



Latitudinal patterns of species richness and range size of ferns along elevational gradients at the transition from tropics to subtropics

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Abstract

Aim: To assess the range size patterns of ferns and lycophytes along elevational gradients at different latitudes in an ecographical transition zone and search for predictors of range size from a set of environmental factors.

Location: Mexico, from 15° to 23° N.

Taxon: Ferns and lycophytes.

Methods: All terrestrial and epiphytic species were recorded in 658 plots of 400 m² along eight elevational gradients. To test whether the range size within assemblages increases with elevation and latitude, we calculated the latitudinal range using the northern and southern limits of each species and averaged the latitudinal range of all species within assemblages weighted by their abundances. We related climatic factors and the changes with latitude and elevation with range size using linear mixed-effects models.

Results: Species richness per plot increased with elevation up to about 1,500–2,000 m, with strong differences in overall species richness between transects and a reduction with increasing latitude. The mean weighted range size of species within assemblages declined with elevation, and increased with latitude, as predicted by theory. However, we also found marked differences between the Atlantic and Pacific slopes of Mexico, as well as low range size in humid regions. The best models described about 76%–80% of the variability in range size and included the seasonality in both temperature and precipitation, and annual cloud cover.

Main conclusion: Latitudinal and elevational patterns of range size in fern assemblages are driven by an interplay of factors favouring wide-ranging species (higher latitudes with increasing temperature seasonality; dryer habitat conditions) and those favouring species with restricted ranges (higher elevations; humid habitat conditions), with additional variation introduced by the specific conditions of individual mountain ranges. Climatically stable, humid habitats apparently provide favourable conditions for small-ranged fern species, and should accordingly be given high priority in regional conservation planning.

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KEY WORDS

distribution, diversity, elevation, endemism, latitude, pteridophytes, Rapoport's rule

1 | INTRODUCTION

One of the most striking patterns in nature is the enormous variation of range sizes of species, ranging from species which occur only in a few square meters to others that are found across the entire globe (Brown, Stevens, & Kaufman, 1996; Gaston, 1998). This variation is not random, but shows distinct patterns related to environmental and geographical conditions as well as the evolutionary history and ecological requirements of the taxa (Kreft, Jetz, Mutke, & Barthlott, 2010; Lomolino, Riddle, Brown, & Brown, 2006; Smith, 1993). Accordingly, a number of ecogeographical rules have been developed to capture these relationships.

One of these rules is Rapoport's rule (RR), which proposes that the latitudinal range size of species is greater at higher latitudes, and that tropical species tend to have smaller ranges allowing more species to coexist in tropical versus temperate regions (Stevens, 1989). Originally conceived for latitudinal gradients, the idea that range sizes may be determined by climatic seasonality was later extended to elevational gradients as well (Stevens, 1992, climatic variability hypothesis). While these patterns have been documented for a wide range of taxa in many regions (Addo-Bediako, Chown, & Gaston, 2000: insects; Ribas & Schoereder, 2006: many groups; Morin & Lechowicz, 2011: trees; Pintor, Schwarzkopf, & Krockenberger, 2015: lizards; Tomašových et al., 2016: birds and marine bivalves), there are also a good number of studies, mainly along elevational gradients in animals but also in plants, that do not corroborate the rule or even reporting a reverse pattern or mixed results suggesting that it varies between taxa and continents (Bhattarai & Veetas, 2006; Pintor et al., 2015; Ribas & Schoereder, 2006; Rohde & Heap, 1996; Rohde, Heap, & Heap, 1993; Ruggiero, 1994; Zhou et al., 2019). Support for the rule is also scarce in the tropics (Blackburn & Gaston, 1996; Rhode, 1996).

Even if a pattern of range size distribution accords to RR, there are a number of complications in understanding the underlying processes. The classic assumption is that temperature conditions are more seasonal at higher latitudes (Stevens, 1989, 1992). When species adapt to these conditions, they widen their niche breadth (tolerance breadth; Slatyer, Hirst, & Sexton, 2013; Stevens, 1992) and thus attain wider geographical ranges. However, the spatial distribution of climatic conditions may vary with latitude or elevation so that even if species have constant niche breadths, this will result in different range size patterns. Furthermore, the classical interpretation of RR focusses only on temperature seasonality, even though seasonal variations in humidity may be equally important for explaining the range size distributions (Gaston & Chown, 1999; Pintor et al., 2015). Especially in the tropics, where there is little seasonal variation in temperatures, variations in precipitation patterns may play an important role. Finally, latitudinal and elevational climatic gradients, while sharing many similarities, also have crucial differences. For instance, elevational ranges (amplitudes)

of species typically increase with elevation (Janzen, 1967; Kessler, 2001; McCain, 2009; Sklenář & Jørgensen, 1999; Stevens, 1989, 1992), which would support RR. However, geographical range sizes (total area) on average decrease with an increase in elevation (Kessler, 2000, 2002, 2010; Kessler & Kluge, 2008; Steinbauer et al., 2016). One explanation is that rugged mountainous terrain habitats with patchy distributions ('sky islands') support fragmented species populations that are more prone to speciation than species inhabiting extensive habitats without geographical barriers (Antonelli, Nylander, Persson, & Sanmartín, 2009; Kessler, 2001; Kruckeberg & Rabinovitz, 1985; McCormack, Huang, Knowles, Gillespie, & Clague, 2009). Besides, past climatic fluctuations determining the connectivity between sky islands may be an important driver of diversification by leading to successive cycles of population expansion and fragmentation ('flickering connectivity systems'; Flantua & Hooghiemstra, 2018; Flantua, O'dea, Onstein, Giraldo, & Hooghiemstra, 2019). Clearly, understanding the spatial variation of species range sizes along latitudinal or elevational gradients requires more detailed understanding than suggested by the conceptually simple RR.

Thus, putting species range sizes into a broader context, range sizes are influenced by a wide range of geographical and evolutionary factors. For instance, species with restricted range sizes are often found in localized habitats, either geographically such as on oceanic islands or environmentally, such as on specialized geological substrates (Carlquist, 1974; Kier et al., 2009; Kruckeberg & Rabinovitz, 1985; Major, 1988). In addition, the geological and evolutionary history of a region also plays an important role in determining current species distributions (Brown et al., 1996; Lomolino et al., 2006). For example, Mexico is exceptionally rich in endemic species in numerous taxonomic groups, which is related to its high geological and environmental heterogeneity (Brummitt, Aletrari, Syfert, & Mulligan, 2016; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000; Rzedowski, 1962, 2006; Tryon, 1972). In particular, dry forest and desert areas are characterized by high endemism and super-endemism (high levels of neo- and paleo-endemics; Sosa & De Nova, 2012; Sosa, De-Nova, & Vásquez-Cruz, 2018). Accordingly, the arid Pacific side of the country is a centre of endemism for many groups of plants and animals, presumably due to the long-term environmental stability of the region (Lott & Atkinson, 2006; Rzedowski, 2006). To a lesser degree, endemism has also been associated with humid forests, which in Mexico are distributed as habitat islands forming an intracontinental habitat archipelago (Llorente-Bousquets, Escalante-Pliego, Darwin, & Welden, 1992).

Determining the causes of the geographical distribution of range sizes is important in a conservational context because a small range size is one of the main predictors of extinction risk of species (Purvis, Gittleman, Cowlishaw, & Mace, 2000). In this sense, the current availability of large databases of species distributions and occurrence records offers outstanding opportunities to document and understand



range size patterns and other large-scale patterns of biodiversity across geographical and environmental gradients. Nevertheless, many biases have been detected in large data banks, such as gaps in the available information, uncertainties in species identification/taxonomy and distributional information, errors in occurrence coordinates, and incomplete species richness for poorly explored regions (Meyer, 2016; Meyer, Weigelt, & Kreft, 2016; Qian et al., 2018). Yet, the improvement of these databases in the last years, and their careful and critical use, depending on the study objectives and region, make them an important tool in macroecology and biogeography.

Ferns and lycophytes (hereafter jointly referred as 'ferns' for simplicity) are taxonomically well-studied and well-suited groups to investigate biogeographical questions because of their spore dispersal (wind-borne), which makes them largely independent from biotic dispersal agents (Barrington, 1993), and thus links patterns of range sizes and endemism mainly to abiotic factors. Additionally, ferns are a moderately species-rich group, still manageable to handle when seeking to conduct a full census within a study area, but diverse enough to show a wide range of range size patterns and to allow for quantitative analyses. With more than 1,088 recorded species (J. D. Tejero-Díez, pers. com., 2019), they are well represented in Mexico, which has one of the best-documented fern floras in the world (Mickel & Smith, 2004). Generally speaking, ferns are physiologically more limited by drought and low temperatures than angiosperms (Brodrribb & McAdam, 2011; Brodrribb, McAdam, Jordan, & Field, 2009) so that their diversity declines more steeply towards arid and cold climatic conditions (Kreft et al., 2010). As a result, fern diversity peaks in tropical montane cloud forests and declines towards lower and higher elevations and higher latitudes (Kessler, Kluge, Hemp, & Ohlemüller, 2011; Khine, Kluge, Kessler, Miehe, & Karger, 2019; Salazar et al., 2015).

Little is known about the distribution of range sizes in ferns. In Costa Rica, Bolivia and Kenia (Kessler, 2001; Kluge & Kessler, 2006; Zhou et al., 2019), fern ranges tend to decrease with elevation, but the latitudinal patterns and the relationship to climatic factors remain unexplored. Nevertheless, considering that fern diversity peaks in the most humid habitats, and that such very wet habitats have a localized and patchy distribution (Killeen, Douglas, Consiglio, Jørgensen, & Mejia, 2007; Llorente-Bousquets et al., 1992; Sanginés-Franco et al., 2015), it seems reasonable to expect that fern species adapted to such conditions have similarly localized and patchy ranges.

In this study, we explored the patterns of latitudinal range size of ferns along eight elevational gradients located at different latitudes in the Mexican transition zone from the tropics (south of Mexico) to the subtropics (30 km south of the Tropic Cancer Line), which is considered a global biodiversity hotspot (Myers et al., 2000) and a centre of fern endemism (Brummitt et al., 2016). We asked whether mean range sizes of fern assemblages vary with latitude and elevation, specifically hypothesizing that mean range sizes increase with latitude as Rapoport's rule proposes (H1) and decrease with elevation (H2). We further hypothesized that mean range sizes increase with increasing environmental stress factors such as low temperature, precipitation, humidity and high climatic seasonality (H3a). Conversely, we predict that mean range sizes decrease with increasing humidity due to the water dependency of the

study group, related to the geographical fragmentation of environmentally suitable areas for specialized ferns (H3b).

2 | MATERIALS AND METHODS

2.1 | Study area

The Mexican transition zone is the complex area where the Neotropical and Nearctic biotas overlap, and in a strict sense corresponds to the mountain highlands of Mexico, Guatemala, El Salvador and Nicaragua (Halffter & Morrone, 2017). We here present data from eight elevational gradients at a range of 0 to 3,500 m elevation at 15–23° latitude N on both the Pacific and Atlantic (Gulf of Mexico) sides of Mexico (Figure 1; Table S4). Three transects have been considered in previous studies: Los Tuxtlas (Acebey, Krömer, & Kessler, 2017; Krömer, Acebey, Kluge, & Kessler, 2013), Perote (Carvajal-Hernández & Krömer, 2015; Carvajal-Hernández, Krömer, López-Acosta, Gómez-Díaz, & Kessler, 2017) and Oaxaca (Hernández-Rojas et al., 2018). Los Tuxtlas including abundances was not published before ('Los Tuxtlas a'). Both transects from Los Tuxtlas were combined for the majority of the analysis.

2.2 | Fern sampling

On each gradient, we sampled the fern assemblages at regular elevational intervals of 100–300 m (every 500 m at Perote), depending on accessibility. At each elevation, depending on the suitability of the slope, 4–8 plots of 20 × 20 m (400 m²) were sampled with a consistent, standardized methodology (Karger et al., 2014; Kessler & Bach, 1999). The plots were established in natural zonal forest, avoiding special structural features like canopy gaps, ridges, ravines, riparian areas, tree fall gaps, landslides and other disturbed areas whenever possible, which all change microenvironmental conditions and have special fern assemblages. In each plot, all fern species and their abundances were recorded for terrestrial (soil, rocks and dead wood) and for epiphytic substrates. Species with long creeping rhizomes were counted as patches. Epiphytes were sampled up to heights of 8 m with trimming poles and recorded at greater heights using binoculars, climbing lower parts of trees, and searching recently fallen trees and branches within and adjacent to the plots (Gradstein, Nadkarni, Krömer, Holz, & Nöske, 2003; Sarmento Cabral et al., 2015).

Samples of all fern species were collected and deposited in the University Herbarium, University of California (UC) in Berkeley, USA, herbarium XAL of the Instituto de Ecología, A. C. (Xalapa, Mexico), MEXU of the Universidad Autónoma de México (Mexico City, Mexico), CIB of the Instituto de Investigaciones Biológicas (Universidad Veracruzana, Xalapa, Mexico), HEM of the Universidad de Ciencias y Artes de Chiapas (Tuxtla Gutiérrez, Mexico) and UAMIZ of the Universidad Autónoma Metropolitana-Iztapalapa (Mexico City, Mexico). Collections were identified by A. R. Smith (UC), A. Hernández-Rojas and C. Carvajal-Hernández. Taxonomy primarily

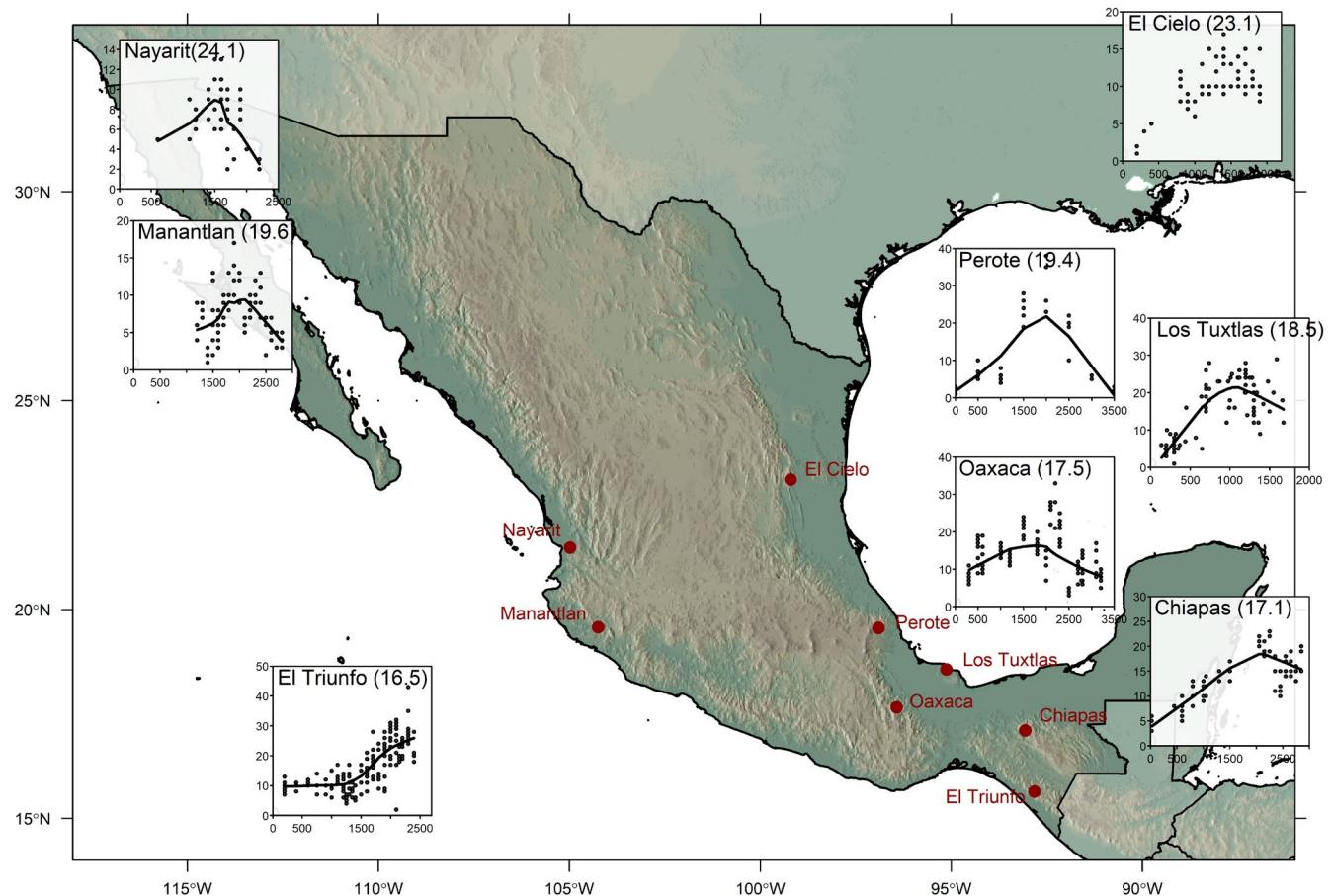


FIGURE 1 Location of the eight study transects and their fern species richness patterns at the transition from tropics to the subtropics in Mexico between 15° and 23° N. Red points represent the mean latitude of all plots per site, indicated in every richness panel [Colour figure can be viewed at wileyonlinelibrary.com]

followed Mickel and Smith (2004) and the current classification for ferns and lycophytes established by the Pteridophyte Phylogeny Group (PPG I, 2016). Species names and authors were checked on the International Plant names Index (IPNI).

2.3 | Explanatory variables

Ferns are closely dependent on climatic variables related to humidity because their sexual reproduction is linked to the presence of water (Page, 2002) and because of their poor stomatal control (Brodrribb & McAdam, 2011; Kessler, 2001). Because water stress is not only determined by water input into a system (by precipitation or fog) but also by evapotranspiration which is related to high temperatures, we specifically included energy- and humidity-related variables as predictors of species distribution and their range size. Besides temperature and precipitation and their temporal variability, cloud cover is also a suitable predictor in this context because clouds reduce solar radiation and provide extra 'occult' precipitation (Bruijnzeel & Veeneklaas, 1998; Hartmann, 1993). Thus, we extracted the following climatic variables per plot from the global climate database set CHELSA (Karger et al., 2017): Annual mean temperature and precipitation (Bio1, Bio12), as well as temperature and precipitation seasonality (Bio4, Bio15). From 'EarthEnv', we extracted

annual cloud cover and its seasonality (CloudA, CloudS; Wilson & Jetz, 2016). We checked for collinearity between the climatic variables using the Variance Inflation Factor (VIF; Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014). Variables with values > 6 were not used in the same model (e.g. elevation and annual temperature), but all variables were included in different models of the same analysis. We also included the position in the country (Pacific and Atlantic side) as a fixed factor because the sides are known to have different biogeographical histories and habitat connectivity, leading to markedly different patterns of endemism for many groups of organisms (Rzedowski, 2006).

2.4 | Species ranges

We used the latitudinal range (range between the northern and southern range limits) of each species as a simple gradual measure of range size. To quantify the latitudinal ranges of the species, we used American species occurrences combined with our own records for a total of 173,110 species records. Data were obtained from the Biodiversity Information Facility (Gbif, www.gbif.org, accessed August–September 2018) databank using the 'RGBI' package in R (R Core Team, 2019). Coordinates of fossil records and specimens from botanical gardens or herbaria were excluded. To detect errors and suspicious patterns



(outliers) within the dataset, we mapped the coordinates and checked the latitudinal range of each species using 'MAPTOOLS' (Bivand & Lewin-Koh, 2019). Range sizes were checked against TROPICOS, Catalogue of Life (Hassler 2020), Mickel and Smith (2004), Labiak and Prado (2007), Vasco, Moran, and Rouhan (2009), Larsen, Martínez, and Ponce (2010), Vasco (2011), Labiak (2011), Lehnert (2013), Smith and Tejero-Díez (2014), Lóriga, Vasco, Regalado, Heinrichs, and Moran (2014), Arana, Larsen, and Ponce (2016), Barbosa-Silva et al. (2016), Villaseñor (2016), Kessler and Smith (2017), Ponce, Rio, Ebihara, and Dubuisson (2017) and Smith et al. (2018), and suspicious and wrong observations were corrected (e.g. coordinates in the sea).

With these latitudinal ranges, we calculated the mean range size of all species (excluding species varieties and species identified only up to genus) in each individual plot as an index of range size within the assemblage (plot). To account for different species abundances within assemblages, we also calculated a 'weighted mean' including the number of individuals of the species, thus down-weighting rare species. The aim of this weighting was to reduce the influence of species that do not belong to the core communities at a site: Because of their spore dispersal, many fern species can occasionally or temporarily occur outside of their core ranges, and such sink populations can strongly impact species richness patterns (Kessler, Hofmann, Krömer, Cicuzza, & Kluge, 2011; Kessler, Salazar, Homeier, & Kluge, 2014).

2.5 | Statistical analysis

We used linear mixed-effects models (LMMs) to control for the non-independence among data points in assessing changes in the species ranges with elevation, latitude and in relation to climatic variables (fixed effects) because these models allow for spatial autocorrelation between neighbours (Crawley, 2007; Zuur et al., 2009), and likelihood ratio tests (LRT) or 'deviance tests' to compare between a null model without the term of interest and the model including this term to determine if one is a better fit to the data than the other (Luke, 2017; Winter, 2019). For the model including climatic variables or many fixed effects, we used the mixed function in the package 'afex' that performs a full suite of likelihood ratio tests for all fixed effects in a model and constructs the correspondent comparison model providing p values for all fixed effects in a model (Singmann, Bolker, Westfall, Aust, & Ben-Shachar, 2019; Winter, 2019). All variables used in the models were scaled.

We also tested the random structure of our models using the restricted maximum likelihood (Winter, 2019) choosing the different transects and groups of plots in the same elevation (Transect/Step) as random effects for the analysis of all transects together. The analysis by individual transects was performed using 'Step' or group of plots in the same elevation as a random effect to avoid overfitting the model with a complex random structure.

To evaluate the association between range size, latitude, elevation and the climatic variables, we calculated the Spearman correlations. Because climatic variables interact in complex ways in relation to latitude, elevation and position in the country (Atlantic and Pacific

sides of Mexico, 'Side') and because our data were not perfectly balanced with regard to these factors (e.g. different elevational spans of the transects), we additionally ran a model with these climatic variables against the residual of the model including latitude, elevation and side.

For model selection, we used the dredge function in the R 'MuMin' package (Barton, 2019). To decide whether such a simplified model was an enhancement to the previous model, we calculated the cAIC (conditional Akaike Information Criterion; Saefken, Ruegamer, Kneib, & Greven, 2018), with a lower cAIC indicating a better model. The amount of variation explained by the fixed (marginal R^2) and random effects (conditional R^2) of each model was calculated using the 'MuMin' package (Barton, 2019; Nakagawa & Schielzeth, 2013). Residuals of models were checked (see example in Appendices). All analyses were performed with the statistical platform R (R Core Team, 2019), using the packages 'usdm' (Naimi et al., 2014), 'LME4' (Bates, Maechler, Bolker, and Walker (2015), 'AFEX' (Singmann et al., 2019) 'MuMin' (Barton, 2019), 'cAIC4' (Saefken & Ruegamer, 2018), 'VEGAN' (Oksanen et al., 2019) and 'GGEFFECTS' (Lüdecke, 2018, to plot the models).

3 | RESULTS

In total, in the 658 plots along the eight study transects, we recorded 410 fern species and 8 varieties, representing about 40% of the Mexican fern flora (Mickel & Smith, 2004; Villaseñor, 2016; J. D. Tejero-Díez, 2019, pers. com., Table S3). Generally speaking, species richness per plot increased with elevation up to about 1500–2000 m, but with strong differences in overall species richness between transects and a reduction with latitude (Figures 1 and 2). No fewer than 17.1% of the species were recorded in only one plot, 26.2% in 2–5 plots, 22.5% in 6–15 plots and only 34.0% in 16 or more plots. The most species-rich families were Polypodiaceae (97), Dryopteridaceae (76), Pteridaceae (44) and Hymenophyllaceae (31). Latitudinal range sizes of species ranged from 0.6° in *Goniopteris tuxtlensis*, a localized endemic, to 138.3° in the widespread species *Cystopteris fragilis*. Overall, mean latitudinal range size was 30.7°. The family Dryopteridaceae presented the smallest mean range sizes ($19.3^\circ \pm 17.7^\circ SD$, latitude), Polypodiaceae ($24.7^\circ \pm 19.2^\circ$), Pteridaceae intermediate ranges ($38.5^\circ \pm 20.3^\circ$) and Hymenophyllaceae the largest ones ($45.1^\circ \pm 15.0^\circ$).

Mean latitudinal range sizes of species in an assemblage increased with latitude ($X^2(1) = 7.71$, $p < .01$) on both the Atlantic and Pacific sides, and decreased with elevation on the Atlantic side ($X^2(1) = 9.56$, $p < .01$). Overall, Pacific and Atlantic sides differed, presenting smaller range sizes on the Atlantic side ($X^2(1) = 11.5$, $p < .01$, Figure 3). Including a random intercept and random slope models (Range size–Elevation) allowed us to see different tendencies between transects (Figure S5 in supplementary material).

The analysis of individual transects showed contrasting results with different climatic factors related to latitudinal range size along each transect (Table 1; Figure 2). The same was true when separating the data by side and by elevational group. When

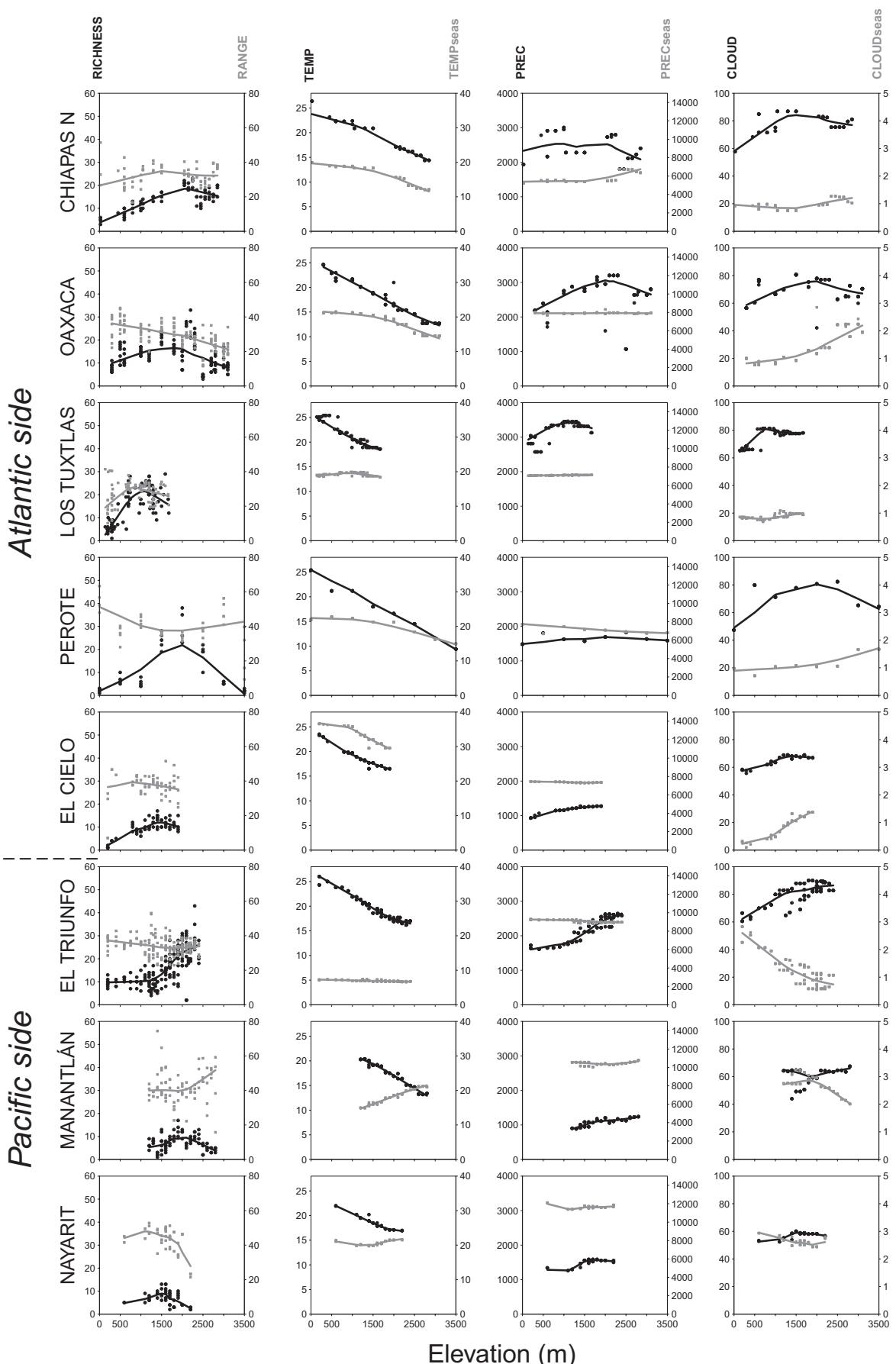




FIGURE 2 Richness and range size patterns of ferns, and environmental factors along eight elevational transects in Mexico at 15°–23° N. Transects are ordered by continental sides (Atlantic, Pacific) and latitude (from south to north within each side)

separating sides, variables related to humidity were important for the Pacific side, whereas the seasonal variability in temperature and humidity were important on the Atlantic side. Incorporating all transects and separating elevational groups, we found that in the upper part of the mountains, temperature was crucial, in the lowlands, precipitation and at intermediate elevations, the seasonal variation of precipitation. Also, using these elevational groups but separated by sides, we found that on the Atlantic side, precipitation seasonality was important at all elevations, whereas on the Pacific side seasonality in both precipitation and temperature was important.

The use of all transects together allowed us to find general patterns and the explanatory power increased significantly in terms of the variance described by the fixed effects when combining all transects using side (Pacific and Atlantic) as fixed effect in the models (Table 1).

Integrating all environmental variables in a global model (full model) including all transects revealed that the most important terms were side, precipitation seasonality annual cloud cover and temperature seasonality (Figure 4b,c,f), this model explained 62% of the variability in range size but even more (70%) when using weighted values (Table 1 and Appendices). With this division, high seasonality in temperature was related to larger range sizes on both sides, whereas high precipitation seasonality was related to small ranges on the Atlantic slope and large ranges on the Pacific slope. Annual cloud cover showed a negative relationship to range size on the Pacific side but not on the Atlantic side (Figure 4c).

When the effect of latitude, elevation and side of the country was controlled using the residuals of this model (Model less) against the climatic variables still some climatic variables remained important (Table 2), showing that they have strong effect on range size, mainly the seasonality.

In general, small values of range size were found at intermediate values of precipitation seasonality, low temperature seasonality and a high annual cloud cover. The humid Atlantic side presented a higher proportion of small range size species relative to the dry Pacific side (Figure 4). All models were checked and no pattern was left in the residuals.

4 | DISCUSSION

The main results of our study can be summarized in the following five points. First, overall latitudinal range size increased with increasing latitude. Second, range size decreased with elevation on the Atlantic slope but not on the Pacific slope. Third, range size decreased in areas with high humidity, low temperature seasonality and intermediate precipitation seasonality, as well as constant cloud cover. Fourth, there was a strong difference in range size between the Pacific and Atlantic sides that was not captured by the climatic factors, with ranges on the Pacific side being much broader. Fifth, we found great variation between individual transects.

Our results confirm the first hypothesis, that on average, latitudinal species ranges become wider at higher latitudes, which is in accordance with Rapoport's Rule (Stevens, 1989). This pattern has been previously documented for algae (Santelices & Marquet, 1998) and other plant (Stevens, 1992) and animal groups (Stevens, 1996: marine fishes; Fleishman, Austin, & Weiss, 1998: butterflies; Swaegers et al., 2014: dragonflies; Böhm et al., 2017: snakes) mainly in the northern hemisphere, and while not fundamentally novel, it is confirmative for ferns and reflects the representativeness of our data. Because temperature and precipitation seasonality showed a linear trend with latitude, we can exclude the possibility that this pattern was driven by a spatially unequal distribution of climatic seasonality, which would result in different range sizes despite equal climatic niche breadths (Gaston & Chown, 1999; Tomašových, Jablonski, Berke, Krug, & Valentine, 2015). Rather, it seems likely that increasingly stressful and variable climatic conditions require broader climatic tolerances of the species, resulting in wider climatic niches and accordingly larger ranges (Janzen, 1967; Stevens, 1989).

In contrast, our second hypothesis that range sizes of ferns should decrease with elevation (Zhou et al., 2019) was supported only on the Atlantic (Gulf of Mexico and Caribbean) side of Mexico, whereas on the drier Pacific side we detected no elevational trend. A decrease in range size with elevation has also been found in ferns in Costa Rica (Kluge & Kessler, 2006) and Bolivia (Kessler, 2002), as well as in other plants and animals (e.g. Gifford & Kozak, 2012; Steinbauer et al., 2016), and is likely linked to topographic complexity, leading to geographically fragmented species ranges which foster allopatric speciation (Antonelli et al., 2009; Kessler, 2001). This effect appears to be most pronounced in wet tropical climates (Kier et al., 2009) or areas of favourable ocean currents that create refugia for endemics (Harrison & Noss, 2017), as found on the Atlantic slope. In addition, formation of endemic species might also be related to past climatic fluctuations that led to successive periods of habitat connectivity and disruption (Flantua & Hooghiemstra, 2018), although this remains to be tested for the Mexican mountains.

The lack of this pattern on the Pacific side is puzzling, but may be related to its overall aridity, since we found that fern range sizes increase with increasing aridity (Figure 4e,f). Interestingly, for drought-adapted plant groups such as *Bursera* (Rzedowski, 2006), *Ipomoea* (Lott & Atkinson, 2006) or many ferns that prefer arid conditions such as *Anemia* or cheilantoid ferns like *Argyrochosma*, *Gaga*, *Myriopteris* and *Notholaena* (Mickel & Smith, 2004), the Pacific slope of Mexico is a well-known centre of endemism. The same is true for insect groups like bees that thrive in arid environments (Bye, Lot, Fa, & Gonzalez-Montagut, 1993). It thus appears that in the case of ferns on the Pacific slope of Mexico, the expected elevational effect on species range sizes is overridden by stressful climatic factors.

In this regard, we found overall that latitudinal range sizes of ferns were smallest in areas of high precipitation and cloud cover.

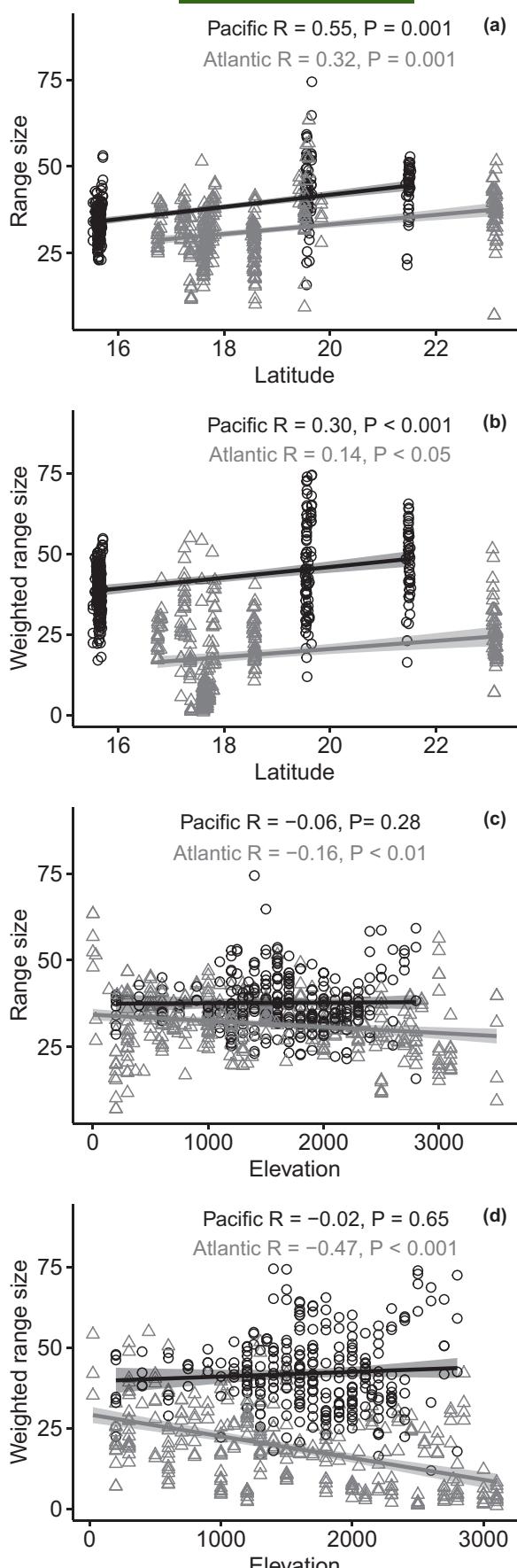


FIGURE 3 Relationship between latitudinal range size of ferns, latitude and elevation along eight elevational transects in Mexico between 15° and 23° N (Spearman correlation). Pacific side, black circles; Atlantic side, gray triangles. For weighted range sizes, only the seven transects were included

Ferns are well known to have highest diversity in wet habitats (Hemp, 2001; Hietz, 2010; Kessler, Kluge, et al., 2011; Kluge & Kessler, 2005), presumably as a result of their less efficient control of stomatal transpiration as compared to angiosperms (Brodrribb & McAdams, 2011; Brodrribb et al., 2009; Page, 2002). Accordingly, it is reasonable to propose that wet habitats, which in Mexico are present mainly on the Atlantic side (e.g. 4,000–7,000 mm/a at Los Tuxtlas; Gutiérrez-García & Ricker, 2011 or La Chinantla; Meave, Rincón-Gutiérrez, Ibarra-Manríquez, Gallardo-Hernández, & Romero-Romero, 2017) and whose distribution decreases northwards, act as localized refuges for many fern species that depend on such conditions. Because of the localized distribution of the habitats, the species will accordingly have localized ranges. In contrast, species capable of surviving in dryer, more widespread habitats will have broader ranges. Species range sizes decreased in areas with less seasonality of both precipitation and cloud cover only on the Atlantic side. This may reflect the generally more favourable conditions for ferns on this side (Figure 4).

In addition, we also found transect-specific patterns that are not captured by the general relationships discussed so far. This supports the idea that individual mountain ranges are unique depending on their geology, topographical profiles and past climatic fluctuations, resulting in individual 'mountain fingerprints' (Flantua & Hooghiemstra, 2018). We refrain from discussing the individual transect patterns in more detail pending replicated sampling in the different mountain ranges to confirm the patterns, but point out that there appear to be range-specific patterns that merit future investigation.

Based on all of the above, we conclude that the distribution of range size of Mexican ferns is driven by an interplay of factors favouring wide-ranging species (higher latitudes with increasing temperature seasonality; dryer habitat conditions) and those favouring species with restricted ranges (higher elevations; more humid habitat conditions), with additional variation introduced by the specific conditions of the individual mountain ranges. The interactions of these factors are complex and are strikingly different between the Atlantic and Pacific slopes of Mexico so that under certain conditions, specific relationships may be overshadowed by other relationships (Tejero-Díez, Torres-Díaz, & Gual-Díaz, 2014). This shows that understanding the distribution of species range sizes should not be simplified too much and that understanding the distribution of range sizes must take into consideration a wide range of factors at various spatial scales. This is also relevant for conservation action, in which range-restricted or endemic species are frequently given priority due to their higher extinction risks (Purvis et al., 2000). Since climatic conditions are currently strongly changing,



TABLE 1 Likelihood ratio test results with p values for all fixed effects in the Linear mixed models (Coefficients), by transects, sides (A = Atlantic and P = Pacific) and elevational groups, using Step or group of plots in the same elevation as a random factors. For all transects together, the Transect/Step random factor structure was used. Similar values in the marginal (R^2m) and conditional R^2 (R^2c) indicates that a linear model is the adequate model with the same coefficients. Bio1, Bio4: annual mean temperature and its seasonality, Bio12, Bio15: annual precipitation and its seasonality and CloudA, CloudS: annual cloud cover and its seasonality. Significance codes: *** $p < .001$, ** $p < .01$, * $p < .05$

Transect	Side	Bio1	Bio4	Bio12	Bio15	CloudA	CloudS	R^2m	R^2c
Triunfo (16.5)			490.06***		80.92***		-15.85***	0.21	0.34
Manantlan (19.6)				-113.45*		-25.92***		0.38	0.38
Nayarit (21.4)		80.88***	187.77*	156.06**	-219.29**			0.41	0.59
ChiapasN (17.1)				-14.94**		-13.03*	-73.85**	0.55	0.55
Oaxaca (17.5)		38.22***	-95.07***			11.14*		0.64	0.83
Tuxtla a(18.5)			72.28*	-22.82**	-462.44**			0.34	0.34
Tuxtla b(18.5)						38.21*	99.60*	0.45	0.45
Perote (19.4)		23.24*				46.97*		0.58	0.62
Cielo (23.1)		-82.21*		-242.12*			-83.17**	0.38	0.57
Pacific: all plots					-15.48*	-10.22***	-12.99***	0.23	0.35
Atlantic: all plots			-3.66*	-5.49***	-7.06**		-8.09**	0.56	0.77
Atlantic per elevational groups									
0-700			-33.51***	-14.98***	-7.08*	-12.84***	-44.82***	0.40	0.40
701-1300			19.66**	10.12*	-11.35**	10.36*		0.76	0.82
1301-1800					-23.48**		-56.58*	0.86	0.86
1801-1400		-17.88*	-9.15**		-10.56**	-33.46**	-40.44**	0.71	0.71
2401-3500			73.30*		-52.53***			0.92	0.92
Pacific per elevational groups									
0-700		138.13*	920.32*		824.89*	-152.64**	-222.10**	0.68	0.68
701-1300			-188.60*		-189.81*			0.24	0.24
1301-1800						-15.60**	-18.95*	0.30	0.34
1801-1400		66.37***	179.57***	63.85***	-119.05***			0.45	0.58
2401-3500								0.46	0.46
By elevational groups (no division between Atlantic and Pacific)									
0-700			-11.09**			-8.14***	-9.68**	0.33	0.33
701-1300				-7.48**				0.58	0.85
1301-1800			-9.46***			-6.94*		0.46	0.68
1801-1400			-8.69**	-6.87**	5.90**			0.50	0.71
2401-3500		32.66**	47.91**					0.76	0.83
All transects (no division between Atlantic and Pacific)				-5.04**	-10.12*	-5.40***	-5.7**	0.23	0.93
All transects (Step as random effect)									
		A: 49.55***		-3.63*	-10.88**	-5.34***	-5.53***	0.62	0.81
Best model (climatic variables)		P: 47.95***	5.62***		-10.85***	-2.96***		0.59	0.76
Random effect: Step)									

understanding the underlying causal relationships rather than only the current patterns of the distribution of range-restricted species is crucial to making informed predictions about the future of many plant

species. Our study points to the overriding importance of climatically humid and stable habitat islands for fern conservation while acknowledging regional variation.

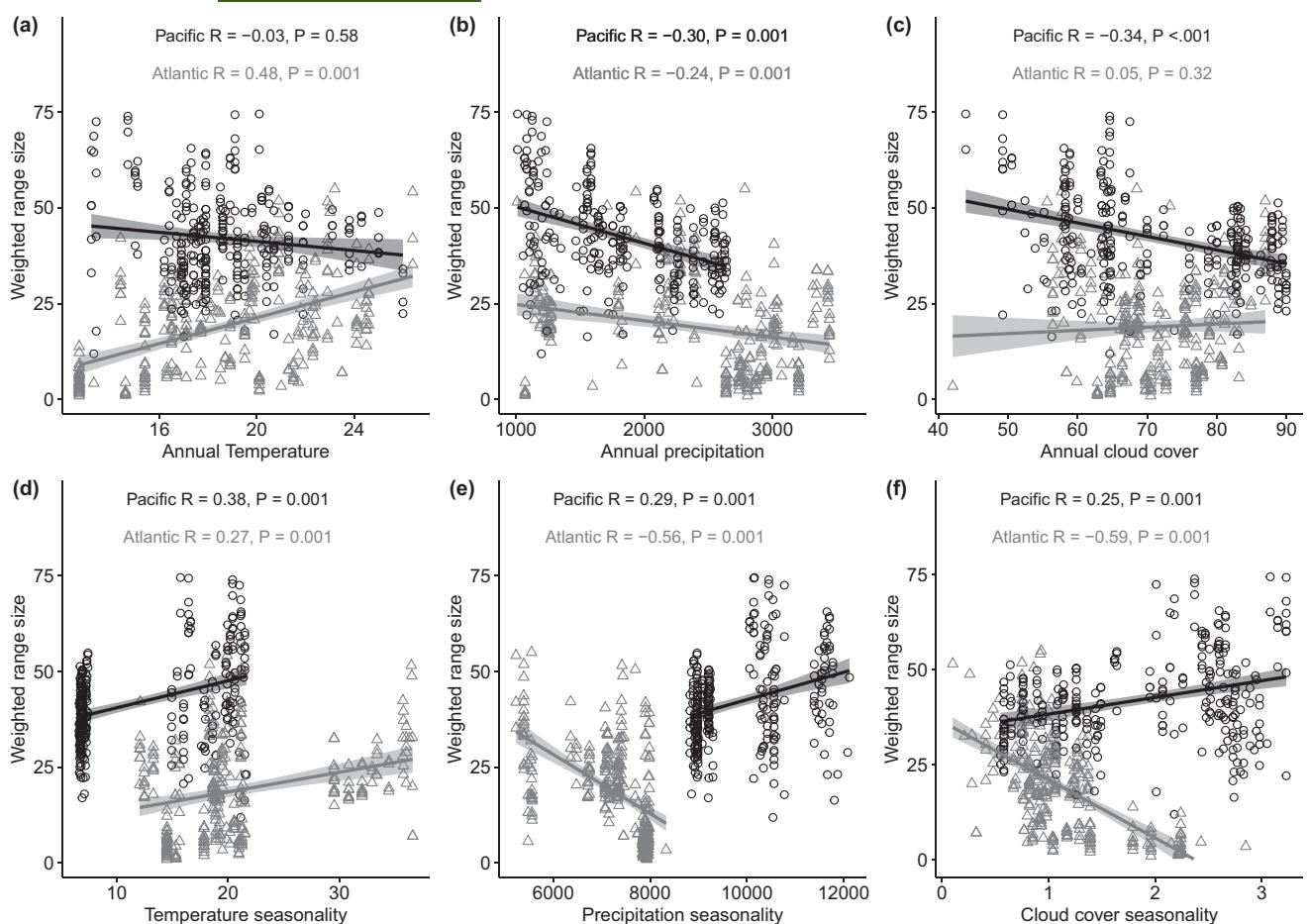


FIGURE 4 Relationship between climatic variables and range size of ferns along eight elevational transects in Mexico between 15° and 23° N (Spearman correlation). Pacific side, black circles; Atlantic side, gray triangles

TABLE 2 Model selection table derived from the model including the residuals of range size (and weighted range size) explained by latitude, elevation and Side (Model les) using as random effect the transect. Full model: Residuals of model les ~ Bio1+Bio4 + Bio12+Bio15 + CloudA+CloudS. Bio1, Bio4: annual mean temperature and its seasonality, Bio12, Bio15: annual precipitation and its seasonality and CloudA, CloudS: annual cloud cover and its seasonality

Model	Response variable	Fixed effects	df	AICc	Delta	Weight
1	Residual of non-weighted range size	Bio15 + Bio4+ CloudA	7	4,306.3	0.00	0.25
2		Bio15 + Bio4+CloudA + Bio12	8	4,306.3	0.04	0.25
3	Residual of weighted range size	CloudS + CloudA+Bio4 + Bio1	8	4,186.0	0.00	0.45
4		CloudA + CloudS+Bio4	7	4,186.4	0.42	0.37

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DATA AVAILABILITY STATEMENT

The data on which this study was based are available in Dryad. Dryad DOI: doi:10.5061/dryad.7h44j0zr2



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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX

TABLE A1 (Continuation) Likelihood ratio test results (Non-weighted range sizes), with p values for all fixed effects in the linear mixed models (Coefficients), by transects, sides (A = Atlantic and P = Pacific) and elevational groups, using step or group of plots in the same elevation as a random factors. For all transects together the Transect/Step random factor structure was used. Similar values in the marginal (R^2m) and conditional R^2 (R^2c) indicate that a linear model is the adequate model with the same coefficients. Bio1, Bio4: annual mean temperature and its seasonality, Bio12, Bio15: annual precipitation and its seasonality and CloudA, CloudS: annual cloud cover and its seasonality. Significance codes: *** $p < .001$, ** $p < .01$, * $p < .05$

Transect (latitude)	Side	Bio1	Bio4	Bio12	Bio15	CloudA	CloudS	R^2m	R^2c
Triunfo (16.5)			196.28**					0.32	0.39
Manantlan (19.6)				-100.21**	50.15*	-19.52***		0.31	0.31
Nayarit (21.4)		48.16***		75.36**	-112.83**			0.60	0.72
ChiapasN (17.1)				-7.45**			-37.43***	0.48	0.48
Oaxaca (17.5)								0.46	0.62
Tuxtla (18.5)b			72.28*	-22.82**	-462.44**			0.34	0.34
Perote (19.4)		23.24*				46.97*		0.58	0.62
Cielo (23.1)		-77.93*		-200.12*			-56.49*	0.29	0.53
Pacific: all plots						-8.21***	-7.40***	0.40	0.52
Atlantic: all plots				-3.64***				0.22	0.63
Atlantic per elevational groups									
0-700		-14.97**	-27.99**	-13.66***		-10.30**		0.47	0.58
701-1300				-5.16***	3.73*	5.06**		0.56	0.65
1301-1800								0.54	0.58
1801-1400			22.24*		-29.39*			0.31	0.65
								0.54	0.64



TABLE A1 (Continued)

Transect (latitude)	Side	Bio1	Bio4	Bio12	Bio15	CloudA	CloudS	R ² m	R ² c
Pacific per elevational groups									
0-700						-62.97*		0.63	0.63
701-1300				81.45*		42.98	-62.16*	0.79	0.79
1301-1800						-6.39*		0.56	0.56
1801-1400		30.76***	91.91***	29.59**	-67.49***			0.36	0.67
2401-3500								0.38	0.38
By elevational groups (no division between Atlantic and Pacific)									
0-700			-8.63*	-7.19**		-6.01*		0.31	0.59
701-1300				-2.53*				0.48	0.75
1301-1800				-2.17*		-4.66**		0.50	0.59
1801-1400				-2.19*				0.17	0.43
2401-3500					6.46*			0.43	0.64
All transects (no division between Atlantic and Pacific)						-2.25**		0.18	0.67
All transects (transect/step as random effects)									
		A: 19.20***		3.7**		-4.83*	-2.49**	0.31	0.65
Best model		P: 17.16***		3.45***		-4.11***	-2.36***	0.28	0.62
Latitude model									
		A: 7.39*	3.42*					0.24	0.61
Elevation model									
			-1.65**					0.13	0.62