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Climate sensitivity and potential vulnerability of Guatemalan fir (*Abies guatemalensis*) forests in Totonicapán, Guatemala

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Introduction

Climate model projections suggest that future decreases in precipitation and rising temperatures will diminish soil moisture and increase aridity throughout Central America and the Caribbean (Magrin *et al.* 2014). These shifts make this region amongst the most susceptible to the consequences of anthropogenic climate change in the world (Giorgi 2006). There is substantial evidence that this combination can also produce “hot drought”, which is expected to increase tree mortality and forest vulnerability from local to global scales (Allen *et al.* 2015). In addition to these significant changes in climate, agricultural expansion and continual increases in deforestation rates endanger forested lands and the ecosystem services they provide. Guatemala now has the highest percentage of degraded land (58.9 percent) in Central America (Magrin *et al.* 2014), primarily a result of the intensification and expansion of agriculture. Consequently, collective forest management by local communities is critical as pressures to decentralize can result in adverse impacts for these communities and can devalue sustainable practices that have contributed to forest conservation for generations (Elías 2012). Places like Totonicapán, Guatemala, where Maya K’iche’ indigenous populations have sustainably managed their forests for centuries, provide a counterpoint to these broader trends and warrant new studies in order to continue to promote and facilitate the century-scale preservation of such regions and to assess their vulnerability in the face of a changing climate.

Totonicapán is a Guatemalan department (a first-order administrative unit) that covers an area of about 1,000 square kilometers in the western volcanic highlands, where over 95 percent of approximately 491,000 inhabitants are K’iche’, an indigenous Maya population (Veblen 1978; Instituto Nacional de Estadística 2003, 2013). Totonicapán experiences a pronounced seasonality in precipitation, with more than 90 percent of annual rain falling between April and October (Veblen 1978). The rainy season is interrupted by the Mid-Summer Drought in July, a short dry period that has an immense influence on agricultural practices (Magaña *et al.* 1999; Maurer *et al.* 2017). Such complex climate and topography support myriad physical environments (Veblen 1976). Totonicapán sustains roughly 39,000 hectares of forest and supports a rich number of conifer species located above 2,700 meters in elevation (Veblen 1976; Regalado *et al.* 2012). Specifically, highland Guatemala contains over seven genera of conifers, which is greater than any other area at this latitude (14°–16°N) (Veblen 1976).

Among these conifers, the forests of Totonicapán host the largest continuous stand of Guatemalan fir (Pinaceae; *Abies guatemalensis* Rehder), at a total of 16,541 hectares (Strandby Andersen *et al.* 2006). Locally known as “pinabete”, the highland conifer is endemic to Central America and extends further south than any species in its genus (Strandby Andersen *et al.* 2006; Kollman *et al.* 2008). Pinabete is widely valued for its ecosystem services and significant role in the Guatemalan economy (Sørensen *et al.* 2013). Erosion control, water storage and purification for

both local communities and those lower in elevation, and a reduction of environmental hazards are among some of the ecosystem services provided by pinabete forests (Strandby Andersen *et al.* 2006). The amount of carbon stored in pinabete stands is also significant; an estimation of carbon storage in Momostenango, a municipality of Totonicapán, concluded that mixed forests store approximately 221.6 tC/hectare, with pinabete as the dominant contributing conifer species and often among the largest trees (>40 cm diameter at breast height) (CEAB 2011). Economically, it is used for construction, charcoal production, Christmas trees, and greenery for holiday decorations (Strandby Andersen *et al.* 2006). Despite its marketable value, pinabete was one of the most prevalent conifers until the 1940's when severe exploitation created a widespread loss in the total number of stands within Guatemala (Standley and Steyermark 1958). Because of substantial loss and unsustainable extraction practices, pinabete was placed on the IUCN's endangered species list in 1997 and has experienced at least a 50 percent loss in the total population within the last three generations (Sørensen *et al.* 2013).

Not only is the prevalence of pinabete in Totonicapán exceptional in comparison to the surrounding areas, the forest cover is also anomalous. Despite multiple generations of intensive forest access and use by K'iche' carpenters, sheepherders, and gatherers of non-wood materials, Totonicapán only recorded a 7 percent decline between 1954–1972, while neighboring departments suffered a 60 percent loss in forest cover (Veblen 1978; Conz 2014). More recently, there was essentially zero (0.04 percent) annual net loss of forest cover in Totonicapán from 2006 to 2010 (Regalado *et al.* 2012). This difference can be attributed in part to the less pronounced dependence on agriculture in comparison to other parts of Guatemala and the establishment of furniture and firewood economies, both of which have depended on sustainable and reliable access to forest products including pinabete (Veblen 1978; Smith 1990; Conz 2014). Imperative to promote economic growth, laws were enforced to prevent the clearing of communal forest lands and to protect the raw materials that formed the foundation of the furniture industry (Veblen 1978). Recent interviews with forest management committees and community members in Totonicapán have further illustrated the importance of historical conservation because it has allowed for the continual use of the forest for fuelwood and timber (vonHedemann and Osborne 2016). Thus, it is evident that close ties between the K'iche' livelihood and these resources have been instrumental in the long-standing preservation of these forests.

This active protection and management by the K'iche' has resulted in the persistence of a mature forest stand that is well suited for dendrochronology, the study of tree rings. New tree-ring data from Totonicapán should improve our understanding of the relationships between climate and tree growth in these forests. Potentially, such records may also be useful for establishing a historical range of climate variability and for analyzing environmental conditions before any meteorological or ecological records are available from the region (Pons *et al.* 2017).

Among their many applications, tree-ring studies can assist in making improved natural resources management decisions and can encompass reconstructions of different regional climate and environmental patterns including drought, streamflow, fire history, and land-use change (Woodhouse and Lukas 2006; Therrell *et al.* 2007; Swetnam *et al.* 2010).

Despite extensive research in dendrochronology during the last century, studies have been more limited in the tropics compared to temperate zones and regions of higher latitudes (Jacoby 1989; Stahle 1999; Roig 2000). A primary reason for this is the complex tree-ring morphology, biodiversity, and climate sensitivity of tropical species. The absence of distinct temperature and daylength seasonality may prevent dormancy and the formation of anatomical ring boundaries typically used to study tree rings (Roig 2000). Without the formation of annual tree rings and large-scale environmental influences on their growth variability, it is impossible to date samples or extract a common signal unless complex chemical analysis tools are utilized (Fritts 1976; Jacoby 1989; Evans and Schrag 2004; Anchukaitis and Evans 2010; Rozendaal and Zuidema 2011). Another challenge related to the development of tropical tree-ring chronologies is the lower potential for replicability, as tropical biodiversity can make it difficult to identify and sample a sufficient number of individual trees of the same species at a site (Jacoby 1989).

Following guidelines for identifying tree species in the tropics that produce annual rings proposed by Stahle (1999), pinabete growing in the mountains of Guatemala was found to be an ideal candidate for tropical investigations (Anchukaitis *et al.* 2013, 2015). While other tropical species of *Abies* have been successfully studied in Mexico (Huante *et al.* 1991), pinabete had not previously been used in tree-ring chronologies. Anchukaitis *et al.* (2013) demonstrated that pinabete growing near 3,500 meters in the Sierra de los Cuchumatanes in western Guatemala forms annual rings, shows consistent detectable interannual growth patterns between trees, and is suitable for the dating process known as “crossdating”. Ring width variation was found to be predominantly influenced by both early growing season soil moisture conditions and late dry season rainfall (Anchukaitis *et al.* 2013). In a further study, Anchukaitis *et al.* (2015) emphasized this connection and statistically reconstructed January through March precipitation levels from 1710 to 2009 using pinabete ring widths. While the reconstruction revealed that current precipitation seasonal patterns are not outside the range of natural variability, future drying is predicted to be a robust regional consequence of anthropogenic climate change and is projected to be more severe in the future (Neelin *et al.* 2006). Though not statistically significant, Anchukaitis *et al.* (2013, 2015) observed negative correlations between ring widths and regional gridded temperature data.

To assess the relationships between western highland forests and large-scale climate dynamics in Central America, Anchukaitis *et al.* (2013, 2015) correlated ring widths with sea surface temperature (SST) anomalies in the eastern tropical Pacific. Significantly negative correlations revealed that El Niño events are often associated

with low growth years for pinabete (Anchukaitis *et al.* 2013). Many models show an increased frequency of El Niño Southern Oscillation (ENSO) in future climate model projections (Steinhoff *et al.* 2015), which could stress ecosystems, limit freshwater availability, and threaten food security (Karmalkar *et al.* 2011; Eitzinger *et al.* 2012). Understanding the regional impacts of large-scale modes like ENSO is of interest, as its frequency and strength have implications that reverberate throughout both the environment and society (Giannini *et al.* 2001; Cai *et al.* 2015).

Our study at Totonicapán contributes a novel and longer-term perspective on the response of pinabete to climate at a distinct location lower in the species' elevational range and distinguished by a strong history of forest conservation. Limited historical climate records and the lack of knowledge surrounding species and regionally specific sensitivities to changing climate conditions impede the potential to propose adaptive management schemes that effectively confront changes in Guatemala (CONAP 2010; INAB 2013a). As an “umbrella species”, additional insights that support managing for the success of pinabete would also result in conditions that benefit many other species living in the same habitat (Strandby Andersen *et al.* 2006). Currently, the endangered status of pinabete and the robust climate projections for future drying throughout Central America place these forests and the ecosystem services and resources they provide at risk. Here, we present analyses of tree rings from pinabete in Totonicapán in order to better understand how climate influences regional forest growth and to explore future vulnerability of this important species and the iconic forests they inhabit.

Methods

Our field and laboratory approach followed methods standard in dendrochronology (Fritts 1976; Cook and Kairiukstis 1990). We collected increment cores in November of 2010 from living *A. guatemalensis* growing in coniferous forests at approximately 3,000 meters in elevation in Totonicapán, Guatemala (14.92°N, -91.32°W) (Figure 1). The pronounced seasonality in precipitation makes Totonicapán an appropriate location for traditional dendroclimatological studies. The specific site was selected in consultation with community forest managers, aiming to include older trees while maintaining relatively homogeneous microsite conditions that were representative of the larger stand characteristics. In order to maximize the length of our tree-ring chronology and the climate signal contained therein, we intentionally sampled older trees that appeared to have limited access to resources, a standard practice in dendroclimatology (Fritts 1976). Two or three samples were collected per tree.

We mounted and sanded each core before using conventional skeleton plotting techniques to crossdate the samples (Douglass 1941). The process of crossdating allows us to match ring-width patterns on specimens from within and between trees to determine and verify the calendar year of formation for each ring (Douglass 1941; Fritts 1976). Though all samples used in this chronology were from

living trees with an outermost ring of 2010, we were unable to simply count the tree rings due to the complex wood anatomy and the previously identified tendency for pinabete trees to occasionally exhibit locally absent rings or suppressed growth (Anchukaitis *et al.* 2013). We used exceptionally narrow, abnormally wide rings, and other distinct anatomical wood characteristics to aid in the crossdating process and to confirm each ring was assigned the correct calendar year. In total, we analyzed 45 cores from 22 trees. The number of cores per tree included in the dataset ranged from one to three.

We completed ring width measurements with 0.001 mm precision using a Velmex unislide stage micrometer connected to a Metronics digital encoder box. We assessed the quality of crossdating and the measurement accuracy of the series using COFECHA (Holmes 1983). After accounting for any potential errors, we calculated the mean site tree-ring chronology using the computer program ARSTAN (Cook 1985) with the same parameters as Anchukaitis *et al.* (2013). Ring widths were first scaled using the adaptive power transformation (Cook and Peters 1997). Detrending curves were calculated using a 50-year cubic smoothing spline to remove the influence of tree geometry and stand disturbances (Cook and Peters 1981). Ring-width indices were calculated as the difference of the measurement value from the fitted curve value. The site level chronology was calculated as the Tukey biweight robust mean value of all indices available for each year, and finally, the low-order serial autocorrelation was modeled and removed. The result of this standardization process, standard to dendroclimatology, is a site-level “residual” chronology free of trends related to age bias, varying tree geometries, and non-climatic biological persistence (Cook *et al.* 1990). In the final site chronology, values greater (less) than one represent above (below) average growth. Statistics of mean between-tree correlation (\bar{r}) and the Expressed Population Signal (Briffa *et al.* 1990) were used to assess the common signal strength of annual growth conditions for *A. guatemalensis* in Totonicapán.

We compared our time series to regional climate data using a seasonal correlation analysis described by Meko *et al.* (2011) for one, four, six, and eight-month time periods. Using the nearest gridpoint to our site, we extracted monthly precipitation data from the Global Precipitation Climatology Centre (GPCC, version 7; Schneider *et al.* 2015) and monthly temperature data from the Climatic Research Unit (HadCRUT4, Morice *et al.* 2012) to compare with our time series. The significance thresholds of $\alpha=0.05$ and $\alpha=0.01$ were evaluated by exact simulation (Percival and Constantine 2006). The temporal stability of these correlations was checked through a comparison of the specified non-overlapping periods from 1914–1979 and 1980–2010 (Meko *et al.* 2011).

We also correlated the chronology with tropical Pacific sea surface temperature (SST) anomalies to investigate the relationship between pinabete growth and ENSO events. We chose the monthly NINO3 SST Index, which computes an average monthly SST value in the eastern tropical Pacific Ocean from 5°S–5°N and

170–120°W using the HadISST1 dataset (Rayner *et al.* 2003). We composited and mapped the monthly SST anomalies for the tree growth years that fell below the 10th and above the 90th percentiles. Although we included years through 1930, *in situ* SST data is extremely limited in much of the tropical Pacific before the 1960's (Deser *et al.* 2010). Lastly, we compared our chronology with the strongest July–September El Niño and La Niña events from the National Oceanic and Atmospheric Administration (NOAA 2017).

Results

We crossdated a total of 45 cores from 22 trees. Three cores (TOT21A, TOT21B, and TOT24A), all from two of the oldest trees, were poorly correlated with the rest of the ring-width series and were not included in the final site chronology due to their recent growth suppression. Therefore, our master chronology from Totoncapán consists of 42 cores from 21 trees, has a mean series intercorrelation of 0.434, and spans the period from 1842 to 2010 (Figure 2A). At 1950, 1900, and 1850, sample size is 41, 24, and six cores, respectively (Figure 2B), with the number of individual trees typically represented by half as many. The Expressed Population Signal (EPS) statistic is above the arbitrary 0.85 threshold for the period 1918–2010, and is above 0.75 back through 1878 (Figure 2C).

Only one ring was locally absent in the entirety of the dataset used to make the master chronology; core TOT24B was missing a ring in 1998. However, growth suppression in the most recent decades and some indistinguishable ring boundaries made it impossible to successfully assign calendar years to the outermost portion of several trees ($n=8$) (Figure 3A). In these periods of suppressed growth, it is likely that there are additional missing rings. For example, in core TOT02B, we identified 41 rings between 1960 and 2010, meaning nine rings were ‘missing’ or so suppressed that they were unidentifiable. Traumatic damage to rings (Anchukaitis *et al.* 2013) was not consistent between trees or even within the core from a single tree, and therefore did not assist in dating the rings. For example, TOT28C displays signs of trauma in 1956 and 1958, but core TOT28B from the opposite side of the tree does not have any anatomical features indicative of damage (Figure 3B), despite a match in the ring widths themselves. Relative ring widths and the presence of false rings proved to be the most reliable markers while crossdating the samples (Figure 3C).

Our climate data comparison results indicate a consistently positive relationship between annual ring-width variability and precipitation that is statistically significant for several individual months and seasonal groupings (Figure 4). For single-month comparisons, October most strongly correlates with precipitation ($r=0.25$, $p<0.05$). August ($r=0.21$) from the year prior to growth, and February ($r=0.21$) from the growth year are also significant at the 0.05 level. August–November and July–October exhibit the strongest relationship with annual tree-ring growth for four-month seasonal correlations ($r=0.34$, $p<0.01$). Ring width is most

highly correlated with the eight-month seasonal value from prior July to present February ($r=0.37$, $p<0.01$).

There is also a consistently negative relationship between annual tree growth and temperature, after accounting for the influence of precipitation (Figure 4). For single-month comparisons, only December is statistically significant at the 0.01 level ($r=0.30$). November ($r=0.22$) and April ($r=0.25$) are also significant, but at the 0.05 level. Statistically significant four-month and six-month correlations demonstrate a similar response; November–February ($r=0.24$) and November–April ($r=0.25$) are both significant at the 0.01 level. Precipitation and temperature correlation coefficients were not statistically different between sub-periods of the record ($p>0.1$), indicating temporal stability in the climate-tree growth relationships over time.

The tree-ring chronology shows significant negative correlations with eastern Pacific monthly SST anomalies from prior June to present February. This implies that years of below average growth are typically associated with warm SST anomalies in the tropical Pacific or El Niño events. Prior August SSTs are most highly correlated with the time series ($r=0.43$, $p<0.05$). During the month of August prior to the years of lowest growth (<10th percentile), a characteristic El Niño SST pattern is common after 1930 (Figure 5). During these nine years, six develop into a stronger El Niño event throughout the boreal winter and peak by February. Contrary to this coherent pattern, the connection between above average growth years (>90th percentile) and cool SST anomalies in the eastern tropical Pacific is less clear. The typical La Niña pattern in the eastern Pacific is either poorly defined or absent during the highest growth years (Figure 6). Only two growth years above the 90th percentile (1925 and 1989) correspond with the top ten La Niña events defined by the July–September season, but five of the lowest growth years (1931, 1958, 1973, 1984, 1998) coincide with the strongest El Niño events.

Discussion

Tree-Ring Chronology & Wood Anatomy

This study confirms the feasibility of developing precisely dated tropical tree-ring records from pinabete in Totonicapán, which is 500 meters lower in elevation than sites sampled in the Sierra de los Cuchumatanes by Anchukaitis *et al.* (2013, 2015). The new site enriches our understanding of tree growth and climate in the western highlands of Guatemala and allows us to compare regions of the country that are distinct in terms of topography, geology, and climate. The chronology has a reasonable sample size of 30 ring-width series back through the year 1916. Although the interseries correlation is somewhat lower than that of other tropical tree-ring chronologies, including those from Stahle *et al.* (2011) and Anchukaitis *et al.* (2013, 2015), the sample size here is smaller and this in part could contribute to the weaker correlation. While the \bar{r} and EPS statistics suggest that inter-annual growth and

ring-width variability are relatively noisy between trees, our sample does contain a stand-wide common response and captures the theoretical population signal (Briffa *et al.* 1990). These statistics might be improved with sampling of additional trees from the stand (Anchukaitis *et al.* 2015), from trees across nearby stands with similar site characteristics, or by developing regional chronologies to identify large-scale common climate forcing. We are actively pursuing other stands of pinabete to continue to increase the number of tree-ring datasets within the tropics and to develop additional high-resolution proxy records. The wide distributional range of pinabete throughout Central America, which includes parts of El Salvador, Mexico, and Honduras (Donahue *et al.* 1985), continues to make it an exceptionally promising candidate for dendrochronology.

While our crossdating of pinabete at Totonicapán was successful, the complexity of its anatomical structure and the significant periods of recent growth suppression within the cores reinforced the challenges in studying tropical tree rings. In total, only 45 of the 92 cores we sampled in 2010 could be successfully crossdated (approximately 49 percent). However, these dating complications were themselves informative and indicated periods of suppressed growth or disturbance in individual trees, providing anatomical evidence of growth stress at different times across the stand.

In some cases, certain tree-ring measurements were truncated as a result of the extended recent growth suppression. Consistencies in these features across multiple cores suggest that periods of disturbance and stress affected much of the study site. The most severe growth suppression was between the 1950's and the 1980's and was associated with relatively low growth among many other trees in the collection. Although low growth was prevalent during this time, the cores with the most indistinguishable rings were often also from the oldest trees. Among the five oldest trees in the chronology, it was necessary to truncate four of them after the 1950's due to severe growth suppression, lack of crossdating, and unidentifiable ring boundaries. It is conceivable that it is especially difficult for pinabete to continue to produce significant stem growth during periods of anomalous climate or disturbance after a certain point in its lifetime and that pinabete forests as a whole may face additional hurdles as more of the tree population ages (Collins *et al.* 2010). Similar patterns of recent growth suppression were noted in Anchukaitis *et al.* (2013), where it also prevented crossdating in several samples, suggesting that recent suppression is common in stands of pinabete in the western highlands. Further investigations are needed to address whether or not the timing is coincident across sites due to large-scale climatic or ecological factors, or whether this simply reflects similar tree age or demography across stands.

Although traumatic resin ducts did not aid in crossdating, they are another intriguing wood anatomical feature found within many of our samples. Our observation that these anatomical features do not occur simultaneously either within trees or across the forest stand confirms similar findings by Anchukaitis *et al.* (2013).

The inconsistency within and between trees suggests that traumatic rings may be a response to individual disturbances, rather than large-scale site perturbations. Although the cause of this trauma is not known, it calls for additional study to help identify events that may compromise the normal growth processes in pinabete. Possible causes of traumatic resin duct formation include fires, insect or fungal attacks, and mechanical wounding associated with human use and management (Bollschweiler *et al.* 2008; Stoffel 2008).

One possible origin of further interest is injury caused by insects; *Mindarus guatemalensis*, an aphid found in Totonicapán, is known to reduce physical growth and to directly cause discoloration of the needles (Reynoso Duarte 2008). *Dendroctonus spp.* has also been known to attack pinabete when growing in stands with *Pinus rudis* Endl. (CAMCORE 1985). Another potential source of disturbance worth additional exploration is the removal of branches for Christmas greenery and trees. Pinabete is a desired species for this purpose and new technologies and increased access to tools including chainsaws and trucks have added to forest thinning today (CONAP/INAB 1999; Conz 2014). Direct impacts from harvesting branches from mature pinabete trees include localized, but severe injury and increased susceptibility to secondary damage (Ignosh and Kilgore 2005). Considering these anatomical features and the climate relationships described below, it is clear that there are multiple factors that influence the growth and vulnerability of individual trees within the stand and across the forests of Totonicapán as a whole.

Climate & Tree Growth Relationships

Guatemala faces likely changes in precipitation that would imperil the western highland forests (Jones *et al.* 2016). In addition to a projected negative trend in summer (JJA) precipitation over the Caribbean Sea and much of Central America (Neelin *et al.* 2006), Rauscher *et al.* (2008) suggests that the peak rainfall in June will diminish and that the Mid-Summer Drought will increase in severity. The period after the Mid-Summer Drought is typically wetter than the first (Taylor and Alfaro 2005), so reduced rainfall during this time in conjunction with declining dry season precipitation would favor species better suited towards dry environments (Imbach *et al.* 2012). Based on our chronology from Totonicapán, pinabete would likely experience increased stress and reduced growth as a result of these changes in precipitation, as the period of rainfall after the Mid-Summer Drought is critical for tree growth in the subsequent year.

Not only is regional summer drying expected, but Magrin *et al.* (2014) project more frequent dry extremes in all seasons. While the influence of early growing season moisture, particularly from February to April, is more important in the Cuchumatanes chronologies (Anchukaitis *et al.* 2013, 2015), both the Totonicapán and Cuchumatanes chronologies are positively correlated with precipitation in the boreal winter and the start of the transition to the rainy season. This relationship indicates the importance of the limited dry season rainfall for total annual tree

growth of pinabete throughout the western highlands and further suggests that model projections of future robust drying in all seasons will have an extensive negative impact across highland forest communities.

Warming temperatures will be an additional stress on tree growth (Neelin *et al.* 2006; Magrin *et al.* 2014). The significant negative relationship between ring-width variability and temperature at our site suggests potential growth consequences from future warming and highlights the sensitivity of pinabete specifically at Totonicapán. While the Cuchumatanes were negatively correlated with gridded temperature data, none of these secondary temperature correlations were statistically significant (Anchukaitis *et al.* 2015). However, a combination of drought and warming temperatures are among the drivers known to increase forest vulnerability and background tree mortality rates across the globe by directly impacting physiological processes and indirectly inducing stress through pests and pathogens (Allen *et al.* 2010; Allen *et al.* 2015). Ultimately, identification of these climate-tree growth relationships here provides species-specific knowledge at a new site and strengthens arguments made in a report by Guatemala's National Institute of Forests (INAB 2013a), which states that effective management strategies are immediately and urgently needed to address changing climate conditions that will likely negatively impact the current ecosystems of the western highlands.

Considering the limited spatial and temporal coverage of meteorological land stations in Central America, the climate record that pinabete holds is especially important. The nearest station to Totonicapán has instrumental records with many temporal gaps and extends only to 1980 (Instituto Nacional de Electrificación 2017). For this reason, we have used gridded climate data in our study, which almost certainly results in lower climate correlations. The lack of instrumental data not only has an impact on our study, but has more generally impeded understanding regional climate dynamics and interannual climate variability, particularly in areas of complex topography like western Guatemala. The number of operational meteorological stations in Central America has decreased over the last several decades, which further complicates monitoring of climate variability and detection and attribution of climate change (Giannini *et al.* 2001). Therefore, the information that can be gained from tree-ring chronologies from pinabete is invaluable for climate adaptation and vulnerability reduction (Pons *et al.* 2017). By increasing sample replication within and between forest stands, we hope that these datasets can lead to robust climate reconstructions, which can be used to evaluate model simulations and to increase their skill in the tropics.

Large-scale variability & a complex relationship with ENSO

The 168-year record developed here also allows us to analyze large-scale modes of variability at interannual to decadal time scales in the context of a changing climate. Due to the critical importance of ENSO on regional hydroclimate in Central America (Steinhoff *et al.* 2015), it is of particular interest to explore its connections to

both forest growth and local climate in Totonicapán using our tree-ring chronology. Although responses to both positive and negative SST anomalies are reflected in our ring-width chronology, the relationship to ENSO appears to be asymmetric, with a stronger response to drying associated with El Niño events and a much less coherent connection to La Niña events. The El Niño signal is strongest from July to October throughout Central America (Ropelewski and Halpert 1987), which agrees with our precipitation correlations and emphasizes the importance of rainfall after the Mid-Summer Drought for tree growth. During the rainy season prior to an El Niño event, centers of convergence shift away from the region and produce drier than average conditions (Ropelewski and Halpert 1987; Giannini *et al.* 2000). Our analysis shows that boreal fall and winter soil moisture deficits negatively affect tree growth in the following calendar year. For example, the 1997–1998 El Niño had a strong SST signal in the eastern Pacific in the summer of 1997 and continued to develop through November. This event was one of the strongest ENSO events in the last century and corresponded with the only missing ring in the dataset as well as the lowest growth year in the overall chronology (1998).

In contrast to the link between tree growth and El Niño events, the relationship with La Niña is less straightforward, and above average growth does not always correspond to cold eastern tropical Pacific SST anomalies. Similar observations for a weaker and more complex La Niña connection have been previously discussed by Ropelewski and Halpert (1989), who characterize the time instability of the connection between La Niña and above average precipitation across Central America and the Caribbean. However, these observations suggest that there are other competing large-scale influences over the climate of Totonicapán that impact rainfall and therefore tree growth and that the ENSO state is, by itself, not sufficient to predict or explain local precipitation anomalies (Enfield and Mestas-Núñez 2000; Anchukaitis *et al.* 2013).

Replication would help us further investigate the influence of ENSO in the western highlands and throughout Central America. Although there is uncertainty in future model projections, Cai *et al.* (2015) conclude that teleconnection patterns are likely to remain stable, suggesting that the western highlands of Guatemala would continue to experience reduced precipitation associated with an El Niño event. The modeling experiments by Cai *et al.* (2015) also indicate SST anomalies characteristic of warm-phase El Niño events are likely to become more common in the future. A higher frequency of El Niño events or the development of a mean state that is similar to El Niño would likely contribute to increased moisture stress and reduced growth in pinabete based on our results. This is somewhat alarming as ENSO related droughts have already increased background tree mortality rates in some places in Central America (Allen *et al.* 2010).

In addition to responding to interannual ENSO events, our tree-ring chronology also demonstrates strong decadal variability. Hastenrath and Polzin (2012) found that the climate of Central America has alternated between periods of

decreased and enhanced rainfall regimes with abnormally high wet periods from 1931–1938 and 1950–1956 and dry from 1939–1947 and 1971–1978. These anomalous periods of wetness and dryness are generally captured by the 10-year spline that overlays the master chronology (Figure 6). Not only does this connection provide useful information regarding tree growth, the existence of persistent wet and dry periods may also be relevant climate knowledge for smallholder farmers in the western highlands (Pons *et al.* 2017).

Importance of the Totonicapán forests in a changing climate

Beyond the vulnerabilities suggested by the climate correlations and potential shifts in mechanisms driving Central American climate, external social and economic pressures will also likely challenge the long history of conservation. In the past, the K'iche' were able to maintain their land, social institutions, and communal identity, which promoted the preservation of the forests, because the Guatemalan state neglected their local governance structures (Ekern 2010). More recent pressures from the state government to convert communal lands into protected areas have often disregarded traditional forms of knowledge, undermining the local governance framework (Elías and Wittman 2005; Elías 2008, 2009). In addition to new top-down management schemes that fail to consider the existing social and management structures, other threats include the cutting of pinabete branches for Christmas trees, overgrazing, land conversion, timber harvest, and the high value of the firewood economy (CONAP/INAB 1999; Taylor *et al.* 2011).

In spite of external pressures from a multitude of sources, the western highland forests remain pivotal in terms of biodiversity and are the headwaters of the majority of Guatemala's watersheds within a region that already experiences limited access to water resources (Elías *et al.* 2009; Elías 2012; Pons *et al.* 2017). INAB (2013b) reports that the areas of greatest forest cover are found in zones dominated by indigenous Maya groups and often coincide with communal forest lands. This observation reemphasizes the critical importance of the forests of Totonicapán, as the location of the largest remaining stand of pinabete in Guatemala. As of 2007, only 14.48 percent of Guatemala remained classified as communal lands (INAB 2013b). Therefore, stands of pinabete and their invaluable environmental and economic resources outside of communal forest lands and protected areas are even more threatened. Although it is beyond the scope of the current study, it would be relevant to investigate sustainable management practices and timber rotation through a tree-ring analysis of growth rates and microsite conditions. These diverse and potentially interacting factors call for continual review of the Totonicapán forests and the development of additional climate knowledge to better understand the environmental risks they confront.

Conclusions

This study develops and interprets a new 168-year long pinabete (*Abies guatemalensis*) tree-ring width chronology from Totonicapán, made possible by persistent and substantial forest cover in the community due to historically active management by the K'iche'. This represents an important geographic and scientific expansion of a burgeoning tree-ring chronology network in Guatemala and confirms annual ring formation and precise annual dating in pinabete, while highlighting regional variation in the seasonal window of climate that influences tree growth. Analysis of complex ring morphology exposes periods of stress, apparently common among the oldest trees, and intriguing wood anatomical characteristics including false rings that may in the future prove useful for studying sub-seasonal environmental conditions. We identify regional climate sensitivity through correlations between the site-level chronology from Totonicapán and regional gridded climate data, demonstrating that late boreal summer to winter precipitation is most significant for the variation in tree growth in the subsequent year. In general, we observe a positive relationship between ring-width variability of pinabete and precipitation and a negative relationship with temperature. On a broader scale, the asymmetrical relationship between tree growth and ENSO reveals pronounced connections to El Niño events and a variable response to La Niña events.

Ultimately, the sensitivity of pinabete at Totonicapán to climate and large-scale mechanisms suggests it will become more vulnerable in the face of anticipated regional drying and warming. Despite the efforts of the local population to protect the forests, these pressures are likely to cause significant challenges for the sustained success of pinabete. Therefore, additional research in collaboration with the local community (Pons *et al.* 2017) is needed to further examine the competing large-scale influences on tree growth in Totonicapán and its applications to adaptive management strategies for these protected, extant forests. Considering the potential climate threat to the Totonicapán forests, we also hope to continue to extend the range of these tree-ring chronologies in order to better understand this spatially complex and diverse region and to provide useful data for climate modeling and forest management.

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Captions

Figure 1. (A) Topographic map of the department of Totonicapán showing 2012 forest cover (GIMBUT 2014) and study site. (B) Photo of the study site in Totonicapán in November 2010. Color version available online.

Figure 2. Totonicapán Chronology. (A) Core-level ring width indices (red) and the robust average site-level chronology (black), calculated as described in the methods section. (B) Sample size. (C) Expressed population signal (EPS) and running interseries correlation (\bar{r}) for 50-year segments, lagged by one year. Horizontal dashed line is fixed at $\text{EPS}=0.85$. Color version available online.

Figure 3. *Abies guatemalensis* tree-ring anatomy. (A) Suppression can result in indistinguishable growth rings, preventing successful crossdating after 1950 for this core. (B) Traumatic rings were inconsistent within and between trees. Trauma is present in both 1956 and 1958 in core TOT28C, but not TOT28B. (C) Distinct false rings (1891, 1895, 1896) and relative ring widths were used to aid crossdating samples. Color version available online.

Figure 4. Correlations and partial correlations (Meko *et al.* 2011) of the master chronology with precipitation totals (P) and average temperatures (T) for one, four, six, and eight consecutive month seasons. Data from 1914–2010. Shaded colors represent significance at the 0.05 level and darkly shaded colors represent significance at the 0.01 level. Color version available online.

Figure 5. August SST anomalies from the HadISST1.1 dataset. Mapped years include those below the 10th percentile beginning in 1930. Maps range from 30°S–30°N and 120°E–60°W. Color version available online.

Figure 6. Average site-level chronology with a 10-year spline overlay to show decadal variability. Circles represent the top 24 July–September El Niño events and squares represent La Niña events ranked by NOAA using the Extended Multivariate ENSO Index. ENSO events that fall below the 10th percentile and above the 90th percentile are represented with solid circles and squares, respectively. Dotted lines mark the 10th (0.809) and 90th (1.173) percentiles. Color version available online.