for plots.

Appendix S2 R syntax formulation of initial models of seedling counts used for backwards selection.

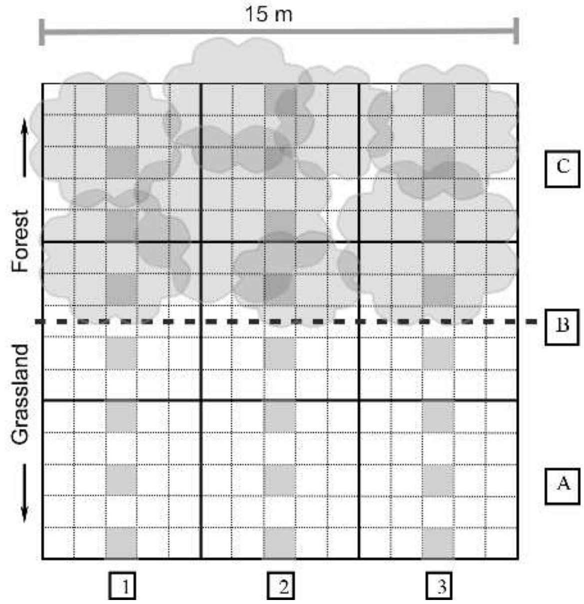
Appendix S3 Results of forward and backward stepwise regression for *P. sericea* seedling density.

Appendix S4 Results of forward and backwards stepwise regression for *P. weberbaueri* seedling density.

Appendix S5 Results of model selection for *P. sericea* and *P.weberbaueri* adult presence.



aec_12588_f1.png



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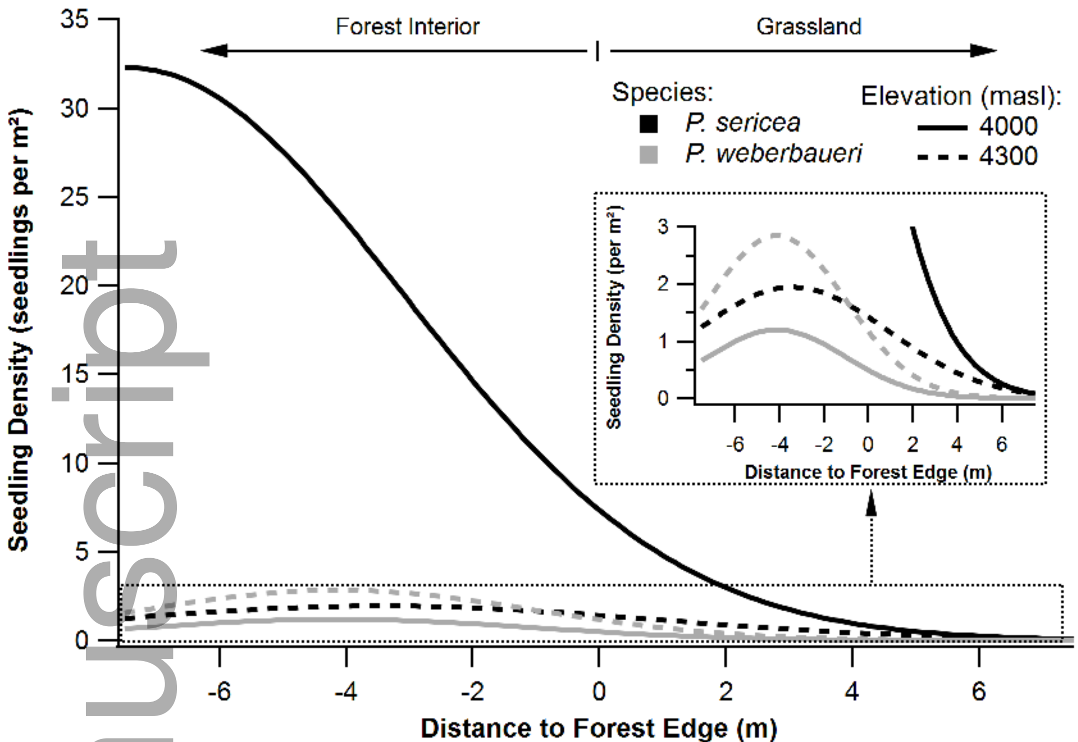

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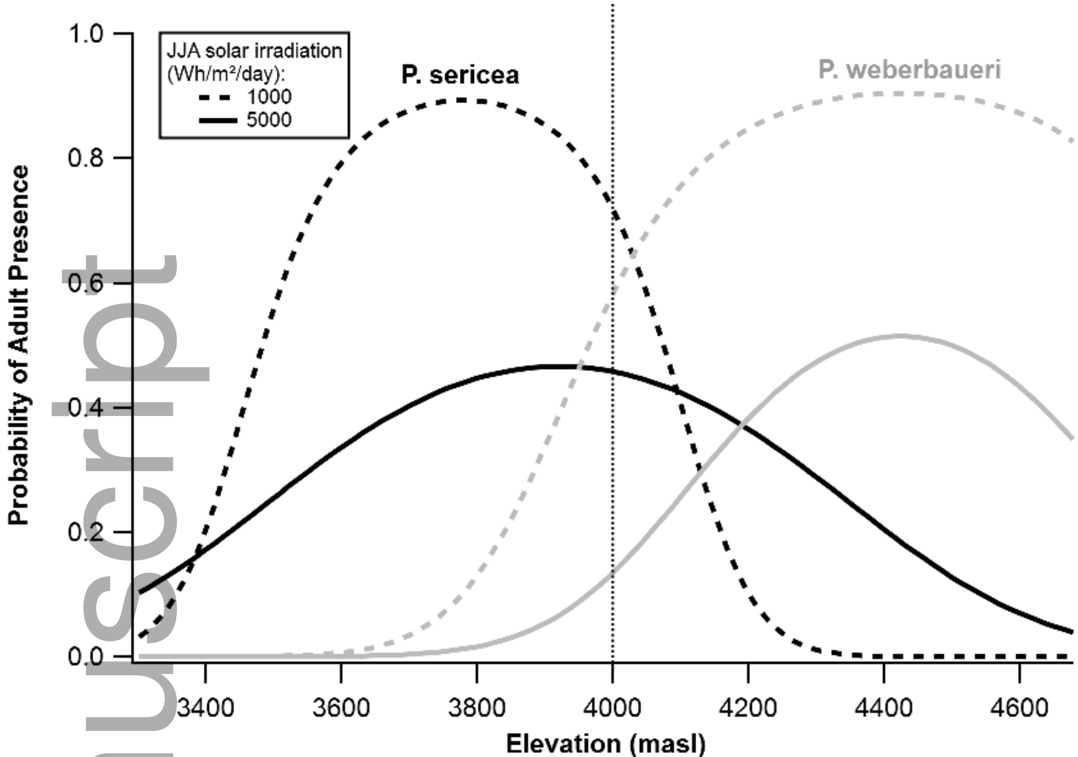

aec_12588_f4.tif