



# Fern and lycophyte niche displacement under predicted climate change in Honduras

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**Abstract** Ferns and lycophytes are excellent model organisms to investigate the effect of climate change on species niches, due to their high sensitivity to changes in temperature and precipitation. In Honduras, this species group is particularly diverse with over 713 known taxa. However, we currently lack a quantitative assessment of the impact that changes in climate might have on these species. This study aimed (1) to explore the structure of the available climatic conditions across the entire country; (2) to determine the extent to which the available climatic space is occupied by different fern and lycophyte species; and (3) to assess which regions of climatic space will be most affected according to scenarios of climate change. We analyzed a newly developed database of herbarium fern records ( $n = 11,791$ ) and used ordination models to compare the climatic niche of all

Honduran fern and lycophyte taxa under present and future climates. We found that species were distributed throughout most of the available climatic space. Under RCP2.6 and RCP8.5 projections 128 to 391 species will have their average niche positions outside of the predicted available climatic space by the years 2049–2099. Particularly affected will be species that grow in low temperature and high precipitation areas, which represent high altitude parks, such as Celaque National Park. Epiphytes showed smaller variance in their climatic niches than terrestrial species. However, terrestrial species showed higher loss in climate space (e.g., 82.9% vs. 17.1% for RCP8.5) and are more likely to be at risk in the future. In general, Honduras is expected to become drier, with more extreme events of severe drought. Considering that ferns are particularly sensitive to changes in climate, if tested in the future, they could be used as a proxy for other Honduran plant taxa.

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## Introduction

The climatic niche—i.e., the climatic conditions associated with the occurrence of a given species—has come to the forefront of much of recent ecological and evolutionary research, given that it provides a natural intersection of many distinct fields, from

ecophysiology and invasion biology to biogeography and macroecology (Petitpierre et al. 2012; Khaliq et al. 2015; Wasof et al. 2015; Atwater et al. 2018). For instance, climatic niches are at the core of the concept of phylogenetic niche conservatism (Wiens and Donoghue 2004), which has been instrumental to understand the biogeographical distributions of a variety of taxa, as well as the origin of latitudinal gradients of species diversity (e.g., Buckley et al. 2010; Kerkhoff et al. 2014). Instead of considering all biotic and abiotic dimensions that can be part of Hutchinson's ecological niche as an  $n$ -dimensional hypervolume (Hutchinson 1957), the focus on a subset of climatic variables that make up the climatic niche is both practical and heuristic. The increasing availability of high-quality climatic layers in recent years, including past, present, and future climatic conditions (Brown et al. 2018; Karger et al. 2017; Sugiyama et al. 2010), has allowed for the first time in recent decades to readily analyze climate data across large geographical regions. In addition, the emphasis on abiotic conditions can provide an overall framework against which biotic conditions such as ecological interactions can be tested against. Indeed, the preeminence of the study of climatic niches is likely to increase in the near future, as we seek to understand how species will respond to the challenges imposed by anthropogenic climate change (Quintero and Wiens 2013; Jezkova and Wiens 2016; Herrera et al. 2018; Meyer and Pie 2022).

A common way in which studies on climatic niche evolution are carried out involves extracting bioclimatic conditions associated with occurrence data of a set of species, calculating species means and then use ordination patterns to understand the structure of interspecific variation in their climatic niches (e.g., Kamilar and Muldoon 2010; Duran and Pie 2015; Ramírez-Barahona et al. 2016; Pie et al. 2017). Although it has provided important insight into how climatic niches evolve in different lineages, one important limitation of this approach is that it does not explicitly take into account the fact that climatic conditions are not isotropic. Rather, some combinations of climatic conditions might be more common in geographical space, whereas other combinations might simply not occur in nature. Such variation in the relative commonness of environmental conditions (environmental prevalence, sensu Meyer and Pie 2018) can constrain the climatic niches that different

species are able to occupy. For instance, interspecific variation in climatic niche breadth might ultimately be the result of the prevalence of different combinations of climatic variables rather than physiological tolerances (Pie et al. 2021). Therefore, it is important that climatic niches should be interpreted with respect to the actual distribution of climatic niche space in which they occur.

Ferns and lycophytes are important components of global plant diversity. Current data suggest that there are approximately 13,000 fern and lycophyte taxa globally (PPGI 2016). They are particularly diverse in the humid tropics (Suissa et al. 2021), making up around 8.2% (1,358) of all vascular plants in Central America (16,335) (Moran and Riba 1995; Ulloa et al. 2017), and in some cases can account for a very large proportion of species in forest inventories (Linares-Palomino et al. 2009). It is believed that approximately 25% of ferns are epiphytes (i.e., plants that live on other plants for physical support but are not parasitic) and it has been shown that they are the third most species-rich group of vascular epiphytes globally (Zotz 2013). In Mesoamerica, for example, the most species-rich countries for ferns are Costa Rica, Mexico, and Panama (Reyes et al. 2021a). Given the prevalence of reproduction through spores, ferns in particular tend to be excellent dispersers and therefore are often believed to be more likely to occur whenever there are suitable conditions for their establishment and growth (although this notion has yet to be tested experimentally, Wild and Gagnon 2005). For instance, dispersal by wind in ferns and lycophytes can vary greatly between taxa but many species are known to have remarkable long-distance dispersal abilities (Barrington 1993; Wolf et al. 2001) and thus are often able to overcome geographical barriers more easily than other taxonomic groups (Tyron 1970). However, our understanding of how fern and lycophyte lineages evolved to occupy their current climatic niches is still incipient (Bystriakova et al. 2011; Hernandez-Rojas et al. 2021). Previous evidence suggests that epiphyte and terrestrial species richness respond differently to environmental gradients (Aros-Mualin et al. 2021), indicating that they might show important differences in their climatic niches, yet the extent of those differences is poorly understood (Nitta et al. 2020). The more restricted growth of epiphytic fern and lycophyte

species, for example, makes them more susceptible to changes in atmospheric conditions (Williams et al. 2020; Hernandez-Rojas et al. 2021) and it has been shown that they are also more likely to be at higher risk under future changes in climate (Reyes et al. 2021b). For example, climate variables that are believed to be particularly important to epiphyte diversity are high temperature, water availability (precipitation/humidity), constant cloud cover, and low seasonality (Kromer 2013; Hernandez-Rojas et al. 2020).

In this study we use a large dataset of carefully curated occurrence records of ferns and lycophytes of Honduras to understand the relationship between their climatic niches and their available niche space. Our goals were (1) to use high-resolution climatic layers of temperature and precipitation variables to describe the structure of the available climatic conditions across the entire country; (2) to determine the extent to which the available climatic space is effectively occupied by different fern and lycophyte species, both with respect to their taxonomy and growth habit; and (3) to assess which regions of the available climatic space will be most affected according to scenarios of climate change.

## Methods

### Occurrence data

Fern and lycophyte data from Honduras were extracted from Batke et al. (2022). Their database held a total of 22,194 herbarium records from the years 1870 to 2018. Following the removal of duplicate entries and entries that could not be assigned a spatial reference, we retained 17,539 records. We taxonomically updated all records by cross-referencing all 17,539 records manually using Reyes et al. (2021a) updated checklist of Honduran ferns and lycophytes. The taxonomic validation resulted in 356 taxonomic changes (e.g., including moving species into different families or replacing species due to synonymy). A further 445 records were identified as invalid and were excluded (e.g., species that do not have a valid name). Moreover, we omitted any records with missing epithet information. Following the exclusion of all of these records, we

retained a total of 11,791 (53% of the original database) for further analysis.

### Growth form classification

We used Zotz et al. (2021) new database of vascular epiphytes and cross-referenced it against our database to separate epiphytes from terrestrial species in our analysis. We manually checked each record to ensure that species were assigned the correct growth form classification, based on published data (e.g., Batke et al. 2016; Reyes et al. 2021b) and field experience by the authors. Epiphytes were defined following Zotz (2013) and Zotz et al. (2021).

### Climatic variables

We obtained climate data from Racines et al. (2018a), which include gridded climate surfaces for Honduras (30-year average) calculated from weather station observations from different official sources (local, national, and regional institutions) for the period between 1981 and 2010 at a spatial resolution of 30 s (~1 km<sup>2</sup>). The entire dataset includes 85 variables, including monthly precipitation (prec), monthly minimum temperature (tmin), maximum temperature (tmax), mean temperature (tmean), and diurnal temperature range (dtr), as well as seasonal and annual rasters derived based on the monthly datasets. However, to reduce collinearity in the dataset, we only included annual and seasonal means for those variables. We then carried out a Principal Component Analysis based on a covariance matrix of the remaining 25 bioclimatic variables, which were scaled and centered (i.e., divided and subtracted by the corresponding means and variances, respectively) prior to the analysis. The number of PCs retained for further analyses was based on a broken-stick criterion, as implemented in ‘vegan’ 2.5–7 (Oksanen et al. 2020). We then extracted bioclimatic data from fern and lycophyte occurrence records using the extract function in ‘raster’ 3.4–13 (Hijmans 2021) and projected them onto the principal components calculated previously. To further explore the extent of occupation of different species across the available climate space, we compared the variance in the scores for different ordination quadrants using Levene’s test, as implemented in ‘car’ 3.0–11 (Fox and Weisberg 2019).

Finally, we explored how expected shifts due to climate change could affect the structure of the available climatic space using the predictions by Racines et al. (2018b). We used RCP2.6 and RCP8.5 IPCC projections, as these represent the best case and worst-case climate forcing scenarios. RCP2.6 projects forecasts under the assumption that atmospheric CO<sub>2</sub> concentration will stabilize by the year 2020 and reduce by the year 2100, keeping global temperature rise below 2 °C by 2100. RCP8.5 has been referred to as the worst-case scenario and assumes that emissions continue to rise throughout the twenty-first century. We obtained the values on each grid cell of the same set of climatic variables obtained above and projected them based on the PCA built from the current climate data. We compared the extent of the corresponding climatic spaces by estimating concave hulls, as implemented in ‘concaveman’ 1.1.0 (Gombin et al. 2020). This approach provides a convenient way to assess which regions of climatic space will be most affected by climate change. All analyses were carried out in R 4.1.1 (R Core Team 2021).

## Results

The PCA was efficient in summarizing the variation in climatic conditions across Honduras, with the first two PCs explaining over 91% of the variance in the dataset. The loadings of the PCA are shown in Table 1. PC1 mostly reflected variation in temperature, especially lower temperatures, whereas PC2 loadings described a trade-off between maximum temperature and diurnal temperature range versus precipitation (particularly during autumn and winter). In other words, PC1 describes overall variation in temperature, whereas PC2 can be interpreted as describing relative aridity, with high PC2 scores indicating regions with high maximum temperatures and low precipitation (Fig. 1).

In general, species were distributed throughout most of the available climatic space, indicating that the climatic conditions found throughout Honduras in general tend to be suitable to fern and lycophyte species (Fig. 1). Furthermore, there were several regions within the available climate space where ferns and lycophytes have not been recorded from. For example, regions that experience high temperature and low levels of precipitation have comparatively fewer fern

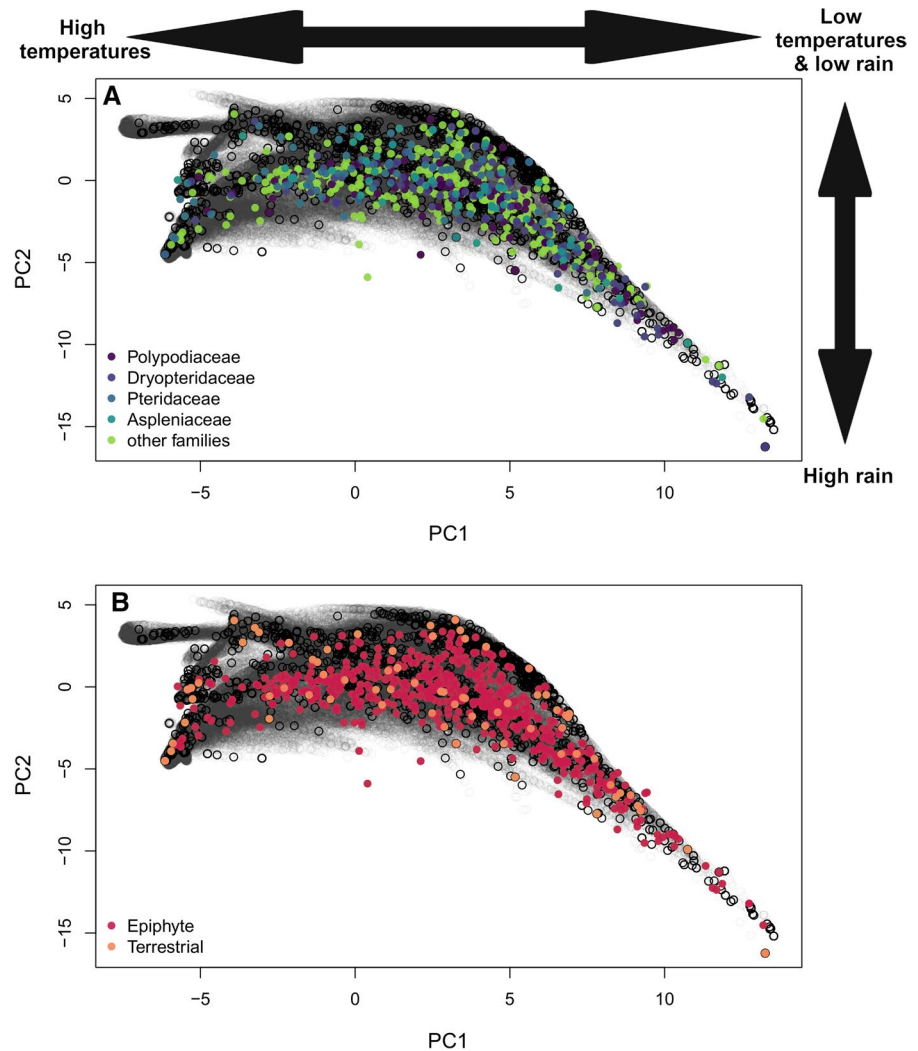
**Table 1** Principal Component Analysis of bioclimatic variables found in Honduras

Variable	PC1	PC2
<i>Annual precipitation</i>	− 0.17	− 0.23
Spring	− 0.14	− 0.15
Summer	− 0.12	− 0.17
Autumn	− 0.18	− 0.23
Winter	− 0.15	− 0.22
<i>Annual diurnal temperature range</i>	0.16	0.28
Spring	0.17	0.26
Summer	0.17	0.27
Autumn	0.14	0.29
Winter	0.15	0.28
<i>Annual maximum temperature</i>	− 0.18	0.26
Spring	− 0.14	0.31
Summer	− 0.2	0.23
Autumn	− 0.2	0.21
Winter	− 0.17	0.27
<i>Annual mean temperature</i>	− 0.24	0.13
Spring	− 0.22	0.17
Summer	− 0.24	0.1
Autumn	− 0.24	0.1
Winter	− 0.24	0.13
<i>Annual minimum temperature</i>	− 0.25	0.01
Spring	− 0.25	0.03
Summer	− 0.25	0
Autumn	− 0.25	− 0.01
Winter	− 0.25	0
Proportion of Variance	0.63	0.29
Cummulative Proportion	0.63	0.92

*DJF* December, January, and February, *JJA* June, July, and August, *MAM* March, April, and May, *SON* September, October, and November

records. Figure 2 shows a geographical projection of the PC scores, clearly indicating that the Departments of Nacaome, Choluteca, and the Rio Ulua in Cortes are comparatively arid. Similarly, the Sierra Madre mountains are defined by lower precipitation and high temperatures, whereas the La Mosquitia region in the northeast are defined by high precipitation and high temperatures (Figs. 1 and 2). In quadrants with negative PC1 scores, species tended to be less frequent, as well as less dense closer to the edges of the available niche space. For example, variance was over four times higher across the available niche space in cooler conditions than in warmer conditions ( $F=45.31$ ,  $p=3.60e-11$ ). It is important to note that

**Fig. 1** Principal component analysis of climatic conditions found in Honduras. All climatic conditions are shown in gray circles. Occurrence of different fern and lycophyte species across the available climate space for **A** the most species-rich families and **B** divided into epiphyte and terrestrial life forms. Closed circles represent species means, whereas black open circles indicate individual records. The arrows on **A** describe the general climate space (see text for details)



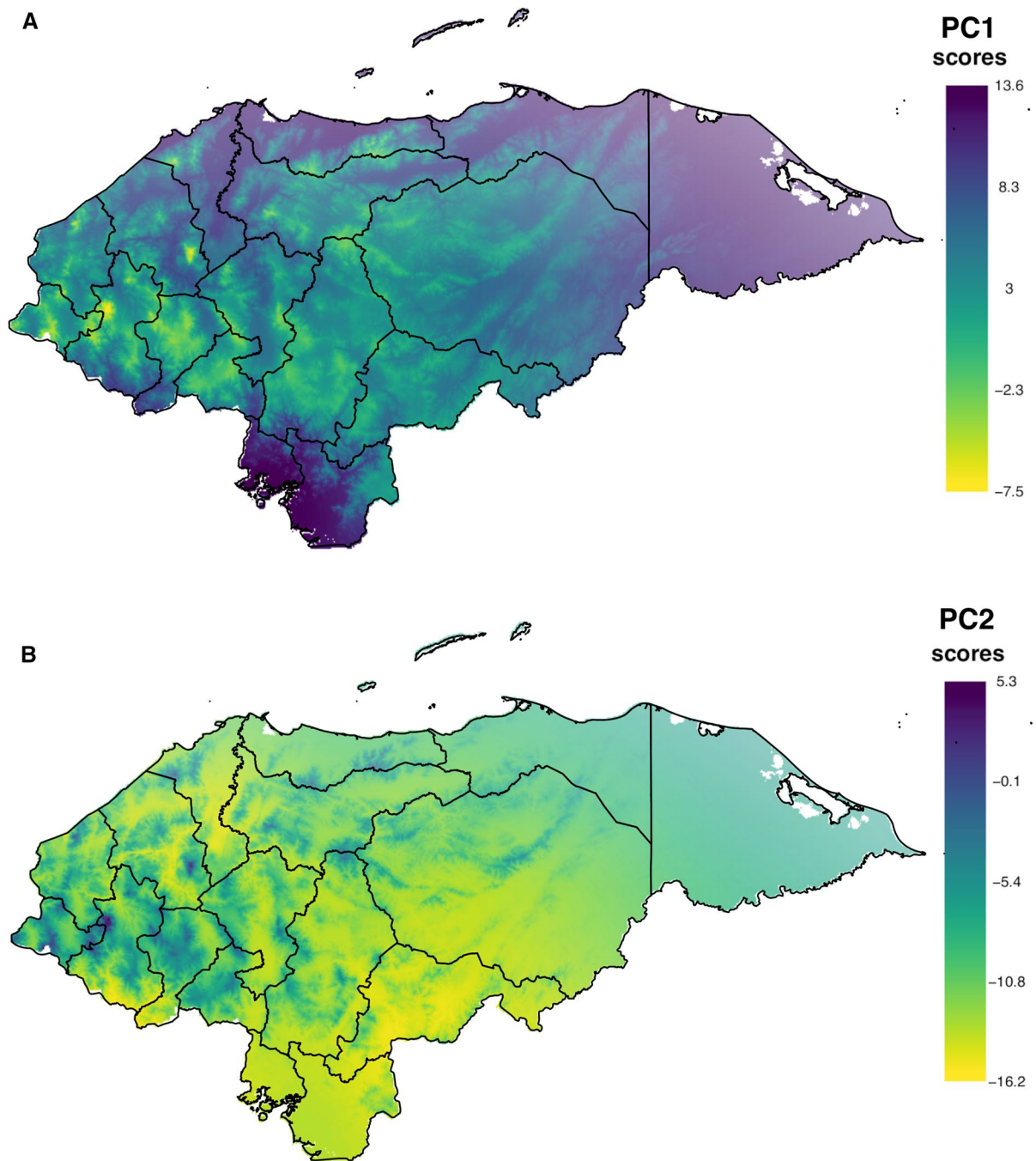
this difference was not a by-product of the variances of the available climatic space when they compared in a similar manner (7.1 vs. 7.2, respectively). We found similar differences when comparing regions with high diurnal temperature and low annual precipitation (i.e., positive PC2 scores), with areas of low diurnal temperature and high annual precipitation (i.e., positive PC1) ( $F=53.55$ ,  $p=7.18e-13$ ). However, in the second comparison, the difference could not simply be explained by differences in the available climatic niche space (8.9 vs. 23.3, respectively).

Interestingly, there were no obvious differences in the pattern of occupation among the most species-rich families (Fig. 1A). When comparing the entire available climatic space, there were significant differences between life forms (i.e., epiphytes vs. terrestrial

ferns) in their pattern of occupation (PC1,  $F=7.35$ ,  $p=0.0069$ ; PC2,  $F=9.19$ ,  $p=0.0025$ ; Table 2, Fig. 1B), with epiphytes showing smaller variance in their climatic niches than terrestrial species (13.38 vs. 21.48 and 8.52 vs. 15.22, for PC1 and PC2, respectively).

Climate projections for the years 2020 to 2099 for RCP2.6 and RCP8.5 suggest how climate space in Honduras will shift in the future (Fig. 3). In general, the climate space will shift to hotter and drier conditions, with RCP8.5 projections showing the strongest shift (Fig. 4). Between 18.9 and 57.8% the analyzed species will have their current average climatic niche outside future climatic spaces (Table 3). This result is not due to a reduction in available climatic space, but rather an overall mismatch between present and future





**Fig. 2** Spatial distribution of principal component scores of the climatic conditions across Honduras. The climatic conditions associated with each grid cell were subject to a principal component analysis and the resulting scores were mapped back to each corresponding cell for visualization. PC1 mostly

reflected variation in temperature, especially lower temperatures (A), whereas PC2 loadings described a trade-off between maximum temperature and diurnal temperature range versus precipitation (particularly during autumn and winter) (B). See text for details

**Table 2** Variance in the scores along different ordination axes of interspecific in occupied climatic niche space of epiphyte and terrestrial plants

Variable	Epiphyte	Terrestrial	<i>F</i>	<i>P</i>
PC1	13.38	21.48	7.35	0.0069
PC1 (PC2+)	5.74	5.05	9.20	0.0025
PC1 (PC2−)	15.27	32.81	2.05	0.15
PC2	8.52	15.22	23.75	1.55e−06
PC2 (PC1+)	9.95	19.05	9.43	0.0022
PC2 (PC1−)	1.82	5.83	11.77	0.0008

“PC1 (PC2+)” and “PC1 (PC2−)” correspond to variance between life forms on PC1 separately for drier (positive PC2 scores) and wetter (negative PC2 scores), respectively. “PC2 (PC1+)” and “PC2 (PC1−)” correspond to variance between life forms on PC2 separately for colder (positive PC1 scores) and warmer (negative PC1 scores), respectively

climatic spaces (Table 3 and Fig. 4). Interestingly, the proportion of impacted species is larger for epiphytic than for terrestrial species, except for the most severe shifts (i.e., RCP8.5 for the year 2069 and RCP8.5 for the year 2099), in which this tendency is reversed (Table 3). It is important to note that there are 23 species that are indicated as outside the present climatic space. Those were species living near the boundaries of the present climatic space but were categorized to be outside because of the way we computed the concave hull. They were left to ensure that all comparisons were carried out using the same framework.

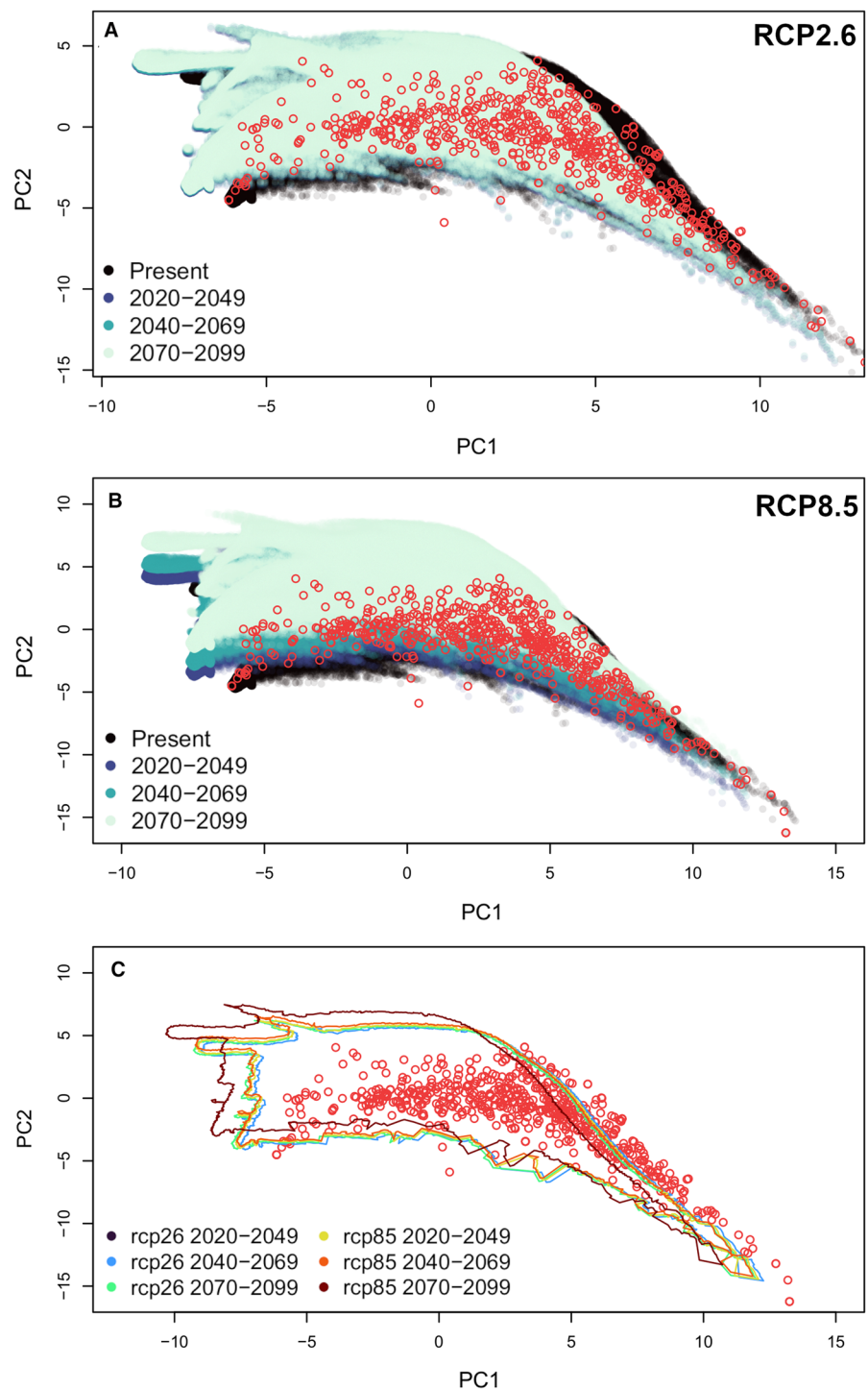
## Discussion

Although fern and lycophte species were widely distributed throughout the available climatic space in Honduras, we found evidence that particular climate conditions were occupied more frequently. In relatively colder conditions (positive PC1 scores), species tended to be distributed throughout the entire available climatic space, whereas in warmer conditions (negative PC1 scores), their distribution became more limited, with precipitation and diurnal temperature being the limiting factors. In addition, terrestrial species showed more variation in their occupied climatic niches compared to epiphytes. This is not surprising, as epiphytes are believed to be more sensitive to variable and extreme climate conditions during different stages of their life (Benzing 1998; Klinghardt and Zotz 2021). To the best of our knowledge, our

study is the first to explicitly demonstrate this pattern for ferns and lycophtes; however, the mechanisms underlying the difference between epiphytes and terrestrial species are not easily determined. We suggest two non-exclusive mechanistic explanations. Firstly, the rate of climatic niche evolution between these two life forms could differ (Hernandez-Rojas et al. 2021). For instance, it has been argued that life history might affect rates of climatic niche evolution in plants, with woody lineages accumulating fewer changes per million years in climatic niche space than related herbaceous lineages (Smith and Beaulieu 2009). A more rigorous test of this hypothesis would be required for our ferns (O’Meara et al. 2006), but more precise phylogenetic and trait data are currently lacking for many of our study species (Kessler et al. 2016). Alternatively, epiphytes are likely to be less well buffered from changes in climate conditions compared to terrestrial species due to their dependence on the forest canopy, often living in less shaded conditions than their conspecific terrestrial taxa and thus being less well buffered higher in the canopy (de Frenne et al. 2019). Assessing the relative importance of these mechanisms might provide valuable insight to understanding how life history traits drive the occupation of the fern climatic niche space in Honduras. It is also worth noting that the higher variance in epiphyte niche occupation could also be partially explained by the lack of host-specific habitat in areas that have high levels of seasonality and low rainfall, such as coastal regions.

There are some important caveats of the approach used in the present study. Firstly, for practical reasons of working with over 700 species, we did not explicitly analyze intraspecific variation in climatic niches. However, it is becoming increasingly clear, particularly in plant species that intraspecific variation in functional traits might lead to marked consequences for community-level dynamics (e.g., Lajoie and Velend 2015; Niu et al. 2020). Secondly, microhabitats might be more important than general climatic conditions to determine the individual distribution of fern and lycophte species (Jones et al. 2011). Finally, the data used in our study were based on Batke et al. (2022) database of fern and lycophte records from Honduras. This dataset was based on herbarium records from the years 1850 to 2018, which can be limiting due to known recorder biases (Daru et al. 2017). However, databases using collated herbarium

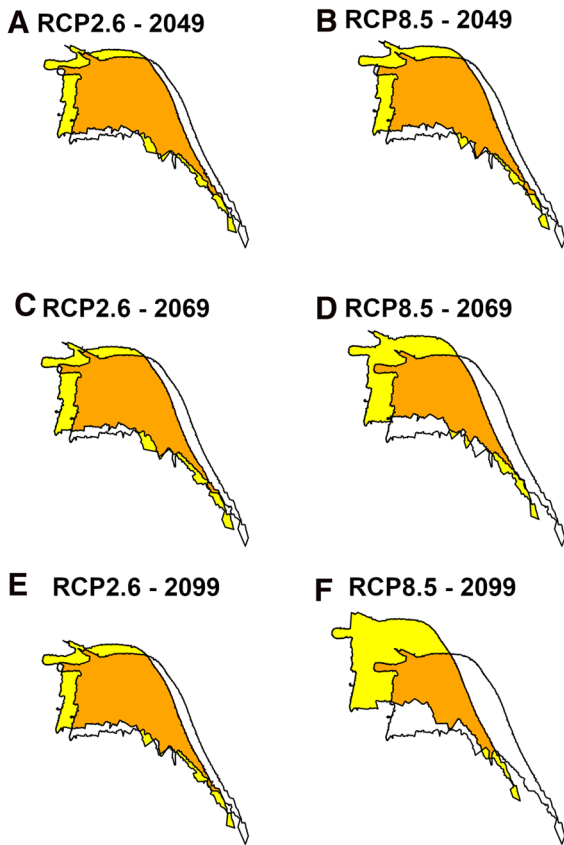
**Fig. 3** Principal component analysis of climatic conditions found in Honduras, including climate space projections under RCP2.6 (A) and RCP8.5 (B) for different years. Panel (C) shows the outline of all the projections. Red empty circles represent the species means



information are often the only and most comprehensive resource to assess the effect of climate change on entire species groups (Loiselle et al. 2007).

Climate change is expected to have a profound influence on fern and lycophyte communities (Gasper et al. 2021), especially epiphytes (Hsu et al. 2011;





**Fig. 4** Predicted consequences of climate space shifts according to different climate change scenarios (A–F). The white area represents the current climate space, yellow the future-predicted climate space, and orange shows the overlap between current and predicted (see Table 3 for details)

Hsu et al. 2014; Reyes et al. 2021b). Our study showed that some regions of the available climatic space will be shifting in Honduras under RCP2.6 and RCP8.5. Particularly species that occurred close to the vicinity of the current climate space or species that have a more restricted climate niche are more likely to experience shifts or losses in the future. For example, areas of moderate precipitation and low temperatures are likely to be decreasing (Fig. 3). Range shifts have frequently been reported for plant and animal species (Magrin et al. 2014) and are believed to be particularly problematic for species that already live close to their climate limit or have a narrow climate range. A recent study by Reyes et al. (2021b) showed that 63 ferns in Celaque National Park, the tallest mountain in Honduras, are likely to shift their range fully or partially above the maximum altitude of the mountain under a RCP2.6 scenario for the year 2050. They also showed that 65% of these species were epiphytes. This is especially concerning, as epiphytic ferns and lycophytes often show exceptional species richness in mid and higher altitudes (Suissa et al. 2021). Celaque is known as one of the most species-rich areas for ferns in Honduras (Rojas-Alvarado 2012) and is believed to have one of the highest levels of endemism in the country. Our climate space analysis showed similar trends as discussed in Reyes et al. (2021b), in that species in high-elevation areas, such as Celaque, are likely to lose their currently occupied climate space (Fig. 3). This is because these high-elevation areas are characterized by low temperature and high precipitation, which is a rare climate niche in Honduras and will be lost as

**Table 3** Predicted consequences of climate space shifts according to different climate change scenarios

Climatic space	Outside			Within			Total area	Overlap
	All	Epiphyte	Terrestrial	All	Epiphyte	Terrestrial		
Present	23	7	16	653	120	533	100.0	100.0
RCP26.49	128	36	92	548	91	457	102.0	79.8
RCP26.69	160	38	122	516	89	427	102.5	76.6
RCP26.99	137	37	100	539	90	449	101.0	77.2
RCP85.49	146	39	107	530	88	442	101.0	75.8
RCP85.69	250	43	207	426	84	342	100.6	62.6
RCP85.99	391	67	324	285	60	225	103.3	47.1

Species counts correspond to the number of species whose mean climatic niche will fall inside or outside each climatic space. Total area indicates the relative size of the climatic space in relation to the present, whereas the overlap indicates the relative area of overlap of the corresponding climatic space in relation to the present (see also Fig. 4)

a result of rising temperatures and a decrease in precipitation (Fig. 2).

We found that terrestrial species are at higher risk in the future, as their climate niche is in closer proximity to their current climate space. Our forecast predictions showed that proportionally more terrestrial species will fall outside the available climate space in the future (Table 3). For example, under a worse-case scenario (RCP8.5) for the year 2099, we estimate that 391 species might shift their average climate niche outside the available climate space. Of the 391 species 17.1% are epiphytes and 82.9% are terrestrial species. For the same projection, we also found that the overlap of climate space between the current and future projection is as little as 47.1%. This is a worrying shift and could result in a large loss of species, in cases where species cannot adopt or have a narrow climate niche (e.g., highly specialized species).

It needs to be noted that we calculated the average niche positions of species in the predicted available climatic space for Honduras. This means that although the average niche positions might fall outside the predicted available climatic space for some taxa, it does not necessarily imply that these species will completely disappear. This is because the shift in climate space might still be suitable for survival but might result in those species being closer to their niche limit. Having a narrower available climate space would make these species more susceptible to sudden perturbations in their environment (e.g., higher predicted extreme events, such as drought, Magrin et al. 2014). Species that are more dynamically capable of physiological response to sudden changes in their environment (e.g., by closing their stomata) and/or are morphologically capable to adapt (e.g., by changing their stomatal density) are less likely to be affected. For example, it has been shown that the predicted increase in atmospheric CO<sub>2</sub> conditions under RCP8.5 for the year 2050 (approximately to 560 ppm) is likely to increase plant water use efficiency as plants close their stomata more (Purcell et al. 2018). Experimental work has demonstrated that this is particularly pronounced in ferns that receive more light (Batke et al. 2018), as would be the case of many epiphytic ferns and lycophytes when compared to lower understory terrestrial species. It is therefore possible that the combined effect of elevated CO<sub>2</sub>, increases in temperature (to a certain point, see

Purcell et al. 2018) and decreases in precipitation, might only negatively affect species that are less physiologically and morphologically adaptable. This is likely to include ferns and lycophytes that require higher availability of water to stay physiologically active to maintain their water to carbon balance, which would include water loving ferns, such as species in the Hymenophyllaceae (i.e., filmy ferns). Currently, there are little detailed data available on the morphological and physiological responses of ferns to changes in climate, making a systematic species comparison difficult (Cheng et al. 2010; Franks et al. 2016).

In summary, our study found that the climate space across Honduras is changing and that some fern and lycophyte species are going to be at higher risk compared to others. Specifically, climate space availability will likely change in areas that experience lower precipitation and temperatures, resulting in unsuitable average niche conditions for up to 57.8% of Honduran fern and lycophyte species. In general, Honduras is expected to become drier in the near future, with more extreme events of high drought (Magrin et al. 2014). It is important to note that, given that we focused on species means, we have not explored intraspecific variation in climatic niche occupation. However, the species near the boundaries of the Honduran climatic niche space are particularly relevant for further studied using ecological niche modeling (Syfert et al. 2018). Nevertheless, the implications of our findings are particularly relevant to conservation management, as our data highlight areas at higher risk for fern and lycophyte species loss and therefore can be used to directly inform policy planning. Ferns and lycophytes constitute the most systematically organized group of Honduran plants (Reyes et al. 2021a) and are ideal for studying Honduran climatic niche variation. Considering that ferns and lycophytes are particularly sensitive to changes in climate, if tested in the future, they could be used as a proxy for other Honduran plant taxa. To test this, more taxonomic work would be required to update the current list of other vascular plant species and to assemble a similar inventory as done by Reyes et al. (2021a).

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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