Conservation applications of ecological niche modeling: non-native ferns may compete with native ferns for limited suitable habitat in Hawaiian dryland ecosystems

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Abstract

Premise

Competition from non-native species and habitat loss are common threats to biodiversity and may act synergistically to increase competition for decreasing habitat availability. We develop a workflow using Hawaiian dryland ferns as a model for the interactions between land-use change and non-native competition in determining available habitat for native species.

Methods

We use fine-resolution climatic variables and carefully curated occurrence data from herbaria and community science repositories to estimate the distributions of Hawaiian dryland. We quantify the degree to which non-natives occupy similar regions of niche space and map the remaining available habitat given land-use change in Hawaiʻi.

Results

The estimated niches for the endemic species (*Doryopteris* spp.) are more narrow than for the indigenous *Pellaea ternifolia*. *Doryopteris angelica* has the lowest proportion of non-native occurrences in its estimated suitable area while *D. decora* has the highest. Both *D. decora* and *D. decipiens* have low proportions (¡20%) of inferred suitable area covering native habitat.

Discussion

Areas characterized by shared environmental preferences of native and non-native ferns may also decrease due to human development and fallowed agricultural lands. Our study demonstrates the value of a novel ecological niche modeling approach for conservation risk assessment in a rapidly changing and urbanized island ecosystem.

Keywords: *climatic niche; conservation; ecological niche modeling; Hawaiian ferns, land use; Pteridaceae*

INTRODUCTION

One of the primary goals of conservation biology is to assess the amount and location of suitable habitat for species of concern. Ecological niche models (ENMs) use occurrence data (records of where individuals of the species have been observed in the past) to estimate the climatically suitable habitat of a particular species (Soberón, 2010). ENMs may allow conservation practitioners to determine the extent of suitable habitat for threatened species, prioritize areas for land conservation, identify regions where a rare species may exist but still be undetected, and many more possible applications (Zhu et al., 2013). However, most traditional approaches to ecological niche modeling confuse theoretical and practical differences between the fundamental and realized niche, confounding the interpretation of such analyses and thus the proper application of ENMS in conservation (Soberón, 2010; Zhu et al., 2013). The fundamental niche is defined as the set of environmental conditions that a species could inhabit in the absence of biotic factors (such as competition) and dispersal limitations, while the realized niche is the set of conditions that a species currently inhabits as a result of the dynamics of biotic interactions and historical dispersal patters (Hutchinson, 1957; Pulliam, 2000; Soberón and Arroyo-Peña, 2017). For the vast majority of niche modeling studies, occurrence data from biological collections describe where a particular species has been observed and represent a sample from the realized niche, which may under-represent the fundamental niche of a species (Jiménez et al., 2019). The dearth of appropriate statistical methods to estimate the fundamental niche from presence-only data had limited the ability of conservationists to expand their efforts to preserve areas where vulnerable species can live—or historically lived—because the right climatic conditions exist, even if the vulnerable taxa currently do not occur in a given location due to biotic interactions. Therefore, it is essential to infer fundamental niches for conservation purposes. New developments in ecological niche modelling can allow conservation practitioners to preserve critical areas where species can survive. These new ENMs modeling approaches are improving our ability to infer the fundamental niche by adding a hypothesis of the accessible area that the species is able to explore (Jiménez and Soberón, 2022).

Additionally, factors beyond the abiotic variables used in ENMs may significantly affect the available area for species of conservation concern. For example, land-use change may mean that areas characterized by the appropriate climatic conditions for a species to thrive are instead unavailable via land conversion from native habitat to areas of intense human development, agriculture, or invasive-dominant ecosystems. Additionally, the fundamental niche intentionally models the range of an organism without considering the impact of biotic interactions such as competition. Thus, competition from non-native species with similar habitat preferences may also significantly affect the amount of available area for native species of conservation concern. These factors are typically not accounted for in traditional ENMs, so conservation applications of ENMs may overestimate the available suitable area of species of interest. In this study, we describe a pipeline for modeling the fundamental niche using the statistical approach in Jiménez and Soberón (2022), while accounting for the impacts land use change and competition from non-native species on available suitable habitat. We apply this methodology to the vulnerable native Hawaiian dryland ferns in the family Pteridaceae and discuss the potential future applications of such approaches for conservation.

Hawai'i is widely known as a biodiversity hotspot, with textbook examples of adaptive radiations following long-distance dispersal to the isolated volcanic archipelago (e.g., the lobeliods, Givnish et al. 2009, silverswords, Baldwin and Sanderson 1998; Witter and Carr 1988, and songbirds, Lovette et al. 2002). Despite the small area of available land, Hawai'i contains an extraordinary diversity of biomes and environmental conditions, which has likely allowed organisms to adapt to novel environments and diversify (Barton et al., 2021). Moreover, because of Hawai'i's isolation and the rarity of long distance dispersal events, rates of endemism are particularly high: 90% of the approximately 1300 native Hawaiian vascular plant species are found nowhere else (Rønsted et al., 2022). Sadly, Hawai'i's spectacular biodiversity is also under immense threat. A recent report on the conservation status of approximately 1000 native Hawaiian vascular plants showed that 75% of the flora is threatened or endangered (Rønsted et al., 2022), while only 33% of that flora receives protection under the U.S. Endangered Species Act and the Hawai'i State Government, implying that much of the native flora is under threat yet unprotected.

Tropical dry forests are one of the most threatened biomes worldwide (Cordell and Sandquist, 2008; Quesada et al., 2009; Wilson et al., 1988). They once made up 42% of the world's tropical regions but currently only 2% remain (Buzzard et al., 2016). Across the tropics, the dry forest biome has attractive features for human use: they tend to be suitable areas for livestock and agri-

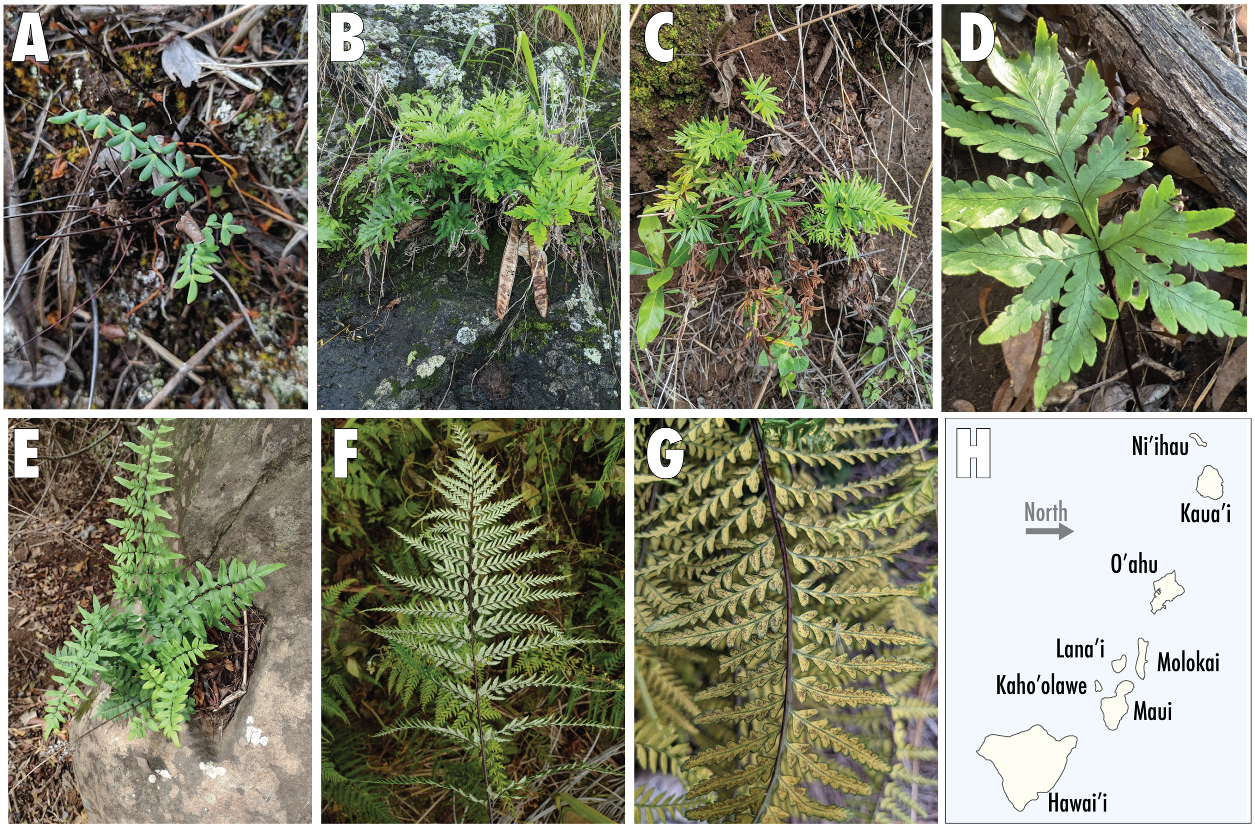

Figure 1: Native (top) and non-native (bottom) dryland ferns in Hawaiʻi. (A) *Pellaea ternifolia*, indigenous to Hawaiʻi (Hawaiʻi island, Maui, and Kauaʻi) and the Americas, (B) *Doryopteris decipiens*, endemic to Hawaiʻi (all major islands), (C) *Doryopteris decora*, endemic to Hawaiʻi (all major islands), (D) *Doryopteris angelica*, endemic to Hawaiʻi (Kauaʻi single-island endemic), (E) *Cheilanthes viridis*, non-native, (F) *Pityrogramma calomelanos*, non-native, (G) *Pityrogramma austroamericana*, non-native, and (H), map of the major Hawaiian islands. Pictures A, B, C, G by C. M. Tribble, picture D by Susan Fawcett, and pictures E and F by Kevin Faccenda.

culture because their soils are often fertile and they possess a marked rainfall season, and they are favored for human development because the dry environment may reduce the risk of disease transmission (Murphy and Lugo, 1986; Portillo-Quintero et al., 2015). These global patterns hold true in Hawaiʻi; most original tropical dry forests in Hawaiʻi have been destroyed (Cordell and Sandquist, 2008) and they are continuously exposed to various threats, mainly due to human activity (Miles et al., 2006). In Hawaiʻi, the leading causes for deforestation of drylands include conversion of former dry forests to agricultural- or pastureland, human development, invasion by nonnative species, and wildfires (D'Antonio and Vitousek, 1992).

While ferns are typically found in moist ecosystems, some ferns have unique adaptations that allow them to thrive in drylands (Sharpe, 2019). In particular, the Cheilanthoideae subfamily of Pteridaceae consists of primarily dry-adapted species worldwide (Gastony and Rollo, 1995; Hevly, 1963). In Hawaiʻi, this subfamily is represented by five native species (*Doryopteris* J.Sm. and *Pellaea ternifolia* (Cav.) Link). Taxonomic classification of *Doryopteris* (like much of Cheilanthoideae) has been a challenge for many years because of the lack of clear morphological characters to identify species (see panels B-D in Fig. 1), causing taxonomic uncertainty within the genus (Bouma et al., 2010; Gastony and Rollo, 1995; Ranker et al., 2019a,b; Rothfels et al., 2008; Schuettpelz et al., 2007; Tryon, 1942, 1944; University Herbarium, 1939; Vernon and Ranker, 2013; Windham et al., 2009; Yesilyurt, 2003; Yesilyurt and Schneider, 2010; Yesilyurt et al., 2015; Zhang et al., 2008, 2007). Despite this uncertainty, to date there are four recognized species of *Doryopteris* that are endemic to the Hawaiian islands: *Doryopteris decora* Brack., *Doryopteris decipiens* (Hook.) J.Sm., *Doryopteris angelica* K.Wood & W.H.Wagner, and *Doryopteris takeuchii* (W.H.Wagner) W.H.Wagner (University Herbarium, 1939; Vernon and Ranker, 2013; Yesilyurt, 2005; Yesilyurt et al., 2015), along with one named hybrid *Doryopteris subdecipiens* W.H.Wagner (Palmer, 2003). Members of this genus reside in warm and dry shrubland, grassland, and forest habitats (Palmer, 2003), and are known to favor rocky substrates within those habitats (Tryon, 1942). *Pellaea ternifolia* is another native Hawaiian Cheilanthoid species (see panel A in Fig. 1) that can also be found in dryland environments (Gastony and Rollo, 1995; Valier, 1995). Unlike the Hawaiian *Doryopteris*, *P. ternifolia* is not endemic to Hawaiʻi; it also occurs in Central and South America. In Hawaiʻi, *P. ternifolia* tends to occur in high elevation montane environments such as Mauna Kea, Mauna Loa, and Kilaeua on Hawaiʻi island and Haleakalā on Maui.

Almost 200 native fern species inhabit the Hawaiian Islands, of which 77% are endemic Palmer (2003). Ranges of ferns are considered to be strongly determined by habitat availability (Smith, 1993; Tryon, 1986); moreover, endemic ferns are generally found at high elevations (Kessler et al., 2010; Kluge and Kessler, 2006, though Hawaiian lowland endemics *Doryopteris* spp. are an exception to this trend). These features make native fern species particularly susceptible to habitat loss, human-induced habitat disturbance, and competition for space against alien species. For example, non-native relatives to the Hawaiian members of Cheilanthoideae may be competing for the same dryland habitat that the native species prefer. *Pityrogramma calomelanos* (L.) Link—which is native to North and South America and the Caribbean (POWO, 2023)—and *P. austoamericana* Domin—which is native to Central and South America (POWO, 2023)— both arrived to Hawaiʻi and are now widespread across the islands (see panels F and G in Fig. 1). Both *Pityrogramma* species are also part of the Pteridaceae family and share morphological characteristics typical of the Cheilanthoideae subfamily (such as farina, a waxy substance on the abaxial surface of the fronds thought to protect the fronds from damage when desiccated, Kao et al. 2019), although they belong to the subfamily Pteridoideae (Zhang et al., 2017). *Cheilanthes viridis* (Forssk.) Sw. (Cheilanthoideae, Pteridaceae) is another non-native dryland fern found in Hawaiʻi (see panel E in Fig. 1) whose native distribution includes most of eastern and southern Africa and the Middle East (POWO, 2023).

Land use has drastically changed over the years in Hawaiʻi. In 1848, The Great Māhele (great land division) was one of the first changes in land usage (Chinen, 2020) and resulted in the partitioning of land in the Hawaiian Islands, changing the feudal system to permit land privatization (Kamakau, 1961; Linnekin, 1983). Following the Great Māhele, Hawaiʻi became attractive to foreign investors who sought to claim lands in an effort to further develop agricultural plantations. In 1835, the first sugarcane plantation was established in Koloa, Kauaʻi (Association, 1992) and, by 1890, foreigners and foreign corporations owned three out of four acres of private lands in Hawaiʻi (Takaki, 1984). Problems of managing plantations arose soon after the Great Māhele. Sugar, pineapple, and macadamia plantations—often established in former tropical dry forest environments—caused shortages of water in West Maui (Association, 1992). Since the early 1900s, agricultural corporations and landholders have diverted natural water resources to plantations in former native dryland habitat, resulting in over 90 billion gallons of water being diverted from natural island streams (John A. Engott, 2007). In more recent years, due to changes in the economy, plantations have largely been abandoned (Zou and Bashkin, 1998), and former plantation land is now primarily dominated by invasive grasses such as guinea grass (*Megathyrsus maximus*, Farrant et al., 2023). These land-use changes are a significant conservation concern because alien species often invade native communities after some type of disturbance (Smith, 1985). In particular, abandoned drylands create potential hazards to native dryland ferns as non-native species invade, changing the biotic and abiotic environment (non-native grasses may suppress native species success) and potentially enhancing competition for limited available suitable habitat (non-native closely related ferns may share similar habitat preferences D'Antonio and Vitousek, 1992).

To better understand the possible adverse effects of (*i*) the presence alien species in the focal species ranges and (*ii*) land-use changes on the survival of native fern species that have become adapted to particular environmental niches in the Hawaiian islands, we developed an integrated ENM pipeline. We first carefully curated occurrence data for seven fern species from herbaria and open-access community science databases and integrated these presence-only data with fine-resolution climatic variables of the main Hawaiian Islands to estimate the fundamental niches of the native ferns *Doryopteris angelica*, *Doryopteris decipiens*, *Doryopteris decora*, and *Pellaea ternifolia*.

We used the novel ENM approach proposed by Jiménez and Soberón (2022). For every recorded location of a given species, there are a series of corresponding climatic values (i.e., annual average temperature). We can plot the occurrences of species in multidimensional environmental space. In this environmental space, the Jiménez and Soberón (2022) model leverages random sampling along with the climatic variables to infer a multivariate normal ellipsoid that represents the probability of a species tolerating combinations of environmental variables. With the multivariate normal probability at hand, we can trace back to the the latitude and longitude in geographical space, but now those localities in the map are associated with a probability of environmental tolerance, and when plotted back in geographical space they create suitability maps for our species. In summary, this methodology takes the geographical occurrence data to climatic space, it calculate probabilities of climatic tolerance, and uses those probabilities to return to geography, where we have now information about the chances for suitable space. Following similar protocols, we curated data of three non-native fern species, *Cheilanthes viridis*, *Pityrogramma calomelanos*, and *P. austroamericana*, and quantified the degree to which non-natives occupy the potential ranges of the native ferns. Finally, using a land-use map of the Hawaiian islands, we identified regions with different degrees of disturbance that hold suitable climatic conditions for the native fern species to evaluate the impact of habitat change.

METHODS

Species occurrence data

We obtained occurrence records of the native and non-native species (Fig. 2 step (1)) from digitized museum collections and human observations via the Pteridophyte Collections Consortium (PCC Consortium, 2022), the Global Biodiversity Information Facility (GBIF GBIF, 2022), the iNaturalist website`https://www.naturalist.org/`), the Herbarium Pacificum (BISH) at Bishop Museum,

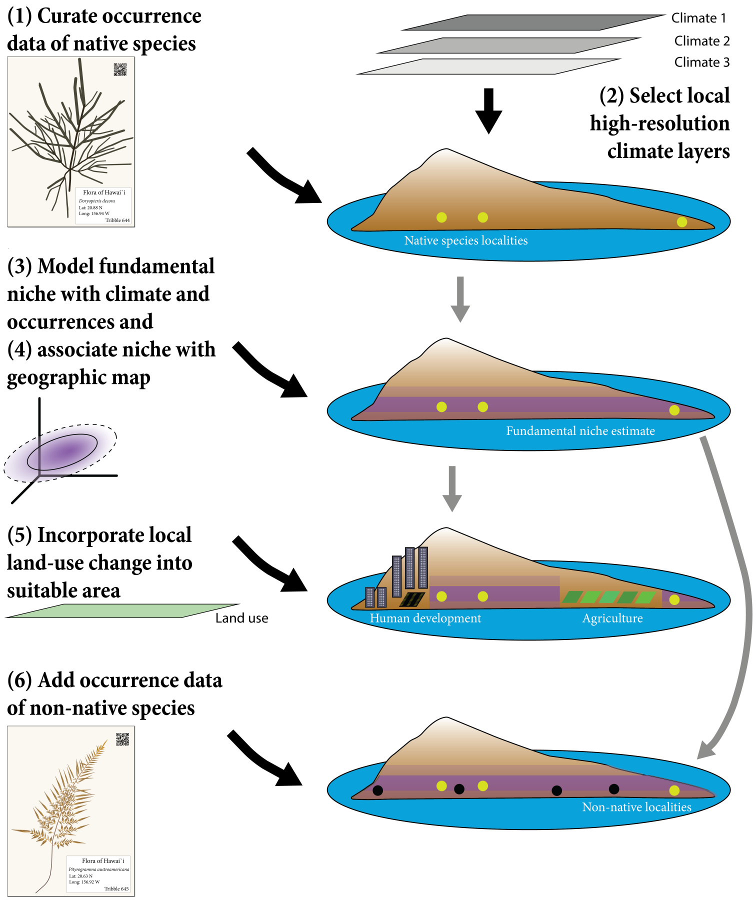

Figure 2: Schematic representation of the analytical workflow. (1) Curate occurrence data of data species. Data from verified physical vouchers is preferred, but iNaturalist or other participatory science databases can supplement if necessary. Curation should include both expert verification of species identifications and careful data cleaning to remove untrustworthy or error-prone GPS data. (2) Gather and transform high-resolution climatic variables, ensuring the variables are not highly correlated and appear sufficient to describe important aspects of the species ecology. (3) Use the data from steps (1) and (2) to estimate the fundamental niche of the native species and (4) identify their potential distributions. The suitability maps created in step (3) were used to: (5) quantify how much suitable area is no longer available to native ferns due to land-use and (6) calculate the percentage of non-native fern occurrences inside the suitable areas.

and the Joseph F. Rock Herbarium (HAW) at the University of Hawaiʻi at Mānoa. We were unable to recover sufficient accurate occurrences to include *Doryopteris takeuchii* or *Doryopteris subdecipiens* in the study, so all downstream analyses focused on the remaining three *Doryopteris* and *P. ternifolia*. Coordinates for *D. angelica* were obscured on iNaturalist because it is a protected species, so we obtained coordinates for *D. angelica* by reaching out to individual observers. In efforts to obtain more occurrences for *D. angelica*, *D. decora*, *P. calomelanos*, and *P. austroamericana*, we received occurrences from the herbaria BISH and HAW. HAW provided access to digitized collections through the database of the Consortium of Pacific Herbaria, and we requested occurrence records from

BISH.

We combined all occurrence data and removed duplicate records. We cleaned the combined dataset to reduce inaccuracies in species occurrences. We excluded records with large coordinate uncertainty as they lacked precision. We prioritized recent occurrences—after 1950—because older records are more susceptible to GPS error and there could be a mismatch between the modern climate data (described below) and the older observations. In one case—*D. decora*—we included older observations due to low sample size. Additionally, we included some localities with unknown years to increase our sample size. We determined the accuracy of the localities based on expected species ranges. We plotted the occurrences over the Hawaiian Islands. We discarded points located in the ocean, outside of Hawai'i, or markedly outside of the species expected range. Lastly, we verified species' identifications by consulting taxonomic experts, including the authors of this study.

Climatic data

To model the fundamental niche of the four focal native species in our study, we selected climatic variables that describe factors we believe are likely to influence species ranges (described in Fig. 2 step (2)). We gathered seven environmental variables from the Climate of Hawai'i website (Giambelluca et al., 2014), which includes detailed breakdowns of climatic and environmental variables: diffuse radiation (W/m^2), leaf area index, relative humidity (%), soil evaporation (mm), solar radiation (W/m^2), available soil moisture, actual evapotranspiration (mm). However, the most up-to-date data on Hawaiian temperature and precipitation is available at the Hawai'i Climate Data Portal (`https://www.hawaii.edu/climate-data-portal/`). We obtained monthly temperature minimum and maximum values and monthly precipitation values from the Data Portal and transformed those data into five additional variables: mean minimum temperature of the coldest four months (cold mean; $^\circ C$), mean maximum temperature of the hottest four months (hot mean; $^\circ C$), mean precipitation of the wettest three months (wet mean; mm), mean precipitation of the driest three months (dry mean; mm), and precipitation seasonality (standard deviation of the monthly precipitation values).

We ensured all climatic variables were the same resolution (250m) and projection (WGS84). The raster layers cover all major Hawaiian Islands except for Ni'ihau, which was excluded from our analyses. As many of the 12 variables may be highly correlated, we estimated the Pearson correlation coefficient (r) for all pairwise comparisons and retained six variables such that all pairwise r values satisfied $-0.7 < r < 0.7$.

Climatic niche modeling of native species

We applied a methodology that enables the identification of the potential distribution of a species (i.e., the set of sites with suitable climatic conditions where the species can inhabit) by modeling its fundamental Grinellian niche (*sensu* Soberón, 2007) in a multivariate space defined by climatic variables relevant for the survival of the species. In particular, we used the model proposed by Jiménez and Soberón (2022) to estimate the fundamental niches of *Doryopters decipiens*, *D. decora*, *D. angelica*, and *Pellaea ternifolia* with occurrence data and information regarding the dispersal limitations and climate availability within the area of study. For each native fern species, we used the curated sample of occurrences (see step 1 in Fig. 2) and extracted the climatic values from the raster layers of the six variables described before. We worked under the assumption that the dispersal abilities of these species allow them to reach any of the main islands within the Hawaiian archipelago, while they cannot disperse to other land areas by natural means. In other words, the main Hawaiian islands (Kaua'i, O'ahu, Moloka'i, Lāna'i, Kaho'olawe, Maui, and Hawai'i) represent our hypothesis about the dispersal abilities of the species (known as the 'M' hypothesis; see Soberón, 2010). We obtained a random sample of eight thousand points within the main Hawaiian islands, extracted their climatic conditions, and use them to estimate the parameters of interest.

Jiménez and Soberón (2022) modeling approach assumes that the fundamental niche of the species has an ellipsoidal shape given by a multivariate normal distribution in environmental space which is described through two parameters of interest: a vector that represents both the optimal environmental conditions for the species and the center of the ellipsoid, and a variance-covariance matrix that defines the shape and size of the niche. We supplied the likelihood function of the model with the occurrence data and the set points representing the available climatic conditions within the study area, and estimated the parameters of interest through a maximum likelihood approach (step 3 in Fig. 2). The Jiménez and Soberón (2022) estimates ellipsoids in multidimensional space where the number of dimensions is equal to the number of climatic layers provided to the model. Estimating the parameters of a model with more than three layers requires an advanced optimization algorithm that is currently not implemented. To address this computational limitation, we created two different models using two sets of three climatic variables each, called Model 1 and Model 2. Model 1 uses the climatic variables diffuse radiation, relative humidity, and precipitation seasonality, while Model 2 uses leaf area index (LAI), hot mean, and dry mean.

After getting the parameter estimates for each model and species, we created different maps to visualize and compare the outputs of Model 1 and Model 2 as follows (step 4 in Fig. 2). First, we used the estimated parameters to create suitability maps by calculating an index, for each cell, whose values range from zero to one (see Jiménez and Soberón, 2022). A suitability index close to 1 means that the environmental conditions associated to that cell are close to the center of the estimated fundamental niche, while a suitability index close to 0 means that the environmental conditions at that cell are either close to the border of the niche or outside of the niche. In each case, we defined the border of the estimated fundamental niche through the 95% confidence ellipsoid of the underlying multivariate normal model. Then, we transformed the suitability maps into binary maps where we assigned a positive value to cells that fall inside the fundamental niche, and a value of zero to cells outside the niche and whose environmental conditions are considered as unsuitable for the survival of the species. For each species, we combined the binary maps for Model 1 and Model 2 by adding the corresponding raster files. With this, we obtained maps whose cells were grouped into four categories: (*i*) *unsuitable*, these correspond to sites with environmental conditions that are outside of the estimated fundamental niches under both Model 1 and Model 2; (*ii*) *suitable under Model 1*, containing sites inside the fundamental niche estimated under Model 1; (*iii*) *suitable under Model 2*, sites inside the fundamental niche estimated under Model 2; and (*vi*) *suitable under Models 1-2*, representing sites predicted as part of the fundamental niche under both Model 1 and Model 2. For further analyses, we only kept regions that were part of the last category.

Impact of non-native species on projected species ranges

We created new maps to evaluate to what extent the non-native ferns, *Pityrogramma calomelanos*, *P. austroamericana*, and *Cheilanthes viridis*, occupy regions identified as the predicted potential distribution of the native species. For each native species, we filtered out the regions identified as suitable under both Model 1 and Model 2 in the previous part of the analyses. We plotted those regions into a new map and added the occurrence data of the non-native ferns on top (step 6 in Fig. 2). Additionally, we calculated the proportion of occurrences of non-native ferns that overlap with the suitable regions of each native species.

Impact of land-use change on projected species ranges

We downloaded a raster file with a land-cover map provided by the U.S. Geological Survey (Jacobi et al., 2017), which was developed as part of a comprehensive assessment of carbon sequestration potential by natural ecosystems in the State of Hawaii (Selmants et al., 2017). This raster layer depicts the land cover and degree of human disturbance to plant communities on the seven main Hawaiian Islands. Each cell in the raster was classified in a hierarchical fashion within 48 detailed land-cover units, which were also grouped into 27 general land-cover units, 13 biome units, and 7 major land-cover units. We reclassified the raster and created two new land-cover classifications (see Table S3 in Supplemental Materials), one were we recombined the biome and general land-cover units into 18 new classes. For the second classification, we considered four habitat statuses: native, mixed (native-alien), alien, and developed, which refer to the degree of disturbance to vegetation.

We calculated the intersection between each of the new land-cover classifications and the binary maps indicating which cells were predicted as part of the fundamental niche of each species under Models 1 and 2 (step 5 in Fig. 2). For this, we first projected and cropped the land-cover rasters so the extent and resolution match the binary maps. We then combined the land-cover and binary rasters into a single raster layer. With the resulting raster, we calculated the proportion of area (relative to the total area predicted as suitable by Models 1-2) covered by the intersection of the suitable areas and each of the land-cover classes. In this way, we were able to quantify how much land in the main Hawaiian islands is climatically suitable for each native fern but is no longer available due land-use changes (Fig. 5).

Code availability

All the analyses described above were performed using R code (R Core Team, 2020), which we share through this GitHub repository: `https://github.com/LauraJim/Hawaiian-Ferns`. More

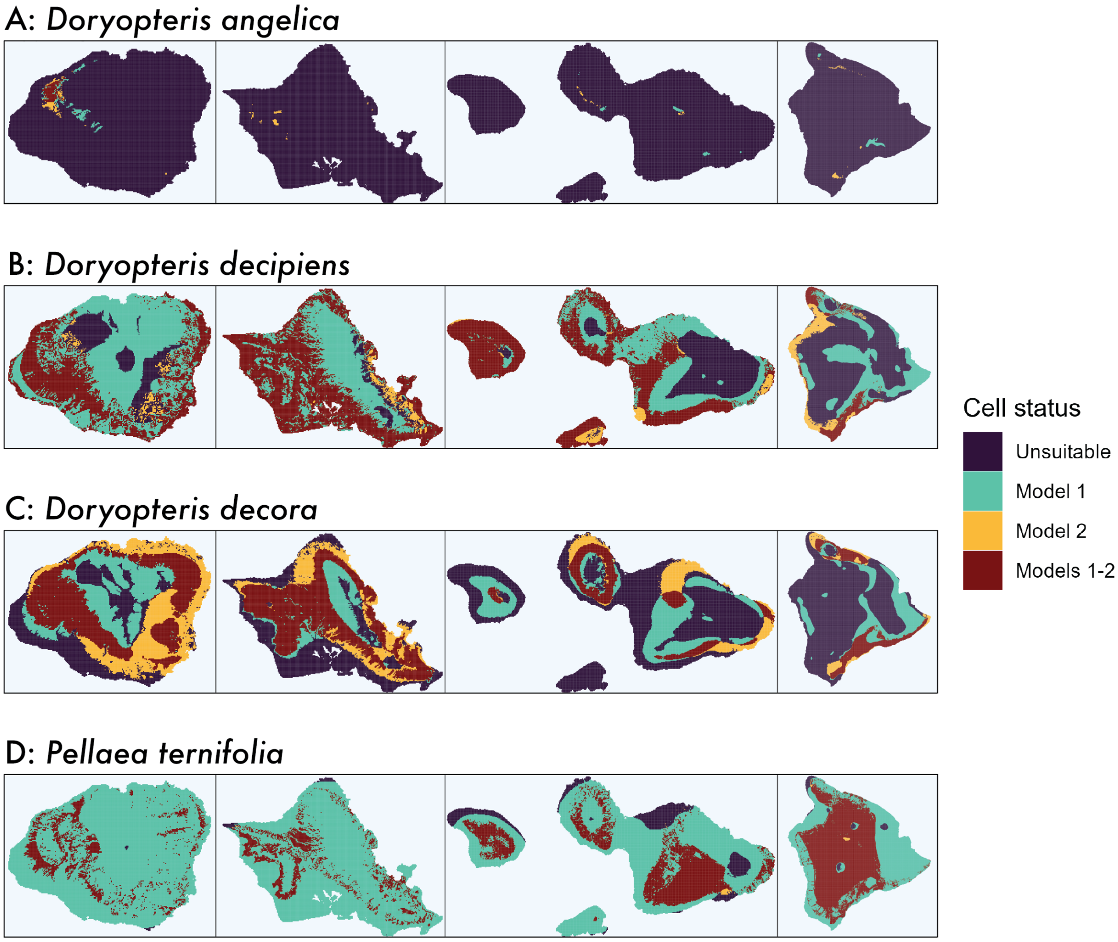

Figure 3: Suitability under Model 1 (teal), Model 2 (yellow), and the overlap of 1 and 2 (burgundy) for native Hawaiian dryland ferns: (A) *Doryopteris angelica*, (B) *Doryopteris decipiens*, (C) *Doryopteris decora*, and (D) *Pellaea ternifolia*.

information regarding the packages and functions we used is provided in the GitHub repository and the Supplemental Material.

RESULTS

Climatic niche of native species

We obtained a total of 25,244 occurrences for the seven (native and non-native) species of interest from all the browsed databases. After data cleaning and filtering, we retained 342 occurrences (shown in Fig. 4). This final dataset includes 55 occurrences of *P. calomelanos*, 82 of *P. austroamericana*, 53 of *C. viridis*, 79 of *P. ternifolia*, 29 of *D. angelica*, 45 of *D. decipiens*, and 15 of *D. decora*. These

Table 1: Percent of occurrences of the listed conspecific native species (e.g., *D. decora* for row *D. decora*) and for all non-native species that fall within the predicted ranges for native species.

	% occurrences in predicted range	
Species	conspecific	all non-native
Doryopteris angelica	82.7	3.2
Doryopteris decipiens	90.1	35.6
Doryopteris decora	90	54.8
Pellaea ternifolia	92.9	33.5

data include occurrences amalgamated by GBIF (2022a,b,c,d,e,f,g,h).

We performed a correlation analysis with the 12 climatic variables we initially selected, retaining six variables such that all pairwise correlation coefficients (r) satisfied $-0.7 > r > 0.7$: diffuse radiation (W/m²), leaf area index, relative humidity (%), maximum mean temperature of the hottest four months (called hot mean; $^{\circ}c$), mean precipitation of the driest three months (called dry mean; mm), and precipitation seasonality (standard deviation of the monthly precipitation values). Figure S1 shows the pairwise correlations between the original 12 variables and Figure S2 shows the pairwise correlations for the selected subset of climatic variables.

For each native fern species, we used the cleaned set of occurrences together with the set of random points—which represent the available climate in the main Hawaiian islands—to estimate the parameters of the models that represent the species' fundamental niche. We fit two 3D models: in Model 1, the niche axes are relative humidity, temperature seasonality, and diffuse radiation. In Model 2, the axes are hot mean, leaf area index, and the dry mean. Parameter estimates are provided in Table S1 at the Supplemental Material. The estimated ellipsoids of *D. angelica* were the smallest and, under Model 1, its niche is nested inside ellipsoids representing the niches of *D. decipiens* and *D. decora* (see Fig. S5 at the Supplemental Material). Under both models, the estimated niches of the ferns in *Doryopteris* are similar to each other—their centers are close and they intersect (see Figures S5 and S6). For *P. ternifolia*, the estimated optimal conditions (ellipsoid's center) were very different from the ones estimated for *Doryopteris* spp. under Model 2. This species seems to be adapted to colder temperatures and presents highest leaf area indices. However, under Model 1, *P. ternifolia*'s niche is quite broad and contains the ellipsoids that represent the niches of the other native species. In the Supplemental Material, we also provide the suitability maps, for each species and model, that were calculated with the parameter estimates (see Fig. S7).

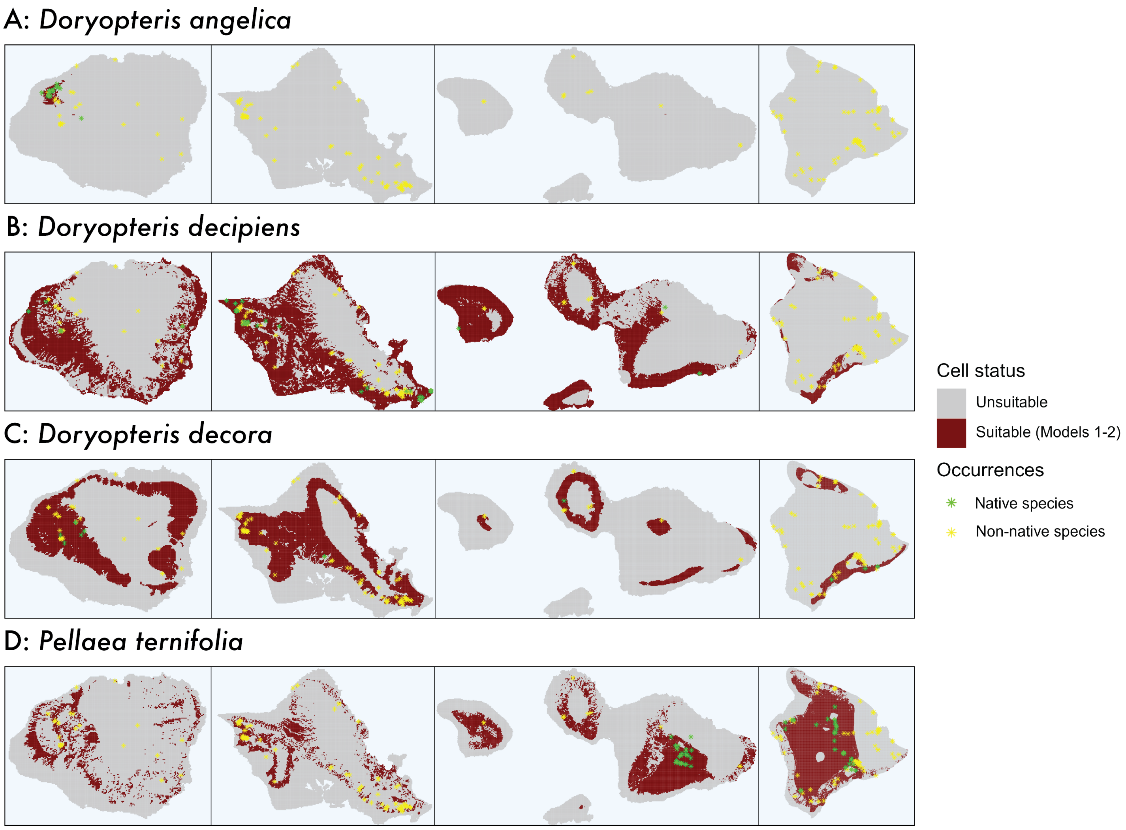

Figure 4: Combined suitability from models 1 and 2 (burgundy) for native Hawaiian dryland ferns: (A) *Doryopteris angelica*, (B) *Doryopteris decipiens*, (C) *Doryopteris decora*, and (D) *Pellaea ternifolia*. Green asterisks represent occurrences of the respective native species, while yellow asterisks represent occurrences of all studied non-natives.

After identifying the 95% confidence ellipsoids of the underlying model for the niche, we obtained binary maps for Model 1 and Model 2, separately. Each pair of binary maps was then combined to obtain the maps shown in Figure 3. All the main Hawaiian islands hold climatically suitable areas for the four native species (except Kahoʻolawe with *D. decora*). For *D. angelica*, only Kauaʻi contains regions identified as suitable under both Model 1 and Model 2. Under Model 1, *P. ternifolia* has the largest potential range, however, after intersecting it with the predicted potential range under Model 2, the final potential range was drastically reduced in Kauaʻi and Oʻahu. For further analysis, we only kept the regions holding climatically suitable conditions under both models.

Impact of non-native species on projected species ranges

Figure 4 shows the binary maps obtained for each native species. The regions colored in burgundy represent cells that were identified as part of the fundamental niche of the species under both Model 1 and Model 2, which we call the predicted potential distribution for the species. *D. angelica* has the smallest predicted potential distribution within the main Hawaiian islands, where only Kauaʻi (left panel in Fig. 4) holds sites with suitable conditions for this species. The predicted potential distributions of *D. decipiens*, *D. decora*, and *P. ternifolia* are wider and all the main islands have regions with suitable conditions (except Kahoʻolawe with *D. decora*). We added the occurrence points of both native (green points) and non-native ferns on top of these maps (yellow points) to evaluate two questions: (1) Does the predicted potential distribution include sites where the species was already identified as present? and (2) To what degree do the non-native ferns occupy the potential distribution of the native ferns? The predicted potential distribution of *D. angelica* correctly predicted 82.75% of the occurrence points, while 3.2% of the non-native ferns occurrence points are inside this range. For *D. decipiens*, the predicted potential distribution prediction included 90.1% of the conspecific native occurrences and 35.6% of the non-native occurrences are inside the species' predicted potential distribution. 90% of the occurrences identified as *D. decora* are inside its corresponding predicted potential niche, which contains the highest percentage of non-native occurrences at 54.8%. Finally, *P. ternifolia*'s predicted potential distribution contained 92.9% of the occurrences and 33.5% of the non-native occurrences.

Impact of land-use change on projected species ranges

We overlaid the potential distribution (under Model 1 and Model 2) of each species with the land-cover layer to partition the climatically suitable areas into land-use types. The bar plots presented in Figure 5 show the proportion of suitable area covered by land-use type, according to each of the land-use classifications of interest (see also Table S2 in the Supplemental Material). Under the land-use classification based on biomes and general land-use units, 17 out of the 18 categories intersected with the suitable area. For *D. angelica*, 80.6% of the suitable area is covered by mesic forest. About 29% of the potential distribution of *D. decipiens* presents some degree of development or is not vegetated. For both *D. decipiens* and *D. decora*, about 6% of their potential distribution is currently used for agriculture. About a quarter of *P. ternifolia*' potential distribution is not vegetated (likely because of this species' affinity for high elevation volcanic habitat with limited plant cover).

Under the second classification, *D. angelica*'s potential distribution is mainly covered by native (58.5%) and alien (35.2%) habitats (see Table S2 in the Supplemental Material). Developed (14%) and alien (69.3%) habitats cover more than 80% of *D. decipiens*'s potential distribution, while only 6.9% of the suitable area is represented by native habitats. We observed a similar pattern for *D. decora* where only a small fraction of the suitable area is covered by native habitats (16.9%). However, *P. ternifolia*'s potential range still presents a native habitat coverage of 37.8%, while the remaining area is mainly covered by mixed (27.9%) and alien habitats (32.4%).

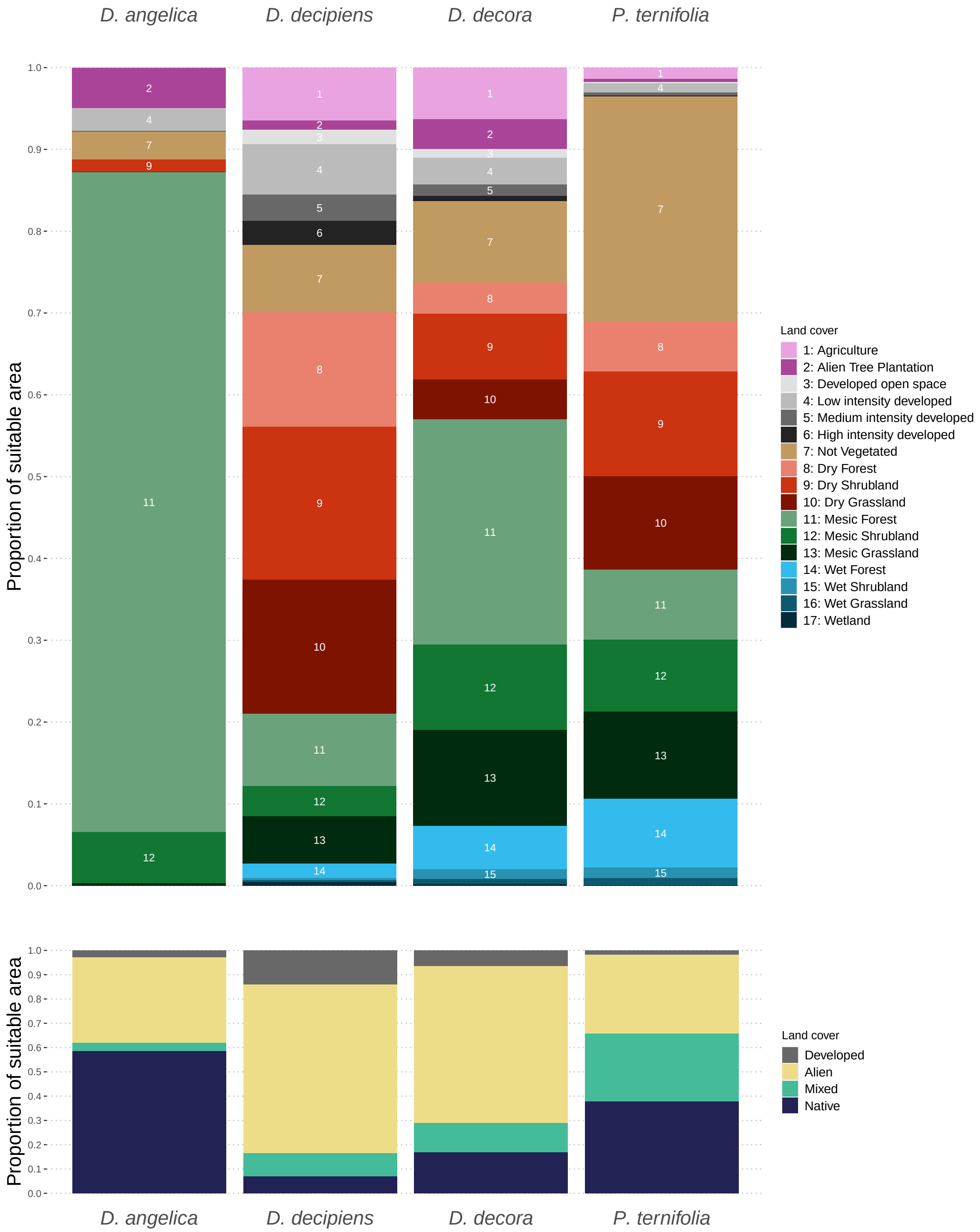

Figure 5: Land uses of inferred climatically suitable areas for native species species. The barplots show the proportion of the total suitable area (sites inside the 95% ellipsoids representing the fundamental niche) that is covered by each land-use type in the corresponding classification. The first classification combines biomes and general land-cover units and the second classification includes four habitat statuses from the most disturbed (Developed) to the most conserved (Native).

DISCUSSION

Hawaiʻi is a longstanding model for understanding ecological and evolutionary processes, and it is exceedingly important to continue studying rapid chances in the islands the face of the global biodiversity crisis. Non-native plant species have a number of very different impacts on native ecological processes in Hawaiʻi. They can deprive native species of water or nutrients and act as primary or alternate hosts for pests and diseases (Smith, 1985). However, a common impact is physical displacement when non-native species colonize disturbed sites and occupy them before the native species can reestablish. Similarly, land-use changes such as agriculture and human development may render climatically appropriate habitat unavailable to native species. Our pipeline for modeling species niche while accounting for competition from non-native species and land-use change demonstrates the importance to conservation efforts of modeling multiple dynamic threats to biodiversity, especially in the highly disturbed habitat of Hawaiʻi dryland ecosystems. We illustrate this pipeline using ferns—plants that tend to not be dispersal-limited given the ability of wind-dispersed spores to travel long distances (Schaefer and Fontaneto, 2011) and thus whose distributions are more likely to be shaped by abiotic and biotic factors.

Importance of land-use data for predicting species' suitable areas

Our results demonstrate an important lesson for plant conservation: an accurate picture of plants' conservation statuses must account for present and historical land use. We demonstrate that while native species *Doryopteris decipiens* and *D. decora* have broader fundamental niches—and thus more suitable land area in Hawaiʻi—than the congeneric *D. angelica*, much of the land predicted as suitable for *D. decipiens* and *D. decora* is dominated by human development or alien habitat (Fig. 5). Of the four native species in our study, only one species (*Doryopteris angelica*) had more than half of its predicted suitable area characterized as primarily native habitat, and this species also has by far the smallest predicted suitable area of all natives. Agriculture accounts for a small percentage of the species' suitable area, though *D. decora* is more affected than the other species. *D. angelica* is considered endangered by the US Fish and Wildlife Service and is the target of several conservation efforts including as Genetic Safety Net Species through the State of Hawaiʻi Department of Land and Natural Resources and the Hawaiʻi State Wildlife Action Plan (DLNR, 2023). In contrast, conspecifics *D. decora* and *D. decipiens* have much larger predicted suitable areas which are much more dominated by non-native habitat (native = 6.95% for *D. decora* and native = 16.92% for *D. decipiens*, see Table 1). Thus, while these species have much larger potential ranges, the quality of this habitat is potentially lower, presenting additional conservation concerns. Our results thus suggest that—by accounting for land use—additional conservation concern may be warranted for these species. Our pipeline thus provides an avenue for conservationists to quantitatively assess the impact of land use on species of interests, as suggested in Gillson et al. (2020).

We contextualize the temporally static land use change data from (Jacobi et al., 2017) with a deeper understanding of the history of land use change in Hawaiʻi. The Jacobi et al. (2017) data represents a snapshot of Hawaiʻi in 2014 when former agricultural lands had been mostly abandoned and had converted—largely through neglect—to non-native grass-dominated landscapes. The low proportion of agricultural land projected as suitable for the species of our study is likely an artifact of this history. This history also illuminates possible conservation futures, and we echo calls for fallowed agricultural land to be targeted for Hawaiian dry forest conservation, including of the native fern flora; restoration of fallow agricultural land has also been suggested as a fire recovery and prevention mechanism (Bond-Smith et al., 2023; Trauernicht et al., 2018).

Impact of non-native ferns

Doryopteris decora is the native fern whose predicted range includes the highest proportion of non-native occurrences (54.8%, Table 1), suggested that this species is the most potentially impacted by competition from related non-native ferns. We emphasize that our study does not demonstrate that non-native ferns are directly competing with natives, nor that these non-natives have negative impacts on native species. Rather, we show that non-native ferns indeed share very similar climatic preferences to native ferns and occur in habitats predicted to be suitable for natives, especially of *D. decora*. While it is possible that *D. decora* persists in these environments despite co-occurrence with non-natives, our difficulty in obtaining recent and accurate occurrence data for this species (see METHODS: Species occurrence data) suggests that *D. decora* may be failing to thrive in an invaded, altered landscape. We suggest that further conservation attention be given to this species. While only 3.2% of non-native occurrences occur in the predicted suitable area for federally listed *D. angelica*, the predicted area itself is significantly smaller than for all other native species in this study. Visual inspect of the occurrences (Fig. 4A) shows many non-native individuals (yellow) in and around the small suitable area (burgundy) and *D. angelica* occurrences (green). Competition from non-native ferns may thus still be a concern for this species.

Accuracy of modeling approach

For most native species, our modeling approach results in predicted suitable areas that include $> 90\%$ of observed occurrences. *D. angelica* is the one exception, with only 83.7% of occurrences falling into the predicted suitable area. This may be because *D. angelica* is predicted to have far less suitable area than the other native species, implying that our model is inferring a very specific set of climatic conditions necessary for *D. angelica* to survive. *D. angelica* is known from only a few populations that are clustered in similar regions of Kaua'i island, and it is possible our model is inferring more strict climatic conditions because the existing individuals and populations are highly clustered in climatic and geographic space.

On the other hand, our predicted suitable area estimate for *Pellaea ternifolia* is quite broad, especially under Model (Fig. 3). Model 1 includes three climatic variables: relative humidity, temperature seasonality, and diffuse radiation, and our results suggest that together these variables hold little to no information about suitability for *P. ternifolia*. In order to compare across species, we used the same set of climatic variables for all estimates, but future studies on *P. ternifolia* should consider other variables that could be more appropriate for modeling suitability. Alternatively, we may be accurately predicting the fundamental niche of *Pellaea ternifolia*, and the discrepancy between observed range and predicted suitable area may be due to the role of biotic interactions in limited where *Pellaea ternifolia* can occur.

Applicability of pipeline to future studies

The pipeline we outline in this study (illustrated in Fig. 2) may guide future studies that use ENMs for conservation applications. Here, we outline three main takeaways for researchers to use moving forward:

1. Our approach allows for and promotes the careful curation of both climatic and occurrence data (steps (1) and (2) in Fig. 2). Rather than use a broad set of generic climatic variables, we

obtained regionally specific and high-resolution climatic layers that describe features likely to be relevant to the species of interest based on their ecology. We encourage researchers to seek out similar datasets whenever possible, though we also acknowledge that many regions of the world do not have access to such data (e.g., see discussion in Soria-Auza et al. 2010). Furthermore, we acknowledge that some of our selected climatic layers appear to be insufficient for *Pellaea ternifolia*, and we recommend that researchers evaluate model predictions given prior information on species ranges and ecology. This may be a challenge for researchers hoping to parallelize analyses of many species (e.g., for regional assessments of the vulnerability of a particular flora). Our approach is thus more appropriate for targeted study of a few species of interest.

2. Our integration of land use into evaluations of predicted suitable area for natives (step (5) in Fig. 2) requires a place-based understanding of the history behind current land use. We position our study within the context of land-use change in Hawai'i; land privatization during Great Māhele encouraged the development of plantations in former Hawaiian drylands. Despite the current abandonment of most plantations, much of that land is still unavailable for native species because non-native species now occupy former native habitat. Our land use change results demonstrate the impact of this history on native dryland plants; only one native species is predicted to have more than 50% climatically suitable area covered by native ecosystems.

3. We emphasize the importance of using a mathematical model that aligns with our theoretical definitions of the niche. Our approach uses the Jiménez and Soberón (2022) model to estimate the fundamental niche—the set of climatic conditions that an organism could inhabit in the absence of biotic interactions. Thus we must also evaluate the potential role of other species. In our case we set out to evaluate how non-natives may impose additional restrictions on where natives occur. We find evidence suggesting that non-native species may be competing with natives (particularly with *D. decora*) for limited available dryland habitat. We encourage researchers to ensure that their model of choice aligns with their theoretical understanding of the ecological niche.

Conclusions

Our novel pipeline unites new developments in ecological niche modeling with a place-based understanding of land-use change and potential competition from non-native species. We demonstrate that native Hawaiian dryland ferns may be competing for limited suitable habitat with non-native relatives, and our results point to the drastic reduction in available area due to land-use changes such as human development and non-native ecosystems, especially fallowed agricultural lands. We advocate for continued conservation efforts for the endangered *Doryopteris angelica*, additional conservation assessment for *D. decora*, and restoration of fallowed agricultural lands to build up more native habitat. Our study also demonstrates the value of our integrative approach and serves as a model for multidimensional conservation assessments based on ecological niche modeling.

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Author contributions

K.E.C, C.M.T., and R.Z.F conceived the study. K.E.C, L.J, and C.M.T performed analyses and wrote the paper. R.Z.F., M.K.T., and K.H. provided feedback on analyses and edited the paper.

Data availability statement

All the R code needed to reproduce all our analyses and figures is available at this GitHub repository: `https://github.com/LauraJim/Hawaiian-Ferns`. The occurrence data for all the species is provided in the same GitHub repository, except for *Doryopteris angelica* given conservation concerns regarding this native Hawaiian species. The rasters with the climate variables and land-use layers can be found at their original sources using the links provided in the Methods section.

References

Association, H. S. P. (1992). Hawaiian sugar manual (1992).

Baldwin, B. G. and Sanderson, M. J. (1998). Age and rate of diversification of the hawaiian silversword alliance (compositae). *Proceedings of the National Academy of Sciences*, 95(16):9402–9406.

Barton, K. E., Westerband, A., Ostertag, R., Stacy, E., Winter, K., Drake, D. R., Fortini, L. B., Litton, C. M., Cordell, S., Krushelnycky, P., et al. (2021). Hawai ʻi forest review: synthesizing the ecology, evolution, and conservation of a model system. *Perspectives in Plant Ecology, Evolution and Systematics*, 52:125631.

Bond-Smith, S., Bremer, L., Burnett, K., Trauernicht, C., and Wada, C. (2023). Reducing fire risk and restoring value to fallow agricultural lands. `https://uhero.hawaii.edu/reducing-fire-risk-and-restoring-value-to-fallow-agricultural-lands/`.

Bouma, W., Ritchie, P., and Perrie, L. (2010). Phylogeny and generic taxonomy of the new zealand pteridaceae ferns from chloroplast rbc l dna sequences. *Australian Systematic Botany - AUST SYSTEMATIC BOTANY*, 23:143–151.

Buzzard, V., Hulshof, C. M., Birt, T., Violle, C., and Enquist, B. J. (2016). Re-growing a tropical dry forest: functional plant trait composition and community assembly during succession. *Functional Ecology*, 30(6):1006–1013.

Chinen, J. J. (2020). *The great mahele: Hawaii's land division of 1848*. University of Hawaii Press.

Consortium, P. C. (2022). Pteridoportal. `https://www.pteridoportal.org/portal/index.php`. Accessed: 2022-06.

Cordell, S. and Sandquist, D. R. (2008). The impact of an invasive african bunchgrass (pennisetum setaceum) on water availability and productivity of canopy trees within a tropical dry forest in hawaii. *Functional Ecology*, 22(6):1008–1017.

D'Antonio, C. M. and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, 23:63–87.

DLNR, H. (2023). Fact Sheet: *Doryopteris angelica*. Accessed: 31 October 2023, `https://dlnr.hawaii.gov/wildlife/files/2013/09/Fact-Sheet-Doryopteris-angelica.pdf`.

Farrant, D. N., Roberts, D. A., D'Antonio, C. M., and Larsen, A. E. (2023). What follows fallow? assessing revegetation patterns on abandoned sugarcane land in Hawaiʻi. *Agriculture, Ecosystems & Environment*, 355:108603.

Gastony, G. J. and Rollo, D. R. (1995). Phylogeny and generic circumscriptions of cheilanthoid ferns (pteridaceae: Cheilanthoideae) inferred from rbcl nucleotide sequences. *American fern journal*, 85:341–360.

GBIF (2022). Global biodiversity information facility. `https://www.gbif.org`.

GBIF (2022a). *Cheilanthes viridis* occurrence download. Retrieved: 14 September 2022, doi = `https://10.15468/DL.TEBH8W`.

GBIF (2022b). *Doryopteris angelica* occurrence download. Retrieved: 16 September 2022, doi = `https://10.15468/DL.HPMECS`.

GBIF (2022c). *Doryopteris decipiens* occurrence download. Retrieved: 9 June 2022, doi = `https://10.15468/DL.RF6Y46`.

GBIF (2022d). *Doryopteris decora* occurrence download. Retrieved: 9 June 2022, doi = `https://10.15468/DL.9Z95M2`.

GBIF (2022e). *Pellaea ternifolia* occurrence download. Retrieved: 20 September 2022, doi = `https://10.15468/DL.3VCVR5`.

GBIF (2022f). *Pellaea viridis* occurrence download. Retrieved: 20 September 2022, doi = `https://10.15468/DL.U7T78F`.

GBIF (2022g). *Pityrogramma austroamericana* occurrence download. Retrieved: 20 September 2022, doi = `https://10.15468/DL.XMGVTS`.

GBIF (2022h). *Pityrogramma calomelanos* occurrence download. Retrieved: 20 September 2022, doi = `https://doi.org/10.15468/DL.2T3DFH`.

Giambelluca, T., Shuai, X., Barnes, M., Alliss, R., Longman, R., Miura, T., Chen, Q., Frazier, A., Mudd, R., Cuo, L., et al. (2014). Evapotranspiration of Hawai'i. *Final report submitted to the US Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawai 'i*.

Gillson, L., Seymour, C. L., Slingsby, J. A., and Inouye, D. W. (2020). What are the grand challenges for plant conservation in the 21st century?

Givnish, T. J., Millam, K. C., Mast, A. R., Paterson, T. B., Theim, T. J., Hipp, A. L., Henss, J. M., Smith, J. F., Wood, K. R., and Sytsma, K. J. (2009). Origin, adaptive radiation and diversification of the hawaiian lobeliads (asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences*, 276(1656):407–416.

Hevly, R. H. (1963). Adaptations of cheilanthoid ferns to desert environments. *Journal of the Arizona Academy of Science*, 2(4):164–175.

Hutchinson, G. E. (1957). Concluding remarks. In *Cold Sprig Harbor Symposia on Quantitative Biology*, chapter 22, pages 415–427. Cold Sprig Harbor Symposia on Quantitative Biology.

Jacobi, J., Price, J., Fortini, L., Gon III, S., and Berkowitz, P. (2017). Hawaii land cover and habitat status: Us geological survey data release.

Jiménez, L., Soberón, J., Christen, J. A., and Soto, D. (2019). On the problem of modeling a fundamental niche from occurrence data. *Ecological Modelling*, 397(February):74–83.

Jiménez, L. and Soberón, J. (2022). Estimating the fundamental niche: Accounting for the uneven availability of existing climates in the calibration area. *Ecological Modelling*, 464:109823.

John A. Engott, T. T. V. (2007). Effects of agricultural land-use changes and rainfall on ground-water recharge in central and west maui, hawai'i, 1926–2004. Scientific Investigations Report 2007-5103.

Kamakau, S. (1961). *Ruling Chiefs of Hawaii*. Kamehameha Schools Press.

Kao, T.-T., Pryer, K. M., Freund, F. D., Windham, M. D., and Rothfels, C. J. (2019). Low-copy nuclear sequence data confirm complex patterns of farina evolution in notholaenid ferns (pteridaceae). *Molecular phylogenetics and evolution*, 138:139–155.

Kessler, M., Mehltreter, K., Walker, L., and Sharpe, J. (2010). *Biogeography of ferns*. Cambridge University Press.

Kluge, J. and Kessler, M. (2006). Fern endemism and its correlates: contribution from an elevational transect in costa rica. *Diversity and distributions*, 12(5):535–545.

Linnekin, J. (1983). The hui lands of keanae: Hawaiian land tenure and the great mahele. *The Journal of the Polynesian Society*, 92(2):169–188.

Lovette, I. J., Bermingham, E., and Ricklefs, R. E. (2002). Clade-specific morphological diversification and adaptive radiation in hawaiian songbirds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1486):37–42.

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., and Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33(3):491–505.

Murphy, P. G. and Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual review of ecology and systematics*, 17(1):67–88.

Palmer, D. D. (2003). *Hawai'i's ferns and fern allies*. Number 2002-2010. University of Hawaii Press.

Portillo-Quintero, C., Sanchez-Azofeifa, A., Calvo-Alvarado, J., Quesada, M., and do Espirito Santo, M. M. (2015). The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for its sustainable management. *Regional Environmental Change*, 15:1039–1049.

POWO (2023). Plants of the world online. Retrieved: 27 September 2023.

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3(4):349–361.

Quesada, M., Sanchez-Azofeifa, G. A., Alvarez-Anorve, M., Stoner, K. E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M. M., Fagundes, M., Fernandes, G. W., et al. (2009). Succession and management of tropical dry forests in the americas: Review and new perspectives. *Forest Ecology and Management*, 258(6):1014–1024.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ranker, T., Imada, C., Lynch, K., Palmer, D., Vernon, A., and Thomas, M. (2019a). Taxonomic and nomenclatural updates to the fern and lycophyte flora of the hawaiian islands. *American Fern Journal*, 109:54–72.

Ranker, T. A., Imada, C. T., Lynch, K., Palmer, D. D., Vernon, A. L., and Thomas, M. K. (2019b). Taxonomic and Nomenclatural Updates to the Fern and Lycophyte Flora of the Hawaiian Islands. *American Fern Journal*, 109(1):54 – 72.

Rønsted, N., Walsh, S. K., Clark, M., Edmonds, M., Flynn, T., Heintzman, S., Loomis, A., Lorence, D., Nagendra, U., Nyberg, B., et al. (2022). Extinction risk of the endemic vascular flora of kauai, hawaii, based on iucn assessments. *Conservation Biology*, 36(4):e13896.

Rothfels, C. J., Windham, M. D., Grusz, A. L., Gastony, G. J., and Pryer, K. M. (2008). Toward a monophyletic notholaena (pteridaceae): Resolving patterns of evolutionary convergence in xeric-adapted ferns. *Taxon*, 57(3):712–724.

Schaefer, H. and Fontaneto, D. (2011). Dispersal limitation or habitat quality–what shapes the distribution ranges of ferns. *Biogeography of micro-organisms: is everything small everywhere*, pages 234–243.

Schuettpelz, E., Schneider, H., Huiet, L., Windham, M., and Pryer, K. (2007). A molecular phylogeny of the fern family pteridaceae: Assessing overall relationships and the affinities of previously unsampled genera. *Molecular phylogenetics and evolution*, 44:1172–85.

Selmants, P. C., Giardina, C. P., Sousan, S., Knapp, D. E., Kimball, H. L., Hawbaker, T. J., Moreno, A., Seirer, J., Running, S. W., Miura, T., et al. (2017). Baseline carbon storage and carbon fluxes in terrestrial ecosystems of hawai 'i. *Baseline and Projected Future Carbon Storage and Carbon Fluxes in Ecosystems of Hawai'I*, pages 75–87.

Sharpe, J. M. (2019). Fern ecology and climate change. *Indian Fern Journal*, 36:179–199.

Smith, A. R. (1993). Phytogeographic principles and their use in understanding fern relationships. *Journal of Biogeography*, pages 255–264.

Smith, C. W. (1985). Impact of alien plants on hawaii's native biota. *Hawaii's terrestrial ecosystems: preservation and management*, pages 180–250.

Soberón, J. (2007). Grinnellian and eltonian niches and geographic distributions of species. *Ecology letters*, 10(12):1115–1123.

Soberón, J. and Arroyo-Peña, B. (2017). Are fundamental niches larger than the realized? testing a 50-year-old prediction by hutchinson. *Plos one*, 12(4):e0175138.

Soberón, J. M. (2010). Niche and area of distribution modeling: a population ecology perspective. *Ecography*, 33(1):159–167.

Soria-Auza, R. W., Kessler, M., Bach, K., Barajas-Barbosa, P. M., Lehnert, M., Herzog, S. K., and Böhner, J. (2010). Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from bolivia. *Ecological Modelling*, 221(8):1221–1229.

Takaki, R. (1984). *Pau Hana: Plantation Life and Labor in Hawaii, 1835-1920*. University of Hawaii Press.

Trauernicht, C., Ticktin, T., Fraiola, H., Hastings, Z., and Tsuneyoshi, A. (2018). Active restoration enhances recovery of a Hawaiian mesic forest after fire. *Forest Ecology and Management*, 411:1–11.

Tryon, R. (1986). The biogeography of species, with special reference to ferns. *The Botanical Review*, 52:117–156.

Tryon, R. M. (1942). A revision of the genus doryopteris. *Contributions from the Gray Herbarium of Harvard University*, (143):1–80.

Tryon, R. M. (1944). Dynamic phytogeography of doryopteris. *American Journal of Botany*, 31(8):471–473.

University Herbarium (1939). *Contributions from the University of Michigan Herbarium*, volume v.1 (1939). Ann Arbor, University of Michigan.

Valier, K. (1995). *Ferns of Hawai'i*. University of Hawaii Press.

Vernon, A. and Ranker, T. (2013). Current status of the ferns and lycophytes of the hawaiian islands. *American Fern Journal*, 103:59–111.

Wilson, E. O. et al. (1988). *Biodiversity*. National Academy Press.

Windham, M. D., Huiet, L., Schuettpelz, E., Grusz, A. L., Rothfels, C., Beck, J., Yatskievych, G., and Pryer, K. M. (2009). Using plastid and nuclear dna sequences to redraw generic boundaries and demystify species complexes in cheilanthoid ferns. *American Fern Journal*, 99(2):128–132.

Witter, M. S. and Carr, G. D. (1988). Adaptive radiation and genetic differentiation in the hawaiian silversword alliance (compositae: Madiinae). *Evolution*, 42(6):1278–1287.

Yesilyurt, J. (2003). *Systematic Revision of the Genus Doryopteris J. Sm. (Pteridaceae-Cheilanthoideae)*. University of Reading, School of Plant Sciences.

Yesilyurt, J. and Schneider, H. (2010). The new fern genus *Calciphilopteris* (Pteridaceae). *Phytotaxa*, 7(1):52–59.

Yesilyurt, J. C. (2005). The Fern Genus *Doryopteris* (Cheilanthoideae-Pteridaceae) in the Hawaiian Islands. *Kew Bulletin*, 60(4):547–558.

Yesilyurt, J. C., Barbara, T., Schneider, H., Russell, S., Culham, A., and Gibby, M. (2015). Identifying the generic limits of the cheilanthoid genus *Doryopteris*. *Phytotaxa*, 221(2):101–122.

Zhang, G., Zhang, X.-C., and Chen, Z. (2008). Phylogeny of cryptogrammoid ferns and related taxa based on rbcl sequences. *Nordic Journal of Botany*, 23:485 – 493.

Zhang, G., Zhang, X.-C., Chen, Z., Liu, H.-M., and Yang, W. (2007). First insights in the phylogeny of asian cheilanthoid ferns based on sequences of two chloroplast markers. *Taxon*, 56:369–378.

Zhang, L., Zhou, X.-M., Lu, N. T., and Zhang, L.-B. (2017). Phylogeny of the fern subfamily pteridoideae (pteridaceae; pteridophyta), with the description of a new genus: Gastoniella. *Molecular Phylogenetics and Evolution*, 109:59–72.

Zhu, G., Liu, G., Bu, W., and Gao, Y. (2013). Ecological niche modeling and its applications in biodiversity conservation. *Biodiversity Science*, 21(1):90.

Zou, X. and Bashkin, M. (1998). Soil carbon accretion and earthworm recovery following revegetation in abandoned sugarcane fields. *Soil Biology and Biochemistry*, 30(6):825–830.