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Publication Date

2018

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UNIVERSITY OF CALIFORNIA

SANTA CRUZ

LOCAL HABITAT MODULATION OF CLIMATE CHANGE EFFECTS ON HIGH-ALTITUDE TROPICAL CONIFERS

AND

TEMPORAL AND GEOGRAPHIC VARIATION IN THE EFFECTS OF HERITAGE CONSERVATION ON POVERTY REDUCTION

A thesis submitted in partial satisfaction

of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In

ENVIRONMENTAL STUDIES

By

Paulo Quadri

December 2018

The Thesis of Paulo Quadri

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LOCAL HABITAT MODULATION OF CLIMATE CHANGE EFFECTS ON HIGH-ALTITUDE TROPICAL CONIFERS

AND

TEMPORAL AND GEOGRAPHIC VARIATION IN THE EFFECTS OF HERITAGE CONSERVATION ON POVERTY REDUCTION

Paulo Quadri Barba

Abstract

Species in tropical mountains are more vulnerable to climate change than species elsewhere because their adaptations are more tightly coupled to their habitats and because tropical high elevations seem to be warming faster than the rest of the planet. However, the vast diversity of habitats that characterizes tropical mountains can also work as refugia during periods of climatic change, potentially conferring greater long-term resilience to species inhabiting these environments. Using a combination of population ecology, dendroecology and stable isotopes, I found important shifts in the distribution and growth of two endemic tropical conifers of Central Mexico. These shifts vary significantly as a

function of local habitat, highlighting the importance of understanding the interactions between local environmental factors and climate change to identify areas of special conservation value during the 21st century.

Conservation policy instruments however, are politically controversial because they compete with other economic land uses. For many years now, critics of modern protected areas (PAs) have claimed that they exacerbate local poverty by restricting access to land and resources. By using cultural heritage sites in Mexico as a surrogate system for PAs, I isolated the effects of attracting tourism (present at cultural heritage sites) from the potential effect of land use restrictions (absent from cultural heritage sites) on poverty. The direction and magnitude of these sites' effects on local poverty reduction shifted between 1990 and 2010, mediated by local and regional geographic differences. Our findings suggest that land use restrictions by PAs are not necessarily responsible for the lack of win-win outcomes in conservation and development, and that other, more complex

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institutional factors may offer better

explanations.

Dedication: To Luz, to my family, and to my friends.

You all are volcanoes and trees.

Who color this world.

With echoes and dreams.

To Diego. With all my love and gratitude.

Introduction

Shifts in tree species growth and distributions are already occurring under climate change, threatening biodiversity and ecosystems integrity. Tropical mountain ecosystems are of special concern because species in these environments tend to have much more restricted distributions than species from higher latitudes. Yet, species distribution shifts in tropical mountains remain largely unexplored. We investigated the modulatory effect of local habitat on the extent and rate of upslope expansion of a montane fir species (*Abies religiosa*) into the habitat of a subalpine pine species (*Pinus hartwegii*), and on the ecophysiological responses of latter to climate change. Our research was conducted on the volcanoes of Central Mexico, where we used population ecology, dendroecological and isotopic methods to explore changes in growth, intrinsic water use efficiency (iWUE), nutrition, and population size structure and abundance in these species as a function slope aspect, elevation, and age.

We found evidence of upslope expansion of fir populations into pine habitat, and of strong modulation of expansion dynamics by local topography. Colonization of the subalpine habitat by firs is occurring mostly along north facing slopes, suggesting that limiting factors for upslope expansion change from moisture dependent to temperature dependent between south and north facing habitats. On north facing slopes, the equilibrium of relative abundances between fir and pine juveniles occurred ~170 m above the current mean elevation of the adult forest ecotone. At any given elevation, interactions between mean annual solar radiation and compound topographic index (CTI) strongly determined the abundance of pine and fir juveniles. Finally, in contrast to fir populations in nearby regions and at lower elevations, fir individuals from these high-elevation locations have experienced substantial growth acceleration in the past three decades, while pine growth seems to have mostly stagnated.

Our analyses from high-altitude (> 3600 m) tropical pine forests in central Mexico show a shift in growth trends between aspects, with trees on south aspects growing significantly less relative to north aspect trees over time (1873 – 1940: -0.066, $p = 0.178$, 1913 – 1950: -0446, $p <$ 0.001, $1945 - 2015$: -0.49 , $p < 0.001$). Stable isotopic analyses of carbon and oxygen and analyses of C:N ratios suggest these trees may have benefited from an interaction between wetter-cooler conditions and CO2 fertilization in recent decades. Intrinsic water use efficiency has been significantly greater in south facing slope trees over the last 140 years and is diverging among young cohorts. ¹⁸O enrichment has only occurred on mature trees. Our findings highlight the importance of considering local-scale environmental and age-dependent factors to better understand current and future population and ecosystem level responses to climate change. Incorporating knowledge of fine scale patterns and processes will improve our ability to detect and protect microrefugia as areas of high conservation value under climate change. However, conservation of these high ecological value areas is sometimes controversial because

of the potential negative local socioeconomic impacts that protection creates through land use restrictions. In the third chapter, we explore the question of what causes win – win outcomes between conservation and poverty alleviation in some instances but not in others. We remove the potential effects of land use and resource use extraction restrictions from PAs by using cultural heritage sites ("INAH" sites) in Mexico as a surrogate system in which these restrictions are non-existent or negligible, but where touristic visitation is substantial. We then estimate the effects of these sites on poverty reduction between 1990 and 2010 in localities in Mexico and compare the effects to protected area impacts. To account for the non-random placement of heritage sites, we model changes in poverty as a function of site density and touristic visitation as well as multiple potentially confounding geographic and social variables. Overall, we find mixed evidence that proximity to one or more cultural heritage sites is associated with poverty reduction benefits. Generalized significant benefits across all

localities from heritage sites occurred only between 1990 and 2000; these benefits fade away in most localities between 2000 and 2010. However, important heterogeneity in impacts between different regions, and by factors such as distance to urban centers and baseline poverty of the localities, suggest substantial variability in the ability of local communities to capture benefits from tourism. This suggests the importance of a better understanding of potential tourism benefits when seeking to predict PA impacts on poverty alleviation.

Chapter 1. Topographic Modulation of Upslope Range Shifts in Tropical Conifers Authors: Paulo Quadri^{1*}, Erika Zavaleta²

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Abstract: Shifts in species distributions are already occurring under climate change, threatening biodiversity and ecosystems integrity. Tropical mountain ecosystems are of special concern because species in these environments tend to have much more restricted distributions than species from higher latitudes. Yet, species distribution shifts in tropical mountains remain largely unexplored. We investigated the extent, rate, and environmental controls on potential upslope expansion of a montane fir species (*Abies religiosa*) into the habitat of a subalpine pine species (*Pinus hartwegii*) on the volcanoes of Central Mexico. We found evidence of upslope expansion of firs

into pine habitat, and of strong modulation of expansion dynamics by local topography. Colonization of the subalpine habitat by firs is occurring mostly along north facing slopes, suggesting that limiting factors for upslope expansion change from moisture dependent to temperature dependent between south and north facing habitats. On north facing slopes, the equilibrium of relative abundances between fir and pine juveniles occurred ~170 m above the current mean elevation of the adult forest ecotone. At any given elevation, interactions between mean annual solar radiation and compound topographic index (CTI) strongly determined the abundance of pine and fir juveniles. Finally, in contrast to fir populations in nearby regions and at lower elevations, fir individuals from these high-elevation locations have experienced substantial growth acceleration in the past three decades, while pine growth seems to have stagnated. Our findings highlight the importance of local-scale environmental factors in modulating species responses to climate change, as well as the need

for targeted, field-based research in tropical mountains to improve our understanding of forest responses to climate change in these unique and complex environments.

Introduction

As climate change progresses, warming trends are occurring most rapidly at higher elevations, especially at tropical latitudes (Loomis et al., 2017; Pepin et al., 2015). As a consequence, tropical mountain ecosystems are at high risk from climate change and are already experiencing changes in hydrology and in species distributions in many regions (Gottfried et al., 2012; Huber, Bugmann, & Reasoner, 2006; Rangwala & Miller, 2012). Shifts in montane species distributions are more likely to alter ecosystem functioning than shifts at lower elevations. This is because climatic zones are compressed over short distances in mountains, such that species functional traits can differ markedly between contiguous vegetation belts. In tropical mountains, there is even less climatic overlap across elevations due to seasonal uniformity (Ghalambor, 2006; Janzen, 1967;

Sheldon, Huey, Kaspari, & Sanders, 2018). Thus, climate change impacts on community structure and ecological processes may be more disruptive in tropical mountains than in other regions in the globe.

Yet, shift dynamics of tree species in tropical high elevation ecosystems remain widely understudied. Based on research from mid and high latitudes, plant populations have shown patterns of range contraction (Zhu, Woodall, & Clark 2012), range expansion (Clements & Ditommaso 2011), full range shifts (Colwell et al. 2008), or have remained static (E. M. Rehm & Feeley, 2015b; E. M. Rehm, Feeley, Rehm, & Feeley, 2018). In montane environments, these dynamics are generally expected to manifest as upslope shifts (Lenoir et al. 2008), although downslope shifts have also been documented (Crimmins et al. 2011; Harsch and Hille Ris Lambers 2014). However, range shifts in mountains do not occur uniformly, and are likely to be strongly mediated by interactions between local topography and regional climate, pushing species towards topographic and

environmental features with more favorable habitat conditions (Gottfried, Pauli, Reiter, & Grabherr, 1999; Greenwood, Chen, Chen, & Jump, 2015; Mclaughlin & Zavaleta, 2012), which can serve as holdouts, stepping stones, and microrefugia during climatic changes (Hannah et al., 2014). The unique levels of species diversity and endemism of tropical mountains, as well as the restricted distributions of these species, magnify the need to understand how local topographic variation and climate change interact to determine the fate of many of these species.

Research on upslope shifts of subalpine treelines has increased substantially over the past years. Yet, global scale studies indicate that only about half of the world's treelines have been moving upwards (E. Rehm & Feeley, 2016), and in fact, tropical treelines appear to have remained stable over the past decades (E. M. Rehm & Feeley, 2015a). This is perhaps because in tropical mountains, locations of timberlines and treelines may be a function of extreme freezing events and not of mean

temperatures (E. M. Rehm & Feeley, 2015a). In addition, at very high elevations $(> 4,000 \text{ m})$, slow biophysical processes such as soil formation may be restricting colonization of trees upslope. However, in montane - subalpine ecotones, environmental conditions may be more conducive to colonization of the subalpine habitat by the lower montane species, potentially threatening the existence of subalpine natives. This possibility is even more concerning if we consider that surface area of 40% of the worlds' mountain ranges peaks at mid elevations and not at their base (Elsen and Tingley 2015). Thus, under climate change, foothills and montane species may be presented with more available area for upslope expansions, while subalpine species may become trapped without further possibility of shifting their populations upward (Macias-Fauria and Johnson 2013).

We investigated potential upslope shifts of a montane fir species (Sacred fir, *Abies religiosa)* into the subalpine habitat of Hartwegii pines (*Pinus hartwegii*), in the volcanic peaks of central Mexico. These species are restricted to

the highest elevations of the Mexican Trans-Volcanic Belt (MTVB). Remote sensing based research in the Sierra Nevada of Central Mexico has shown that Hartwegii pine populations may be advancing upslope at a rate of 1.4 meters/year, especially on the warmest flanks of the mountains (Torres - Beltran 2013). Growth analyses of both species in nearby, lower elevation sites, have shown substantial growth declines (Gómez-Guerrero et al., 2013; Silva, Gomez-Guerrero, Doane, & Horwath, 2015).

Both Hartwegii pines and Sacred firs provide valuable ecosystem services to one of the most densely populated regions in the world; sacred firs also provide wintering habitat for the iconic monarch butterfly (*Danaus plexippus*), while Hartwegii pine forests support the remaining populations of the highly endangered volcano rabbit (*Romerolagus diazi*).

Our goal was to understand the influence of local-scale environmental variation on the extent of upslope fir movement and their potential encroachment into the pine zone. To examine this, we explored interactions between

topography (mesic valleys and exposed, xeric slopes), aspect (mesic north-facing slopes and warmer, drier south-facing slopes), and elevation.

Methods

Study Site and Recent Fire History

The research sites of our study are located on the western slopes of the Iztaccihuatl volcano located in the Sierra Nevada range (19° 07´43´´, 98° 39´ 37´´). The climate of the Sierra Nevada region is considered temperate subhumid, with an average annual precipitation of 928 mm and annual mean temperature of 14º C. The region receives most of its precipitation during summer and not during winter. At high elevations, this means cool - wet summers, and cold – dry winters, with almost no snowpack to provide moisture during the hot and dry springs (García Amaro de Miranda, 2003), and as in other similar climates, precipitation peaks at about 2000 m and then declines with elevation (Anders & Nesbitt 2015).

Figure 1.1. Study area. Yellow line depicts the fir - pine ecotone. Habitat below the yellow line corresponds to the montane zone. Blue line marks the upper limit of the Hartwegii pine forest. White dashed lines represent our ecotone transects (not real scale). Pink circles represent our subalpine plots (not real scale).

Firs are monodominant along the montane belt $(2,800 - 3,500 \text{ m})$ on the western and northern slopes of the Sierra Nevada. *A. religiosa* is a relatively fast-growing species that is shade-tolerant but can grow successfully in full sunlit conditions as long as soil moisture is sufficiently available. *P. hartwegii* is fire and drought tolerant with preferences for well drained soils.

The region features low to mid intensity forest fires as part of its natural disturbance regime (Rodríguez-Trejo & Fulé, 2003). To rule out the possibility of shifts in fir population ranges confounded by fire suppression practices in the area, we conducted a series of supervised land cover classification analyses. We used Landsat imagery between 1986 and 2014 and bands 4,7,2 (RGB) (Koutsias & Karteris, 2000) (Supplemental Materials 1.1). Ground truthing field work was done during early summer 2015 after a series of small fires occurred in the region. We conducted observations on the number of fire scars on trees and had informal interviews with park officials to understand more about the recent fire history of the area.

Fir age structure at the ecotone

To explore changes in age structure of firs along at the fir – pine forest boundary, we

placed 10 transects running along the bottom of the ravines of 10 elevation gradients and representing north and south aspects (Figure 1.1). Transects were established cutting across approximately the last 50 meters of dense fir forest and ended where the last individuals of the contiguous forest stood. Elevation gain of transects varied between 42 - 100 m and between 100 and 150 m of linear distance. In each transect we measured and recorded diameter at breast height (DBH), altitude, and transect distance or position of the largest three fir individuals intercepting $a \sim 20$ m belt (10 m on each side) obtaining a total sample size of 238 firs. To assess the current position of the fir forest line (i.e. fir – pine ecotone) we used Google Earth imagery to extract multiple sample points $(N = 20)$ representing the maximum and average elevations of fir forest lines on north and south aspects at different topographic positions (i.e. ravine bottoms or steep slopes).

Fir and pine age structure in the subalpine zone

To explore the spatial distribution and abundance of juvenile of both species we established 30 plots within the pine forest (subalpine zone), with radii varying between 15 and 20 m (Figure 1). Six plots were placed right at the fir – pine forest boundary and the rest located systematically at approximately 200 m intervals of linear distance up to the upper limit of the contiguous pine forest. In each plot, we recorded DBH of all trees larger than 5 cm DBH, and root collar (RC) measurements of all individuals smaller than 5 cm DBH, and registered habitat variables such as canopy and functional understory cover, slope, aspect, elevation, number of dead individuals. Using ArcMap 10.3 we calculated solar radiation and compound topographic index (CTI) (Gessler, Moore, McKenzie, & Ryan, 1995), from a 15 m resolution digital elevation model (DEM) obtained from the National Institute of Statistics and Geography of Mexico (INEGI, 2018).

Tree Rings Samples Collection

To estimate age and growth trends, we collected two increment cores from 43 firs and from 30 pines greater than 5 cm of DBH. Tree cores were mounted, sanded, polished, scanned and cross-dated, and ring widths were measured using Image-J (Abràmoff, Hospitals, Magalhães, & Abràmoff, n.d.). We converted raw ring widths into ring width index (RWI) using the Cstandardization method (Biondi & Qeadan, 2008a), and basal area increment (BAI) to remove the natural declining trend of raw ring width data in mature trees. BAI conversion assumes an annual time step resolution where one full ring (early wood $+$ late wood) equals one year and assumes the observed increment in each core is uniform around the whole tree, and it is expressed as follows:

$$
BAI = \pi * (R_t^2 - R_{t-1}^2)
$$

Where R is the radius and t is the year of ring formation.

Data Analysis

All analyses were performed using R v 3.4 (R Core Team, 2012) and ArcMap 10.3 The presence of fires was confirmed by mapping and calculating the percent area registered as "burned" during multiple years over the past three decades.

Changes in age-size structure with elevation

We assessed differences in the current position of the fir forest line were using t-tests of the maximum elevations between north and south facing habitats on different topographic slope categories. To infer potential changes in population age structure across the elevation gradient we first regressed tree age or number of rings on DBH from sampled individuals ($n = 43$, *A. religiosa*, n = 30, *P. hartwegii*). We then modeled the change in age – size structure across the elevation gradient using linear mixed models with elevation and aspect as fixed effects and transect as a random effect (using both, random slopes and random intercepts). Model selection was done using likelihood tests and Akaike's Information Criteria (AIC).

Spatial distribution and abundance of fir and pine juveniles

Differences in growth between firs and pines were analyzed calculating confidence intervals throughout the whole basal area increment time series. Above the mature fir – pine forest ecotone, size and elevation relationships were assessed by regressing the sizes of the 10 largest individuals of each species found in every plot on elevation. To examine the relationship between abundance of juvenile firs and pines above the ecotone as a function of key environmental variables, we used generalized linear models (GLM) with a negative binomial error distribution and a loglink function. Model specifications were built after exploring the data through pairwise correlations. Differences in age – based relative abundances between firs and pines as a function of elevation and aspect were calculated using a log-transformed interspecific juvenile to adult ratio, or the number of juvenile individuals (< 10 cm DBH) from one species divided by the number of adults $(> 10 \text{ cm} \text{ DBH})$. We then regressed the ratios on altitude including species as interaction term and controlling for slope

aspect. We also ran separate individual linear models to compare differences in regression slope coefficients between north and south aspect habitats. Finally, to estimate the differences in elevation between the present firpine adult and the present equilibrium of interspecific juvenile to adult ratios, we inverted our model using elevation as dependent variable and the juvenile to adult ratios as independent, fitting a separate model for each slope aspect. Here, the intercept of each model is the elevation at which both species balance each other in terms of their relative abundances.

Results

Fire events and Fir Forest Line Position

Years with fire episodes recorded as burned areas occurred mostly in 1986, 1998, and 2011, with the greatest burned area recorded in 1998, when a strong positive Southern Oscillation phase (ENSO) brought very hot and dry conditions to central Mexico (Supplemental Materials 1.2).

Maximum elevation of firs between north and south facing aspects at the fir forest limit did not differ significantly $(-0.749, p =$ 0.463). However, in less steep sites (i.e. along ravines), maximum elevation of firs tended to be higher on south facing slopes than on north facing slopes (t = -1.78, $P = 0.131$).

Age – size relationship and growth.

Tree ring analysis of firs growing above the fir forest line indicate that average age of these trees was 57.6 years (range 6-117). DBH and age (Fig. 1.2) show a relatively strong relationship ($R^2 = .722$, $p = < 0.0001$) in firs, estimated at almost 1 cm of increase in DBH per year of age. The relationship for pines was substantially weaker ($R^2 = .534$, $p = < 0.0001$).

Basal area increment differences between firs and pines become significant after 1947 and nonsignificant again only during the mid 1980s (confidence intervals shown in Figure 1.3). Ring Width Index data (Supplemental Material 1.3) showed some periods of divergent growth and others of convergent growth, but no

indication of growth decline for any of the

species.

Figure 1.2. Linear regression of age and diameter at breast height for firs located on and above the treeline on the Western slopes of the Iztaccihuatl volcano.

Figure 1.3. Basal Area Increment of Hartwegii pines and Sacred firs: BAI in mm² . Shaded areas represent 95% Confidence Intervals. Dark line represents growth of firs, and light gray line represents growth of pines.

Fir age-size structure at the fir forest edge

Maximum fir size (age) decreased with increasing elevation. The full mixed effects model including altitude and aspect habitat as fixed effects performed better than both reduced models ($p < 0.0001$). While the decline in fir size with elevation along north facing habitats was slightly steeper, according to the AIC scores the use of an interaction between elevation and aspect did not improve the model significantly, and in fact the interaction was marginally nonsignificant (0.264, $t = 1.804$).
Table 1.1. Linear mixed effects model for change in age – size structure of firs along the upper edge of the contiguous fir forest (ecotone). (A) Full model including altitude and aspect as fixed effects, (B) reduced model without aspect as interaction term (C) reduced model with only random effects.

		⋖				≃						
		DBH (cm)				DBH (cm)				DBH (cm)		
<i>redictors</i>	Estimates	Error std.	Statistic	\overline{p}	Estimates	std. Error	Statistic	\overline{p}	Estimates	Error std.	Statistic	p
Intercept)	4114.6951 542.306		7.5874		< 0.001 1589.1925 276.7754		5.7418		< 0.001 1589.1925 276.7754 5.7418			0.001
Altitude	-1.1213	0.1494			-7.5048 <0.001 -0.4235		0.076 -5.5753		-0.001 -0.4235	0.076	-5.5753	0.001
South		-916.2124 529.8319	-1.7293	0.0851								
ltitude:AspectS	0.26	0.1457	1.785	0.0756								
Random Effects												
	664.22				809.58				809.58			
₀₀	318.32 $_\mathrm{Transect}$				47.96 $_{\mbox{\small\sc T}$ mase t				47.96 $_{\text{Tarnsect}}$			
	0.32 $_{\rm Tamsect}$				10.06 $_\mathrm{Transect}$				0.06 $_{\rm{Transect}}$			
Observations	238				238				238			
Marginal R ² / Conditional R ² $ 0.384/0.584$					0.160 / 0.207				0.160 / 0.207			
AIC		2249.933				2283.885				2283.885		

Fir and pine size structure in the subalpine zone

Above the mature fir – pine ecotone, maximum size of firs decreased sharply with elevation, but larger sizes were much more persistent along north facing habitats as elevation continued to increase (North: -0.201, p < 0.0001 , South: -0.214 , $p < 0.0001$, Figure 1.4). In contrast, pine maximum size increased with elevation on north facing habitats and remained unchanged on south facing habitats (North: 0.141, $p < 0.0001$, South: -0.0036, $p =$ 0.889).

Juveniles' abundance and environmental factors

Our model indicated a significant interaction between CTI and solar radiation predicting the abundance of both species (Firs: - 5.46, p < 0.001, Pines: 7.29, p < 0.0001) (Supplemental Material 1.5). For both species the effect of CTI was only significant at low levels of solar radiation; however, the direction of the relationship changed from high CTI values (i.e. drainage areas) having more juvenile firs at low levels of solar radiation, to low CTI values (i.e. more exposed sites) having more individuals at high levels of solar radiation. The

exact opposite trend was true for pines

(Supplemental Material 1.6).

Figure 1.4. Change in maximum size of pines and firs in the Western slopes of the Iztaccihuatl volcano. Maximum DBHs of pine (A) and fir (B) individuals with elevation along north and south facing slopes at the subalpine zone.

Relative abundances and elevation

The elevation at which relative abundances of juvenile pines exceeded that of firs occured at approximately 3,767 m on north facing slopes $(p < 0.0001)$, and 3,698 m on south facing slopes ($p < 0.0001$, Table 1.2). Figure 1.5 shows individual regression plots by aspect and the differences in elevation between adult and

juvenile ecotones (Supplemental Material 1.7). Considering a 57-year period (the same one used by Torres – Beltran (2013,) to estimate the speed of advance of pines towards higher elevations), and assuming an average fir – pine ecotone of 3,600 m, then firs have advanced approximately 2.9 m*year-1 on north facing habitats, and 1.7 m*year⁻¹ on south facing habitats.

Table 1.2. Interaction between the juvenile to adult ratios and species to estimate the differences in ecotone between juveniles and adults on different slope aspect habitats.

Figure 1.5. Interspecific juvenile to adult ratios (log transformed). Solid vertical line represents the approximate adult ecotone. Longdashed line represents the juvenile ecotone on south facing habitats. Short-dashed line represents the juvenile ecotone on north facing habitats.

Discussion

We found evidence of recent upslope colonization of pine (subalpine) habitat by firs (montane species). However, this colonization process is strongly modulated by local habitat characteristics. The progressive decline in maximum size of fir individuals with increasing elevation found across the ecotone transects is consistent with a gradual expansion of the fir forest line over the past four or five decades. The trend of higher maximum elevations reached by firs on south facing slopes could be explained by the topographic characteristics of the transects, which we placed along the lower sections of the ravines where soil moisture may be sufficient for fir seedlings to establish and recruit. Our results indicate that on more exposed sites, firs reach higher elevations on south facing slopes only along the ravines, and not on steeper - exposed slopes, where the critical threshold for tree development determined by moisture can occur before than that of temperature (Mountains et al., 2018; Wilmking, 2012).

In high latitudes where trees are limited mostly by low temperatures, it is common to find higher timberlines and treelines on equatorial slopes (Danby & Hik, 2007; Vitali, Camarero, Garbarino, Piermattei, & Urbinati, 2017). Thus, under mild or initial warming, any progression of trees into higher elevations should be expected on south facing slopes first (Danby & Hik, 2007; Elliott & Kipfmueller, 2010). In this case however, expansion along south facing habitats is halted less than 100 m above the average fir forest line elevation but progresses along north facing habitats up to an elevation of nearly 3,900 m; almost 300 m beyond the mean elevation of the fir - pine forest ecotone.

Distribution shifts in the subalpine zone.

The change in maximum fir size with elevation inside the subalpine zone suggests that the adult fir – pine ecotone would likely be found at substantially higher elevations, even if warming trends were to halt. Moreover, given the speed of advancement of fir trees on north facing habitats is twice as fast as that found for

pines at their upper distribution limit (Torres – Beltran, 2013), it is plausible to expect local extirpations of Hartwegii pine populations along the more mesic areas of the subalpine vegetation zone.

Importantly, the use of age-based relative abundances would be ineffective in detecting distribution shifts in a mixed forest ecosystem simply because different species have different reproductive and competitive traits, as is the case with these two species. However, in the case of two neighboring monodominant species and an environmental gradient responsible for their spatial segregation, using relative abundance ratios based on species ontogeny is important because under stable environmental conditions (i.e. no climate change), the population age structure should remain fairly similar across the gradient (e.g. elevation). In other words, if the observed pattern of firs above the adult ecotone was solely the expression of an equilibrium condition in which outpost individuals are maintained at high elevations through a rescue effect from low

elevations, the population age structure should not decrease with elevation.

Our growth results further support the idea that firs have increasingly favorable conditions over pines, and contrast with those of Gomez-Guerrero et al (2013), who found notorious growth declines in populations of *A. religiosa* inhabiting lower elevations. This also reinforces the hypothesis that the upslope expansion is more likely to be related to changing climatic conditions than to land use change or management practices. While this portion of the Mexico City Valley is considered a low nitrogen deposition site relative to the rest of the region (Silva et al., 2015), we cannot completely discard the potential role of nutrient deposition driving these patterns. Yet, Hartwegii pines should be expected to respond similarly.

The inverted U-shape relationship between abundance of juvenile firs and annual mean solar radiation suggests that in the subalpine zone firs have not invaded some of the colder areas. If temperatures continue to increase in the next decades, firs may be able to colonize

areas were soil temperatures are currently too cold, or where sporadic extreme low temperatures have prevented them from establishing successfully so far. In contrast, the relationship between pine juveniles and solar radiation appears to follow a U-shape, where higher number of juveniles are found either at very low or very high solar radiation levels. When looking at adult individuals and solar radiation, we found the opposite trend than for juveniles, and thus we believe this could be indicative of a displacement process in which juvenile pines are being pushed towards more extreme habitats by juvenile firs.

In areas of high solar radiation, juvenile firs exist mostly on more depressed drainage areas. However, as solar radiation decreases, juvenile firs become abundant on more exposed sites. Pine juveniles on the other hand, are more abundant on less well drained soils (i.e. high CTI values) when solar radiation is high (i.e. warmer sites). This pattern is consistent with Hartwegii pine's preference for well drained soils, presumably to avoid root damage under

freezing conditions (Ramírez-Contreras & Rodríguez-Trejo, 2009).

Our findings resonate with the differences found between slope aspect habitats in the St. Elias Mountains by Danby and Hik (2007), and those found by Elliott and Kipfmueller (2010) in the southern United States Rocky Mountains, where treeline expansion was detected on south facing habitats at the Canadian sites (high latitudes), and seemed to be switching from south to north facing habitats at the southern sites (mid latitudes). Thus, our results in Central Mexico could be considered an additional observation along a latitudinal gradient.

Future of Sacred Fir and Hartwegii Pine Distribution

Our results indicate an uncommon case of upslope shift in which factors limiting the upward colonization of fir populations seem to have changed over time depending on local topography. Evidence of recent colonization of firs along north facing habitats likely indicates

that that their upper range may not have been always limited just by soil moisture, and in the past may also have been limited by low temperatures. As conditions began to warm up, firs may have begun colonizing south facing slopes right at their upper distributional limit. Continued warming probably prevented further expansion upslope along south facing slopes. Along north facing slopes however, as minimum temperatures increased, juvenile pines likely started losing their cold-tolerant competitive advantage over firs, opening a niche for the latter.

Because of intense land use change dynamics at the lower distribution of firs in this region*,* it is difficult to know if the range of the species is retreating from lower elevations. However, modelling efforts for the entire distribution of the species have determined that range contractions of up to 69.2% by 2030 are likely to happen, and in fact research has discussed assisted migration into higher elevations (Sáenz-Romero, Rehfeldt, Duval, & Lindig-Cisneros, 2012). Other studies have

predicted future distributions of firs to reach elevations of up to 3,900 m between 2020 and 2030 (Lourdes & Diana, 2015). Our results show that firs may already be shifting upslope, but it is likely that this is only occurring in mountains where topographic complexity is adequate as to provide *stepping stone* habitats that enable their upward migration (Hannah et al., 2014). In addition, our results indicate that, as firs advance into the subalpine zone, Hartwegii pine populations and their associated understory community could become locally extirpated from mesic areas, pushing them towards more drought and fire prone sites.

Given the marked structural and functional differences between these two species, ongoing and future changes in their distributions are likely to have important consequences at the community and ecosystem level (Agramont, Maass, Bernal, Hernández, & Fredericksen, 2012; Pérez-Suárez, Fenn, Cetina-Alcalá, & Aldrete, 2008). Moreover, their ability to continue migrating upslope will likely be determined by feedback loops of habitat

modification related to their functional traits. For example, the dense canopies of mature firs provide habitat for a diverse community of shade tolerant herbaceous understory species of mesic affinity while preventing shade intolerant species from establishing, including Hartwegii pine seedlings (Sánchez-González & López-Mata, 2003). How fast can Hartwegii pines occupy currently unavailable niches will depend partly on their ability to alter the physical and chemical properties of soil at higher elevations.

While shifts in species distributions in mountain ecosystems are expected and already occurring under climate change, results have shown that the processes and patterns associated to these shifts can vary substantially between regions and species (Rabasa et al., 2013). Bioclimate modelling efforts to predict these shifts typically lack the capacity to accurately assess local scale interactions between species traits and local habitat variation (Jonathan Lenoir, Hattab, & Pierre, 2017). However, strategic or targeted ecological fieldwork has the potential to reveal these interactions which can

then be scaled up to better inform conservation and management plans.

Increasing field-based research efforts on climate change impacts in tropical high elevations is central to global biodiversity conservation because these environments are likely to experience disproportionate local and global extinctions compared to extra tropical mountains (Dullinger et al., 2012). At the same time, many species may be able to persist through local habitat refugia created by local scale environmental heterogeneity (Keppel et al., 2012). Our research highlights the relevance of understanding how this local habitat variability is and will continue to mediate climate change impacts in mountain ecosystems.

Chapter 2. Climate Change Reverses Growth Trends between Topographic Aspects Authors: Paulo Quadri^{1*}, Lucas Silva², Erika

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Abstract: Under climate change, cold-limited, high-altitude tree species are expected to experience growth acceleration. However, mixed results in high-altitude tree growth trends and range shifts continue to dominate the literature, suggesting that local environmental factors and species adaptations play a key role in modulating species responses to climate change. We used dendroecological and isotopic methods to study this modulation as an expression of developing climatic microrefugia. Our analyses from high-altitude $(> 3600 \text{ m})$ tropical pine

forests in central Mexico show a shift in growth trends between aspects, with trees on south aspects growing significantly less relative to north aspect trees over time (1873 – 1940: - 0.066, $p = 0.178$, 1913 – 1950: -0446, $p < 0.001$, 1945 – 2015: -0.49, p < 0.001). Stable isotopic analyses of carbon and oxygen and analyses of carbon:nitrogen ratios suggest these trees may have benefited from an interaction between wetter-cooler conditions and CO2 fertilization in recent decades. Intrinsic water use efficiency has been significantly greater in south facing slope trees over the last 140 years and is diverging among young cohorts, and ¹⁸O enrichment has only occurred on mature trees. Our findings highlight the importance of considering localscale environmental and age factors to better understand current and future population and ecosystem level responses to climate change. Incorporating knowledge of fine scale patterns and processes will improve our ability to detect and protect microrefugia as areas of high conservation value under climate change.

Introduction

Under climate change, species in mountain ecosystems are expected to shift upslope as a response to warming temperatures (Breshears, Huxman, Adams, Zou, & Davison, 2008; J Lenoir, Gegout, Marquet, De Ruffray, & Brisse, 2008). However, sessile species such as trees may instead rely more on the development of holdouts or *in situ* microrefugia (Ashcroft, 2010; Hannah et al., 2014) for their persistence and not so much on upslope migration. This is especially true for subalpine tree species, which may be constrained not just by low temperatures, but also by geomorphic factors, moisture availability, or poorly developed soils (Andre & Gonza, 2015; Loranger, Zotz, & Bader, 2016a, 2016b; Macias-fauria & Johnson, 2013). Most research on the development of these holdouts or microrefugia comes from modeling approaches, and direct evidence from the field remains surprisingly scarce, especially from tropical high-altitude ecosystems.

In high-elevation forest ecosystems, much attention has been given to the role of low

temperatures in limiting tree species' distribution and growth, and how this limitation may be affected by global environmental change (Holtmeier & Broll, 2018; Korner, 2018; Wilmking, 2012). Accordingly, if tree growth is limited mostly by low temperatures, a warming climate should lead to increased productivity (Paulsen, Weber, & Korner, 2017; Wilmking, 2012). However, mixed results of growth acceleration and growth declines from subalpine forest ecosystems dominate the literature (Dulamsuren, Hauck, Kopp, Ruff, & Leuschner, 2017; Gómez-Guerrero et al., 2013; Liang, Leuschner, Dulamsuren, Wagner, & Hauck, 2016; Silva et al., 2016). Similarly, theory and evidence from controlled experiments suggest that rising atmospheric $CO₂$ concentrations should stimulate tree productivity and resource use efficiency (Körner, 2003). Yet, in natural systems, evidence of such $CO₂$ driven stimulation has been scarce and sometimes contradictory. The lack of a coherent response from these ecosystems could arise because rising $CO₂$ and warming are not the only factors

determining tree productivity; many other hydrologic, biogeochemical and ecological factors play important roles (de Andrés, Camarero, & Büntgen, 2015; Loranger et al., 2016a; Maxwell, Silva, & Horwath, 2018; Peñuelas, Canadell, & Ogaya, 2011). In mountains, these factors can vary significantly across small spatial scales, potentially leading to spatially heterogenous responses to warming and rising CO2. Understanding how local scale environmental heterogeneity mediates species responses to climate change is fundamental because it can help identify potential microrefugia, which will likely play a central role in preventing regional extinctions and securing long term ecosystem resilience (Birks & Tinner, 2016; Dobrowski, 2011; Mclaughlin & Zavaleta, 2012).

Using a combination of dendroecological and isotopic analyses, we examined how contrasting local topographic aspects may be affecting physiological performance in Hartwegii pines (*Pinus hartwegii*) in Central Mexico during the past

~140 years. Topographic aspect is a major factor influencing the amount solar radiation received by soils or organisms. Solar radiation in turn, is the main component of surface energy budgets which strongly determine key components of microclimates (e.g. soil moisture, evaporative demand) (Bennie, Huntley, Wiltshire, Hill, & Baxter, 2008).

We expected factors limiting growth to shift between aspects, from temperature limitation on north aspects, to moisture limitation on south aspects (Mccullough et al., 2016), and tree growth tends to change according to these resource shifts. We expected individuals growing on north facing slopes (colder, wetter habitats receiving less solar radiation) to be experiencing more favorable conditions than in the past. In contrast, due to potential recent water limitation, we expected trees on south-facing slopes (warmer, drier habitats) to be experiencing growth declines. Simultaneous increases in intrinsic water use efficiency (iWUE) and 18 O enrichment over time, is considered to be indicative of reduced

stomatal conductance due to increasing leafsurface temperatures leading to evaporative fractionation of oxygen isotopes, and photosynthetic fractionation in carbon isotopes (McCarroll & Loader, 2004). Thus, we expected to find evidence of greater and steeper increases in iWUE in south aspects accompanied by more enrichment of ¹⁸O relative to north aspects.

Methods

Our study site was located approximately 70 km southeast of Mexico City, on the Iztaccihuatl – Popocatepetl National Park (19° 07´43´´, 98° 39´ 37´´) in the Trans Mexican Volcanic Belt (TMVB) ecoregion of central Mexico, between the states of Puebla and Mexico (Figure 2.1). The whole research area spanned an altitudinal gradient between 3,600 m asl and 3,950 m asl. At the lowest portion of the gradient, the *P. hartwegii* forest is met by a montane forest entirely dominated by sacred firs (*Abies religiosa*). At their upper distributional limit, the pines dissolve gradually into a system of alpine grasslands dominated by *Festuca tolucencis* and *Muhlenbergia quadridentata.*

Other important understory species are *Lupinus montanus* and *Senecium spp*. The regional climate is considered as sub-humid temperate, characterized by cool wet summers with rains beginning in early June and extending sometimes as far as October or November. Average precipitation is 928 mm and average annual temperature on the lower slopes is 14°C. Winters are cold and dry with January averaging 10.8°C and February only 6.9 mm of rainfall. Springs are dry and warm when most of the fires occur in the region.

Figure 2.1. Study Site: Left Panel: **A)** Mexico and the Trans-volcanic Belt Ecoregion. **B)** Study site ~ 70 km southeast of Mexico City**. C)** Location of sampling plots. **D)** and **F)** Western slopes of the Iztaccihuatl volcano, where multiple canyons create north (D) and south facing aspects (F).

We used a systematic sampling design along the western canyons of the Iztaccihuatl volcano, where we worked on six transects, three on south facing slopes and three on north facing slopes. On average, gradients span 1.4 km of distance and 200 m of altitudinal change. On each gradients, four to six plots of radii ranging between 15 and 20 m were used to collect when possible two cores (one 5 mm and one 12 mm, ~ 1.3 m above ground level) from the five or four *P. hartwegii* individuals with the least amount of apparent biological or physical damage representing multiple size classes all > 10 cm DBH ($N = 86$ trees, High Elevation ($\sim 3,850$ m) $= 28$ trees, south $= 13$, north $= 15$. Mid Elevation $(-3,740 \text{ m}) = 28$, south = 14, north = 14. And Low Elevation $({\sim} 3,640 \text{ m}) = 30$, south = 15 and north $= 15$.

Growth measurements

We used ring width index (RWI) measurements from all trees and converted them into basal area increment (BAI). The use of BAI provides accurate metrics for above ground productivity and because it detrends ontogenic

effects from ring widths, it reliably estimates growth throughout the tree lifespan (R. L. Peters, Groenendijk, Vlam, & Zuidema, 2015). To do this, tree cores were mounted, sanded, polished, and cross dated. Ring width measurements were performed on high resolution scanned images using Image J (software info). BAI was calculated as follows:

$$
BAI = \pi * (R_t^2 - R_{t-1}^2)
$$

Where *R* is the tree radius, and *t* is the year of ring formation. The formula assumes basal uniformity of annual increments.

Isotopic and nutrient measurements

For stable isotopic analyses we selected eight individuals representing the oldest and youngest age groups from both aspect habitats, and with the strongest correlations to the mean ring width index series on each habitat. To avoid additional confounding elements, only trees growing above 3,700 m on more exposed sites and away from potential competition factors with *A. religiosa* trees and other species from the montane communities. Individual rings of each

tree were sliced off the tree cores and grinded as whole wood. Sample material was then weighted and packed in tin and silver capsules. Rings sampled were selected based on analysis of RWI curves of both habitats. Carbon isotopes were used to understand changes in iWUE and its potential relationship to changing growth patterns. For carbon isotopes we generated yearly resolutions between 1978 and 2015 to capture the growth reversal pattern. Between 1878 and 1978we selected rings based on periods of divergence and convergence between both habitats RWI series. Oxygen isotopes a typically used in tandem with carbon isotopes to identify the likely environmental mechanisms responsible for changes in iWUE. Usually, higher leaf surface temperatures lead to ¹⁸O enrichment of leaf water (McCarroll & Loader, 2004). Examination of carbon-to-nitrogen ratios in tree rings is considered standard analysis for changes in NUE (Hart & Classen, 2003). Isotopic analyses were performed at the Stable Isotope Facility of the University of California, Davis and are characterized as follows:

$$
\delta\binom{0}{00} = (R_{sample} - R_{standard} - 1) * 1000
$$

Where *Rsample and Rstandard* are the carbon isotopic ratios in the sample material and a reference standard respectively (the Vienna Pee Dee Belemnite formation for $\delta^{13}C$, and the Vienna Standard Mean Ocean Water for $\delta^{18}O$),

For meaningful interpretations of carbon isotopes the following derivations are necessary to correct for changes in atmospheric $\delta^{13}C$ (Farquhar, O'leary, & Berry, 1982; McCarroll & Loader, 2004)

 $\Delta^{13}C = (\delta^{13}C_{\text{air}} - \delta^{13}C_{\text{plant}})/ (1 + \delta^{13}C_{\text{air}} / 1000)$

Where Δ^{13} C is the discrimination against ¹³C, δ^{13} C_{air} represents the isotopic ratio of the atmosphere (the source), and $\delta^{13}C_{\text{plant}}$ is the isotopic ratio of plant biomass (the product). Isotopic discrimination in turn is described as follows:

$$
C_i = C_a * (\Delta^{13}C - a)/(b - a)
$$

Where a is the discrimination against ${}^{13}CO_2$ occurring through stomata diffusion during the gaseous phase $(4.4 \frac{0}{00})$, and *b* is the net

discrimination occurring during carboxylation $(27 \frac{0}{00}).$

Finally, intrinsic water use efficiency (*iWUE*) is given by:

$$
iWUE = A/g = C_a * [1 - (C_i / C_a)] * 0.625
$$

Where A is net carboxylation, g is the leaf stomatal conductance, and 0.625 is the constant relating conductance of $CO₂$ molecules and water vapor.. Δ^{13} C in plants is directly related to changes in C_i / C_a at the leaf level which, as described above, is controlled by the net assimilation rate (*A*) and by stomatal conductance (*g*). Therefore, changes in ^{13}C discrimination can be cause either by drought conditions (affecting mostly stomata conductance), or by changes in nutrition or temperature (mostly related to net assimilation rate). Thus, oxygen isotopes, carbon to nitrogen ratios, and climate data from nearby weather stations were used to strengthen our interpretation of iWUE and its relationship to tree growth.

Climate data

Temperature and precipitation by season were obtained from a network of weather stations in and around the Izta – Popo National Park. Data exists only between 1961 and 2015 and weather stations are operated by the National Meteorological Service of Mexico (Supplemental Material 2.1). $CO₂$ concentrations and δ^{13} C_{air} values were obtained from existing publications (McCarroll et al., 2009), and complemented from NOAA's CarbonTracker, version CT2017 (W. Peters et al., 2007). To confirm environmental differences between aspects, we calculated mean incident annual radiation using a 15 m resolution digital elevation model (DEM) (Supplemental Materials 2.2)

Statistical Analyses

To explore the associations between our main variables we used pairwise correlations on the entire data set. Standardization of tree rings measurements was performed using the C-

method (Biondi & Qeadan, 2008b). Selection of cohorts was done based on the distribution of age frequencies, where roughly three periods of recruitment can be identified and classified as "Old", "Mid" and "Young" cohorts (Supplemental Material 2.6). Least-squares regressions were used to evaluate and compare growth and isotopic trends among aspect habitats and cohorts over the different periods of interest. adjusted coefficients of determination $(r²)$, estimates, and probabilities are reported where appropriate (Supplemental Material 2.7 – 2.13b). Periods of growth analysis were determined based on visual inspection of contrasting trends. Two sets of mixed-effects models were also generated to examine the magnitude and direction of different relevant parameters based on our correlation matrix (Supplemental Material 2.16). The first one includes the entire study period using aspect, age, and year as fixed effects with interactions, and altitude and sampling plot as random effects (Table 2.2). Different versions of the model were tested using Akaike's information criterion

(AIC) defined as $AIC = -2L + 2K$, where L is the maximum log-likelihood of the model, and K is the number of parameters. The second set focuses on recent decades, when meteorological data is available for the region, and incorporates other physiological and environmental variables as fixed effects (iWUE, temperature, precipitation) using "year" as random effect to understand the effect of these environmental variables in any given year (Supplemental Material 2.14a and 2.14b). All models from this set use year as random effect to reveal effects of relevant variables in any given moment.

Results

Growth trends

We sampled 86 *P. hartwegii* individuals ranging from 45 to 143 years old. Growth curves of the entire sample show three distinctive periods of growth: 1873 – 1939, 1940 – 1978, and 1980 – 2015 (Supplemental Material 2.4). AIC comparisons of our mixed-effects models indicate that aspect and age are significant factors explaining changes in growth $(t = 6.799)$, p < 0.001) (Table 2.1, interaction plots in
Supplemental Material 2.5), with the effect of age being much stronger on north aspects. Although our sample shows high age variation, three different events of recruitment were identified based on age frequency distribution (Supplemental Material 2.6). Individual regressions using interactions between year and aspect for the periods indicated confirm these results showing a progressive and significant decline in south aspect trees relative to north aspect trees over time $(1873 - 1940: -0.066, p =$ 0.178, 1913 – 1950: -0446 , p < 0.001, 1945 – 2015: -0.49, p < 0.001). Comparisons of early life stages (~ first 50 years of life) between trees of different cohorts show that pines on south aspects recruited after 1940 are growing approximately four times slower than those recruited before the 1900s $(0.147 \text{ cm}^2 \text{ yr}^1)$, and $0.57 \text{ cm}^2 \text{ yr}^1$ respectively). In contrast, young trees on north aspects have reached the fastest growth rates ever recorded by these pines in either north or south facing slopes $(.586 \text{ cm}^2 \text{ yr}^1)$ (Supplemental Material 2.7).

Table 2.1. Changes in growth of pines over time across aspect and age using plot and altitude and random effects. (A) is full model with three-way interactions between fixed effects. (B) model excluding age, and (C) model excluding aspect.

Carbon isotopes

We observed significant declines in tree ring δ^{13} C values in both cohorts reflecting atmospheric enrichment of $CO₂$ during the last century (old: -0.01, *t* = -11.885, p < 0.001, young: -0.016 , $t = -7.98$, $p < 0.001$) (Figure 2.2). However, enrichment was greater on south aspects (old: 0.975, *t* = -16.885, p < 0.001, young: 0.431, *t* = 5.898, p < 0.001) (Supplemental Material 2.8, 2.9). We also found significant declines in atmosphere to plant discrimination of ${}^{13}CO_2(\Delta^{13}C)$ in trees from both old and young cohorts (old: -0.005 , $t = -1$ 6.945, $p < 0.001$, young: -0.01 , $t = -4.595$, $p <$ 0.001). However, discrimination on young south aspect trees was stronger than that from young north aspect trees (old: -1.027, *t* = -19.17, p < 0.001, young: -0.423, *t* = -5.407, p < 0.001) (Supplemental Material 2.11). Changes in intrinsic water-use efficiency (iWUE) followed those of Δ^{13} C, with steeper increases in young trees relative to old ones (old: 0.172 , $t = 31.53$, p < 0.001 , young: 0.299, $t = 23.14$, p < 0.001). Differences between aspects were more

pronounced in old trees than in young ones (old:

6.142, *t* = 15.84, p < 0.001, young: 2.356, *t* =

4.99, $p < 0.001$) (Figure 2.3. and Supplemental

Material 2.10).

Figure 2.2. Basal area increment by cohort indicating average growth of trees of all ages. South and north facing aspects are depicted in red and blue, respectively. Shaded areas represent standard errors. Inner table: average growth rates from the slopes of linear regressions ($p < 0.001$) that allows comparison of growth in same life stages between trees from different cohorts.

Figure 2.3. Carbon isotope results from old and young pines. Upper panel: atmosphere-towood carbon isotope fractionation $(\Delta 13C)$. Lower panel: iWUE by aspect habitat.

Oxygen Isotopes

Contrary to our expectations, oxygen isotopes showed no differences between aspect habitats, and no changes over time except in old trees, where δ^{18} O has increased significantly (old: 0.0092 , $t = 2.77$, $p = 0.0062$) (Figure 2.4 and Supplemental Material 2.12).

Carbon to Nitrogen Ratios

Carbon to nitrogen ratios (C:N) increased overall between 1892 and 1950 with marginally nonsignificant slower rates on south aspects $(-0.35, t = 1.84, p = 0.071)$. Whereas during the period between 1950 and 2015 C:N declined sharply with marginally nonsignificant differences between aspects again $(-642.6, t = -$ 1.69, $p < 0.093$). In young individuals, however, trends were much more contrasting and south aspect trees showed sharp declines in C:N ratios following the same trend than old cohorts during the second period (year - south:-0.75, $t = -7.22$, p < 0.001). North aspect trees unexpectedly showed increases in C:N ratios, following trends

of old cohorts during the first period (Figure 2.4, Supplemental Material 2.13)

Environmental variables, carbon isotopes, and growth.

We generated model specifications to analyze growth trends (Supplemental Material 2.14a and 2.14b) based on our set of pairwise correlations of environmental and ecophysiological variables during the last 55 years for which there are weather stations records (Supplemental Material 2.3).

Mixed-effects models showed significant interactions between iWUE and aspect, indicating reduced growth on south aspects relative to north ones associated to increasing iWUE (-2.36, *t* = -7.82, p < 0.001). In turn iWUE decreased in absolute terms with increasing spring precipitation (-1.39, *t* = -2.47, p < 0.016), and increased with increasing winter and summer temperatures (1.31, $t = 5.47$, $p <$ 0.001, and 1.588, *t* = 4.63, p < 0.001 respectively) (Supplemental Material 2.14a).

Summer precipitation was associated to reduced growth on south aspects relative to north ones (- 3.246, $t = -2.45$, $p = 0.014$), while spring precipitation was associated to more growth on south aspects relative to north aspects $(6.864, t =$ 4.60, p < 0.001). Lastly, both, maximum winter and summer temperature was associated to less growth on south aspects compared to north aspects (winter: -3.79, *t* = -5.22, p < 0.001, summer: -4.342, *t* = -4.34, p < 0.001).

Figure 2.4. Oxygen isotopes and carbon-tonitrogen ratios for old and young pines.

Discussion

Our observations of growth trends shifting in time from faster growth on south aspects, to faster growth in north aspects suggest that limiting factors to pine growth may be

shifting from energy limitation (low temperatures) to moisture limitation. Faster growth rates on south facing slopes during the late 1800s and early 1900s should be expected if low temperatures were the primary limiting factor for tree growth in those years. However, faster growth rates on north facing slopes would be expected in the second half of the $20th$ century (warmer conditions), as moisture availability becomes the primary limiting factor. The fact that this shift is mostly driven by the younger cohorts of pines is somewhat puzzling, especially considering the increase in C:N ratios in these individuals. Growth acceleration in subalpine trees has been attributed to synergies between rising $CO₂$ concentrations (C_a) and increasing nitrogen availability from warming soils (Silva et al., 2016). In our case, growth acceleration is accompanied by seemingly decreasing nitrogen availability. One possible explanation for this could be increasing nitrogen use efficiency (NUE), which is known to occur with increasing C^a (Drake, Gonzàlez-meler, & Long, 1997). N storage in evergreen conifers

occurs primarily in RuBisCo, making them particularly sensitive to changes in C_a (Millard & Grelet, 2010). The observed changes over time in C:N could thus be a consequence of the combination of sufficient soil moisture on north facing slopes with increased C_a stimulating photosynthesis (i.e. more nitrogen in RuBisCo) rather than of reduced soil N availability.

Higher winter and summer temperatures and more summer precipitation are associated to more growth on north aspects relative to south aspects. This supports our hypothesis of warming temperatures and increased, or at least, sustained soil moisture allowing trees in north aspects to grow faster, releasing them from the constrains of low temperatures. In contrast, spring precipitation, which occurs sporadically during the hottest months (April - May) favors growth on south aspect trees relative to north aspect ones. South aspect trees showed absolute growth declines with increasing winter and summer maximum temperatures, and absolute growth gains with increasing spring precipitation. Thus, as warming has progressed,

spring precipitation may now be a major limiting factor for tree growth on south aspects.

Carbon Isotopes

While increases in iWUE are expected solely from rising CO₂ concentrations, the comparison of aspects allowed us to focus on the effect of other environmental factors on iWUE, such as water limitation and increases in temperature. Given the relationships between temperature, precipitation, and growth described above, it is likely that the differences in iWUE not accounted by increasing C_a are a consequence of water limitation and warming on south aspects. Importantly, growth declines on south facing habitats in both, old and young trees coincide with the time when iWUE reached \sim 57 (mmol mol⁻¹), which is in 1939 in old individuals, and 1965 in young individuals at \sim 55 (mmol mol-1). For old trees on north facing slopes, iWUE values were approximately 52 $\text{(mmol} / \text{mol}^{-1})$ in 1939 when they started showing growth declines. Young individuals on

north aspects however, continued to accelerate their growth even beyond $65 \, \text{(mmol / mol}^{-1})$. In other words, at \sim 56 mmol of carbon fixed per mol of water, trees on south aspects started to decline regardless of their age, while on north aspects young trees had been able to maintain positive growth trends at \sim 44% more iWUE than what old trees on north aspects experienced during their initial period of growth, approximately 100 years ago.

High iWUE coupled with growth declines or stagnation on south aspects can thus be interpreted as water stress or limitation, especially because our models indicate that iWUE decreased with increasing spring precipitation and increased with increasing summer and winter temperatures.

Oxygen Isotopes

We expected δ^{18} O to increase over time tracking iWUE and temperature trends, supporting the hypothesis of increasing temperatures at a leaf surface level, especially on south aspects, reducing stomatal conductance

(Sternberg, 2009). Lack of a consistent pattern of ¹⁸O enrichment in young trees is therefore unexpected, especially since we observed significant increases in δ^{18} O values in old trees, indicating that the differences between cohorts cannot be explained by regional variations in isotopic signatures of precipitation. One likely explanation could be that only dominant trees, with directly exposed canopies to solar radiation, are susceptible to oxygen isotopic fractionation due to increased evapotranspiration (ET).

Using dendroecological and isotopic methods we showed that rising temperatures and CO² concentrations do not necessarily translate into tree growth acceleration. Instead, critical interactions between changing environmental conditions at global and regional scales (i.e. temperature, precipitation, $CO₂$), and local environmental heterogeneity (i.e. local topography) are likely to produce variable outcomes, even within populations of long-lived organisms such as trees.

Previous research has shown how variation in these interactions produces

contrasting outcomes across regional scales (Camarero, Gazol, Galván, Sangüesa-Barreda, & Gutiérrez, 2015; Martínez-Vilalta, López, Adell, Badiella, & Ninyerola, 2008; Reed, Ballantyne, Annie, & Anna, 2018; Van Der Sleen et al., 2015). Here we showed how disparate results can also occur across smaller spatial scales and across different generations in a population, thus adding complexity to our understanding of species responses to climate change. The differences across different-aged cohorts in particular, emphasize the importance of sampling trees from different sizes instead of just following the traditional dendroecological approach of studying dominant individuals.

While previous research and theory suggest that nitrogen use efficiency (NUE) in conifers typically increases with iWUE, the combination of growth acceleration and increasing C:N ratios observed in young north facing trees is quite unexpected and deserves further exploration. Future research here should focus on the role of species interactions such as

fungal-plant associations and its effect on competition and facilitation dynamics.

The detection of shifting growth patterns and their associated limiting factors over such small spatial scales, highlights how thresholds of ecological stability can vary significantly over short distances, and how can they be crossed in just a few decades. At the same time, these shifts point at a potential link between physiological responses and the future distribution of Hartwegii pines. Exploring how factors such as local topography, age, increasing $CO₂$, and rising temperatures interact affecting physiological responses in trees is key to understand whether species will be able to persist in the future, as well as where and for how long. While more research is needed in tropical high-altitude forests, our work, along with other recent studies from Mediterranean and temperate latitudes (de Andrés et al., 2015; Elliott & Cowell, 2018; Elliott & Kipfmueller, 2010; Silva et al., 2016), indicate that as $CO₂$ and temperatures continue to rise, north facing slopes may work as climatic holdouts or

microrefugia. Protection of these areas will therefore be increasingly prioritized in conservation strategies.

Chapter 3. Using Archeological Heritage Sites in Mexico to Understand the Poverty Alleviation Impacts of Protected Areas. Authors: Paulo Quadri Barba¹, Katharine Sims², Adam Millard - Ball 1 ¹ Department of Environmental Studies,

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Abstract: Win – win outcomes between conservation and local economic development have been detected in several countries, challenging the general notion that protected areas (PAs) tend to create poverty traps for local communities by restricting resource extraction activities. In this paper, we explore the question of what causes win – win scenarios in some instances but not in others. We remove the potential effects of land use and resource use extraction restrictions from PAs by using cultural heritage sites ("INAH" sites) in Mexico as a surrogate system in which these restrictions are non-existent or negligible, but where

touristic visitation is substantial. We then estimate the effects of these sites on poverty reduction between 1990 and 2010 in localities in Mexico and compare the effects to protected area impacts. To account for the non-random placement of heritage sites, we model changes in poverty as a function of site density and touristic visitation as well as multiple potentially confounding geographic and social variables. Overall, we find mixed evidence that proximity to one or more cultural heritage sites is associated with poverty reduction benefits. Generalized significant benefits across all localities from heritage sites occurred only between 1990 and 2000; these benefits fade away in most localities between 2000 and 2010. However, important heterogeneity in impacts between different regions, and by factors such as distance to urban centers and baseline poverty of the localities, suggest substantial variability in the ability of local communities to capture benefits from tourism. This suggests the importance of a better understanding of potential

tourism benefits when seeking to predict PA impacts on poverty alleviation.

Introduction

As the world seeks to meet the Millennium Ecosystem and Development Goals, it is fundamental that researchers continue exploring the existing linkages between biodiversity conservation and human development to adequately inform policy decisions. One of the biggest challenges for researchers in sustainability and conservation science has been to find evidence of whether conservation instruments, such as protected areas, promote or hinder local development (Roe, Fancourt, & Sandbrook, 2015). In the past decade, thanks to the generation of more reliable data, it has been possible to conduct more rigorous studies at larger spatial and temporal scales, many of which have demonstrated that conservation and local development can indeed be compatible. Fewer studies, however, have examined the potential causes and mechanisms that might explain the

wide observed variation in outcomes, with studies finding both positive, negative and neutral impacts of PAs on local livelihoods (Ferraro, Hanauer, & Sims, 2011; Oldekop, Holmes, Harris, & Evans, 2016). Identifying these mechanisms is critical to the successful design of policies that enable governments and societies to address conservation and poverty in an effective way (Ferraro & Hanauer, 2015). Identifying mechanisms or causes, however, is typically a challenging endeavor because the complex nature and scale of the study systems make it difficult to isolate specific channels at play.

One of the main mechanisms through which PAs are thought to negatively impact local economies is by limiting access to land resources and activities (e.g. agriculture, fuelwood), creating so-called *poverty traps* (Barrett, Travis, & Dasgupta, 2011). Conversely, PAs may help local economies by encouraging tourism or increasing amenity values. However, testing these mechanisms empirically is problematic because even when different

categories of PAs with different levels of strictness can be compared, many other factors influence changes in local socioeconomic conditions (e.g. location, PAs budget, land ownership). In Mexico, for example, Sims and Alix – Garcia (2017) found that on average PAs had no impact on local changes in poverty, with the notable exception of certain biosphere reserves, which allow for sustainable resource use and tend to have more budget than other PAs. Moreover, they found no association between the revenue generated by PA entrance fees (a reasonable proxy for tourism visitation) and poverty reduction levels, except when the opportunity cost of the land was low (e.g. far away from urban areas).

These null results could be assumed to be the product of opposing effects: negative economic impacts from land use / resource extraction limitations imposed by PAs on one side, and a combination of benefits from tourism and government subsidies to PAs on the other. In this study, we seek to separate the effects of land use and resource use extraction restrictions

from the effect of touristic activity, using the case of archeological heritage sites in Mexico ("INAH" sites; administered by the *Instituto Nacional de Antropología e Historia*). In archeological heritage sites, resource use restrictions are minor, but touristic visitation is substantial (Table 3.1). In a similar way to protected areas, archeological (cultural) heritage conservation sites have been designed to protect places that are considered to have high public value, with some even designated as World Heritage sites by UNESCO. However, restrictions on land use in cultural heritage sites are minor; they are typically limited to a small area, and focused on regulating architectural styles and other aesthetic elements. Importantly, cultural and natural heritage conservation in Mexico have similar socioeconomic and cultural motivations and share multiple institutional elements in their designation and management. As with protected areas, archeological heritage sites also experience similar threats and challenges, such as increased touristic demand and limited

carrying capacity (Shackley, 2006), and can be central protagonists in social and political conflict scenarios (Labadi, 2017).

A relevant and distinct institutional characteristic of Mexico when compared to other nations is its vast amount of privately owned land. Mexico´s territory is only 2% public property, with the remaining 98% being either individual or collective private property (SEDATU, 2015). This characteristic is relevant as land use restrictions from PAs over private property could carry greater negative economic implications for local inhabitants than restrictions over public lands.

Thus, from a comparative perspective, it would be logical to expect more conspicuous benefits from archaeological sites than from PAs. In other words, if PAs reduce poverty reduction through promoting tourism, but increase poverty through resource extraction limits, we would expect to see substantial economic benefits from cultural heritage sites.

We first review relevant concepts and results in the conservation and development literature. Next, we present our hypotheses and explain why Mexico presents a unique

possibility to test these hypotheses. We then introduce our data and methods and lastly, we discuss our findings and how they contribute to our understanding of conservation and local development outcomes.

Conservation and Poverty Reduction

The modern paradigm of conservation has, at its core of policy instruments, the concept of protected areas, which are well-defined areas in which land use and resource extraction are regulated or restricted. While PAs have proven to be effective policy tools to protect biodiversity (Contu et al., 2016) , the designation of PAs and their central role in conservation has been historically controversial from some political, cultural, and socioeconomic perspectives because in their institutional "genetics," PAs carry with them a legacy of oppression and inequality rooted in their colonial origins (West, Igoe, & Brockington, 2006). Conceived originally as exclusive institutions for the benefit of European rulers and elites in both Europe and the colonies,

modern PA systems commonly struggle to achieve social inclusivity. Indeed, many of the contemporary criticisms of PAs focus on their character as external impositions on resource uses by local communities (West et al., 2006), and concerns that they will lead to local poverty traps, impeding access to land resources by local or native rural communities who may already face challenging socioeconomic conditions (Roe, 2008; Roe & Elliott, 2006). Thus, one of the key challenges in conservation science is to better understand how this historical trajectory may constrain the evolution of PAs into more effective and inclusive institutions, and through what specific mechanisms these constraints affect socioeconomic outcomes.

Accordingly, researchers and practitioners have increasingly sought to find evidence of whether, and how, biodiversity conservation reduces poverty for local or regional communities (Brockington & Wilkie, 2015; Holmes & Brockington, 2012; Roe, 2008). With the access to longer-term and more reliable national- and subnational-scale data,

new findings that show positive impacts of PAs on poverty reduction are emerging in the literature. In Thailand, Sims (2010), found that PAs increased average consumption and reduced poverty rates, even though the Thai model of "strict" PAs (categories I and II in the IUCN classification) restricts use of the land for local communities. Andam *et al* (2010) also found significant poverty reduction benefits from PAs in Costa Rica. In Bolivia, Canavire-Bacarreza and Hanauer (2013) found that municipalities with at least 10% protected area cover experienced greater poverty reduction than similar municipalities without PA coverage. At smaller spatial scales, in Uganda, Naughton-Treves, Alix-Garcia, and Chapman (2011), found that households located closer to the perimeter of Kibale National Park faced less risk of being force to sell their land due to economic pressures. Similarly, in Cambodia, households bordering PAs showed increased socioeconomic benefits compared to control localities (Clements, Suon, Wilkie, & Milner-Gulland, 2014).

In the cases of Thailand and Costa Rica, the results point towards tourism as the major driver of poverty alleviation (Andam et al., 2010; Ferraro & Hanauer, 2015; Sims, 2010). In the case of Cambodia, on the other hand, the authors attribute the causes of wellbeing to access to markets and security in access to and management of forest resources.

In more wealthy countries, there is also some evidence for positive socio-economic impacts. In the United States, for example, Rasker (1993) points out that between 1969 and 1989, Yellowstone National Park transformed the entire regional economy, as 80% of all new jobs and 65% of the growth in labor income took place in the service sector rather than the traditional mining, agriculture, and manufacturing sectors. More recently, strong evidence of increased economic performance as a function of the extent of protected federal lands was found for the non – metropolitan U.S. West (Rasker, Gude, and Delorey 2012). Even in the more urbanized landscapes of Germany for example, some PAs have shown important

local economic contributions during the past decades due to tourism visitation (Mayer, Müller, Woltering, Arnegger, & Job, 2010). Likewise, national parks in Austria were found to significantly contribute to local economies, mainly through tourism but also by attracting new investments and companies (Getzner, 2003).

Null and negative impacts of PAs on local communities have been widely reported too. In the northern midwestern United States, for example, Marcouiller and Deller (2005) did not find strong associations between natural amenities (e.g. rivers, lakes) and indicators of economic, employment and population growth. In the northwestern United States, Eichman et al. (2010) found negative impacts on employment growth due to the reallocation of federal lands from timber production to protection of old growth forest. In developing countries, negative or null impacts seem to be more pervasive, and negative economic effects are often accompanied by social impacts, particularly the direct or indirect displacement of people when

PAs are designated or after they start operating (Holmes & Brockington, 2012). Displacement can in turn produce significant economic impacts, as in the Congo basin where thousands of people were displaced and impoverished due to national parks establishment and management (Cernea & Schmidt-Soltau, 2006).

Importantly, just as the benefits of PAs vary significantly from region to region or country to country, so do their negative effects. In Australia, for example, the social impacts of PAs on native communities tend to stem from the management and decision making process, whereas in Latin America PAs sometimes work—whether intentionally or inadvertently- as a gateway into indigenous communities for commercial agriculture or resource extraction interests (West et al., 2006).

The case of Mexico is particularly interesting. Here, Sims and Alix-Garcia (2017) did not find significant contributions of protected areas to local economies, opening the door to the question of why do PAs provide benefits in countries like Thailand and Costa

Rica and not in others like Mexico? In the case of Thailand and Costa Rica, the authors state that, compared to most developing countries, Thailand and Costa Rica have made strong investments in their PA systems, have had successful eco-tourism sectors, and in general have experienced accelerated macroeconomic growth in the last decades (Andam et al., 2010). Thus, it is unknown whether their results would hold for other developing nations. Yet, Mexico shares many of the characteristics of countries such as Thailand and Costa Rica, where PAs have yielded poverty-reduction benefits. Specifically, Mexico has had relatively stable macroeconomic growth during the past 25 years, and the contribution of the tourism industry and service economies to GDP has also risen significantly (The World Travel & Tourism Council, 2018). Furthermore, there is a strong institutional framework to manage protected areas, though the National Commission of Natural Protected Areas (CONANP) which was instituted in 2000. In addition to the lack of benefits from PAs in Mexico, surprisingly, Sims

and Alix-Garcia (2017) found no relationship between the number of visitors to PAs and local poverty reduction except where opportunity costs were low. While the revenue collected by CONANP from PAs access fees from tourists does not necessarily return in the form of investments to the PAs where it was collected from¹, it would still be logical to expect more visitation to translate into local economic benefits.

Mechanisms for poverty impacts

Because the overwhelming majority of protected area surface in Mexico exists on private lands (just over 80%), and since one of the main mechanisms through which PAs can have an adverse socioeconomic effect in local communities is by imposing extensive land use and resource use restrictions, we seek to find evidence of these factors hindering positive effects of conservation on local poverty reduction. Our reasoning is that, if PA

¹ Bernardez, Amaya, phone conversation with lead author, October 29, 2018.

restrictions are neutralizing positive effects from tourism visitation to PAs, then, if we could simulate the removal of PAs restrictions, we should see substantial and consistent benefits to local communities from tourism. To test this reasoning, we use archeological sites in Mexico as a surrogate system for protected areas and estimate their effects on poverty reduction between 1990 and 2010 in localities across 20 states of Mexico.

Our main hypothesis is that localities that have more nearby archeological sites should experience more poverty reduction. Second, we expected more visitation by tourists to be associated with more poverty reduction, and that the more sites with more visitation should lead to greater poverty alleviation. Third, we considered the possibility of important regional differences, and expected localities in regions with more developed touristic infrastructure, like the Yucatan peninsula, or those that are closer to major sources of domestic and international tourism, like Central Mexico, to be able to take greater advantage of proximity to archeological
sites (Supplemental Figure 3.1). Our reasoning here is that, if a strong tourism sector is one of the main channels through which conservation can reduce poverty at local scales, then we should expect higher levels of poverty reduction in localities that are near clusters of such sites, especially in those with higher visitation. Further, we were interested in knowing whether wealthier or poorer localities at baseline benefited more from INAH sites. Lastly, we expected that being closer to urban areas should produce more poverty alleviation by being closer to sources of tourism and markets.

Compared to PAs, archeological sites cover only a small area of land. Even Teotihuacan, the largest of these sites, extends over an area of only 246 hectares. Thus, any potential negative economic impact caused by land use restrictions in cultural heritage sites is experienced by few land owners or communities. This is a clear and important difference between archeological sites and PAs, which cover extensive tracts of privately owned land, and where land use restrictions affect

hundreds or thousands of land owners. Hence, it would be reasonable to expect stronger benefits from archaeological sites than from PAs.

In México, the National Institute of Anthropology and History (INAH) is the agency directly responsible for the management of the country´s archeological areas. In the case of PAs, CONANP (National Commission of Natural Protected Areas) is the agency responsible for their management. Supplemental materials 3.2 and 3.3 provide comparative data on budgets and tourism visitation for the two agencies, and the spatial overlap of archeological sites and protected areas.

Methods

Unit of Analysis and Response Variables

Our unit of analysis is the locality, which represents the smallest administrative entity in Mexico. Spatial data on the 105,647 localities existing in 1995 are from the National Institute of Statistics and Geography of Mexico (INEGI). While the source data represent each locality as a point feature, we use the

representation of Thiessen polygons following Sims and Alix-Garcia (2017). In our analysis, we use the subset of the 10,465 localities within 50 km of any INAH archeological site, in order to compare localities that vary in their local proximity to the archeological sites but are relatively similar on other dimensions (Figure 3.1).

Poverty outcome data were obtained from Sims and Alix-Garcia (2017), who used the index of marginality calculated by CONAPO to generate a poverty alleviation index. CONAPO's index of marginality is a weighted indicator that incorporates a variety of aspects such as schooling, availability of potable water, electricity access, housing characteristics, among others. The weights are established by principal components analysis performed by CONAPO² . The index used here was generated using area weighted means of CONAPO's marginality index for each locality, then renormalizing these values to have mean zero and

² Full methodology is documented in: http://www.conapo.gob.mx/work/models/CONAPO/i ndices_margina/2010/anexoc/AnexoC.pdf

standard deviation one, and inverted so that

higher values indicate more poverty alleviation.

Figure 3.1. Spatial distribution of INAH Sites and localities included in the study.

Treatments and Covariates

Spatial data of INAH sites were obtained through the INAH Geo-Portal System³, and visitation data for archeological sites were downloaded from the Institutional Visitor Statistics System⁴. Visitation data has been recorded since 1996, but not every site has complete records for this period; a few sites were not opened to the public until after 1996, and a small number were open in early years but have now been closed to the public. After matching sites with visitation records to those that have spatial reference data, we retained 141 archeological sites distributed across 20 states in the southern half of Mexico that we grouped by geographic region: Central, South, Yucatan Peninsula, Gulf Coast, and North within these 20 states⁵.

³ http://www.geoportal.inah.gob.mx/

⁴ http://www.estadisticas.inah.gob.mx/

⁵ Most of the great cities and infrastructure of the precolonial civilizations were built south of the 21 °N parallel. Therefore, almost all of the archeological sites are found in the central and southern half of the Mexican territory.

We obtained a detailed network dataset of Mexico's roads from OpenStreetMap (OSM)⁶ and used ArcMap 10.2 to calculate the network or road distance between every locality and every INAH site within 50 km. We then calculated derivative distance variables for each locality as follows: (i) site density, i.e. the number of INAH sites found within in a series of network distances (30 and 50 km); (ii) the cumulative number of sites within each network distance band; and (iii) the network mean distance between the locality and all corresponding INAH sites within the 50 km (Euclidean distance) zone. Approximately half of the localities were "untreated" (no INAH site within 30 km network distance).

Visitation data were assigned to each locality as the sum of the mean year visitation between 1996 and 2011 of all the corresponding INAH sites. Because a few sites in Mexico receive disproportionately more tourism than

⁶ "Map data copyrighted OpenStreetMap contributors and available from [https://www.openstreetmap.org"](https://www.openstreetmap.org/)

most other sites, visitation values were log transformed.

In addition to poverty indicators, Sims and Alix-Garcia (2017) generated a series of covariates for each locality. We used a subset of those covariates that could explain the locations of INAH sites and that might be correlated with outcome variables. For instance, although all INAH sites are by definition historical, and so predate our outcome variables, many of them may exist in less economically productive locations, or in majority indigenous areas that are politically and socially disadvantaged. If baseline controls are not included, this type of relationship could erroneously lead to the conclusion that INAH sites are creating poverty. We model the change in poverty as a linear function of two main predictors (site density and visitation levels) and a series of covariates that control for geographical and historical socioeconomic differences across localities. Our main estimating equation is of the following form:

$\Delta POV_{ij} = SiteDensity_{ij}\beta_1 + Vistation_{ij}\beta_2$

 $+ Z_{ij} \Gamma + E_{ij}$

Where $\triangle POVij$ is the change in poverty alleviation index in locality *i* and *j* is decade $(1990 - 2000,$ and $2000 - 2010)$, *SiteDensity* and *Visitation* are vectors of the main predictors, and Z_i is a vector of controls. The most important components of this term are geographic region (which is associated with the level of tourism infrastructure development) and baseline poverty. Other relevant components are population size, average slope, distance to main roads, distance to urban centers, and whether the locality is found within a protected area or not.

Results

All individual components show reductions in the percent of populations, indicating that all localities, with INAH sites and no INAH sites, were better off in 2010 compared to 2000 in absolute terms (Supplemental Material 3.4).

Our analysis yields mixed results across time and space of local poverty reduction driven by proximity and visitation to INAH

archeological sites. Supplemental Material 3.5 shows the results and specifications from our base model. The effect of the number of INAH sites on poverty reduction is positive and statistically significant between 1990 and 2000 $(0.0449, p < 0.0001)$, but negative and also statistically significant between 2000 – 2010 (- 0.019, $p = 0.023$).

Table 3.3. Coefficients of base models and models with interactions of poverty alleviation associated to INAH sites.

As expected, the Yucatan Peninsula (states of Campeche, Quintana Roo and Yucatan) is the only region in which positive and significant benefits are found during both decades (0.217, p $= 0.0488$, and 0.1362, $p < 0.001$). In contrast, the south region, which includes the three poorest states of Mexico (Guerrero, Oaxaca and Chiapas), shows positive, albeit smaller than those of the Yucatan peninsula, between 1990 and 2000 (0.0745, p < 0.01) but negative between 2000 and 2010 (-0.0538, $p = 0.0147$). For the Gulf region (states of Veracruz and Tabasco), results indicate positive effects on poverty alleviation from the presence and number of INAH sites but, again, only during the first decade of the study $(0.0891, p =$ 0.0487), as there is no detectable effect during the second decade. Lastly, the northern portion of the region shows much smaller and nonsignificant effects during both decades (0.02012, $p = 0.654$, and 0.05161 , $p = 0.168$ respectively) (Table 3.4).

Surprisingly, our model estimates the average effects of visitation to be non-significant in both decades. This is the case regardless of whether the number of sites (our other main predictor) is included in the model (Table 3.4). The effects of visitation however, do follow the same trend as the number of sites, being positive during the first decade and negative during the second one $(0.015485, p = 0.116, and -0.0078, p)$ $= 0.278$). However, and even more unexpectedly, when examining the interaction between number of visitors and number of sites, we find that during the first decade, benefits from having more sites nearby were greater from sites receiving less visitation $(-0.0486, p < 0.05)$, and during the second decade, when benefits from having more INAH sites nearby decline across all localities, this decline is not significantly different from zero when visitation is low.

The interaction between number of sites and the distance to cities from every locality, we see that between 1990 and 2000, localities further away from cities benefited more from having more INAH sites nearby $(0.142, p <$ 0.001), and between 2000 and 2010, the further

away a locality is from a city, the more likely to continue receiving benefits from being close to multiple INAH sites $(0.066, p < 0.01)$.

Finally, results from an interaction between number of sites and baseline poverty of every locality indicate that during both decades, poorer localities captured most of the benefits $(0.172, p < 0.001$ for the first period, and 0.044, p < 0.05 and for the second period).

Discussion

The possibility of finding substantial evidence of local development thanks to the presence of INAH archeological sites was a plausible expectation. The INAH sites attract substantial numbers of tourists but, in contrast to PAs, do not impose land use limitations on a large number of land owners or communities. Furthermore, Mexico is a nation with one of the largest tourism industries in the world, with moderate but stable macroeconomic growth, and with established institutional and management agencies such as INAH, whose budget has been steadily increasing in the past decades. Such an economic and institutional framework would

seem well-suited to capturing local economic benefits from visitor spending and preservation activity. Therefore, our results are interesting in a variety of ways.

Visitation: more is not necessarily better

First, contrary to one of our main expectations, our results show that visitation to INAH sites, after controlling for the number of sites, has no significant effect on local poverty. As explained earlier, our theory of change features spending on local goods and services by tourists as a main driver of local economic benefits and thus, we expected greater number of visits to provide a development advantage for localities near INAH sites compared to those further away. One possible explanation for this lack of impact may be related to the distribution of visitation numbers among INAH sites, where a few receive a disproportionately large number of visitors, but are isolated from other INAH sites or other touristic attractions. Accordingly, if INAH sites are too far from one another, visitors arriving from nearby urban centers may

not remain for a sufficient time in the adjacent localities for their spending on local goods and services to be substantial. This possibility has been documented in Bwindi Impenetrable National Park in Uganda, where length of stay of visitors turned out to be a stronger predictor of locally retained spending than visitor profile (Sandbrook, 2010).

Alternatively, or in addition, it is possible that visits organized through private tour companies bypass nearby local communities, preventing visitor interactions in local markets (Walpole & Goodwin, 2000). This may be especially true for popular sites such as such as Chichen – Izta or Teotihuacan, where there are a large number of tourists but a high proportion of them are being transported door to door by private tours. This possibility is further substantiated by the results from the interaction between number of sites and number of visitors, and number of sites and distance to cities. In the first case, we can see how less visitation, not more, is associated with more poverty alleviation as the number of INAH sites nearby increases. In the second case, more

poverty alleviation is associated to being further away from cities. These results suggest that local spending by visitors may increase when INAH sites are further away from urban centers (i.e. spending more time in local accommodations), and that sites with lower visitation may be less appealing for private, non-local tour companies and thus any spending from visitors is entirely captured by the local economy (Figure 3.2).

Benefits from clustering.

In contrast to visitation numbers, our other main predictor, the number of sites within 30 km of road distance, seems to have had poverty alleviation benefits, though only during the first decade of the study. As explained earlier, networks of INAH sites within short distances of each other may provide poverty reduction benefits, if they increase the time spend by tourists in and around nearby localities. The more time visitors spend, the more likely they are to consume local goods and services (e.g. spending the night in local accommodations, buying local foods, hiring local guides). It is also possible that the presence of multiple INAH

sites in a small area attracts attention from local

and federal governments, resulting in more

infrastructure investments such as roads and

electricity (Figure 3.2).

Figure 3.2. Overall effect of number of INAH sites and visitation on poverty alleviation. Higher coefficients represent greater poverty alleviation. Lines show 95% confidence intervals.

Regional Differences and Baseline Poverty Effects.

Our expectation about differences among regions of Mexico was that more or better levels of infrastructure potentially relevant for tourism development (i.e. roads, airports, more urbanization, education) would increase the probability of local benefits from proximity to INAH sites. Accordingly, the Yucatan peninsula is the only region in which proximity to INAH sites seems to have generated sustained socioeconomic benefits over time (Figure 3.3).

Figure 3.3. Interaction effect between the number of INAH sites located < 30 km from any locality and region and the change in poverty index between 1990 – 2000 (A), and in 2000 – 2010 (B).

The results from the interaction between number of sites and baseline poverty , concur with those found in Thailand and Costa Rica (Ferraro et al., 2011), where poorer localities at baseline benefited the most from the designation and management of protected areas. Economic theory would suggest that it is easier for PAs to reduce poverty when they are designated over marginal lands with low opportunity cost, and thus it is relatively easy or inexpensive to offset any losses from forgone agricultural activities (Andam, Ferraro, Pfaff, Sanchez-Azofeifa, & Robalino, 2008). From this perspective it makes sense that more isolated and marginalized localities benefited more from being close to INAH sites. This is supported too by the positive relationship between distance to cities and poverty alleviation due to proximity of INAH sites.

Together, our analyses suggest that localities that were poorer at baseline but that are in states or regions that are wealthier or with better infrastructure were more likely to experience poverty alleviation benefits from being close to INAH sites.

Ephemeral Benefits from Tourism from Archeological Sites and Protected Areas in Mexico.

Perhaps the most puzzling result from our analysis is the inconsistency of the INAH sites impacts between decades. What causes this inconsistency is unclear, especially because many INAH sites opened to the public in the late 1990s and the year 2000 (see Table 3.4) and thus we expected any benefits from these new openings to be reflected during the second decade.

Any explanation is necessarily speculative. However, one possibility relates to changes in the national economic picture over the two decades. During the 1990s, the INAH sites were working as a development insurance against the national background crisis that started in the country early in 1995, providing a moderate but sustained influx of income to nearby localities.

After 2000, the Mexican economy was steadily recovering and in fact experiencing an economic transition towards a bigger and stronger manufacturing economy (Villareal and Fergusson 2014), and these improvements may have accelerated economic growth in non-INAH tourism dependent localities, leaving behind INAH dependent ones. Likewise, the role of better government poverty reduction programs and remittances from immigrants in the US has also been highlighted as one of the main drivers of improvements in inequality and income documented between 2000 and 2010 (Esquivel and Cruces 2011) This suggests that when other economic activities are present or thriving, the poverty alleviation effects of tourism due to INAH sites may be diluted.

What is most interesting to us is that this pattern of ephemeral benefits seems to be the case for PAs too. Between 2000 and 2010, Sims and Alix – Garcia (2017) found that PAs had a small negative and not significantly different from zero effect on poverty alleviation. (They estimated results only for the more recent decade because the analysis compares PAs to payments for ecosystem services, which began only in 2003). When running a model using the same covariates but just for our study localities (for $2000 - 2010$ only), we also find a small negative and non-significant effect of all PAs together (Table 3.5). However, when we look at the effects of different PA types in both decades, we see that strict and mixed-use PAs had positive and significant effects in the earlier decade, between 1990 and 2000 (Table 3.4) but not in the more recent decade.

Biosphere Reserves, which were mainly designated during the late 1990's, had a positive and significant impact in our data during the 2000's. This suggests a generalized trend over time in which both, INAH sites and PAs seem to provide initial benefits that level off, saturate (or possibly become negative in the case of strictly protected areas) after a few years. We discuss possible explanations for these trends next.

Conclusions

This study explores the mechanisms behind the poverty reduction potential of protected areas, through using the analogous system of archeological sites. While assessments of protected area impacts must include both the forgone opportunity cost of land for local communities within PAs and the benefits from tourism, our study isolates the impact of tourism alone. Our findings from the first decade of the study are consistent with the idea that PAs and cultural heritage sites should both contribute to local development through tourism (Nijkamp, 2012). However, in the second decade, we found no positive impacts of INAH sites.

One possible explanation is the existence of structural deficiencies hindering the possibility of achieving local poverty reduction through tourism. Such deficiencies are typically manifested in the form of economic leakages that tend to occur in enclave tourism schemes, in which foreign companies and investors control the local tourism industry, thus fostering an extractive economic system that prevents local economic growth (Mbaiwa, 2005). Details about the mechanisms and consequences of economic leakage issues in tourism have been reviewed in detail by Lacher and Nepal (2010). According to them, without adequate linkages between the tourism industry and local economies, it is very difficult to have a multiplier effect in which rounds of spending stay in the local markets promoting investments that further enable the development of these local economies and the formation of local human capital. In our case study, these structural deficiencies are probably a direct consequence of inadequate local institutions, and the lack of sufficient investments in public infrastructure, rather than

something inherent to the mere designation of these conservation areas (both INAH sites and PAs).

In summary, our results suggest that, in Mexico, both PAs and INAH sites provide some local poverty alleviation benefits but only during a short period of initial investment that comes with the designation or opening to the public of these conservation sites. This initial period may be successful at generating positive outcomes because the types of human and social capital existing in these localities are adequate or sufficient to capture some benefits provided by INAH sites and PAs during this early period. However, sustained long term benefits may not be possible if communities or localities fail to develop new forms of human and social capital that are adequate in the context of tourism in PAs and cultural heritage places such as the INAH sites in Mexico.

Our study makes two important contributions to the existing literature on conservation and development. First, we provide evidence suggesting that the lack of local

economic benefits from visitation to PAs, may not necessarily be the product of compensatory negative impacts due to of land use restrictions imposed by PAs. Instead, other structural characteristics such as infrastructure, and social and human capital, may determine the ability of local populations to capture and take advantage of the tourism industry associated to PAs and cultural heritage sites. This is a crucial finding because it suggests that land use restrictions from PAs may not be the problem, or at least it doesn't need to be if other social impacts of heritage conservation are addressed adequately. Second, we provide one of the first national level quantitative studies measuring the influence of cultural heritage conservation sites on local economies, something relevant as UNESCO World Heritage designations rise as key touristic destinations (Timothy & Boyd, 2006).

We believe that as new data are generated by governments and international organizations, researchers will have more opportunities to test hypotheses about the

mechanisms underlying conservation and development outcomes. In this context, it will be crucial to continue building upon existing research to try to identify these mechanisms and elucidate how exactly they operate

Appendix Chapter 1

Supplemental Material 1.1. (A) Study region. Landsat 5, TM image. May 1986. Black rectangle denotes area of field data collection. Land cover change analysis was performed on entire image. (B) Approximate ecotone isocline (where mature *A. religiosa* forest transitions into *P. hartwegii* forest), approximately 3,600 m above sea level.

Supplemental Material 1.2. Land cover change between 1986 and 2014 across the study region. Increases in Pine forest cover are potentially due to active reforestation / afforestation efforts carried out by the park staff.

Supplemental Material 1.3. Ring Width Index of *A. religiosa* and P. *hartwegii*

matrix of main variables by aspect (A) south, (B) north.

 $\widehat{\mathfrak{C}}$

Supplemental Material 1.5. Results from negative binomial generalized linear models of juvenile abundance of *A. religiosa* **and** *P. hartwegii:* Annual Mean Incident Solar Radiation (SR) and Compound Topographic Index (CTI) as interaction terms and controlling for elevation (1,4), without controlling for elevation (2,5), and using only elevation as predictor (3,6)*.*

Supplemental Material 1.6. Simple Slopes

Analysis: plots showing interactions between CTI and Solar Radiation for *A. religiosa* juvenile abundance (A), and for *P. hartwegii* (B). CTI values are rescaled to have mean = 0.

Supplemental Material 1.7. OLS model results for change in interspecific juvenile to adult ratios across elevation gradient. Separate models fit for north aspect (left column) and south aspect (right column).

Appendix Chapter 2

Supplemental Material 2.1. Temperature and precipitation trends since 1960 from six local and regional weather stations located above 2,700 m: change in minimum (A) and maximum (B) temperatures, and precipitation (C) by season ($F = fall$, $S = spring$, $SM =$ summer, $W =$ winter). Error bars represent SEs. (D) location of weather stations.

Supplemental Material 2.2. Annual mean

incident solar radiation by slope aspect extracted from a 15 m resolution DEM using 30 points (15 per aspect).

Supplemental Material 2.3. Correlation

matrix of all relevant environmental and ecophysiological variables aggregated by aspect.

Supplemental Material 2.4. Basal area

increment. Main curves: average growth of trees of all ages sampled in south (red) and north (blue) facing aspects. Shaded areas represent SEs. Regression lines are also shown by aspect and by three periods of evident growth acceleration or decline. Inner table: average growth rates from the slopes of linear regressions ($p < 0.001$).

Supplemental Material 2.5. Interaction plots for Age and Aspect from mixed-effects model in Table 1: Solid lines represent + 1 standard deviation of tree age, thick-dashed line represents the mean, and light-dashed line is -1 standard deviation of age. **In (A) south aspects and in (B) north aspects.**

recruitment can be detected. For the last one (young cohorts) we aggregated the last 80 years to have enough representation of both aspects.

Supplemental Material 2.7. Individual OLS regressions with Year: Aspect interactions split by age class and periods of growth decline or acceleration. (A) oldest cohort growth increased steadily for their first $63 - 68$ years of life. Middle age trees only experienced accelerated growth during their first $38 - 35$ years of life. Young cohorts on north facing slopes growing steadily and at the fastest rate for 76 years now. On south aspects, tree growth stagnated after less than two decades since recruitment. (B) shows linear growth trends for periods of growth decline in old and mid cohorts. After the initial period of growth increase shown in panel A, old cohorts decline after 1940 for 75 years. Something similar occurs in middle aged trees.

Supplemental Material 2.8. OLS model of

d ¹³C. Main effects: Year and Aspect. Estimates show more ${}^{13}C$ enrichment in south aspects relative to north aspects.

Supplemental Material 2.9. Graphic output of OLS model for d¹³C.

Supplemental Material 2.10. OLS model of

∆ ¹³C**.** Main effects: Year and Aspect. Estimates show less 13 C discrimination in south aspects relative to north aspects, especially for young trees.

Supplemental Material 2.11. OLS model of

iWUE. Main effects: Year and Aspect. Estimates show greater increases of iWUE in young cohorts relative to old ones, and higher values in south aspects relative to north aspects, especially for old trees.

Supplemental Material 2.12. OLS model of

d18O. Main effects: Year and Aspect. Estimates show significant enrichment of ${}^{18}O$ in old individuals only. No significant differences between aspects were detected.

Supplemental Material 2.13. OLS model of carbon-to-nitrogen ratios (C:N). Main effects: Year, Period (for old cohort only), Aspect, and

their interactions. The model shows contrasting significant differences C:N trends. Steeper increments in old north aspect trees than on south aspect ones during the first period (1873 – 1947), and then C:N ratios decline similarly during the second period $(1950 - 2015)$. Young trees also show a similar trend than that of old trees during their first period of growth; increasing C:N in north aspects and decreasing on south aspects.

Supplemental Material 2.14a. Mixed-effect models of environmental and physiological variables. (A) General model. Fixed effects: iWUE, aspect, maximum winter and summer temperatures, and summer and spring precipitation. Random effect: Year. **(B)** Fixed effects: Aspect and iWUE and their interaction showing iWUE being significantly associated to

less growth on south aspects relative to north aspects.

 \overline{B}

 \widehat{A}

Supplemental Material 2.14b. Mixed-effect models of environmental and physiological variables. (C) Fixed effects: aspect, summer, spring precipitation and their interaction showing that greater summer precipitation is associated to reduced growth on south aspects relative to north ones, while more spring precipitation is associated with enhanced growth in south aspects relative to north aspects. and minimum and maximum temperatures in winter. Random effects: Year, Altitude and Plot. And, **(D),** fixed effects: aspect, maximum winter temperatures, and maximum summer temperatures, and their interaction showing how higher temperatures lead to less growth on south aspects relative to north aspects.

Appendix Chapter 3

Supplemental Figure 3.1. Example of distribution of localities along the roads network in the Yucatan peninsula.

Supplemental Material 3.2. Differences in budget and visitation between both agencies

our study
** Estimated from entrance fees data

Supplemental Material 3.3. INAH sites found

within protected areas in Mexico.

Supplemental Material 3.4. Summary statistics for percent change in poverty in all localities with different amount of INAH Sites within 30 km or road distance.

Supplemental Material 3.5. Base model results for both decades.

Supplemental Material 3.6. Model

specifications from Sims and Alix – Garcia (2017) with (1) and without (2) our main predictors. Robust standard errors in parentheses.

Significant
Codes:

 $r_{p<0.05}$; " $p<0.01$; "" $p<0.001$

Supplemental Material 3.7. Marginal Contribution of INAH Sites to Poverty Reduction. Standard errors in parentheses

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