

# Global and regional drivers of abundance patterns in the hart's tongue fern complex (*Aspleniaceae*)

Namjoo Heo<sup>\*,</sup>, Donald J. Leopold, Mark V. Lomolino, Seona Yun and Danilo D. Fernando

Department of Environmental Biology, State University of New York College of Environmental Science and Forestry, One Forestry Drive, Syracuse, NY 13210, USA

\* For correspondence. E-mail [nheo01@esf.edu](mailto:nheo01@esf.edu)

Received: 19 July 2022 Returned for revision: 6 October 2022 Editorial decision: 20 October 2022 Accepted: 21 October 2022

- **Background and Aims** The hart's tongue fern (HTF) complex is a monophyletic group composed of five geographically segregated members with divergent abundance patterns across its broad geographic range. We postulated hierarchical systems of environmental controls in which climatic and land-use change drive abundance patterns at the global scale, while various ecological conditions function as finer scale determinants that further increase geographic disparities at regional to local scales.
- **Methods** After quantifying the abundance patterns of the HTF complex, we estimated their correlations with global climate and land-use dynamics. Regional determinants were assessed using boosted regression tree models with 18 potential ecological variables. Moreover, we investigated long-term population trends in the USA to understand the interplay of climate change and anthropogenic activities on a temporal scale.
- **Key Results** Latitudinal climate shifts drove latitudinal abundance gradients, and regionally different levels of land-use change resulted in global geographic disparities in population abundance. At a regional scale, population isolation, which accounts for rescue effects, played an important role, particularly in Europe and East Asia where several hot spots occurred. Furthermore, the variables most strongly influencing abundance patterns greatly differed by region: precipitation seasonality in Europe; spatial heterogeneity of temperature and precipitation in East Asia; and magnitudes of past climate change, temperature seasonality and edaphic conditions in North America. In the USA, protected populations showed increasing trends compared with unprotected populations at the same latitude, highlighting the critical role of habitat protection in conservation measures.
- **Conclusions** Geographic disparities in the abundance patterns of the HTF complex were determined by hierarchical systems of environmental controls, wherein climatic and land-use dynamics act globally but are modulated by various regional and local determinants operating at increasingly finer scales. We highlighted that fern conservation must be tailored to particular geographic contexts and environmental conditions by incorporating a better understanding of the dynamics acting at different spatiotemporal scales.

**Key words:** Abundance, *Asplenium scolopendrium*, BRT modelling, climate change, conservation, geographic disparity, global scale, habitat protection, land-use, rarity, regional scale, population trends.

## INTRODUCTION

As species rarity is generally a biological phenomenon, conservation biologists face the daunting task of identifying the underlying causes of rarity and integrating them into political and economic decisions (Schemske *et al.*, 1994). Along with geographic range and habitat specificity, local abundance is one of the key attributes accounting for species rarity (Rabinowitz, 1981; Rabinowitz *et al.*, 1986). In nature, spatial and temporal variations in local abundance are omnipresent, resulting from dynamic interactions between species traits and ecological and biogeographic factors (Brown, 1984; Sporbert *et al.*, 2020). Given that abundance is more conducive to quantitative analysis than other rarity attributes, elucidating the factors and dynamics underpinning abundance patterns is essential to understanding species persistence and developing conservation plans (Gaston, 1994; Brown *et al.*, 1995). Climate and land-use patterns generally explain the global abundance patterns of species (Cahill *et al.*, 2013; Newbold *et al.*, 2015). Climate change is a pervasive

threat, affecting even species in protected areas (Monzón *et al.*, 2011). It interacts with the biological traits of organisms such as growth rates, reproduction and dispersibility, which control vital rates and hence population abundance (Walther *et al.*, 2002; Parmesan, 2006). Climate change has resulted in relatively predictable and gradual changes in abundance, with many ecological impacts projected to come from rising temperatures and modified precipitation patterns (Wu *et al.*, 2011; Cahill *et al.*, 2013; Palmer *et al.*, 2015).

The effects of land-use dynamics on patterns of population abundance are also globally widespread (Newbold *et al.*, 2015). Today, >75 % of Earth's ice-free land has been altered by human land use (Ellis and Ramankutty, 2008), which together with overexploitation, introduction of non-native species and chains of co-extinction comprise Diamond's (1984) the evil quartet of anthropogenic threats. During the Late Pleistocene and into the Holocene, dynamics in climates and landcover have been particularly intense (Barnosky *et al.*, 2004), and both may

have interacted synergistically to cause catastrophic changes in population abundance at regional scales (Brook *et al.*, 2008).

Abundance patterns are also shaped by factors that operate on finer scales, including local topography, microclimate and edaphic conditions (Coudun and Gégout, 2007; Ohler *et al.*, 2020; García-Girón *et al.*, 2021). Biological processes between spatially close populations (e.g. colonization and recolonization through dispersal processes in a metapopulation or source–sink dynamics) can also influence species abundance patterns at local to regional scales (Hanski, 1989; Eriksson, 1996). These local-scale determinants can modulate species responses to global and regional drivers, or delay their effects for decades (de Frenne *et al.*, 2013). The importance of each determinant greatly depends on location, and interactions among determinants can vary considerably across temporal and spatial scales. Hence, our understanding of the factors driving abundance patterns, and therefore patterns in rarity, is often complicated by interactions of factors operating across a broad range of spatial and temporal scales (García-Girón *et al.*, 2021).

As ferns are typically independent from the constraints of mutualistic coevolutionary relationships, their abundance patterns are more closely tethered to local environmental conditions (Barrington, 1993). Subsequently, geographic disparities in abundance patterns often occur within species complexes of ferns which consist of closely related but geographically segregated infraspecies. The hart's tongue fern (HTF, *Asplenium scolopendrium*) complex provides a highly informative case study to address this phenomenon and explore the underlying factors influencing abundance and rarity across its globally disjunct range. As a temperate evergreen plant, it has a circumpolar distribution in the Northern Hemisphere, but recently introduced populations also occur in New Zealand (Brownsey and Perrie, 2017). Each complex member is geographically segregated and exhibits vastly different patterns of abundance and rarity, thus providing an important opportunity to investigate potential drivers across the range of this intriguing species complex. The three main population clusters occur in Europe, North America and East Asia, and are broadly characterized by decreasing north to south gradients of abundance. In Europe, abundance is relatively high throughout the north-west, particularly in the British Isles, but tends to decrease towards southern and eastern Europe (Löve, 1954).

The north to south gradient is most apparent in North America where northern populations located along the Niagara Escarpment are relatively abundant, while populations occur sparsely in southern areas including Alabama and Tennessee, inhabiting specific habitats such as cave mouths and sinkholes (COSEWIC, 2016; USFWS, 2020). The southernmost populations in Mexico and the Caribbean are extremely rare; thus, detailed information on this species' distributional range and habitat characteristics is lacking (Viane and Reichstein, 1991; Wagner *et al.*, 1993; USFWS, 2020). Mainland East Asian populations such as those in the Russian Far East, North-eastern China and the Korean Peninsula also are generally rare, but many islands including the Japanese Archipelago, Jeju and Ulleung Islands host relatively abundant populations (Korea Forest Research Institute, 1997; Lin and Viane, 2013; Shiyong *et al.*, 2017). However, even in the Japanese Archipelago, population abundance declines in south-western regions (e.g. Chiba and Aichi) and northern Kyushu (e.g. Saga and Kumamoto),

being listed as provincially endangered in these prefectures (Murakami, 2020).

Historically, these geographic disparities in abundance patterns across the broad range of this species complex have drawn considerable scientific interest, with numerous studies focusing on various characteristics of local populations, including ecological and habitat characteristics (Maxon, 1900; Petry, 1918; Gates, 1962; Futyma, 1980; Cinquemani Kuehn and Leopold, 1993; Keil *et al.*, 2012; Ok and Yoo, 2012; Ismail *et al.*, 2017), development and ecophysiology (Testo and Watkins, 2011, 2013; Grašičet *et al.*, 2020), and population genetics (Ok and Yoo, 2012; Fernando *et al.*, 2015; Weber-Townsend, 2017). Long-term population studies have also been performed to understand the temporal dynamics of local population abundance, particularly for the American HTF (Hunter, 1922; Faust, 1960; Cinquemani *et al.*, 1988, Cinquemani Kuehn and Leopold, 1992; Brumbelow, 2014).

Comprehensive studies of the global and regional drivers of HTF patterns in abundance and rarity, however, are still lacking, despite there being requisite insights for successful conservation of these species. Several HTF members such as *A. scolopendrium* var. *lindenii* and *A. scolopendrium* subsp. *antrijovis* are seriously threatened, and a population of these may disappear before they can be examined (Viane and Reichstein, 1991). Ongoing discussion regarding delisting *A. scolopendrium* var. *americanum* from the Lists of Endangered and Threatened Wildlife and Plants in the USA also requires a clear understanding of the dynamics underlying abundance patterns across its range (USFWS, 2020).

Here, we expand our understanding of the factors that determine local- to global-scale patterns in abundance and rarity of the HTF complex. We postulated hierarchical systems of environmental controls in which climatic and land-use change drive abundance patterns at the global (i.e. inter-regional) scale, while various ecological conditions act as finer scale determinants that further increase regional and local geographic disparities. To address this hypothesis, we first quantified the abundance patterns of the HTF complex by comparing the densities and geographic isolation among populations. We then investigated the potential impacts of climate and land-use change by comparing changes in climatic suitability and protected area coverage for each region. Regional determinants were assessed using boosted regression tree models with 18 potential explanatory variables. Furthermore, we examined population trends in the USA based on >100 years of census data to understand temporal dynamics and the interplay of climate change and anthropogenic activities. Overall, this study provided key insights for assessing species rarity and persistence and for developing effective strategies for the conservation of this iconic species complex.

## MATERIALS AND METHODS

### *Taxonomic framework*

Five taxa have generally been recognized as members of the HTF complex and generally reflect geographic segregation: two European taxa *A. scolopendrium* subsp. *scolopendrium* and *A. scolopendrium* subsp. *antrijovis*, two American taxa

*A. scolopendrium* var. *americanum* and *A. scolopendrium* var. *lindenii*, and one East Asian taxon *A. komarovii* (Tropicos, <https://www.tropicos.org>; GBIF, <https://www.gbif.org/>; World Plants, <https://www.worldplants.de/>) (Fig. 1).

#### Abundance data

Given the difficulty of estimating local population size without thorough censuses and demographic studies (Delgado *et al.*, 2008), we measured the average number of occurrences per sampling unit (100 × 100 km grid cells) as a proxy for population abundance. The georeferenced occurrence records (with each considered as a single population) were obtained from the GBIF database by querying ‘*Asplenium scolopendrium*’ as well as its subspecies, varieties and synonyms (Supplementary data Table S1). We cleaned the data by removing duplicates and flagged records with co-ordinate errors, such as country centroids and capitals, zero or equal co-ordinates and locations of biodiversity institutions, using the R package CoordinateCleaner v.2.0-20 (Zizka *et al.*, 2019). To reduce the effects of spatial clustering due to sampling bias, we rarefied the occurrences with a resolution of 10 km using the R package humboldt v.1.0.0.420121 (Brown and Carnaval, 2019). Outliers and taxonomically misclassified records were manually identified based on herbarium specimens and meta-data from GBIF, which resulted in 7082 occurrence records. The Create Fishnet and Spatial Join tools in ArcGIS Pro 2.8.3 were respectively used to generate the 100 × 100 km grid cells as sampling units and to summarize population abundance by counting the number of cleaned occurrence records entirely within an associated sampling unit. The resulting 630 spatial datasets of population abundance were used as response variables in spatial analyses (Supplementary data File S1).

#### Explanatory variables

We considered 18 potential predictors, including those regarding current climatic conditions, the magnitude of past climatic change, climatic spatial heterogeneity, topographic variables, edaphic conditions, anthropogenic impacts and population isolation (Table 1). Current climate raster data with 30 arc-second spatial resolution were downloaded from WorldClim 2.0 (<https://www.worldclim.org/>, Fick and Hijmans, 2017). According to Hamann *et al.* (2015), the magnitude of past climate change (i.e. temperature and precipitation) was estimated by computing the distance from a grid cell with a climate value of the Last Glacial Maximum (LGM, approx. 21 000 years ago) to a neighbouring grid cell with the present matching climate value. Both LGM and current (1979–2013) temperature and precipitation raster data with 10 min spatial resolution were downloaded from PaleoClim (<http://www.paleoclim.org/>, Karger *et al.*, 2021). We estimated the spatial heterogeneity of temperature, precipitation and elevation with a coefficient of variation between a focal cell and its neighbouring cells using the Focal Statistics tool in ArcGIS Pro 2.8.3. Terrain ruggedness was derived from elevation raster data downloaded from WorldClim 2.0 using Esri's Arc Hydro tools implemented in ArcGIS Pro 2.8.3. Soil raster data with 250 m spatial resolution including pH, water content, cation

exchange capacity and organic carbon were downloaded from the ISRIC Soil Data Hub to investigate the effect of edaphic conditions on local population abundance (<https://www.isric.org/>). The raster human footprint data were obtained from the NASA Socioeconomic Data and Applications Centre (<https://earthdata.nasa.gov>). This index was used to estimate recent anthropogenic pressures on natural ecosystems by incorporating information about population density, human land use and infrastructure (Sanderson *et al.*, 2002). The distance to the nearest population was used as a proxy for population isolation and was computed using the Near tool in ArcGIS Pro 2.8.3. We homogenized these spatial data from various sources, and all values of these explanatory variables were summarized for each sample unit using the Zonal Statistics as Table tool in ArcGIS Pro 2.8.3. Principal component analysis was performed to investigate the correlation of the explanatory variables using the R package stats v.4.2.0 (R Core Team, 2021), and the resulting loadings of the variables are shown in Supplementary data Table S2 and Fig. S1.

#### Quantification of population abundance patterns

We quantified population abundance patterns using the area occupied by HTF populations, density (mean number of populations per 100 km<sup>2</sup>) and isolation (distance to the nearest population) within regions and then summarized these data using bar plots. Geographical distributions of the HTF populations were displayed along with the locations of biomes identified by the UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC, <https://www.unep-wcmc.org>). We conducted pairwise *t*-test comparisons to indicate the significance of the mean difference between each region using Europe as a reference.

#### Changes in climatic suitability

We estimated changes in climatic suitability by comparing the current and past distributions of optimal climatic spaces. These were predicted based on the maximum entropy model (MaxEnt) using the R package dismo v.1.3-5 (Hijmans *et al.*, 2021). Both present (1979–2013) and historical climate data (LGM) with 2.5 min spatial resolution were retrieved from PaleoClim. Considering the compatibility between two different periods of suitability, we used the same 18 explanatory bioclimatic variables. A total of 80 % of occurrence data were randomly selected to train the model, with the other 20 % used to test the model. Model performance was assessed based on AUC (area under the receiver operator curve), a commonly used discriminant measure for models, in which AUC > 0.7 generally indicates good performance (Raes and ter Steege, 2007). The plot showing changes in climatic suitability was produced by contrasting the current and past predicted distributions using the basic plot function in R v.4.2.0 (R Core Team, 2021). The relationships between latitude and changes in climatic suitability of local populations were plotted using the R package ggplot2 v.3.3.6 (Wickham *et al.*, 2022). Regression lines from generalized linear models (GLMs) and correlation values were computed and displayed with scatterplots to identify relationships between two variables.



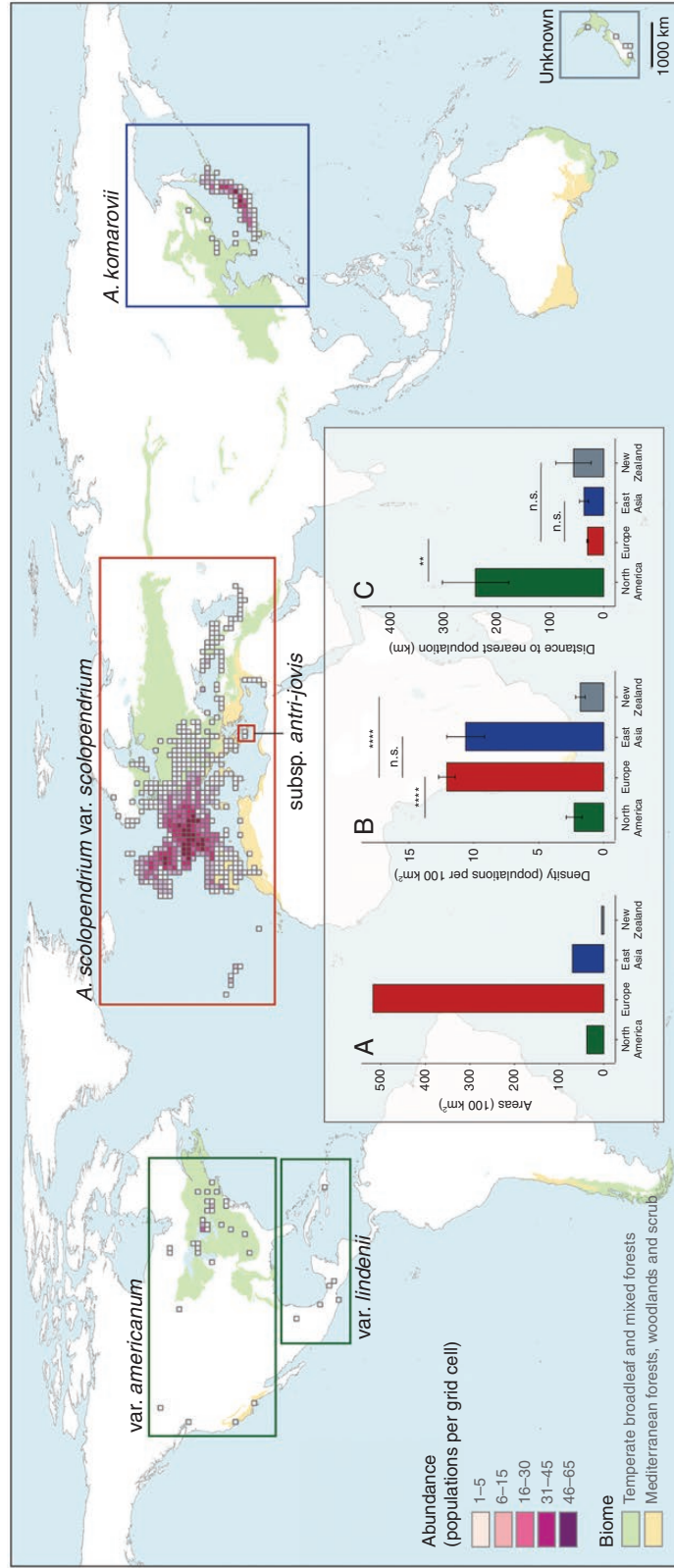


FIG. 1. Distributions and differences in geographic range, population density and geographic isolation among taxa of the hart's tongue fern complex. The purple gradient in each grid cell indicates local population abundance (i.e. number of populations per 100 x 100 km grid cell). Bar charts compare (A) areas occupied by HTF populations, (B) mean density of local populations and (C) mean distance to the nearest populations. *P*-values of the pairwise *t*-tests indicate the significance of the mean differences between the reference group (Europe) and others (North America, East Asia and New Zealand). n.s. *P* > 0.05, \*\**P* ≤ 0.01, \*\*\*\**P* ≤ 0.0001.

TABLE 1. Explanatory variables used in spatial analyses.

Categories	Variables (acronym)	Units	Resolution	Sources
Current climatic variables	Annual mean temperature (BIO1_pre)	°C	30 sec	WorldClim 2.0 (Present, 1970–2000)
	Temperature seasonality (BIO4_pre)	°C		
	Annual precipitation (BIO12_pre)	mm		
	Precipitation seasonality (BIO15_pre)	mm		
Magnitude of past climate change	Average velocity of temperature change (CV_BIO1)	m year <sup>-1</sup>	10 min	Derived from PaleoClim (LGM and present) based on Hamann <i>et al.</i> (2015)
	Average velocity of precipitation change (CV_BIO12)	m year <sup>-1</sup>		
Climatic heterogeneity	Spatial heterogeneity of annual mean temperature (BIO1_het)	°C	30 sec	Derived from current climatic variables using Focal statistics tool in ArcGIS
	Temperature seasonality (BIO4_het)	°C		
	Spatial heterogeneity of annual precipitation (BIO12_het)	mm		
	Precipitation seasonality (BIO15_het)	mm		
Topographic variables	Spatial heterogeneity of elevation (ELE_het)	m	30 sec	Derived from the elevation data (WorldClim 2.0) using Arc Hydro tools
	Terrain ruggedness (TRI)	m		
Edaphic conditions (topsoil)	Soil pH (Soil_pH)	–	250 m	ISRIC Soil Data Hub
	Soil water contents (Soil_WC)	kPa		
	Soil cation exchange capacity (Soil_CEC)	cmolc kg <sup>-1</sup>		
	Soil organic carbon (Soil_OC)	%		
Anthropogenic impacts	Human footprint (HF)	0–100	1 km <sup>2</sup>	NASA Socioeconomic Data and Applications Centre
Population isolation	Distance to the nearest population (ISO_pop)	m	–	Derived from occurrence data

### Coverage of protected areas

We used the coverage of protected areas as a proxy to estimate the impact of land-use change on abundance patterns, given the difficulty in quantifying global land-use change as well as the limitations in inferring its past impact using current abundance data. We computed the proportion of regions within protected areas using data from the World Database on Protected Areas (WDPA) available in ArcGIS Pro 2.8.3 (Dinerstein *et al.*, 2017). The data sorted the regions into four categories based on the extent of remaining natural habitat and protected land: ‘Half protected’ (>50 % of the total ecoregion area is protected), ‘Nature Could Reach Half’ (<50 % of the total ecoregion area is protected but the sum of the total protected area and remaining unprotected natural habitat exceeds 50 %), ‘Nature Could Recover’ (the sum of the total protected area and the amount of unprotected natural habitat remaining is <50 % but >20 %) and ‘Nature Imperiled’ (the sum of the total protected area and the amount of unprotected natural habitat remaining is ≤20 %). We generated stacked bar charts to visualize the proportional differences between regions using the R package ggpubr v.0.4.0 (Kassambara and Kassambara, 2020).

### BRT modelling for assessing regional determinants

The relative importance of explanatory variables was assessed at a regional scale using boosted regression tree (BRT) models, which can fit complex non-linear relationships and are insensitive to outliers and collinearity between predictors (Elith *et al.*, 2008). The BRT approach fundamentally differs from traditional regression methods in that it uses a boosting technique to adaptively combine large numbers of predictions from multiple regression decision trees to optimize predictive performance (Elith *et al.*, 2006). Using the R package dismo

v.1.3-5, we performed BRT modelling using the datasets divided into Europe, North America and East Asia. Each model was fit with a Poisson distribution, tree complexity of 5, learning rate of 0.01 and bag function of 0.7. Final models were validated using 10-fold cross-validation. The relative importance (or contribution) of each predictor variable was estimated based on the number of times a variable was selected for each decision tree and scaled to a percentage, with a higher number indicating a stronger influence on the response (Friedman and Meulman, 2003; Elith *et al.*, 2008). Regional differences in the relative importance of explanatory variables were visualized with a heatmap using the R package ggplot2 v.3.3.6. The fitted functions of a BRT model that showed the effect of an explanatory variable on the response were displayed as partial dependence plots.

### Hot spot analysis

We identified the spatial clusters of population abundance in each region of Europe, North America, East Asia and New Zealand because metapopulation dynamics such as rescue effects can affect abundance patterns. Hot spots, the areas with a higher concentration of abundant populations (i.e. high/high local relationships) compared with the expected number given a random distribution of populations, were identified based on Getis-Ord  $G_i^*$  statistics and visualized using the Hot Spot Analysis tool in ArcGIS Pro 2.8.3. High  $z$ -scores of the  $G_i^*$  statistic ( $G_i^*Z$ ) indicate hot spots where abundant populations are spatially clustered.

### Case study: population trends in the USA

We used the available long-term field census data (1898–2018) for American HTF in the USA to investigate how the

interplay of climate change and anthropogenic activities influenced the population trajectory across a detailed temporal scale. The census data were compiled from multiple sources (McGilliard, 1936; Cinquemani Kuehn and Leopold, 1992; Brumbelow, 2014; USFWS, 2019), and the status of habitat protection of each population was identified based on the species status assessment report (USFWS, 2019) (Supplementary data File S2). We generated scatterplots of population abundance (number of individuals per population) over time with a log transformation to account for large differences in the abundances between populations. Trend lines from generalized linear models (GLMs) and correlation coefficients were generated using the R package ggplot2 v.3.3.6.

## RESULTS

### *Abundance patterns in HTF complex*

Hart's tongue ferns were mostly distributed in a single biome (i.e. Temperate Broadleaf and Mixed Forests) with a few found in Mediterranean Forests, Woodlands and Scrub (Fig. 1). However, their geographic ranges, abundance patterns and isolation varied among regions. The areas occupied by HTF populations were largest in Europe (51 700 km<sup>2</sup>), followed by East Asia (70 km<sup>2</sup>), North America (38 km<sup>2</sup>) and New Zealand (5 km<sup>2</sup>) (Fig. 1A). The mean population density was the highest in Europe (12.08 populations per 100 km<sup>2</sup>), but the difference from East Asia (10.63 populations per 100 km<sup>2</sup>) was not significant ( $P > 0.05$ ). Those of North America (2.26 populations per 100 km<sup>2</sup>) and New Zealand HTF (1.8 populations per 100 km<sup>2</sup>) were significantly lower than those of the other two regions ( $P < 0.0001$ ) (Fig. 1B). Mean population isolation, calculated by an average distance of a population to its nearest population, was significantly higher in North America (240.63 km,  $P < 0.01$ ) than in Europe (30.12 km,  $P < 0.01$ ), which did not differ significantly from isolation of populations in East Asia (36.96 km) or New Zealand (56.56 km) ( $P > 0.05$ ) (Fig. 1C).

### *Impact of global drivers*

Our predictions for climatic suitability performed well, with an AUC value of 0.812. Globally, and in both Northern and Southern Hemispheres, it appears that climatic change has driven latitudinal shifts in the climate suitability (space) of the HTF complex away from the tropics and towards higher latitudes (Fig. 2A). Shifts in climatic suitability were positively correlated with latitude in Europe ( $R = 0.78$ ,  $P < 0.01$ ), East Asia ( $R = 0.30$ ,  $P = 0.01$ ) and North America ( $R = 0.58$ ,  $P < 0.01$ ), and negatively correlated in New Zealand ( $R = -0.41$ ,  $P = 0.49$ ) (Fig. 2B).

The four regions varied in the degree to which their current distributions included protected areas, demonstrating that the impact of land-use change differed among regions (Fig. 2C). North America (39.5 %) had the highest proportion of populations exposed to low levels of protection ('Nature Imperiled'), followed by Europe (20.89 %), East Asia (4.29 %) and New Zealand (0 %). In contrast, the proportion of populations in highly protected areas ('Nature Could Reach Half Protected')

was highest in East Asia (88.57 %), followed by North America (47.37 %) and Europe (15.47 %). All populations in New Zealand were under intermediate levels of protection ('Nature Could Recover'), followed by Europe (63.25 %), North America (10.53 %) and East Asia (7.14 %).

### *Regional determinants of abundance patterns*

BRT models performed well, showing from 97.47 % to 98.96 % of deviance with cross-validation correlation (0.598–0.927) (Supplementary data Table S3). All regions had population isolation (ISO\_pop) as the most important variable explaining regional abundance patterns, though its relative importance differed by region (Europe = 55.8 %, East Asia = 50.5 % and North America = 29.4 %) (Fig. 3A). Precipitation seasonality (BIO15\_pre, 17.2 %), terrain ruggedness (TRI, 8.2 %) and magnitude of past temperature change (CV\_BIO1, 3.4 %) also affected abundance patterns in Europe, with all showing negative relationships to fitted functions (Fig. 3C). In East Asia, spatial heterogeneity of precipitation (BIO15\_het, 11.8 %), temperature (BIO1\_het, 11.4 %) and temperature seasonality (BIO2\_het, 5.8 %) all had positive relationships with fitted functions. In North America, magnitude of past temperature change (CV\_BIO1, 17.2 %), spatial heterogeneity of temperature seasonality (BIO4\_het, 12.3 %) and soil pH (6.8 %) were important variables. In addition, the spatial pattern of hot spots (clusters of high abundance populations) differed between regions, with most (GiZ score  $\geq 1.65$ ) distributed in north-west Europe (55 significant hot spot clusters), followed by the Japanese Archipelago in East Asia (five significant hot spot clusters). No hot spots occurred in North America (Fig. 3B).

### *Case study: population trends in the USA*

A long-term population trajectory in the USA demonstrated the interplay of climatic and anthropogenic activities (Fig. 4). Although the degrees of stochasticity differed between populations, southern populations such as those of Morgan (Alabama,  $R = -0.37$ ), Jackson (Alabama,  $-0.98$ ) and Marion (Tennessee,  $R = -0.63$ ) showed clear decreasing trends regardless of habitat protection. In contrast, northern populations, including those of Madison, Onondaga (New York) and Mackinac (Michigan), tended to have increased during the census periods, but population trends differed depending on levels of habitat protection. Despite occurring at the same latitude (Onondaga and Madison, 43°N), unprotected populations such as those on privately owned lands generally showed declining trends ( $R = -0.24$  to  $-0.23$ ), while protected or government-managed populations showed increasing population trends ( $R = 0.19$ – $0.37$ ).

## DISCUSSION

Ferns, often considered bio-indicators, are particularly sensitive to environmental conditions. Clear correlations between local abundance and climatic conditions have been reported for several fern species (Kessler et al., 2011; Pouteau et al., 2016; de Gasper et al., 2021; Bonari et al., 2022), and their vulnerability to anthropogenic threats has also been widely

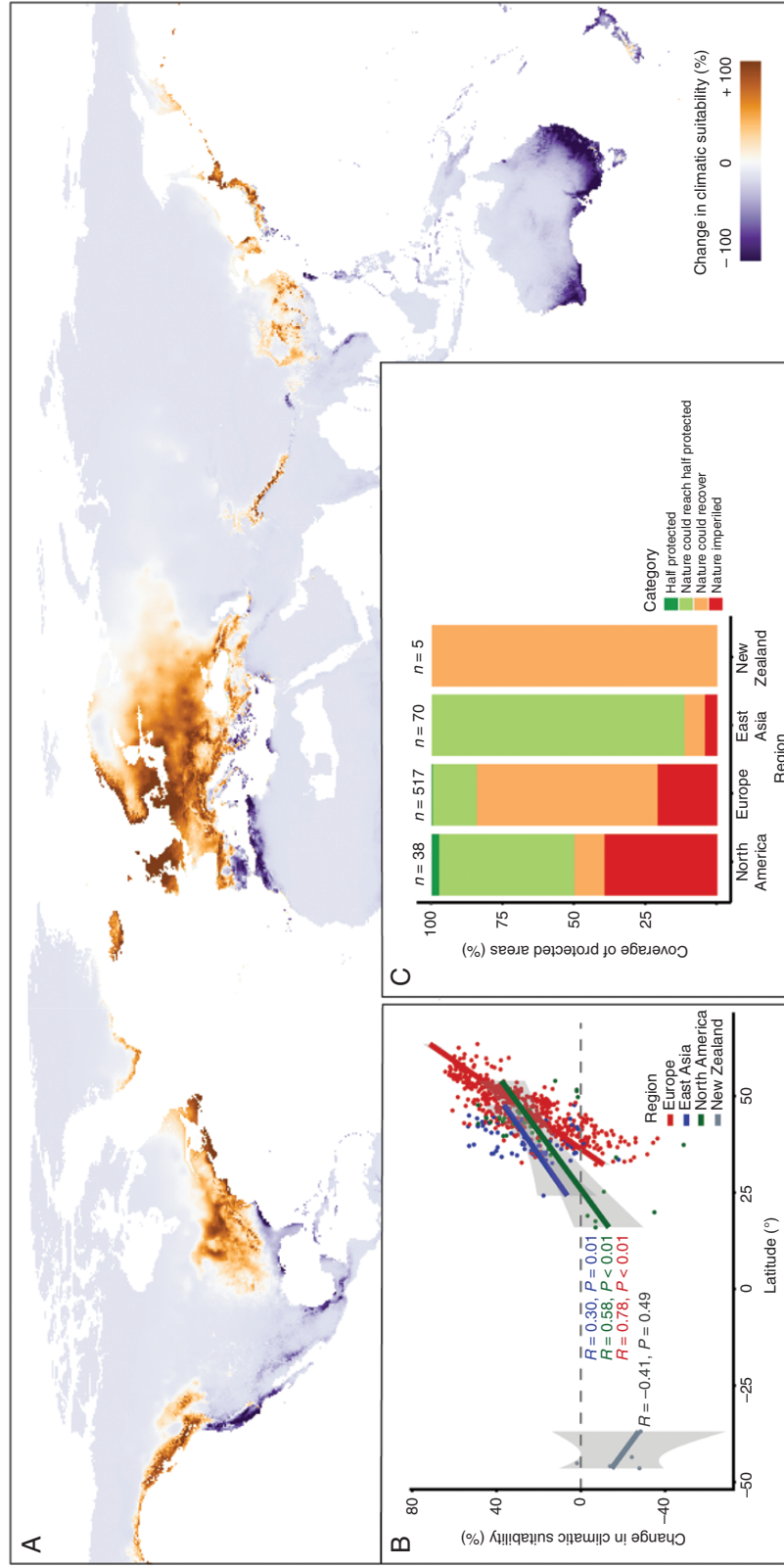


FIG. 2. Impacts of global drivers of climate and land-use change. (A) Geographical changes in climatic suitability since the LGM. Brown areas indicate that climatic conditions have become more suitable for HTF, while purple indicates the opposite. (B) Scatterplot showing the relationship between latitude and changes in climatic suitability of local populations. Each point represents a sample unit. Positive values on the x-axis indicate that the climatic condition has become more suitable, whereas negative values indicate the opposite. (C) Coverage of protected areas of HTF populations for each region.



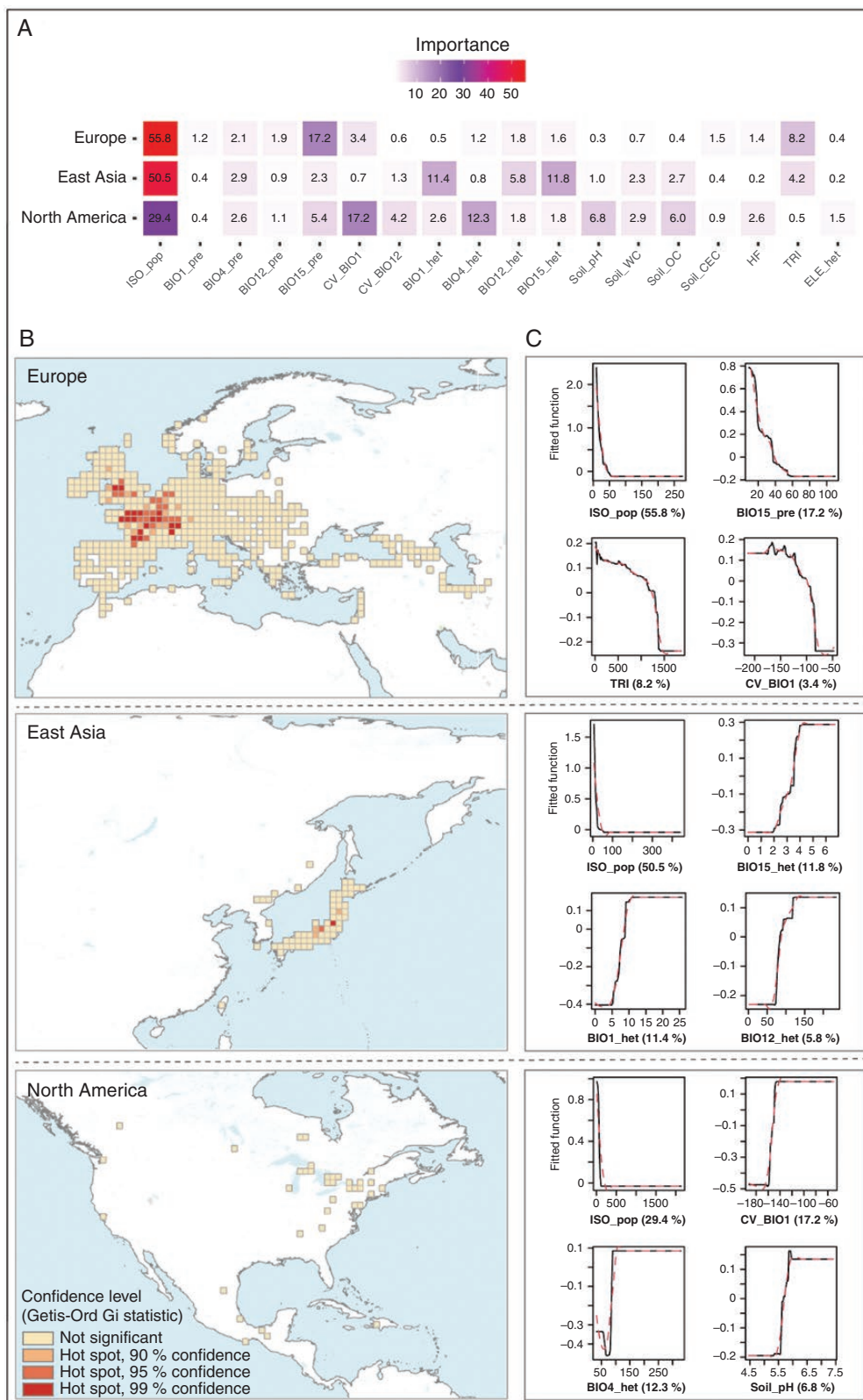


Fig. 3. Regional determinants of abundance patterns and hot spots. (A) Relative variable importance from the BRT models (i.e. the relative contribution of the variable to the full model) across Europe, East Asia and North America. (B) Getis-Ord  $G_i^*$  statistics representing hot spots of local population abundance. The red gradient indicates the significance of hot spots. (C) Partial dependence plots from the BRT models. The top four significant explanatory variables are shown with their relative importance values. The x-axis indicates the actual values of each variable in the units shown in Table 1. A smoothed version of the fitted function is added as dashed red lines. New Zealand was excluded from this analysis due to small sample size.



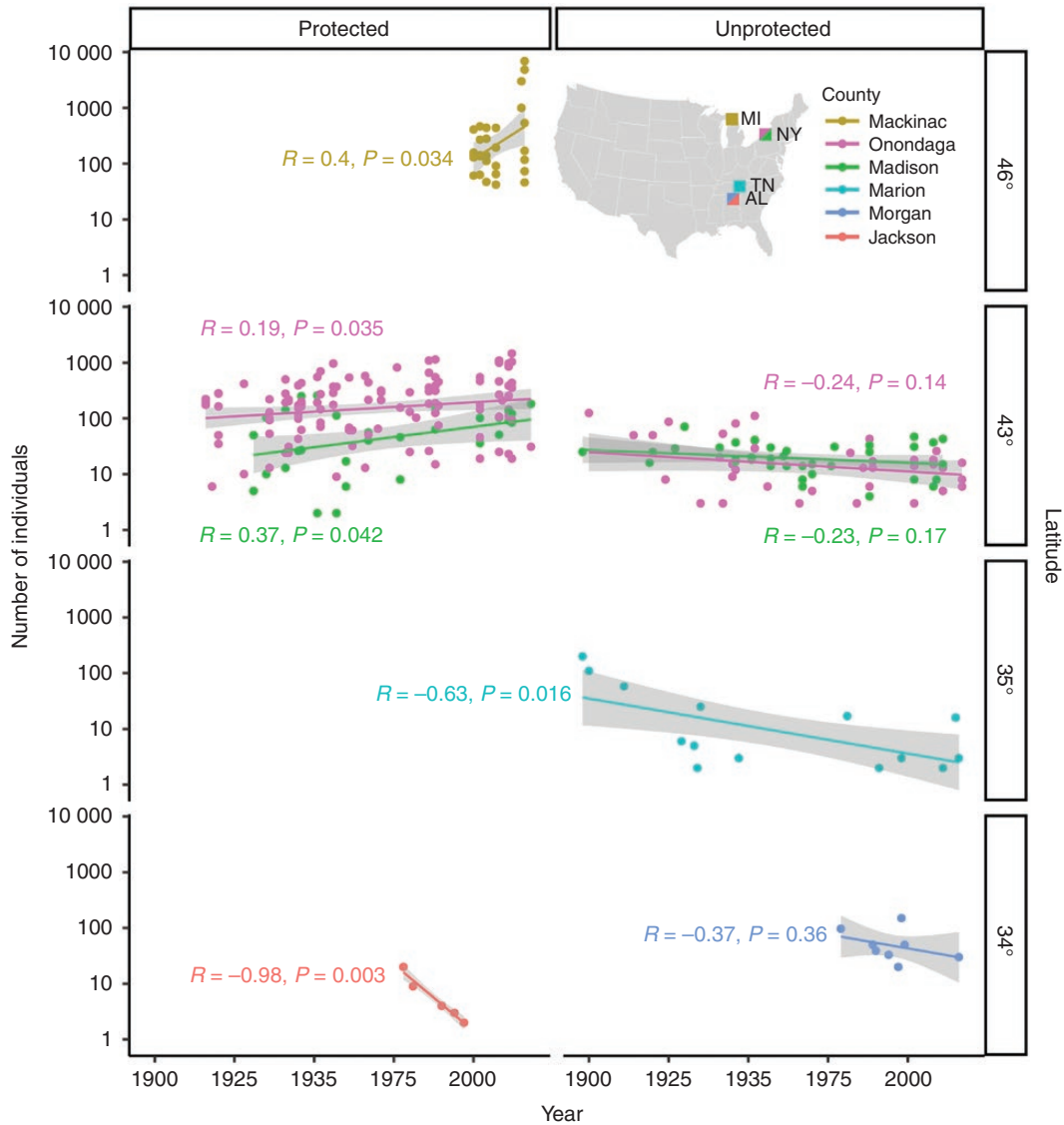


FIG. 4. Population trends in the USA. Each point represents a single census for a specific population and year. Colours represent different locations (counties), and correlation coefficients ( $R$ ) represent the direction of population trends. The grey shade represents the 95 % confidence intervals of regression lines. Note that the  $y$ -axis (number of individuals) is shown on a logarithmic scale due to large differences in population sizes.

recognized (Giudice *et al.*, 2011; Marini *et al.*, 2011; Brummitt *et al.*, 2016). Nonetheless, the spatial heterogeneity of local abundance in the HTF complex suggested a potential role for regional or local factors in their abundance patterns. Hierarchical systems of environmental controls probably determine abundance patterns, such that climatic and land-use dynamics act globally but are modulated by regional- to local-scale determinants such as topography, geology and microclimate, which operate at increasingly finer scales (Howard, 2015). This hierarchical framework was reflected in the abundance patterns of the HTF complex, and the complicated relationships between their abundance and factors at various scales were revealed with BRT's machine learning method, thus overcoming the challenges of disentangling complex situations using a relatively simple and conventional linear regression model (Elith *et al.*, 2008).

#### Global drivers

At the broadest scale, global abundance patterns were strongly associated with specific bioclimatic conditions. HTFs were almost exclusively abundant in a single biome (i.e. temperate broadleaf and mixed forests) with minimal exceptions (Fig. 1). Thus, the ecological niche and climate space of the HTF complex corresponds to that favouring temperate seasonal forests with a typical temperature range of 10–30 °C and annual precipitation of 50–150 cm (Gilliam, 2016). These habitats are currently distributed widely but disjunctively in temperate regions of the Northern Hemisphere, including Europe, eastern North America, East Asia and several islands, which mirrors the current global disjunct distribution of the HTF complex. Globally non-uniform distribution of these habitats may subsequently explain the uneven abundance pattern of the HTF complex.

Europe differs from other regions in that alternative niches are contiguous with major habitats, as opposed to North America in which the Mediterranean climate regions along the California coast are far from the temperate forests of the eastern USA. Thus, relatively abundant and contiguous suitable habitats may contribute to increasing regional abundance in Europe by providing wide-range refugia in the event of disturbances such as glaciation. In the case of North America, the populations that occur in different biomes appear to be remnant populations whose local extinction was delayed due to the existence of microrefugia such as caves or sunken limestone areas (USFWS, 2020; Heo et al., 2022).

Nevertheless, changing climate conditions over time and space appear to play essential roles in shaping global HTF abundance patterns. Our results revealed a global latitudinal shift of the climate space for the HTF complex such that suitability decreased for populations near the tropics but increased for those at higher latitudes since the LGM (21 000 years ago) (Fig. 2). These shifts occurred across all regions of North America, Europe, East Asia and New Zealand, thus affirming that climate change was a global driver of the observed latitudinal pattern in abundance among regional populations. According to the distance decay effect, environmental conditions tend to become more different and less favourable with distance from the centre of main populations (Nekola and White, 1999). In the case of the HTF complex, this distance decay effect is directional, and thus extinction pressures should become stronger from higher to lower latitudes. Populations distributed at low latitudes should therefore face stronger extinction pressure, which aligns with the current rarity of two southern taxa, *A. scolopendrium* var. *lindenii* and *A. scolopendrium* subsp. *antri-jovis*.

Anthropogenic threats from land-use change were also a global driver of abundance patterns among regional populations (Ellis and Ramankutty, 2008; Newbold et al., 2015). However, the particular impacts of land-use dynamics varied by region, presumably due to regional differences in levels of habitat protection. In particular, these anthropogenic threats probably play a major role in determining abundance patterns in East Asia. Almost all current East Asian populations were within highly protected regions ('Nature Could Reach Half Protected'), implying that populations in less protected regions have already become locally extinct due to intensive land use. Subsequently, they would be fairly abundant on several islands but sparse in inland areas where anthropogenic threats are most severe, such as the Russian Far East, North-east China and the Korean Peninsula (Zhu et al., 2007; Bergen et al., 2020). Even within the Japanese Archipelago where HTF populations are abundant, the populations usually occurred on the steep slopes of high-elevation mountains where land use is less intense. In contrast, about 70 % of the populations in North America were under low levels of protection, meaning that they have been surviving without intense protection, probably under less severe land-use change than in East Asia. However, the loss of multiple populations due to limestone quarrying and timber harvesting warns that persisting populations in North America are still at risk of local extinction (Benedict, 1927; USFWS, 2019). Given that only 5 % of the European population was highly protected ('Nature Could Reach Half Protected'), the abundance of the European taxon is more likely to be explained by natural factors rather than anthropogenic disturbance of persisting populations.

### Regional determinants

The importance of variables explaining abundance patterns differed among regions. Although population isolation (ISO\_pop) was the most significant variable in all regions, its importance varied, being much higher in Europe and East Asia than in North America (Fig. 3A). Isolation is likely to be an indicator of metapopulation dynamics and the potential for dispersal and recolonization ('rescue') among populations after disturbance or local extinction (Tilman and Kareiva, 1997; Dormann et al., 2007). Consistent with this, several hot spots in Europe and East Asia were comprised of highly clustered (low isolation) neighbouring populations (Fig. 3). On the contrary, population isolation was less influential in North America, possibly because isolation among these populations far exceeded the dispersal range and, therefore, the range of rescue effects as well. The sunken habitats separated by steep ridges and surrounding vegetation may effectively impede dispersal and disrupt any substantial metapopulation dynamics among these North American populations (Brumbelow, 2014; Fernando et al., 2015).

In addition, the influence of other ecological factors also varied among regional populations (Fig. 3A, C). Precipitation seasonality (BIO15\_pre) was the primary determinant of abundance patterns in Europe. A negative relationship between precipitation seasonality and abundance explained higher HTF abundance in the oceanic climate of western Europe including the British Isles, which were identified as hot spots for European HTF. Spatial heterogeneity of precipitation (BIO15\_het) followed by temperature (BIO1\_het) and terrain ruggedness (TRI) were the major determinants of abundance patterns in East Asia. Here, higher abundance occurred in the cloud forests of island mountains, where constant water sources support both survival and reproduction. High volcanic or volcano-influenced mountains in the Japanese Archipelago, Taiwan and the Jeju and Ulleung Islands in Korea may also provide a variety of climatic conditions over short distances and microhabitats along rocky slopes. Collectively, these stable but diverse island habitat conditions may have promoted high abundance, creating several insular hot spots, particularly in the Japanese Archipelago (Fig. 3B).

In contrast to patterns across Europe and East Asia, several alternative determinants of population abundance, including magnitude of past climate change (CV\_BIO1), temperature seasonality (BIO4\_het) and edaphic conditions (Soil\_pH), influenced HTF across North America, indicating the likely influence of long-term, historical events including glaciation and climatic dynamics since the LGM. Abundant populations of North American HTF are mostly distributed along the Niagara Escarpment, which was extensively covered by ice sheets during the Wisconsin Glaciation and currently has prominent lake effect precipitation (Fulton and Prest, 1987; USFWS, 2020). Following glacial retreats, open niches and locally favourable climatic conditions may have promoted recolonization by HTFs prior to that of other plants.

Edaphic conditions defining the niche space of HTFs also appear to vary substantially among regional populations. Compared with other regions whose populations occur in various habitat and soil types, including the crevices of stone walls, river channels, mountains and even concrete blocks

(Preston *et al.*, 2002; Keil *et al.*, 2012; Murakami, 2020), US populations exclusively occurred in glacial plunge basins, ravines, cave mouths and sink holes within calcareous substrates (USFWS, 2020). These concave sites are often identified as karst habitats, which frequently become refugia for certain taxa under climate change, thus preserving relict and endemic species that become extinct in the surrounding alternative habitats (Bátori *et al.*, 2009). Subsequently, the concave karst and related habitats of US populations may function as microrefugia, which maintain milder microclimates with higher and more stable minimum daily temperatures and humidity as well as fewer freezing days in winter (Maxon, 1900; Petry, 1918). Empirical evidence supports a climatic buffering effect of these concave refugia, where the declines of the HTF populations in New York were typically accompanied by extreme climate events such as regional drought rather than prevailing local climate conditions (Cinquemani Kuehn and Leopold, 1992). Therefore, it is not likely to be the calcareous substrates themselves, but rather the microclimates associated with these concave karst regions that enable these North American populations to persist during periods of generally unfavourable climate conditions across the region.

#### Population trends in the USA

Population trends projected with nearly 100 years of census data demonstrated a northward range shift in which northern populations have generally increased, while southern populations have decreased. However, regardless of the particular region in North America, populations protected and managed by the conservation-related government sector showed increasing population trends compared with those at the same latitude without protection, illustrating the importance of habitat protection and conservation measures.

#### Conservation implications for vulnerable HTF taxa

Based on our findings on HTF abundance patterns and underlying factors, southern populations (i.e. *A. scolopendrium* var. *lindenii* and *A. scolopendrium* subsp. *antri-jovis*) appeared most vulnerable to local extinction given predictions that they will be greatly affected by climate change. Most populations of *A. scolopendrium* var. *lindenii* occur in sinkholes, and very limited and geographically isolated niches are available for colonization/recolonization from dispersal. Thus, habitat microclimate management and assisted migration are necessary measures for their persistence. *Ex situ* conservation can also be considered if climatic change continues to decrease the abundance of *in situ* populations. Conversely, the persistence of *A. scolopendrium* subsp. *antri-jovis* appears much more probable than that of *A. scolopendrium* var. *lindenii* because its populations occur in a milder Mediterranean climate, but the risk from a small population size should be managed to promote long-term persistence.

In comparison with the above, the American HTF (*A. scolopendrium* var. *americanum*) has the next highest conservation priority; however, its rarity and persistence differed between southern and northern populations. The northern populations, such as those near the Great Lakes region, are relatively

abundant primarily because they have more extensive and stable refugia, particularly those along the Niagara Escarpment. Fortunately, all known populations of *A. scolopendrium* var. *americanum* in New York are currently protected from future anthropogenic threats, which the USFWS has asserted justifies its decision that *A. scolopendrium* var. *americanum* no longer meets the definition of a threatened species (USFWS, 2020). Nonetheless, the long-term extinction risk of *A. scolopendrium* var. *americanum* remains high due to the intrinsic factors of small and fragmented populations. USFWS (2020) has subsequently suggested reintroduction/augmentation programmes for future conservation actions. As habitat protection was identified as one of the critical determinants of abundance, the conservation strategies for unprotected Canadian populations should focus on improving the extent of protected areas. Like *A. scolopendrium* var. *lindenii*, assisted migration or reintroduction may be necessary for southern populations of *A. scolopendrium* var. *americanum*, depending on the strength of climatic pressures. If only mild pressure is expected, augmentation programmes may be sufficient to manage demographic risk, taking care to preserve their evolutionary distinctiveness and adaptive traits of local populations.

The East Asian HTF (*Asplenium komarovii*) is fairly abundant on several islands, but sparse in inland areas with severe anthropogenic threats. The conservation strategies for this taxon can focus on increasing population connectivity, particularly from the abundant island source (hot spots) to scarce populations, thus maximizing rescue effects. Securing the areas capable of functioning as stepping-stones could be an effective conservation strategy. Although populations in New Zealand were rare, this unknown variety was probably introduced and naturalized (Brownsey and Perrie, 2017). Given that other taxa of *A. scolopendrium* are typically abundant on islands, these populations are thought to have the potential to expand. Thus, the origin of the New Zealand taxon and the dynamics of its dispersal and population expansion should be studied to provide insights into the conservation of other taxa, as well as to control any undesired population increase and range expansion.

#### Conclusions

We investigated geographic disparities in abundance patterns of the hart's tongue fern complex and revealed hierarchical systems of environmental controls in which climatic and land-use change drives abundance patterns at the global scale, while various ecological conditions act as finer scale determinants that further increase geographic disparities at regional and local scales. A clear understanding of these drivers can ultimately provide insights for assessing the rarity and persistence of the HTF complex as well as developing effective strategies for the conservation of its vulnerable taxa. As the abundance of ferns is typically tethered to climate and substrate, global drivers such as climate change and anthropogenic disturbances probably affect other fern taxa in similar ways. However, the impacts of these drivers may greatly differ depending on the geographic distribution of species and the interactions among their regional and local ecological determinants. Fern conservation must therefore be tailored to the particular geographic context and environmental conditions of a taxon by incorporating



a better understanding of the interactions among factors at different spatiotemporal scales. Future studies may benefit from incorporating high-resolution microclimate data to reveal more micro-scale factors and processes related to abundance patterns and conservation.

#### SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. **Table S1**: information on the occurrence dataset downloaded from GBIF. **Table S2**: principal component analysis (PCA) loadings of the 18 explanatory variables. **Table S3**: performances of the BRT models. **Figure S1**: principal component analysis (PCA) biplot of the 18 explanatory variables. File S1: BRT dataset. File S2: census dataset.

#### ACKNOWLEDGEMENTS

We thank Dr James E. Watkins Jr and Dr Martin Dovciak for discussions during the preparation of this manuscript.

#### CONFLICT OF INTEREST

We have no conflicts of interest to declare.

#### LITERATURE CITED

- Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB. 2004. Assessing the causes of late Pleistocene extinctions on the continents. *Science* **306**: 70–75. doi:10.1126/science.1101476.
- Barrington DS. 1993. Ecological and historical factors in fern biogeography. *Journal of Biogeography* **20**: 275–279. doi:10.2307/2845635.
- Bátori Z, Csiky J, Erdős L, et al. 2009. Vegetation of the dolines in Mecsek Mountains (South Hungary) in relation to the local plant communities. *Acta Carsologica* **38**: 237–252.
- Benedict RC. 1927. Is the distribution and naturalization of the hart's tongue scientifically defensible? *American Fern Journal* **17**: 19–23. doi:10.2307/1543748.
- Bergen KM, Loboda T, Newell JP, et al. 2020. Long-term trends in anthropogenic land use in Siberia and the Russian Far East: a case study synthesis from Landsat. *Environmental Research Letters* **15**: 105007. doi:10.1088/1748-9326/ab98b7.
- Bonari G, Fattorini N, Fruchter SR, et al. 2022. Fine-scale fern ecological responses inform on riparian forest habitat conservation status. *Biodiversity and Conservation* **31**: 2141–2161.
- Brook BW, Sodhi NS, Bradshaw CJ. 2008. Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**: 453–460. doi:10.1016/j.tree.2008.03.011.
- Brown JH. 1984. On the relationship between abundance and distributions. *American Naturalist* **124**: 255–279. doi:10.1086/284267.
- Brown JH, Mehlman DW, Stevens GC. 1995. Spatial variation in abundance. *Ecology* **76**: 2028–2043.
- Brown JL, Carnaval AC. 2019. A tale of two niches: methods, concepts, and evolution. *Frontiers of Biogeography* **11**: e44158.
- Brownsey PJ, Perrie LR. 2017. Taxonomic notes on the New Zealand flora: lectotypes in the fern family Aspleniaceae. *New Zealand Journal of Botany* **55**: 249–257.
- Brumelow TR. 2014. *Population and microclimate studies of the American hart's-tongue fern (Asplenium scolopendrium var. americanum (fern.) Kartsch and Ghandi) in central New York*. MS Thesis, State University of New York College of Environmental Science and Forestry, USA.
- Brummitt N, Aletrari E, Syfert MM, Mulligan M. 2016. Where are threatened ferns found? Global conservation priorities for pteridophytes. *Journal of Systematics and Evolution* **54**: 604–616. doi:10.1111/jse.12224.
- Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, et al. 2013. How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* **280**: 20121890. doi:10.1098/rspb.2012.1890.
- Cinquemani DM, Faust ME, Leopold DJ. 1988. Periodic censuses (1916–1986) of *Phyllitis scolopendrium* var. *americana* in central New York State. *American Fern Journal* **78**: 37–43. doi:10.2307/1547666.
- Cinquemani Kuehn DM, Leopold DJ. 1992. Long-term demography of *Phyllitis scolopendrium* (L.) Newm. var. *americana* Fern. in central New York. *Bulletin of the Torrey Botanical Club* **119**: 65–76.
- Cinquemani Kuehn DM, Leopold DJ. 1993. Habitat characteristics associated with *Phyllitis scolopendrium* (L.) Newm. var. *americana* Fern. (Aspleniaceae) in central New York. *Bulletin of the Torrey Botanical Club* **120**: 310–318.
- COSEWIC. 2016. *COSEWIC assessment and status report on the American Hart's-tongue fern, Asplenium scolopendrium var. americanum, in Canada*. Ottawa: Committee on the Status of Endangered Wildlife in Canada.
- Coudun C, Gégout JC. 2007. Quantitative prediction of the distribution and abundance of *Vaccinium myrtillus* with climatic and edaphic factors. *Journal of Vegetation Science* **18**: 517–524. doi:10.1111/j.1654-1103.2007.tb02566.x.
- Delgado P, Eguarte LE, Molina-Freaner F, et al. 2008. Using phylogenetic, genetic and demographic evidence for setting conservation priorities for Mexican rare pines. *Biodiversity and Conservation* **17**: 121–137.
- Diamond JM. 1984. 'Normal' extinction of isolated populations. In: Nitecki MH ed. *Extinctions*. Chicago: Chicago University Press, 191–246.
- Dinerstein E, Olson D, Joshi A, et al. 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* **67**: 534–545. doi:10.1093/biosci/bix014.
- Dormann C, McPherson J, Araújo M, et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**: 609–628.
- Elith J, Graham CH, Anderson P, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**: 129–151.
- Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* **77**: 802–813. doi:10.1111/j.1365-2656.2008.01390.x.
- Ellis EC, Ramankutty N. 2008. Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* **6**: 439–447. doi:10.1890/070062.
- Eriksson O. 1996. Regional dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. *Oikos* **77**: 248–258. doi:10.2307/3546063.
- Faust ME. 1960. Survival of hart's-tongue fern in central New York. *American Fern Journal* **50**: 55–62. doi:10.2307/1545243.
- Fernando DD, Discenza JJ, Bouchard JR, Leopold DJ. 2015. Genetic analysis of the threatened American hart's-tongue fern (*Asplenium scolopendrium* var. *americanum* [Fernald] Kartsch and Ghandi): insights into its mating system and implications for conservation. *Biochemical Systematics and Ecology* **62**: 25–35. doi:10.1016/j.bse.2015.07.034.
- Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315. doi:10.1002/joc.5086.
- de Frenne P, Rodríguez-Sánchez F, Coomes DA, et al. 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences, USA* **110**: 18561–18565. doi:10.1073/pnas.1311190110.
- Friedman JH, Meulman JJ. 2003. Multiple additive regression trees with application in epidemiology. *Statistics in Medicine* **22**: 1365–1381. doi:10.1002/sim.1501.
- Fulton R, Prest V. 1987. Introduction: the Laurentide ice sheet and its significance. *Géographie Physique et Quaternaire* **41**: 181–186.
- Futyma RP. 1980. The distribution and ecology of *Phyllitis scolopendrium* in Michigan. *American Fern Journal* **70**: 81–87. doi:10.2307/1546987.
- García-Girón J, Heino J, Iversen LL, Helm A, Alahuhta J. 2021. Rarity in freshwater vascular plants across Europe and North America: patterns, mechanisms and future scenarios. *Science of the Total Environment* **786**: 147491. doi:10.1016/j.scitotenv.2021.147491.
- de Gasper AL, Grittz GS, Russi CH, et al. 2021. Expected impacts of climate change on tree ferns distribution and diversity patterns in subtropical Atlantic Forest. *Perspectives in Ecology and Conservation* **19**: 369–378.

- Gaston KJ. 1994. *Rarity*. London: Chapman & Hall.
- Gates ME. 1962. *A microclimate study of the h tongue fern in central New York*. MS Thesis, Syracuse University, USA.
- Gilliam FS. 2016. Forest ecosystems of temperate climatic regions: from ancient use to climate change. *New Phytologist* **212**: 871–887. doi:10.1111/nph.14255.
- Giudice GE, Ramos Giacosa JP, Luna ML, et al. 2011. Diversidad de helechos y licófitas de la Reserva Natural Punta Lara, Buenos Aires, Argentina. *Revista de Biología Tropical* **59**: 1037–1046.
- Grašič M, Sovdat T, Gaberščik A. 2020. Frond optical properties of the fern *Phyllitis scolopendrium* depend on light conditions in the habitat. *Plants* **9**: 1254. doi:10.3390/plants9101254.
- Hamann A, Roberts DR, Barber QE, Carroll C, Nielsen SE. 2015. Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology* **21**: 997–1004. doi:10.1111/gcb.12736.
- Hanski I. 1989. Metapopulation dynamics: does it help to have more of the same? *Trends in Ecology & Evolution* **4**: 113–114. doi:10.1016/0169-5347(89)90061-X.
- Heo N, Lomolino MV, Watkins JE Jr, Yun S, Weber-Townsend J, Fernando DD. 2022. Evolutionary history of the *Asplenium scolopendrium* complex (Aspleniaceae), a relictual fern with a northern pan-temperate disjunct distribution. *Biological Journal of the Linnean Society* **137**: 183–199. doi:10.1093/biolinnean/blac080.
- Hijmans RJ, Phillips S, Leathwick J, et al. 2021. Package ‘dismo’. Species distribution modeling, version 1.3-5. <https://cran.r-project.org/web/packages/dismo/index.html>
- Howard C, Stephens PA, Pearce-Higgins JW, et al. 2015. The drivers of avian abundance: patterns in the relative importance of climate and land use. *Global Ecology and Biogeography* **24**: 1249–1260.
- Hunter M. 1922. The present status of *Scolopendrium* in New York state. *American Journal of Botany* **9**: 28–36.
- Ismail AM, Maulood BK, AL-Khasraji TO. 2017. An ecological and morphological study on (*Asplenium scolopendrium*) *Phyllitis scolopendrium* (L.). Newman within Howler (Erbil) City-Kurdistan of Iraq. *Journal of Garmian University* **4**: 555–562.
- Karger DN, Nobis MP, Normand S, et al. 2021. CHELSA-TraCE21k v1.0. Downscaled transient temperature and precipitation data since the last glacial maximum. *Climate of the Past Discussions* <https://doi.org/10.5194/cp-2021-30>.
- Kassambara A, Kassambara MA. 2020. ggpubr: ‘ggplot2’ based publication ready plots. R package version 0.4.0. <https://cran.r-project.org/web/packages/ggpubr/index.html>
- Keil P, Buch C, Fuchs R, et al. 2012. Areal expansion of Hart's-tongue (*Asplenium scolopendrium* L.) at the edge of northwestern Germany's low mountain range in the Ruhr area. *Decheniana (Bonn)* **165**: 55–73.
- Kessler M, Kluge J, Hemp A, Ohlemüller R. 2011. A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography* **20**: 868–880. doi:10.1111/j.1466-8238.2011.00653.x.
- Korea Forest Research Institute. 1997. *Illustrated rare and endangered species in Korea*. Seoul: Korea Forest Research Institute.
- Lin YX, Viane RLL. 2013. Aspleniaceae. In: Wu ZY, Raven PH, Hong DY, eds. *Flora of China*, vols 2–3 (Pteridophytes). Beijing: Science Press; St. Louis: Missouri Botanical Garden Press, 267–316.
- Löve A. 1954. Cytotaxonomical remarks on some American species of circumpolar taxa. *Svensk Botanisk Tidskrift* **48**: 211.
- Marini L, Bona E, Kunin WE, et al. 2011. Exploring anthropogenic and natural processes shaping fern species richness along elevational gradients. *Journal of Biogeography* **38**: 78–88.
- Maxon WR. 1900. On the occurrence of the Hart's tongue in America. *Fernwort Papers* **2**: 30–46.
- McGilliard E. 1936. The Hart's-tongue in Tennessee 1878–1935. *American Fern Journal* **26**: 113–122. doi:10.2307/1543694.
- Monzón J, Moyer-Horner L, Palamar MB. 2011. Climate change and species range dynamics in protected areas. *Bioscience* **61**: 752–761. doi:10.1525/bio.2011.61.10.5.
- Murakami K. 2020. A record of hart's-tongue fern (*Asplenium scolopendrium* L.) inhabiting holes in concrete armor blocks on the coast of southern Hokkaido, Japan. *Journal of Hokkaido University of Education (Natural Sciences)* **70**: 1–6.
- Nekola JC, White PS. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**: 867–878. doi:10.1046/j.1365-2699.1999.00305.x.
- Newbold T, Hudson LN, Hill SL, et al. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* **520**: 45–50. doi:10.1038/nature14324.
- Ohler LM, Lechleitner M, Junker RR. 2020. Microclimatic effects on alpine plant communities and flower–visitor interactions. *Scientific Reports* **10**: 1–9.
- Ok GH, Yoo KO. 2012. Habitats ecological characteristics of *Asplenium scolopendrium* L. and its RAPD analysis. *Korean Journal of Plant Resources* **25**: 719–730. doi:10.7732/kjpr.2012.25.6.719.
- Palmer G, Hill JK, Brereton TM, et al. 2015. Individualistic sensitivities and exposure to climate change explain variation in species' distribution and abundance changes. *Science Advances* **1**: e1400220. doi:10.1126/sciadv.1400220.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**: 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.
- Petry LC. 1918. Studies on the vegetation of New York State-II. The vegetation of a glacial pluge basin and its relation to temperature. *Bulletin of the Torrey Botanical Club* **45**: 203–210. doi:10.2307/2479657.
- Pouteau R, Meyer JY, Blanchard P, Nitta JH, Terorotua M, Taputuarai R. 2016. Fern species richness and abundance are indicators of climate change on high-elevation islands: evidence from an elevational gradient on Tahiti (French Polynesia). *Climatic Change* **138**: 143–156. doi:10.1007/s10584-016-1734-x.
- Preston CD, Pearman DA, Dines TD. 2002. *New atlas of the British and Irish flora*. Oxford: Oxford University Press.
- Rabinowitz D. 1981. Seven forms of rarity. In: Syngge H, ed. *The biological aspects of rare plant conservation*. New York: Wiley, 205–217.
- Rabinowitz D, Cairns S, Dillon T. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In: Soulé ME, ed. *Conservation biology: the science of scarcity and diversity*. Sunderland, MA: Sinauer Associates, 182–204.
- Raes N, ter Steege H. 2007. A null-model for significance testing of presence-only species distribution models. *Ecography* **30**: 727–736. doi:10.1111/j.2007.0906-7590.05041.x.
- R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Sanderson EW, Jaitheh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience* **52**: 891–904. doi:10.1641/0006-3568(2002)052[0891:thfat]2.0.co;2.
- Schemske DW, Husband BC, Ruckelshaus MH, et al. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**: 584585–584606. doi:10.2307/1941718.
- Shiyong D, Zhengyu Z, Yuehong Y, et al. 2017. Red list assessment of lycophytes and ferns in China. *Biodiversity Science* **75**: 765–773.
- Sporbert M, Keil P, Seidler G, et al. 2020. Testing macroecological abundance patterns: the relationship between local abundance and range size, range position and climatic suitability among European vascular plants. *Journal of Biogeography* **47**: 2210–2222. doi:10.1111/jbi.13926.
- Testo WL, Watkins JE Jr. 2011. Comparative development and gametophyte morphology of the hart's-tongue fern, *Asplenium scolopendrium* L. *Journal of the Torrey Botanical Society* **138**: 400–408. doi:10.3159/torrey-d-11-00054.1.
- Testo WL, Watkins JE Jr. 2013. Understanding mechanisms of rarity in pteridophytes: competition and climate change threaten the rare fern *Asplenium scolopendrium* var. *americanum* (Aspleniaceae). *American Journal of Botany* **100**: 2261–2270. doi:10.3732/ajb.1300150.
- Tilman D, Kareiva PM. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton, NJ: Princeton University Press.
- USFWS. 2019. *Species status assessment report for the American hart's-tongue fern (Asplenium scolopendrium var. americanum) version 1.3*. Cortland: U.S. Fish and Wildlife Service New York Field Office.
- USFWS. 2020. *American Hart's-tongue fern (Asplenium scolopendrium var. americanum) 5-year review: summary and evaluation*. Cortland: U.S. Fish and Wildlife Service New York Field Office.
- Viane RLL, Reichstein T. 1991. Notes about *Asplenium*: some new names and combinations in *Asplenium* L. (Aspleniaceae, Pteridophyta). *Biologisch Jaarboek Dodonaea* **59**: 157–165.

- Wagner WH, Moran RC, Werth CR. 1993.** Aspleniaceae. In: Flora of North America Editorial Committee, eds. *Flora of North America north of Mexico*, vol. 2. New York: Oxford University Press, 228–245.
- Walther GR, Post E, Convey P, et al. 2002.** Ecological responses to recent climate change. *Nature* **416**: 389–395. doi:[10.1038/416389a](https://doi.org/10.1038/416389a).
- Weber-Townsend JR. 2017.** *Contributions of genetic data to the conservation and management of the threatened American hart's-tongue fern (Asplenium scolopendrium var. americanum)*. MS Thesis, State University of New York College of Environmental Science and Forestry, USA.
- Wickham H, Chang W, Henry L, et al. 2022.** Package 'ggplot2': Create elegant data visualisations using the grammar of graphics, version 3.3.5. <https://cran.r-project.org/web/packages/ggplot2/index.html>
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. 2011.** Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* **17**: 927–942. doi:[10.1111/j.1365-2486.2010.02302.x](https://doi.org/10.1111/j.1365-2486.2010.02302.x).
- Zhu J, Mao Z, Hu L, Zhang J. 2007.** Plant diversity of secondary forests in response to anthropogenic disturbance levels in montane regions of northeastern China. *Journal of Forest Research* **12**: 403–416. doi:[10.1007/s10310-007-0033-9](https://doi.org/10.1007/s10310-007-0033-9).
- Zizka A, Silvestro D, Andermann T, et al. 2019.** CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* **10**: 744–751. doi:[10.1111/2041-210x.13152](https://doi.org/10.1111/2041-210x.13152).